
Exploring the Role of Plant-Microbe Interactions in Improving Soil Structure and Function Through Root Exudation: A Key to Sustainable Agriculture

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Abstract

The most astonishing feature of plant roots is their capability of secreting a broad variety of compounds ranging from low molecular to high molecular weights into the rhizosphere. These compounds act as signals for establishing and regulating the interactions among plant roots and microorganisms present in rhizosphere through different mechanisms. The mechanism of establishment of these relationships includes complex signaling cascades and involves different transporter proteins. Exudation is an important process that influences the microbial diversity and relevant biological activities. In addition, these secretions mediate the phenomena of mineral uptake in soil with low nutrient content either through chelation directly or by affecting biological activity of microbes. Further,

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microbes associated with plants have the potential to upgrade phytoremediation efficiency by facilitating phytoextraction and phytostabilization and through increase in biomass production by plants. Overall these exudation-mediated plant-microbe interactions influence the soil structurally and functionally via orchestrating microbial richness, nutrient acquisition, and phytoremediation. Hence, in light of this, the chapter is intended to provide the perceptivity to comprehend the impact of root exudation-mediated plant-microbe interactions in enriching the structural and functional characteristics of soil.

Keywords

Root exudates • Microbial diversity • Soil • Phytoremediation • Rhizobacteria

23.1 Introduction

Among different metabolic features of plant roots, one of the utmost amazing properties is to secrete out numerous substances into rhizosphere. These secretions are outlined as lightweight permeable excreted substances which can be eliminated out without any trouble through passive diffusion, and for this process, plants don't have to spend their energy (Bertin et al. 2003; Bais et al. 2006). Root secretions are broadly classified as (i) lightweight molecules like organic acids, amino acids, sugars, and some secondary metabolites, which include most of the excreted products from roots, and (ii) heavyweight secretions that include reminiscent of mucilage (polysaccharides) and proteins, which are large biomolecules in terms of weight Badr and Vivanco 2009. This mechanism involves replenishment of soil with micro- and macronutrients excreted out through roots (Hutsch et al. 2000; Nguyen 2003). The qualitative and quantitative nature of root secretions are reliant on the age and type of the plant, and other physical and biological parameters. Owing to the process of root exudation, various biochemicals excreted from plant roots have the capacity to control microbial growth, allow symbiotic relationship, prevent the development of parasitic and pathogenic species in the surrounding area of roots, and regulate the composition of soil (Nardi et al. 2000; Walker et al. 2003). Around 5–21% of whole photosynthetic carbon is being circulated throughout the rhizosphere by means of root exudation (Nguyen 2003; Derrien et al. 2004). Although the exudates excreted from roots supply biomass and energy to soil, they also help the plant to establish communication with other microbes and regulate their growth. The crops facilitate each positive and negative communication within the rhizosphere by the means of root exudation (Bais et al. 2006; Philippot et al. 2013). The positive communication comprises symbiotic associations with useful microorganisms, similar to rhizobium, mycorrhizae, and plant growth-promoting rhizobacteria (PGPR). The existence of numerous microbes in rhizosphere impacts the soil by performing various processes like transportation of water and nutrients through roots, maintaining fertility of soil, and nodule formation (White 2003). These root secretions symbolize a vital role in plants for

maintaining interactions with rhizosphere-inhabiting microbes. To support communication, many types of substances and signaling substances are secreted from plant roots, known as autoinducers. However, several types of compounds are released from plant roots, and most of them belong to compounds having low molecular weight, referred to as secondary metabolites (Bais et al. 2004). Few of these secondary metabolic products had been recognized earlier, and their roles within the rhizosphere have been studied and explained in detail.

23.2 Root Exudation and Its Mechanism

The mode of secretion of root exudates involve the release of carbon into soil from plant roots (Hutsch et al. 2000; Nguyen 2003; Vishwakarma et al. 2016). Roots usually secrete by secretion of particular proteins and small molecules (Stotz et al. 2000). These secretions are utilized by bacteria present in soil for biomass and energy production. Root exudates might exhibit both positive and negative association within the rhizosphere. The investigation of these secretions released from roots help to have in-depth knowledge of communication among plants and microbes (Broeckling et al. 2008; Weir et al. 2004; Bais et al. 2004, 2006). The optimistic interaction includes symbiotic relationship with invaluable microbes, corresponding to PGPR. Rhizobia, mycorrhizae, and negative response incorporate organization with parasitic and pathogenic microbes. Rhizospheric bacteria are responsible to remove these contaminants, while the roots supply nutrients for microbial growth (Bais et al. 2008). Workers have explained the enhanced mechanism for isolation of microorganisms from soil which have the following properties: (1) breakdown of particular contaminant and (2) enriched medium for growth of microorganisms. Shukla et al. (2010) explained the approach “rhizo-remediation” to describe the significance of root exudates and the rhizospheric microorganisms.

23.2.1 Diffusion

The passive process involves transport of natural substances like phenolics, carboxylic acids, sugars, and amino acids according to the formation of gradient of concentrations between cytosol of root cells (high concentration) and soil (low concentration). Due to membrane permeability for natural compounds, it allows movement of compounds through lipid bilayer of the plasma membrane. The factors accountable for permeability are concentration and polar nature of the compounds. This system allows the transport of lipophilic substances. Under a particular cytosolic pH of 7.1–7.4, small polar intracellular molecules together with carboxylic acids and amino acids occur as anions which move slowly through the plasma membrane. However, during the process of K^+ ion diffusion and the transfer of protons with the help of ATPase, there is generation of positive-charge gradient which allows influx of cations and efflux of carboxylate anions by diffusion. Root

secretion of sugars and amino acids occurs through diffusion under stress (Jones and Darrah 1994a, b).

23.2.2 ABC Proteins

They are the proteins that are most widely present in nearly all families. Many substances like metabolic products, anions, and cations are transported by utilizing energy generated by ATP hydrolysis. Hence, they are the primary active transporters having the property to drive substances against the electrochemical gradient (Krattinger et al. 2009). In eukaryotes, these proteins help in export of substances from cytoplasm to apoplast and transfer from cytoplasm to organelles like mitochondria. About more than hundreds of ABC transporters were reported in the genome of rice and *Arabidopsis*, and few of them were observed to be associated in the transportation of compounds like glutathione (Martinoia et al. 2002), auxins (Noh et al. 2001), and anthocyanins (Goodman et al. 2004) and antifungal components. Furthermore, ABCs are assumed to transfer diterpene sclareol from *N. plum-baginifolia* leaves (Jasinski et al. 2002) and the isoflavone genistein (antifungal agent) from the roots of soybean (Sugiyama et al. 2007). These proteins also act as phytoalexin because of their activities against microbes (Geibel 1994). However, around 25 ABC transporter genes showed significant increase in gene expression levels in *Arabidopsis* root which are responsible for exudation processes (Badri et al. 2008). In an experiment, such genes were knocked out and secretions released from wild type and mutants were analyzed. It was observed that the nature of these secretions from wild type and mutants was different. It was concluded that ABC transporter proteins were in regulation of exudation process. The other example in which a gene responsible for powdery mold resistance in *Arabidopsis* codes an ABC transporter is known as PEN3. It is located in the membrane of the cell, and its movement toward infected area on the epidermis and hair of roots is regulated by structures present on pathogens like chitin and flagellin (Stein et al. 2006). This active transporter releases antimicrobial substances including derivative of glucosinolates into the apoplast to stop the pathogenic microbial movement further into the cell. However, PEN3 ($\frac{1}{4}$ AtPDR8) also inhibits toxic effect exhibited by heavy metal by transferring cadmium ions from cells of root (Kim et al. 2007) showing that the identical transporter protein is responsible for many functions in the other tissue.

23.2.3 Multidrug and Toxic Compound Extrusion (MATE) Proteins

Interestingly, MATE proteins facilitate the transportation of secondary metabolites. They are expressed in both eukaryotic and prokaryotic species (Hvorup et al. 2003; Magalhaes 2010), and some bacterial species and mammals are accountable for multidrug resistance. Although not much information is reported about these proteins, MATEs act as secondary transporters that transport ions (H^+ and sodium ions)

along the electrochemical gradient allowing the transport of substance across the membrane. According to data reported, *Arabidopsis* genome has 58 MATE genes, and description about these transporters has been already reported in detail. ALF5 is expressed in cortical root cells and the epidermis and is suggested to guard plants from xenobiotics by removing them from root cells (Diener et al. 2001). In a study by Li et al. (2002), *Arabidopsis* gene named AtDTX1 is found to encode a protein located in the plasma membrane and helps in the exportation of antibiotics, alkaloids, and toxic components from roots. Some other MATE genes present in different plants like *H. vulgare* (HvAACT1), *Sorghum* (SbMATE1), and *Arabidopsis* (AtMATE1) show Al resistance by allowing an Al-activated outward movement of citrate ions from root tips (Furukawa et al. 2007; Magalhaes et al. 2007; Liu et al. 2009).

23.2.4 Aluminum-Activated Malate Transporter (ALMT) Proteins

ALMT proteins are accountable for discharging malate ions from roots, thereby providing resistance against aluminum toxicity in both dicotyledons and monocotyledons (Ryan et al. 2011). These protein families are found only in plants and not in animals and bacteria. These proteins form anion-transporting networks that create pores with selective nature in membranes and initiate flaccid transport of substrates along electrochemical gradients (Lynch and Whipps 1990). This clearly elucidate that due to movement of anions outward or cations inward along ion channels, there is generation of difference in potential across the cell membrane ranging from -100 to -200 mV or across tonoplast ranging from -10 to -50 mV. They are present on the cell membrane of roots and help in Al resistance. Gene TaALMT1 present in wheat is shown to be expressed in suspension cultures of tobacco (*Nicotiana tabacum* L.), *Arabidopsis*, wheat, and barley and is responsible for malic acid transportation facilitating Al tolerance (Delhaize et al. 2004, 2007; Ryan et al. 2011).

23.2.5 Major Facilitator Superfamily (MFS) Proteins

This family of proteins is among the prevalent class of transporter proteins in biological systems. The release of phytosiderophores (secondary metabolites) displays a substantial part in providing iron (Fe) nutrition to the grasses (Marschner et al. 1987). The produced secondary metabolites remove Fe^{+3} from the rhizospheric soil and form complex with these ions which is further delivered to plant root cells by H^+ -linked transporters of OPT family (Kim and Guerinot 2007).

MFS proteins are responsible for initial export of the compounds. These are categorized into different classes based on their function such as antiporters, co-transporters, or uniporters. The gene named as TOM1 expanded as “transporter of mugineic acid family phytosiderophores1” in rice discharges avenic acid and deoxymugineic acid from roots of rice plant (deficient in iron) (Nozoye et al. 2011). During decrease in iron supply, the gene expression of TOM1 is enhanced, and

overexpression of TOM1 in transgenic plants exhibited enhanced release of deoxymugineic acid with better Fe tolerance.

23.2.6 Hot Spots of Exudations from Root

The spots of exudation from roots are foremost since they show a predominant impact on the arrangement of microbial communities alongside the plant roots. The most important regions of secretion are the root tip with destructive cells invading from the tip region to the region of death of outer cells (Bowen and Rovira 1991). Utilizing a ^{14}C -labeling manner, McDougali and Rovira (1970) and Rovira (1973) confirmed that both main and lateral roots are among the major areas of root secretion followed by the elongation of roots. Bowen (1979) used *Pseudomonas fluorescens* as a model for identifying areas of secretion on *Pinus radiata* by coating disinfected seedlings with the bacteria and analyzing their spots of progress alongside roots. From this observation, it was elucidated that cell junctions present in longitudinal axis had been the major hot spots. However, the amount of root exudation of several substances from different sites of roots is inadequate.

23.3 Interaction of Root Exudates

23.3.1 Roots and Rhizosphere Interactions

Plants have the capability to adapt to the local environment by perceiving changes in a specific rhizospheric environment. These subsequent changes in a particular rhizosphere include variations in the growth of neighboring plants and microbes invading in close vicinity. Due to presence of any external organism, roots retort by secreting some proteins and molecules (Stotz et al. 2000; Stintzi and Browse 2000). Furthermore, the root exudates can show mutualistic or protective roles in positive or negative interaction, according to other constituents in the rhizosphere. Although numerous reports are present to show plant's association with microbe and insect in the plant organs such as stems and leaves, only a small amount has been concentrated during interaction of root with microbes and soil inside the rhizosphere.

Root exudates are also observed as a mode of interaction among plant roots and PGPR inside the rhizosphere (Hirsch 2003; Bais et al. 2006) and comprise of proteins, phenolics, organic acids (OAs), and sugars (Bais et al. 2006; De Weert et al. 2002). Although root secretions deliver nutrients to PGPR, they also differentiate microbes inhabiting in soil (Badri et al. 2008). As per the data published about the low molecular weight OAs such as malate, fumarate, and citrates exuded from roots hairs, it was observed that it allowed PGPR growth (De Weert et al. 2002; Kamilova 2006; Rudrappa et al. 2008; Ling et al. 2011). Organic acids of tricarboxylic acid cycle are also responsible for playing a key role as molecular signals (Jones 1998).

23.3.2 Root-Root Communication

The occurrence of one root system prevents the invasion to the other by releasing some chemical substances. The mechanism of allelopathy inhibits the progression of other plant species in vicinity by excreting chemical inhibitors. It also has importance in agriculture as it does not allow growth of weeds and acts as natural weedicide (Callaway and Aschehoug 2000). Bais et al. (2002c) found that (\pm)-catechin prevents growth of knapweed within rhizosphere by releasing phytotoxin from roots. The aforementioned example illustrates how these plant roots interact with neighboring roots. Plants have capability to utilize exuded secondary metabolites to control the rhizospheric conditions for causing damage to neighboring plants. Plants with this nature have the capacity to utilize metabolites released from roots as chemical linkers for haustorial growth needed for heterotrophic development of plant (Keyes et al. 2000). Some parasites of food crops including rice (*O. sativa*), legumes, millet, and sorghum (*S. bicolor*) and from Scrophulariaceae family particularly invade the root of nearby plants to acquire mineral, water, and other beneficial growth-promoting compounds from host plant (Yoder 2001). Some of the allelochemicals like flavonoids, quinones, cytokines, and para-hydroxy acids are reported to facilitate formation of haustoria (Becard et al. 1995; Estabrook and Yoder 1998; Yoder 2001); however, detailed structures of released compounds for formation of haustoria are not still clear.

23.3.3 Root Exudate-Mediated Mutualistic Interactions

Mutualism among plants and microbes is principally mediated by exudation of roots. Generally, three specific microbial groups have been observed, i.e., mycorrhizal fungi, N_2 -fixing bacteria, and other beneficial bacteria (Azcon-Aguilar and Barea 1996) (Fig. 23.1). One more mode of communication that characterizes underground zone is root-microbe interactions. The compounds which play an essential part in interaction between roots and microbes are flavonoids existing in the exudation from leguminous roots and stimulate genes of *Rhizobium meliloti* involved in the process of nodulation (Peters et al. 1986). Many molecular signaling mechanisms are included in the process of identifying plant secretions by bacteria. The mutualistic relationship between rhizobia family and their leguminous plant hosts from Fabaceae family is attributed to the signals produced and compounds secreted by both of them. During this process, the exudation by roots generates signals, which further stimulates the genes involved in nodulation process (nod genes) (Hirsch et al. 2001). According to the analysis, flavonoids are accountable for nod gene activation (Wang et al. 2012; Peck et al. 2006). Flavonoids are known to act as agonists for some rhizobia species but inhibitors for other species (Cooper 2007). Chemical compounds like flavonoids are continuously secreted into the rhizospheric soil, but their concentration is considerably enhanced in the presence of a particular *Rhizobium* species (Becard et al. 1992).

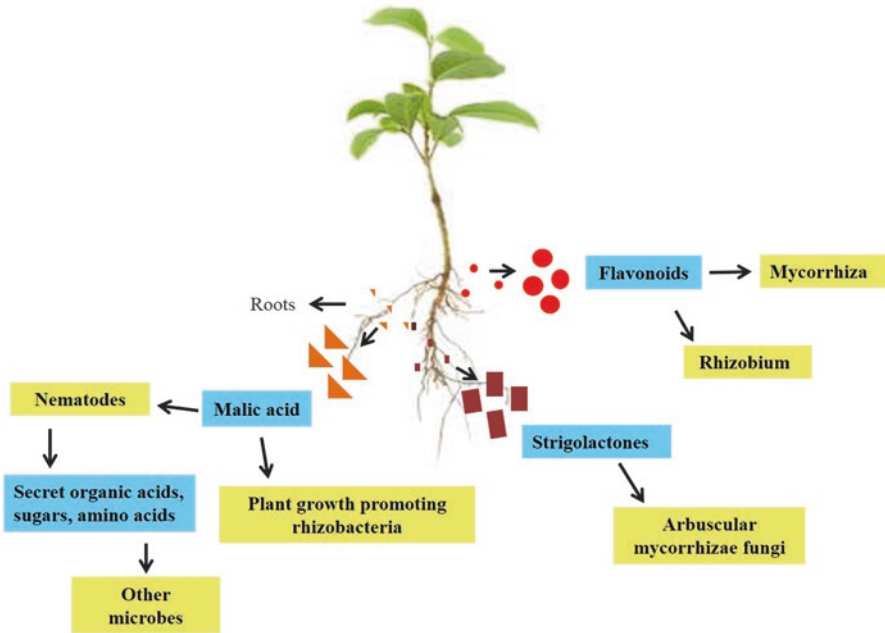


Fig. 23.1 Root exudation-mediated microbial colonization in rhizosphere

The symbiotic interactions between *Frankia* (*Actinobacteria*) and eight families of dicotyledonous plants are known as actinorhizal (Wall 2000). There are series of regulatory events happening during the course of symbiosis and they start with an infection. Further, a common step both in *Rhizobium* and *Frankia* known as curling of the root hair is preceding nodule development. However, the phenomenon of nodule formation is regulated by phenolic compounds (benzoic and cinnamic acids) and flavonoid-like components (flavanone and isoflavanone) (Ishimaru et al. 2011; Benoit and Berry 1997). It was reported that curling of the root hair is improved in *Alnus glutinosa* root filtrate (Van Ghelue et al. 1997; Prin and Rougier 1987). Popovici et al. (2010) observed that plants of Myricaceae family regulate their root secretions in the presence of *Frankia* and that flavonoids might determine its micro-symbiont specificity. The chief plant substances which were modulated by inoculating *Frankia* are hydroxycinnamic acids, flavonoids, and phenols. It was reported that genes accountable for synthesis of flavonoids are stimulated in *A. glutinosa* when co-inoculated with *Frankia* (Kim et al. 2003; Hammad et al. 2003).

Among most of terrestrial plants, arbuscular mycorrhizal fungi (AMF) and plant roots are considered to form symbiotic associations (Van der Heijden and Sanders 2002). These relationships facilitate the nutrient and mineral uptake by plants; nevertheless, fungi exploit the lipids and carbohydrates from host root. By increasing resistance against pathogens and herbivores, AMF have shown to benefit the plants indirectly by modulating its tolerance against pathogens and herbivores in several

known systems (Pozo and Azcon-Aguilar 2007; Cameron et al. 2013; Bennett et al. 2006). Since these are obligate organisms, therefore their survival is governed by their potentiality to develop rapid symbiotic relation with the roots. The branching and hyphae growth prior to infecting the roots need the presence of compounds secreted by plant roots (Giovannetti et al. 1996). A number of researches have performed studies on AMF and exudation process by roots (Nagahashi 2000; Nagahashi and Doudes 2003; Yu et al. 2003; Vierheilig and Bago 2005; Harrison 2005). Root exudates were also shown to involve in the establishment of symbiotic relationships of AMF (Vierheilig and Bago 2005). The signals provided by host plant roots facilitate the development of infection structure and AMF (Czarnota et al. 2003; Smith and Read 1997). As flavonoids persist in root exudates, their connection with signaling in establishing plant-AMF relationships has been explicated. Flavonoids are also regarded as a key compound for transforming nonsymbiotic AMF into symbiotic one (Besserer et al. 2006). Plentiful data have speculated the effects of flavonoids on growth of hyphae, differentiation, and colonization in the roots (Morandi 1996). Flavonoids show chemical structure-dependent stimulatory impact on growth of hyphae in AMF. However, in occurrence of CO₂, the flavonoids' stimulatory effects were found to be more pronounced (Bécard et al. 1992; Chabot et al. 1992; Poulin et al. 1993). Recently, in several studies, it is described that flavonoids show AMF species-specific effects through pre-symbiotic growth and its exposure to plants (Scervino et al. 2005). Colonization of AMF has been observed to amend the qualitative and quantitative nature of root exudates in the host system (Azaizeh et al. 1995) and chemotactic response of soil microbes (Sood 2003; Buee et al. 2000). However, strigolactones (carotenoid-derived terpenoids) were reported to promote branching in *G. margarita*, spore germination in *Glomus intraradices*, and cell proliferation in *Gigaspora rosea* (Akiyama et al. 2005).

23.3.4 Root-Insect Communication

Root-insect interaction has been localized to stems and leaves, but studies relevant to them are very few in numbers because of complex rhizospheric system of and unavailability of proper devices for experimentation (Koricheva et al. 2009). Root-insect interaction by bugs/pests like aphids can result in major damage to crops including *Beta vulgaris* and *Solanum tuberosum* (Hutchison and Campbell 1994). In observations made by Wu et al. (1999) on in vitro simultaneous cultures of aphids and hairy roots, it was elucidated that aphids decreased the vegetative growth and enhanced the polyacetylene synthesis with a similar response to phytoalexin (Flores et al. 1988). Fluorescent-carboline alkaloids were characterized from root secretions of *O. tuberosa* (*oca*) by Bais et al. (2002a). The main fluorescence showing compounds was recognized as harmaline (3,4-dihydroharmine) and harmine (7-methoxy-1-methyl-carboline). These alkaloids possess the fluorescence as well as phototoxic activities against insects (Larson et al. 1988).

23.3.5 Root-Pathogen Communication

The survival of root cells against pathogenic microorganisms depends on the release of chemicals like phytoalexins and defense proteins (Flores et al. 1999). This would have led the scientists to explore the chemodiversity present in root exudates for new biological entities including antimicrobials. Rosmarinic acid (RA) was found to be released from hairy root tips of cultures of *Ocimum basilicum* when stimulated by extracts of the cellular wall of fungi, i.e., *Phytophthora cinnamom* (Bais et al. 2002b). Roots were elicited to secrete rosmarinic acid by incorporation of *Pythium ultimum* in situ. This secondary metabolite exhibited antimicrobial activity against a diverse group of soil microbes including *Pseudomonas aeruginosa* (Bais et al. 2002b). Similarly, in other studies, hairy root cultures of the plant *Lithospermum erythrorhizon* were induced for producing cell-specific pigmented naphthoquinones and other biochemical entities against bacteria and fungi present in the soil (Brigham et al. 1999). The abovementioned examples proved that RA and naphthoquinones released as root exudates had defensive mechanisms against pathogenic microorganisms. Both Gram-positive and Gram-negative bacteria comprising of essential plant pathogens such as *Agrobacterium* and *Erwinia* spp. hold quorum-sensing mechanisms that regulate the transcription of genes needed for their pathogenic activities (Fray 2002). It is the cell-cell interaction between bacteria controlled by autoinducers. They are peptide-signaling molecules for Gram-positive bacteria and acylated homoserine lactones (AHLs) for Gram-negative bacteria. After reaching to saturation level in bacterial growth, it automatically activates certain transcription regulatory proteins which regulate particular genes (Teplitski et al. 2000). Hence, these signals allow bacterial cells to modulate the expression of genes in variation to population. Therefore, roots develop defense mechanism by releasing components in the rhizospheric soil that block quorum-sensing responses in bacteria, like signal blockers and signal-degrading enzymes. Further practices in this direction are still required to aid the isolation and characterization of these compounds.

23.4 Effects of Root Exudates on Soil Structure and Function

It is well known that roots of plants exude a huge number of biochemicals into the rhizosphere. Through this exudation, roots may regulate the microbes available in the vicinity of soil, deal with herbivores, restrain the development of competitors, and promote useful symbiosis (Rougier 1981). Abiotic stress is one of the severe stresses of environment that lowers the growth and yield of any crop even on irrigated land throughout the world (Vishwakarma et al. 2017). Root exudates mediate the beneficial alternations in soil function and structure by promoting microbial richness and facilitating mineral uptake in soil as well as removing of toxic substances from the soil (Nardi et al. 2000).

23.4.1 Maintenance of Microbial Diversity

Plants use the exuded molecules to protect themselves against pathogenic and parasitic organisms and to attract positive ones. These root exudates are used by bacteria present in close vicinity for production of biomass and energy. In addition, 20% of photosynthetic products are released by plants which form the basis for plant-microbe interactions. These interactions support the growth of plants by increasing the accessibility of minerals, promoting synthesis of phytohormones, degrading phytotoxic compounds, and suppressing pathogenic activities of microorganisms (Bais et al. 2006). The reported demonstrations clearly signify the value of understanding the functional attributes of microbial colonies available in the soil and the modes by which root exudates affect activity and microbial diversity.

The bacterial and fungal growth in the rhizospheric soil are selectively influenced by root exudates by altering the soil chemistry and allocating specific substrates for microbial growth. In turn, microorganisms affect the constitution and amount of various root exudates by influencing its secretion from plant root cells along with metabolism and nutrition of plants. Alternations in root exudations and rhizodeposition in distinct zones of roots form the foundation of variation of structure of present microbial communities and other species in different locations of roots (Paterson et al. 2007). In addition, soil type, status of nutrition, and environmental factors are also responsible for variation in rhizospheric microbial communities (Yang and Crowley 2000).

Studies depicting the close connection between root exudation and microbial composition in rhizosphere are increasing dramatically (Broeckling et al. 2008; Badri et al. 2008, 2013a; Chapparro et al. 2012, 2013; Micallef et al. 2009). In these studies, chemical compounds occurring in the exudates were reported as signaling molecules, substrates, or attractants that mediate the variations in microbial community (Shaw et al. 2006; Jain and Nainawatee, 2002; de Weert et al. 2002; Horiuchi et al. 2005; Badri and Vivanco 2009; Bais et al. 2006; Badri et al. 2013a, b; Neal et al. 2012). Moreover, it was explicated that root seedlings secrete sugars as substrates for the early development of extensive types of microbes and antimicrobial compounds for selecting particular microbial populations present in rhizospheric soil (Badri et al. 2013a; Chapparro et al. 2013). Rhizospheric microbial diversity is also affected by different varieties of plants (Smalla et al. 2001; Kowalchuk et al. 2002; Costa et al. 2006). This perhaps can be correlated with the constituents secreted in the form of exudates as it alters with the age, type, and location of plant along the root system (Lupwayi et al. 1998; Hertenberger et al. 2002; Yang and Crowley 2000).

23.4.2 Phytoremediation

Environmental pollution is a problem of concern nowadays and it is harshly affecting the soil-plant systems. Phytoremediation has become the emerging topic in the recent days due to its environmentally safe and cost-effective properties. Root

exudates facilitate phytoremediation by varying the physicochemical characteristics of rhizosphere by affecting absorption of metals (Lebeau et al. 2008). The modes through which root exudates scavenge heavy metals include pH modification of rhizosphere, chelation, complex formation, and alternation of microbial diversity within the rhizosphere. Through these processes, root exudates alter the chemical subsistence of heavy metals, enhance their bioavailability, make soil microbes active, and thus reduce the pollution. Ectoenzymes present in the root exudates mediate the elimination of organic contaminants by either directly degrading the pollutants or indirectly invigorating the microbial activity (Kuang et al. 2002). In general, the microbial activities occurring in the rhizosphere augment the effects of phytoremediation by two pathways:

1. *Direct pathway* in which microbes concomitant with plants increase translocation of metals and hence mediate phytoextraction or decrease mobility of metal pollutants from the rhizosphere contributing in phytostabilization
2. *Indirect pathway* in which microorganisms attribute metal tolerance to the plants or increase the biomass production by plants to arrest/remove the metal pollutants.

The rhizosphere bacteria have gained the special interest among microbes participating in heavy metal removal owing to their capability to improve the process directly by altering availability of metals by changing pH of soil and secreting chelators (e.g., siderophores, organic acids) and by redox reactions (Khan et al. 2009a, b; Gadd 2000; Kidd et al. 2009; Rajkumar et al. 2010; Ma et al. 2001, 2011; Uroz et al. 2009; Wenzel 2009).

There are numerous advantages for using microbe-mediated heavy metal mobilization as compared to chemical methods because metabolites synthesized by microbes are degradable, have low toxicity, and can easily be formed under in situ conditions in rhizosphere. However, plant growth-enhancing substances like plant growth hormones, siderophores, and ACC (1-aminocyclopropane-1-carboxylic acid) deaminase synthesized by microbes can interact with plants to help in plant growth in heavy metal-polluted soils (Wu et al. 2006; Babu and Reddy 2011; Glick 2010, 2012; Glick et al. 2007; Kuffner et al. 2010; Luo et al. 2011; Luo et al. 2012; Ma et al. 2011; Rajkumar et al. 2010; Miransari 2011) (Fig. 23.2).

23.4.3 Mineral Acquisition

As previously mentioned, the compounds secreted as exudates from roots serve as signals for numerous heterogenous, diverse, and active microbial communities available in soil. They make the soil system dynamic for nutrient turnover and sustainable for crop productivity with improved physicochemical structure (Chandler et al. 2008). By modifying physicochemical properties of soil, root exudates control the framework of microbial community present in close proximity of root surface (Dakora and Phillips 2002). Few molecules are metabolized by rhizospheric

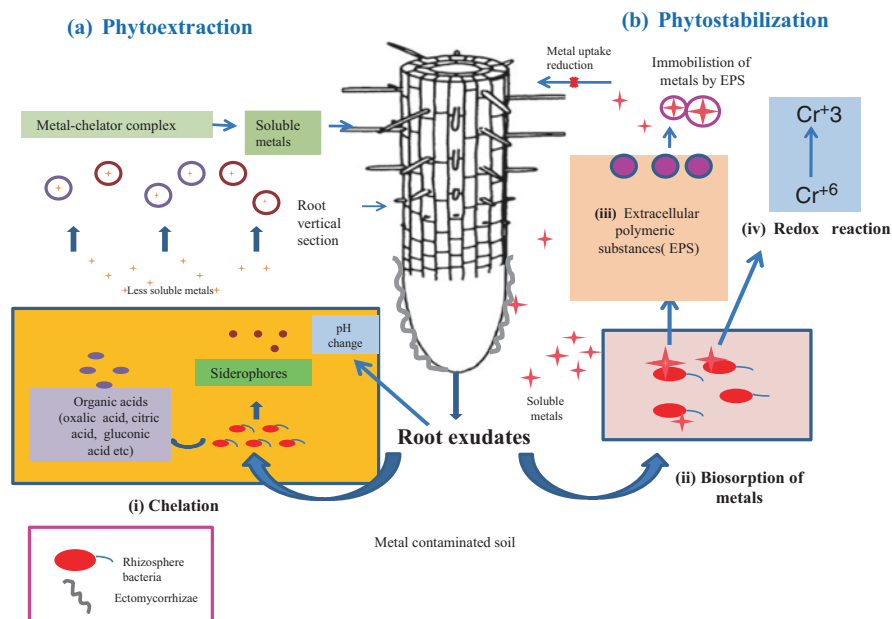


Fig. 23.2 Root exudation-mediated plant-microbe interactions facilitate **a** phytoextraction **b** phytostabilization process in metal-polluted soil by (i) chelation, (ii) biosorption, (iii) immobilization of metals by EPS, and (iv) redox reactions (modified from Rajkumar et al. 2012)

microbes as C and N sources, while other molecules which are secreted out by microbes are subsequently utilized by plant species for their development and growth (Kang et al. 2010).

Various agricultural soils lack adequate amount of iron, phosphorus, and nitrogen that results in minimal growth of plants. Majorly, the nutrients are taken up by the plants via rhizosphere when microorganisms interact with compounds in root exudates. They contain the combination of inorganic ions, organic acids, enzymes, vitamins, and amino acids. Aldonic acid and phenolics released by plant roots of N_2 -fixing legumes trigger the root-nodule-forming bacteria, i.e., *Rhizobiaceae*. These signals activate nod gene expression in symbiotic bacteria and thus facilitate nitrogen fixation. Biological nitrogen fixation represents economically and environmentally favorable substitutes to the chemical fertilizers (Munees and Kibret 2014).

Root exudates are utilized by plants growing in the low-nutrition condition not only as symbiotic attractants of microbes involved in mineral acquisition but also in other ways. Extracellular enzymes present in root exudates release phosphorus from organic compounds and other molecules (Richardson 2001). Further by chelation, these enzymes make P available to the plants. In addition, organic ions can also mediate the mobilization of phosphorus through decreased sorption of phosphorus by altering soil topological properties, chelation of cations, and desorption of orthophosphates from a particular region (Bar-Yosef 1991; Jones 1998).

23.5 Conclusion

Several researches have elucidated that root exudates act as key factor for establishment of plant-microbe symbiotic relationships. However, there is requirement of investigating other factors to understand these relationships in ecological point of view. Recent advancements in technology have a significant role in knowing multifaceted interactions between plants and microbes. Furthermore, it is also important to study the root exudation phenomenon in specific environmental conditions for exploring many other soil microbes, biological activities, and related genes to demonstrate their applications in acquiring nutrients, scavenging toxins from contaminated soils, attracting plant growth-promoting microbes, and improving the quality of soil. Although significant researches have been carried out in exploring the capability of rhizospheric microbes in heavy metal toxin phytoremediation, more advances in this aspect are still required to be anticipated. In this context, future researches are required to completely study the genomics of rhizospheric microbes, uptake mechanism of metal-chelator complex in plant, signaling cascades involved in activation of microbes under stress induced by heavy metal, and various factors affecting acquisition of minerals. Such studies might provide sufficient knowledge for utilizing these microbes efficiently in scavenging of soil contaminants and improving structural and functional properties of soil to facilitate sustainable agriculture.

Acknowledgment The authors are thankful to Director MNNIT Allahabad and Design and Innovation Centre (DIC) MNNIT Allahabad for providing necessary facilities to carry out the research work.

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