Review Article

AN OVERVIEW: INTERACTION BETWEEN MICROBIAL ENDOPHYTES AND ROOT EXUDATES

Abstract:

Rhizosphere bacterial endophytes reside in a vast number of plant tissues as a microbiome and from their they positively induce plant growth. Endophytic community structure within the plant cells is dynamic and is influenced by various abiotic and biotic factors such as soil conditions, biogeography, plant species, microbe–microbe interactions and plant–microbe interactions, both at local and larger scales. Root exudates are a complex mixture of soluble organic substances, which constitute sugars, amino acids, organic acids, enzymes, and other substances. The root surroundings also contain cell lysates, which are released when root cortex cells are ruptured by external mechanical damage, microbial graze, microbial infection, or the natural pores formed in the process of lateral roots emergence that break through the root epidermis. Since root exudates have abundance roles in plant growth promotion at different stages of plant life cycle. In view of this hypothesis, the present review has attempted to describe the various functions of root exudates and their interactions with microbial community present with in the plant tissues and their positive effects on plant health.

Keywords: Root exudates, plant growth promotion, endophytes, biocontrol.

Introduction:

The interaction between plants and microorganisms in the soil is well recognized. Hiltner **[1];** Hartmann et al. **[2]** initial observations made evidenced that microorganisms (both beneficial & pathogenic) are more abundant in the rhizospheric soil surrounding the plant roots than in soil that are away from the root area. Plant roots exude various organic compounds that promote microbial growth conditions which shows major impact on the

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composition of the rhizosphere microbiome **[3,4,5]**. In recent times, research is more focused on the composition of the rhizosphere microbiome, exploring the impact of them on plant growth and health **[6,7,8]**. The microbial endophyte life cycle is inextricably linked with that of the host plant and is influenced by the plant species, plant life stage and plant health. Some characteristics of plant-endophytic colonization are well programmed, for example, endophytic microorganism take advantage of plant wounds for entry into tissues, but plants also control which endophytes are favored before and after tissue penetration **[9,10]**. This results in plants of different species grown on the same soil harboring distinct groups of endophytes **[11,12]**. For evaluation of microbial population, Dong et al. **[13]** stated that monocots have 100-fold higher number of *Klebsiella pneumonia* cells than dicots. The reason for differential populations is unknown, but in fact, the alterations root architecture, host-bacteria interactions, precise selection/recruitment, or the types of chemicals in root exudates attracting specific endophytes may be factors. On other hand, root exudates may alter microbial populations in the rhizosphere, determining their abundance and diversity of microbial species that colonize the host plant **[8]**. The nature of chemicals in root exudates released by plants can act as signals for beneficial bacteria identify suitable hosts **[14,9,15]**. n

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Plants produce various secondary metabolites to protect themselves against pathogens and to attract beneficial microbes. *For example*, the symbiotic associations of *Rhizobium* and mycorrhizal (VAM) interactions in which roots secrete compounds that act as messengers to attract *Rhizobium* and arbuscular mycorrhizal fungi **[16,17]**. Regardless of progression in understanding the symbiotic plant-microbe interactions, little progress has been made in genetic and biochemical changes responsible for the attraction of non-symbiotic microbes towards plants. Plant associations with plant growth-promoting rhizobacteria (PGPR) provide protection from soil-borne plant pathogens by antagonistic mechanisms **[18,19]**. Plant and endophytic colonization are a complex process that requires the capacity to compete with other bacteria in the rhizosphere soil and communicate, interact with plant roots. Root exudates are chemically diverse attracting microorganisms to colonize roots, or to be able to colonize the internal plant tissues for endophytes. A whole genome sequence approach was studied by Shidore et al. **[20]** to know the endophyte genes that help in root colonization. Furthermore, they also exposed the bacterial endophyte *Azoarcus* spp. strain BH72 to exudates of rice plants (*Oryza sativa* cv. *Nipponbare*) and analyzed the endophyte's gene expression changes. As expected, many genes known to be involved in rhizosphere competence were found to be upregulated; Several other genes were altered in substantiate their role for endophytic colonization, such as gene for minor pilin PilX, signal transduction

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proteins and a serine–threonine kinase as a putative component of the type IV secretion system (T6SS). Based on the results of Shidore et al. **[20]** it was suggested that rhizosphere competence, as well as endophytic colonization was induced by root exudates. Although evidence exists for intra-plant communication, but, as such proven reports were not existed demonstrating whether plants exude specific chemical signals through their roots to attract beneficial bacteria in the rhizosphere. Furthermore, it is very hypothetical to explain whether shoot infection by pathogenic bacteria will induces recruitment of beneficial rhizobacteria to the root surface. The microbe-microbe signaling under distress conditions, especially between aboveground and belowground tissues, are poorly documented. Such signaling, although potentially complex due to the involvement of significant physical distances, may be an important and effective strategy in plant defense that has thus far been overlooked **[15]**. In this scenario, the present review focused on the interaction between the microbial endophytes and plant root exudates and their mechanisms for plant health.

Interaction between endophytes and root exudates:

The microorganisms with colonizing ability in colonization around or in the plant are collectively called colonization properties. In the interactive colonization processes, communication between the plant and bacterium (and vice versa) has a key role **[9]**. Bacterial root colonization often starts with the recognition of specific compounds in the root exudates **[21]**. These compounds probably also have major roles in below-ground community interactions **[18]**. At same time plants communicate with almost all the groups of commensalistic, mutualistic, symbiotic and pathogenic microorganisms *via* chemicals exuded by roots **[22]**. Chemotaxis is important factor in colonization around roots with the help of motility directed by chemotactic response to root exudates **[23]**. Chemotaxis is not common in all endophytic species, and other multiple parallel paths have evolved during different plant–microbe interactions. Root-exuded organic acids are major chemo-attractants for *P. fluorescens* and has close association with tomato plant **[21]**, whereas carbohydrates and amino acids attract *Corynebacterium flavescens* and *Bacillus pumilus* to rice **[24]**. The apparent specificity in these interactions probably relates to bacterial nutritional requirements and, in each of these cases, chemotaxis towards specific resources probably determines the specificity of the interaction.

Among plant materials, seeds carry a range of endophytes **[25,26]**. Seedborne endophytes confirm their presence in new germination. Unlikely, in vegetative propagation (such as potatoes or sugarcane) transmission of their endophytes to the next generation and would not require the infection process. In the rhizosphere there is a selection of the microorganisms that can survive in the root exudates and compete with others. Rosenblueth and Martínez-Romero **[27]** found that some strains can act as both epiphytes and endophytes for colonizing the rhizosphere surface and inside tissues. Beneficial microbes in the rhizosphere is important not only as the first step in biocontrol, but also is crucial in plant growth. It has been assumed that many microorganisms are attracted by carbon-containing compounds exuded by plant roots. Indeed, this phenomenon was first described by Hiltner **[1]**, who observed increased numbers and activity of microorganisms near plant roots. Evidence continues to accumulate which suggests a major role for root exudates in determining the fate of microbial species in the rhizosphere (saprophytes/endophytes).

The most complex interactions in the rhizosphere surrounding were differentiated by chemical, physical and biological properties among land plans. For the last one decade, the biological importance of root exudates by plants is grained as one of important trait in the rhizosphere in mediating interactions among plants and microbes **[28,29,30,31]**. Root exudates classified as low molecular weight compounds such as amino acids, organic acids, sugars, phenolics, and other secondary metabolites and high molecular weight compounds include mucilage and proteins. Root exudation represents a major carbon cost to the plant **[32]**. Plant roots even responds to various environmental factors through the secretion of a wide range of compounds, depending on nutritional status and soil conditions **[33,34]**. This action interferes with the plant-bacteria interaction and an important factor contributing to the efficiency of the inoculant **[33,35,34]**. Apart from low and high molecular weight compounds, root exudation includes the secretion of ions, free oxygen species, water, enzymes, mucilage and a diverse array of carbon containing metabolites **[22]**. In plants, roots alone excretes 10-44% of photosynthetically fixed carbon, which acts as primary energy source, signaling molecules or antimicrobials for soil microorganisms **[36]**. The release of exudates purely depends on plant age, genotype and microorganisms response and interaction with different host plants **[37,38,39]**. Thus, artificial microbial inoculants are generally guided to the one specific plant from which the bacterium was isolated.

Root exudates in plant growth promotion

Plant–microbe interactions can positively influence plant growth through a variety of mechanisms includes nitrogen fixation by alpha and betaproteobacteria **[40]**, biotic and abiotic stress tolerance communicated by the presence of endophytic microbes **[41]**, and direct and indirect applications by PGPR **[42]**. Several proved interactions prove the importance of root exudates in positive plant–microbe interactions, where they act either directly or indirectly for healthy plant growth promotion **[43]**. The classical example for positive plant-microbe interaction is legume roots and *Rhizobia* bacteria interactions, which can form dinitrogen-fixing nodules in the roots of legumes. Similarly, vascular arbuscular mycorrhizal (VAM) fungi symbiotically interacts with plant roots more than 80% of terrestrial plants. Mycorrhizal fungus and bacterial rhizobial associations are thought to derived from a common-ancestral and plant–microbe interaction likely of fungal origin and demonstrated that some host proteins regulates both mycorrhizal and rhizobial interactions with roots **[44]**. Root exudates play a role in the recognition of mycorrhizal fungi with compatible host plant **[45,46]**. Although root exudates have been suspected to play a communicative role in mycorrhizal associations, the identification of specific molecule interactions from AMF and host remains elusive. Akiyama *et al.* **[47]** stated that, a sesquiterpene called strigolactone 5-deoxystrigol was identified in the root exudates of *Lotus japonicus* which is responsible for inducing VAM fungi hyphal branching in germinating spores. In the presence of VAM symbiosis, plants trade carbon with phosphate from their fungal partners **[48,49,50]**. Recently, a leucine-rich-repeat receptor kinase (SymRK) was identified as a common genetic basis for plant root endosymbiosis with AMF, *Rhizobia*, and *Frankia* bacteria **[51]**.

Root exudates in biocontrol activity

Certain strains of root-colonizing fluorescent pseudomonads can provide efficient protection of crop plants against a variety of soilborne phytopathogenic fungi, notably by the secretion of extracellular antimicrobial secondary metabolites into the rhizosphere **[52]**. In another study *in vitro* screened *Bacillus subtilis* and *Bacillus licheniformis* MSEB (Maize seed endophytic bacteria) showed strong antifungal property against three broad fungal pathogens *Rhizoctonia solani*, *Sclerotia rolfsii* and *Macrophomina phaseolina* and these were seed treated with tagged rifampicin mutant endophytic bacteria (*Bacillus* spp.) before sowing showed potent root and stem colonizers **[53]**. Werra *et al.* **[54]** investigated the impacts of 63 different low-molecular-weight compounds, most of them plant derived, on the *in vitro* expression of two antifungal biosynthetic genes by the plant-protecting rhizobacterium *Pseudomonas fluorescens* CHA0. Most of the compounds tested, affected the expression of one or both antifungal genes. This suggests that biocontrol activity in plant-beneficial pseudomonads is modulated by plant-bacterium signaling. It was well documented that

Trichoderma spp. as effective biological control agents of plant diseases caused by soilborne fungi **[55]**. Seeds treated with *Trichoderma lignorum* plants had roots with lower levels of *Rhizoctonia solani* in their rhizosphere than roots of untreated seeds. *Trichoderma* had little effect on the survival of *Rhizoctonia solani* in non-rhizosphere soil. However, application of *Trichoderma lignorum* as a wheat-bran preparation, conidial suspension or seed coating reduced the pathogen counts in the rhizosphere soil of beans **[56]**.

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Compounds secreted from plant roots often alter the gene expression of benefitted microorganisms by acting as signals that either induce or repel the interaction with beneficial and or harmful strains, respectively. The prominent unknown fact is whether two distinct groups of beneficial bacteria, such as soil microorganisms (not plant associated) and plant endophytic strains (plant colonizers) strains, respond uniformly or variably to the root exudates. In a study, *Bacillus mycoides*, a potential biocontrol and plant growth promoting bacterium strain, was isolated from the endosphere of potatoes and also from soil of the same geographical region. To characterize their phenotypic differences, the whole genome of the two strains were sequenced and the transcriptome response to potato root exudates was compared. The transcriptome profiles showed that endophytic strains responded more distinct than the soil-derived isolate and a higher number of significant differentially expressed genes were detected **[57]**. Biocontrol inoculants often show inconsistency in their efficacy at field scale and the reason for this remains often unclear. A high rhizosphere competence of inoculant strains is assumed to be a key factor for successful biocontrol effects as the biocontrol strain must compete with the indigenous microbial community in the rhizosphere. It is known that many factors, among them plant species and soil type shape the rhizosphere microbial community composition. However, microbial community composition in the rhizosphere can also be influenced by the presence of a pathogen **[58]**. The biological control process mediated by microbes relies on multiple interactions among plants, pathogens and biocontrol agents (BCAs). One such efficient BCA is *Bacillus cereus* AR156, a bacterial strain that controls a broad spectrum of plant diseases and potentially works as a microbe elicitor of plant immune reactions. The strain *B. cereus* AR156 has induced some specific components in plant root exudates was probably involved in further biocontrol processes **[59]**.

Root exudates and their mechanisms to establish endophytic colonization:

Plants often use transport mechanisms to distribute and produce compounds into the rhizosphere surroundings **[60,61]**. In general, root exudates can be released by plant roots *via* either passive (diffusates) or active (secretions) mechanisms by different transport methods. Most of them were low molecular weight organic compounds through a passive process. Small polar and uncharged molecules are transported by direct passive diffusion, a process that depends on (i) membrane permeability, (ii) the polarity of the exuded compounds and (iii) cytosolic pH **[60]**. Plant root cells secrete other compounds, such as secondary metabolites, polysaccharides and proteins, with the help of different membrane-bound proteins **[61]**. Such as, ATP-binding cassette (ABC) transporters **[62,63,64,65]**, MATE family (multidrug and toxic compound extrusion) **[66]**, the major facilitator superfamily **[67]** and the aluminum-activated malate transporter family **[61]**. Although, there are not many reports on the details of these membrane-bound transport protein functions, they have been associated with the transport of a wide range of compounds into the rhizosphere.

For the last two decades, interactions in rhizosphere mediated by root exudates were widely studied **[68,69,70,71,72,73]**. Plant root associated phytochemicals can facilitate several interactions, such as plant–plant, plant–microbe, and plant–faunal. These interactions can vary from neutral to beneficial or deleterious **[74,75]**. In some cases, microbes can transition from pathogenic to symbiotic depending upon the environmental conditions **[76]**. For example, *rhizobia*, symbiotic nitrogen (N)-fixing bacteria, range from a symbiotic to a neutral interaction with plants depending on soil N levels **[77,78]**. Furthermore, under N-limiting conditions, legumes secrete more flavones and flavonols to attract and initiate legume–rhizobia symbiosis **[79,80]**.

Table 1: Potential functional role of root exudate components identified from different plant rhizospheres, for example tomato, Brassica napus etc., adapted from **[81,69,82]**.

Exudates component	Functions	Specific compounds identified in root exudates
Organic acids	Nutrient source Chemoattractant signals to microbes Chelators of poorly soluble mineral	Citric, glutaric, oxalic, malonic Malic, aldonic, fumaric, erythronic Succinic, ferulic, acetic, butanoic

	nutrients Acidifiers of soil Detoxifiers of Al nod gene inducers	Butyric, syringic, valeric, rosmarinic, lactic, glycolic trans-cinnamic, piscidic, formic aconitic, pyruvic vanillic, tetronic
Amino acids	Nutrient source Chelators of poorly soluble mineral nutrients Chemoattractant signals to microbes	a- and b-alanine proline asparagine, valine, threonine, aspartate, tryptophan cystein, ornithine, cystine, histidine, glutamate, arginine, glycine, homoserine, isoleucine, phenylalanine, leucine, -Aminobutyric acid, lysine a-Aminoadipic acid, methionine, serine, homoserine
Sugars & Vitamin	Promoters of plant and microbial growth nutrient source	Glucose, desoxyribose, oligosaccharides galactose, biotin, maltose, thiamin, ribose, niacin, xylose, raffinose pantothenate, rhamnose, rhiboflavin, arabinose, fructose
Proteins and enzymes	Catalysts for P release from organic molecules Biocatalysts for organic matter transformations Plant defense	Acid/alkaline, phosphatase amylase, invertase, prot!ease PR proteins, lipases, b-1,3-glucanases
Inorganic ions and gases	Chemoattractant signals to microbes	HCO_3" OH" Hþ CO_2 H_2
Phenolics	Nutrient source Chemoattractant signals to microbes Microbial growth promoters nod gene inducers and inhibitors in rhizobia Resistance inducers against	Liquiritigenin, luteolin Daidzein, 40,7-dihydroxyflavanone Genistein, 40,7-dihydroxyflavone Coumetrol, 4,40-dihydroxy-2'-methoxychalcone Eriodictyol, 40-7-dihydroxyflavone 3,5,7,30-tetrahydroxy- 40methoxyflavone

	phytoalexins Chelators of poorly soluble mineral nutrients Detoxifiers of Al Phytoalexins against soil pathogens	naringenin isoliquiritigenin, 7,30-dihydroxy-40-methoxyflavone umbelliferone, (þ)- and (")- catechin
Root border cells	Produce signals that control mitosis Produce signals controlling gene expression Stimulate microbial growth Release chemoattractant Synthesize defense molecules for the rhizosphere Act as decoys that keep root cap infection-free Release mucilage and proteins	

Transport mechanisms of root exudates:

During the last one decade many researchers substantially gained progress in isolation and characterization of root exudates and their important interactions in rhizosphere soil. However, the mechanism of root exudates secretion is poorly understood. The production and release of root-derived compounds are commonly constitutive but, may be induced by biotic or abiotic stress as described previously in this article. The secretion of root exudates by plant roots is initially thought to be a passive process which dependent on three separate pathways: diffusion, ion channels and vesicle transport **[83]**.

Diffusion process:

During diffusion, small polar molecules and uncharged molecules are transported through permeability nature of lipid membranes **[84]**. This passive diffusion process depends on membrane permeability **[85]** and cytosolic pH **[86]**. Other compounds like sugars, amino acids and carboxylate anions were transported across membranes by the aid of proteins, and their direction of movement is dependent on their electrochemical gradient that allows them to pass from the cytoplasm of intact root cells to the soil. Samuel et al. **[87]** showed that the large cytosolic K^+ diffusion potential and the extrusion of protons through ATPase generate a positively charged gradient that promotes the release of carboxylate anions. Factors that affect membrane integrity could also promote the release of organic acids **[88]**. In such cases, mediate the controlled release of these compounds mediated by anion channels in the roots **[89,90,91,92]**.

Ion-exchange method:

Sugars, amino acids and metals were specifically transported by the compounds that in turn involved in the secretion of other compounds from root cells [**93,94,95,96,97,98,99,100]**. Plants cells possess metal homeostasis to avoid excess concentrations of free metal ions inside the cells (e.g. Fe, Zn, Mn and Cu); these mechanisms involve coordination of metal ion transporters for uptake, translocation and compartmentalization **[101]**. For e.g. graminaceous plants secrete mugineic acid, a metal-binding ligand secreted into the rhizosphere, and form Fe(III)-MA ligand to reduce the Fe (iron) toxicity and then enter into the root cells *via* a specific transporter YSL identified in maize **[102,103]**. Recent evidence demonstrated that the silicon efflux transporter from rice is involved in efflux of silicon from root cells **[104,105]**. Similarly, it has been demonstrated that malate transporter (AtALMT1) plays a critical role in releasing malate from root cells under aluminium toxicity in *Arabidopsis* **[106]**. There are other transporters like monosaccharide transporters that are involved in transporting hexoses, pentoses including ribose and polyols such as myo-inositol and glycerol **[107,108]**.

Vesicular transport system:

Vesicular transport mechanisms involves in secretion of high-molecular weight compounds by roots **[109]**. Knowledge of the vesicle-mediated trafficking of proteins is well understood **[110]**, but the mechanism of vesicle-mediated transport of phytochemicals is not fully characterized **[111,112]**. There are reports demonstrating that plant defense responses are accompanied by trafficking of antimicrobial compounds to the site of pathogen infection. For e.g. pigmented vesicles accumulate on sorghum leaves at sites of attempted fungal infection they often termed as antimicrobial pigments **[113,114]**. Similar reports by **[115],** Yazaki et al. **[116,117]** suggested the pigmented antimicrobial napthoquinones are secreted in response to fungal elicitation. into the apoplast of the boraginaceous plant, *Lithospermum erythrorhizon* by a vesicle-mediated mechanism.

Membrane bound transport proteins:

Membrane-bound proteins offer an alternative transport mechanism for the release of metabolites from cells and different proteins have been involved in the transport of secondary compounds across plant membranes. Among these, some localize to the plasma membrane which directly export compounds from the cell. Others localize to inner membranes where they can help sequester compounds into subcellular compartments or perhaps load vesicles ready for exocytosis. These proteins include the ABC family, the MATE family, the major facilitator superfamily (MFS), and the ALMT (aluminium-activate malate transporter) family of transport proteins **[118]**.

ABC proteins mediated transport system:

ABC proteins comprise a large and ancient family of proteins found in all phyla. They drive the transport of various substrates (metabolic products, ions, lipids and xenobiotics) using the energy of ATP hydrolysis. Hence, these are primarily active transporters that have the potential to transport substrates against their electrochemical gradient. In eukaryotic cells, ABCs export substrates from the cytosol to the apoplast through the plasma membrane or from the cytosol to other internal organelles such as the vacuole. There are >100 putative ABCs in the rice and Arabidopsis genomes, some of which are involved in the transport of glutathione conjugates **[119]**, chlorophyll catabolites **[120]**, auxins **[121,122]**. For example, ABCs are thought to export the antifungal diterpene sclareol from the leaves of Nicotiana plumbaginifolia **[123]** and the isoflavone genistein from soybean roots **[124]**. Genistein is a signaling molecule that is released from the roots of many legume species to stimulate nodulation. It may also function as a phytoalexin due to its slight antimicrobial activity **[125]**. Another gene required for powdery mildew resistance in *Arabidopsis* encodes an ABC transporter called PEN3 and it localizes to the plasma membrane, and its recruitment to sites of pathogen attack on the epidermal cells and root hairs is triggered by pathogen-associated molecular patterns such as flagellin and chitin **[126]**. PEN3 could be releasing antimicrobial compounds, including glucosinolate3 which derivatives into the apoplast adjacent to the appressoria to restrict pathogen invasion. Interestingly, PEN3 (=AtPDR8) also prevents heavy metal toxicity by exporting cadmium ions or cadmium conjugates from root cells **[127]**, suggesting that the same transporter serves different functions in different tissues. Another example related to leaf pathogens is Lr34, one of the most important disease resistance genes in wheat. Lr34 is a full-sized ABC transporter expressed in leaves that is necessary for durable rust resistance in wheat around the world **[128]**. The function of Lr34 remains unclear, but one model proposes that Lr34 protects infected cells by exporting antimicrobial compounds into the apoplast in response to pathogen attack. Badri et al. **[62]** identified 25 ABC transporter genes highly expressed in *Arabidopsis* root cells that are likely to be involved in secretion processes. Plants with knockout mutations in these genes were obtained, and the exudates collected from wild-type plants and mutant lines were compared. They found that exudate composition differed between the wild-type and mutant plants and that more than one ABC transporter could be involved in the secretion of a specific phytochemical.

MATE proteins

The MATE genes encode transporters that also export a variety of substrates, including secondary metabolites. The family is found in eukaryotes and prokaryotes **[129,130]**, and certain members in bacteria and mammals are responsible for multidrug resistance. Details of their function are not well understood, MATs appear to function as secondary active transporters using the electrochemical gradient of other ions (sodium or protons) to drive substrate motion Arabidopsis gene called AtDTX1 encodes a plasma membrane-located protein that facilitates the efflux of plant alkaloids, antibiotics and other toxic compounds from the roots **[131]**. Other MATE genes in sorghum (SbMATE1), barley (HvAACT1), and Arabidopsis (AtMATE1) confer resistance to aluminum by facilitating aluminum-activated efflux of citrate anions from root tips **[132,133]**. Citrate released from the roots is thought to chelate the toxic Al^{3+} cations in the apoplast and prevent damage occurring to the rapidly dividing and elongating cells in the apices **[134,135]**. More recently a MATE protein in rice, named PEZ1, was shown to export phenolic compounds into the xylem **[136]** and it was speculated that similar proteins might also be facilitating the transport of phenolic compounds into the rhizosphere.

MFS proteins

Release of a special class of secondary metabolites, the phytosiderophores, is an important iron nutrient in grasses **[137]**. These phytosiderophores chelate iron(III) in the rhizosphere and the entire complex is then transported to root cells by proton-coupled transporters belonging to the oligopeptide transporter family **[138]**. However, the initial export of these compounds from roots involves the MFS proteins, one of the largest and most diverse.TOM1 expression is induced when iron supply is restricted, and transgenic plants overexpressing TOM1 show increased release of deoxymugic acid and increased tolerance to reduced iron supply.

Future aspects

The quantities of organic compounds exuding from roots is not large, about only 0.4% of the total carbon photosynthesized, they do exert a very strong influence on the soil microorganisms attraction and may be significant in affecting plant nutrient availability. There is evidence that exudates from the roots of some plants are toxic to roots of neighboring plants and to some germinating seeds. The present review compilation is based data generated from the experiments carried on media based solution-grown plants so that there are still some important questions to be answered about root exudates from soil-grown plants: (i) How much organic material is exuded from roots into soil ? (ii) How far from roots do the compounds diffused from diffusion site ? (iii) What concentration gradients exist ? (iv) What effects do soil properties have upon exudation ? (v) What are the main sites of exudation ? The application of C^{14}-labeling techniques offers a powerful tool which answer these questions. Use of radioisotopes to investigate the sites of exudation along roots and the role of lateral roots in the exudation process should enable us to determine what part of the soil will be most affected by root exudates.

Conclusion

Based on the current status, rhizosphere microbial community in the soil is closely linked to plant growth, and it can be changed by alteration of root exudate secretion pattern. Studies proved that changing the root exudate patterns by modifying ABC transporter could affect the rhizosphere microbiome levels. However, benefits of PGPR to plants in terms of growth and yield are well-documented and majority of the studies have only emphasized on plant parameters aboveground. But, in fact the interactions of PGPR with the plant starts in the rhizosphere through root exudation followed by attraction, movement and colonization on the rhizoplane, and/or in the endorhizosphere. In rhizosphere, most of the biological activities guided by the root exudates. Chemotaxis is a vital motility property that allows bacteria to move towards the rhizosphere and this process of chemotaxis towards root exudates has been suggested to be the first step of bacterial colonization on root surface. It was concluded that root exudates transported through the various mechanisms for the movement of secondary plant metabolites in roots are probably similar to those used elsewhere in the plant, but much larger quantities of these compounds are released from roots than from leaves. A variety of transport mechanisms are employed to move bioactive secondary products around root cells and into the rhizosphere, and these fluxes are often highly dependent on the local soil environment and root health. This review has highlighted the possible pathways for the safe transport of secondary metabolites and their interactions with microbial communities especially endophytes in inducing plant growth.

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