Review Article

AN OVERVIEW: INTERACTION BETWEEN MICROBIAL ENDOPHYTES AND ROOT EXUDATES

Abstract:

Bacterial endophytes of rhizosphere were able to reside in different plant tissues as a microbiome and from there they positively induce plant growth. Endophytic community structure in plant tissues is active and is altered by various biotic and abiotic stresses such as soil parameters, crop locations, plant verities, microbe–microbe interactions and plant–microbe interactions, both at local and larger scales. Root exudates include soluble organic substances, constitutes sugars, amino acids, organic acids, enzymes, and other substances. Apart from these compounds, the root surroundings contains lysates of cells, which released when root cortex cells are subjected mechanical damage, microbial graze, infection, or the natural pores formed in the process of lateral roots emergence. Since root exudates have abundance roles in plant growth promotion at different stages of plant life cycle. In recent times, the nature of compounds released by plant roots could attract group of microorganisms (beneficial) and particularly focus is more attracted towards the endophytic bacteria moved towards root surfaces and their entry into the plant tissues. 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: biocontrol, endophytes, plant growth promotion, root exudates

Introduction:

The rhizosphere plant – microbe interactions were well recognized feature. The initial observations of Hiltner **[1];** Hartmann et al. **[2]** revealed that microorganisms are richer in rhizospheric soil surrounding plant roots. Plant roots are capable to exude various organic compounds that promote microbial growth conditions which impact on the composition of the rhizosphere microbiome **[3,4]**. In recent times, research is more focused on the structure of the soil microbiome, exploring the impact on plant protection **[5,6]**. The microbial endophytes often inseparably linked with plants and is influenced by the plant species, life stage and health. 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 **[7,8]**. This results states that different species of plants grown on the same soil conditions sheltering distinct groups of endophytic microorganisms **[9]**. For evaluation of microbial population, Dong et al. **[10]** 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, 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 **[7]**. The nature of chemicals in root exudates released by plants can act as signals for beneficial bacteria identify suitable hosts **[11,7,12]**.

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 to act as messengers in attracting *Rhizobium* and arbuscular mycorrhizal fungi **[13,14]**. Plant growth-promoting rhizobacteria (PGPR) provide antagonism to plans in protecting from soil-borne plant pathogens **[15,16]**. Plant-endophytic associations 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 microbes 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. **[17]** 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. Based on the results of Shidore et al. **[17]** it was reported both epiphytic and endophytic colonization was induced by root exudates. Although evidence exists for intra-plant communication, but, as such proven reports were not existed to prove whether plants exudates signals through their roots to attract beneficial bacteria in the rhizosphere. Furthermore, it is hypothetical to explain whether pathogenic bacteria will induce recruitment of beneficial rhizobacteria in the root surface by infecting the shoots. The microbe-microbe signaling such stress conditions, especially between aboveground and belowground tissues, are poorly documented **[12]**. 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 ability in colonization around or in the plant are collectively termed as colonization properties. In this process, signaling between the plant and bacterium (and vice versa) has a key role **[7]**. "Bacterial below ground colonization always starts with the recognition of key compounds in the root exudates. These compounds may also have major roles in microbial community interactions" **[15]**. At same time plants communicate with groups of commensalistic, mutualistic, symbiotic and pathogenic microorganisms *via* root exudates **[18]**. Chemotaxis is important factor in colonization around roots with the help of motility directed by chemotactic response to root exudates **[19]**. "Chemotaxis is not common in all endophytic species, there are other parallel paths have recognized during plant–microbe interactions. Organic acid exudates are major chemo-attractants for *P. fluorescens* and has close association with tomato plant, in another study carbohydrates and amino acids attract *Corynebacterium flavescens* and *Bacillus pumilis* to rice plants" **[20]**. The possible explanation in these interactions is 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 **[21]**. Seeds associated endophytes confirm their abundance in new germination. Unlikely, in vegetative propagation transmission, endophytes automatically appear in next generation and so they would not require the infection process. In the rhizosphere, selective microorganisms can only survive the root exudates and compete with others. Rosenblueth and Martínez-Romero **[22]** 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 root exudates with carbon rich attracts more microorganisms. Indeed, this speculation was first described by Hiltner **[1]**, stated that abundant activity of microorganisms near plant roots. Evidence continues to accumulate that a major role for root exudates in determining the fate of microbes 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, root exudates by plants marked as one of the biological important trait in the rhizosphere in facilitating singnals among microbes and plants **[23,24,25]**. "Root exudates classified as low and high molecular weight compounds such as amino acids, organic acids, sugars, phenolics, and other secondary metabolites and mucilage and proteins comes under high molecular weight compounds. Major carbon depositions to plants derived from root exudates" **[26]**. "Plant roots even responds to various environmental factors through the secretion of a wide range of compounds, depending on nutritional status and soil conditions" **[27,28]**. "This action interferes with the plant-microbe interactions and a key factor contributing to the efficacy of the inoculants" **[27,29]**. "Apart from low and high molecular weight compounds, root exudates also secrets ions, free oxygen species, water, enzymes, mucilage and a diverse array of carbon containing metabolites" **[29]**. "In plants, roots alone excrete 10-44% of photosynthetically fixed carbon, which acts as primary energy source, signaling molecules or antimicrobials for soil microorganisms" **[30]**. The release of exudates purely depends on plant age, genotype and microorganisms response and interaction with different host plants **[31,32,33]**. Thus, artificial microbial treatments usually guided to the one specific plant from which the bacterium was isolated.

Root exudates in plant growth promotion

Plant–microbe interactions often induce plant growth *via* variety of mechanisms such nitrogen fixation by alpha and betaproteobacteria **[34]**, "biotic and abiotic stress tolerance communicated by the presence of endophytic microbes" **[35]**, and "direct and indirect applications by PGPR" **[36]**. "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" **[37]**. "The classical interaction of legume and *Rhizobia* is best example for positive plant-microbe interaction which forms fixing nodules in the roots of legumes. Similarly, vascular arbuscular mycorrhizal (VAM) fungi symbiotically interact with plant roots of >80% of terrestrial plants. Mycorrhizal fungus and bacterial rhizobial interactions are thought to be derived from a interaction likely of fungal origin of plant-microbe associations states that host proteins regulates both mycorrhizal and rhizobial interactions with roots" **[38]**. "Root exudates has special role in the recognition of mycorrhizal fungi with host plant" **[39,40]**. Although, the identification of specific molecule interactions from AMF and host remains elusive. Akiyama *et al.* **[41]** stated that, "a sesquiterpene called strigolactone 5-deoxystrigol compound was identified in the root exudates of *Lotus japonicus* which is responsible for inducing VAM fungi hyphal branching in germinating spores and plants trade carbon with phosphate from their fungal partners" **[42,43,44]**. "Recently, a leucine-rich-repeat receptor kinase (SymRK) was found and known to be genetic basis for plant root endosymbiosis with AMF, *Rhizobia*, and *Frankia"* **[45]**.

Root exudates in biocontrol activity

"In general, particular *Pseudomonas* spp. strains provide efficient crop protection against a variety of soilborne phytopathogenic fungi, by secretion of extracellular antimicrobial secondary metabolites into the rhizosphere" **[46]**. 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 **[47]**. Werra *et al.* **[48]** 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 *P. fluorescens* strain CHA0. Most of the compounds tested, affected the expression of one or both antifungal genes". "This suggests that biocontrol activity in pseudomonads strains is modulated by plant-bacterium signaling. It was well documented that *Trichoderma* strains were most effective biological control agents against several soilborne fungi" **[49]**. "For examples, seeds treated with *T. lignorum* strains showed that plants roots with lower levels of *Rhizoctonia solani* in their rhizosphere than control plants. *Trichoderma* had little effect on the survival of *Rhizoctonia solani* in non-rhizosphere soil. However, application of *T. lignorum* as a wheat-bran preparation, conidial suspension or seed coating reduced the pathogen counts in the rhizosphere soil of beans" **[50]**.

Compounds secreted from plant roots change the pattern of gene expression of benefitted microbes by acting as signals that either induce or inhibit 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 PGP strain, was isolated from the endosphere of potatoes and 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 **[51]**. "*In vitro* screened biocontrol isolates often show inconsistency in their efficacy at field level and the best reason for this remains often unclear till date. 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" **[52]**. "The biological control relies on multiple interactions among plants, pathogens and biocontrol agents (BCAs). One such efficient BCA is *Bacillus cereus* AR156, which 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" **[53]**.

Root exudates and their mechanisms to establish endophytic colonization:

"Plants often use transport mechanisms to distribute and produce compounds into the rhizosphere surroundings" **[54,55]**. "In general, root exudates were released by *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" **[56]**. "Plant root cells secrete other compounds, such as secondary metabolites, polysaccharides and proteins, with the help of different membrane-bound proteins **[57]**. Such as, ATP-binding cassette (ABC) transporters" **[58,57,58]**, MATE family (multidrug and toxic compound extrusion) **[59]**, the major facilitator superfamily **[60]** and the aluminum-activated malate transporter family **[55]**. 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 **[61,62,63,64,65]**. “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” **[66,67]**. “In some cases, microbes can transition from pathogenic to symbiotic depending upon the environmental conditions” **[68]**. “For example, *rhizobia*, symbiotic nitrogen (N)-fixing bacteria, range from a symbiotic to a neutral interaction with plants depending on soil N levels” **[69,70]**. “Furthermore, under N-limiting conditions, legumes secrete more flavones and flavonols to attract and initiate legume–rhizobia symbiosis” **[71,72]**.

Table 1: Important roles of root exudate components identified from different plant rhizospheres. For example, Tomato, Brassica napus etc., adapted from **[62,73,74]**.

Components of Root Exudates	Key Functions	Specific compounds identified in root exudates	References
Organic acids	Nutrient source Chemoattractant signals to microbes Chelators of poorly soluble mineral nutrients Acidifiers of soil Detoxifiers of Al nod gene inducers	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, tetronic	**74**
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	**73**
Sugars &	Promoters of plant and	Glucose, desoxyribose,	

Vitamin	microbial growth nutrient source	oligosaccharides galactose, biotin, maltose, thiamin, ribose, niacin, xylose, raffinose pantothenate, rhamnose, rhiboflavin, arabinose, fructose	**62**
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	**62**
Inorganic ions and gases	Chemoattractant signals to microbes	HCO_3" OH" Hþ CO_2 H_2	**62**
Phenolics	Nutrient source Chemoattractant signals to microbes Microbial growth promoters nod gene inducers and inhibitors in rhizobia Resistance inducers against phytoalexins Chelators of poorly soluble mineral nutrients Detoxifiers of Al Phytoalexins against soil pathogens	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 naringenin isoliquiritigenin, 7,30-dihydroxy-40-methoxyflavone umbelliferone, (þ)- and (")-catechin	**73**
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		**73**

Transport mechanisms of root exudates:

During the last one decade many researchers substantially gained progress in isolation and characterization of root exudates and their associations 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 **[75]**.

Diffusion process:

During diffusion process, lipid membrane mediates the transport of small polar molecules and uncharged molecules **[76]**. This passive diffusion process depends on membrane permeability **[77]** and cytosolic pH **[78]**. Apart from this, compounds like sugars, amino acids and carboxylate anions were transported by the aid of proteins, and their direction of movement is supported on electrochemical gradient that allows them to pass from the cytoplasm of intact root cells to the soil. Samuel et al. **[79]** 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 **[80]**. In such cases, mediate the controlled release of these compounds mediated by anion channels in the roots **[81,82,83]**.

Ion-exchange method:

The compounds specifically transported sugars, amino acids, and metals, which aids in the secretion of other compounds from root cells **[84,85,86,87,88,89,90]**. Plant cells have metal flow balance mechanisms to prevent excessive concentrations of free metal ions (e.g., Fe, Zn, Mn, and Cu) inside the cells; these mechanisms involve coordination of metal ion transporters for uptake, translocation, and compartmentalization **[91]**. 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 **[92,93]**. Recent evidence suggests that the rice silicon efflux transporter is involved in silicon efflux from root cells **[94,95]**. Similarly, malate transporter (AtALMT1) has been shown to play an important role in the release of malate from root cells in Arabidopsis under aluminum toxicity **[96]**. Other transporters involved in transporting hexoses, pentoses including ribose, and polyols such as myo-inositol and glycerol include monosaccharide transporters **[97,98]**.

Vesicular transport system:

Vesicular transport mechanisms involve in secretion of high-molecular weight compounds by roots **[99]**. Knowledge of the vesicle-mediated trafficking of proteins is well understood **[100]**, but the mechanism of vesicle-mediated transport of phytochemicals is not fully characterized **[101]**. 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 **[102]**. Similar reports by **[103],** Yazaki et al. **[104,105]** 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:

Different proteins have been engaged in the transport of secondary metabolites across plant membranes, and membrane-bound proteins provide an additional transport pathway for the release of metabolites from cells. Some of them accumulate at the plasma membrane and send substances out of the cell directly. Others concentrate near inner membranes where they can aid in securing substances in subcellular compartments or potentially fill vesicles with material in preparation for exocytosis. The ALMT (aluminum-activate malate transporter) family of transport proteins, the ABC family, the MATE family, the major facilitator superfamily (MFS), and others are among these proteins **[106]**.

ABC proteins mediated transport system:

ABC proteins are a large and ancient protein family found in all phyla. They use ATP hydrolysis energy to drive the transport of various substrates (metabolic products, ions, lipids, and xenobiotics). As a result, these are primarily active transporters with the ability to transport substrates against an electrochemical gradient. ABCs transport substrates from the cytosol to the apoplast via the plasma membrane or from the cytosol to other internal organelles such as the vacuole in eukaryotic cells. There are >100 putative ABCs in the rice and Arabidopsis genomes, some of which are involved in the transport of glutathione conjugates **[107]**, chlorophyll catabolites **[108]**, auxins **[109]**. For example, ABCs are thought to export the antifungal diterpene sclareol from the leaves of Nicotiana plumbaginifolia **[110]** and the isoflavone genistein from soybean roots **[111]**. Genistein is a signaling molecule produced by the roots of many legume species to promote nodulation. Because of its minor antimicrobial activity, it may also serve as a phytoalexin **[112]**. Another gene required for powdery mildew resistance in Arabidopsis encodes an ABC transporter called PEN3, which localizes to the plasma membrane and is recruited to pathogen attack sites on epidermal cells and root hairs by pathogen-associated molecular patterns like flagellin and chitin **[113]**. To limit pathogen invasion, PEN3 may release antimicrobial compounds such as glucosinolate3 derivatives into the apoplast adjacent to the appressoria. Surprisingly, PEN3 (=AtPDR8) protects against heavy metal toxicity by exporting cadmium ions or cadmium conjugates from root cells **[114]**, suggesting that the same transporter serves different functions in different tissues. Lr34, one of the most important disease resistance genes in wheat, is another example related to leaf pathogens. Lr34 is a full-sized ABC transporter expressed in leaves that is required for long-term rust resistance in wheat worldwide **[115]**. Lr34's function is unknown, but one theory suggests that it protects infected cells by exporting antimicrobial compounds into the apoplast in response to pathogen attack. Badri et al. [56] discovered 25 ABC transporter genes that are highly expressed in Arabidopsis root cells and are most likely involved in secretion processes. Exudates collected from wild-type plants and mutant lines were compared to plants with knockout mutations in these genes. They discovered that the composition of exudate differed between wild-type and mutant plants, and that more than one ABC transporter could be involved in phytochemical secretion.

MATE proteins

MATE genes encode transporters that export a wide range of substrates, including secondary metabolites. The family is found in both eukaryotes and prokaryotes **[116,117]**, and certain members of the family are responsible for multidrug resistance in bacteria and mammals. Although the specifics of their function are unknown, MATs appear to function as secondary active transporters that use the electrochemical gradient of other ions (sodium or protons) to drive substrate motion. AtDTX1, an Arabidopsis gene, encodes a plasma membrane-located protein that aids in the efflux of plant alkaloids, antibiotics, and other toxic compounds from the roots **[118]**. Other MATE genes found in sorghum (SbMATE1), barley (HvAACT1), and Arabidopsis (AtMATE1) confer aluminum resistance by facilitating the aluminum-activated efflux of citrate anions from root tips **[119,120]**. Citrate released by the roots is thought to chelate the toxic Al3+ cations in the apoplast and protect the rapidly dividing and elongating cells in the apices from damage **[121,122]**. PEZ1, a rice MATE protein, was recently shown to export phenolic compounds into the xylem **[123]**, and it was speculated that similar proteins might also facilitate phenolic compound transport into the rhizosphere.

MFS proteins

The phytosiderophores, a type of secondary metabolite, are an important source of iron in grasses [124]. In the rhizosphere, these phytosiderophores chelate iron (III), which is then transported to root cells by proton-coupled transporters from the oligopeptide transporter family [125]. However, the MFS proteins, which are among the largest and most diverse, are involved in the initial export of these compounds from roots. When iron supply is limited, TOM1 expression is induced, and transgenic plants overexpressing TOM1 exhibit increased deoxymugic acid release and tolerance to reduced iron supply.

Future aspects

Although the number of organic compounds exuded from roots is small (about 0.4 % carbon photosynthesized), they have a strong influence on soil microorganism attraction and may be significant in affecting plant nutrient availability. There is evidence that exudates from some plants' roots are toxic to neighboring plant roots and some germinating seeds. The current review compilation is based on data generated from experiments conducted on media-based solution-grown plants, so some important questions about root exudates from soil-grown plants remain unanswered: (i) How much organic material is exuded into the soil by roots? (ii) How far are the compounds diffused from the diffusion site from the roots? (iii) Are concentration gradients present? (iv) How do soil properties influence exudation? (v) What are the primary exudation sites? The use of C14-labeling techniques provides a powerful tool for answering these questions. The use of radioisotopes to investigate root exudation sites and the role of lateral roots in the exudation process should allow us to determine which parts of the soil will be most affected by root exudates.

Conclusion

According to the current situation, the rhizosphere microbial community in the soil is closely related to plant growth and can be altered by changing the pattern of root exudate secretion. Changing the root exudate patterns by modifying the ABC transporter has been shown in studies to affect the rhizosphere microbiome levels. The benefits of PGPR to plants in terms of growth and yield, on the other hand, are well documented, and most studies have only focused on plant parameters aboveground. However, PGPR interactions with plants begin in the rhizosphere with root exudation, followed by attraction, movement, and colonization on the rhizoplane and/or in the endorhizosphere. Most of the biological activities in the rhizosphere are guided by root exudates. Chemotaxis is a vital motility property that allows bacteria to move towards the rhizosphere, and it has been proposed that chemotaxis towards root exudates is the first step in bacterial colonization on the root surface. It was concluded that root exudates transported through the various mechanisms for the movement of secondary plant metabolites in roots are likely to those used elsewhere in the plant, but that roots release far more of these compounds than leaves. To move bioactive secondary products around root cells and into the rhizosphere, a variety of transport mechanisms are used, and these fluxes are frequently highly dependent on the local soil environment and root health. This review has highlighted the potential pathways for the safe transport of secondary metabolites, as well as their interactions with microbial communities, particularly endophytes, in promoting plant growth.

References:

1. Hiltner L. Uber neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berucksichtigung der Grundungung and Brache. Arb Dtsch Landwirsch Ges, 1904;98:59.
2. Hartmann A, Rothballer M, Schmid M, Lorenz H. A pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil, 2008;312:7–14. https://doi.org/10.1007/s11104-007-9514-
3. Lemanceau P, Corberand T, Gardan L, Latour X, Laguerre G. Effect of two plant species, flax (*Linum usitatissinum* L.) and tomato (*Lycopersicum esculantum* Mill.),

on the diversity of soilborne populations of fluorescent Pseudomonads. Applied and Environmental Microbiology, 1995;61:1004–1012.

4. Grayston S, Wang JS, Campbell CD, Edwards AC. Selective influence of plant species on microbial diversity in the rhizosphere. Soil Biology & Biochemistry, 1998;30:369–378.
5. Berg G, Smalla K. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiology Ecology, 2009;68:1–13.
6. Mendes R, Kruijt M, De Bruijn I, Dekkers E, Van Der Voort M, Schneider JHM, Piceno YM. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science, 2011;332:1097–1100.
7. Rosenblueth M, Martínez-Romero E. Bacterial endophytes and their interactions with hosts. Molecular Plant-Microbe Interactions, 2006;19:827–837.
8. Hardoim PR, van Overbeek LS, van Elsas JD. Properties of bacterial endophytes and their proposed role in plant growth. Trends in Microbiology, 2008;16:463–471.
9. Olivares F, Baldani V, Reis V. Occurrence of the endophytic diazotrophs *Herbaspirillum* spp. in roots, stems, and leaves, predominantly of Gramineae. Biology and Fertility of Soils, 1996;21:197–200.
10. Dong Y, Iniguez AL, Triplett EW. Quantitative assessments of the host range and strain specificity of endophytic colonization by *Klebsiella pneumoniae* 342. Plant and Soil, 2003;257:49–59.
11. Mathesius U, Mulders S. Extensive and specific responses of a eukaryote to bacterial quorum-sensing signals. Proceedings of the National Academy of Sciences, USA, 2003;100:1444–1449.
12. Rudrappa T, Czymmek K, Paré PW, Bais HP. Root-secreted malic acid recruits beneficial soil bacteria. Plant Physiology, 2008;148:1547–1556.
13. *Kent Peters N, Long SR. Alfalfa root exudates and compounds which promote or inhibit induction of Rhizobium meliloti nodulation genes. Plant Physiol, 1998;88:396–400.*
14. *Besserer A, Puech-Pagès V, Kiefer P, Gomez-Roldan V, Jauneau A, Roy S, Portais JC, Roux C, Bécard G, Séjalon-Delmas N. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. PLoS Biol, 2006;4:e226.*

15. *Bais HP, Fall R, Vivanco JM. Biocontrol of Bacillus subtilis against infection of Arabidopsis roots by Pseudomonas syringae is facilitated by biofilm formation and surfactin production. Plant Physiol, 2004;134:307–319.*
16. *Cavaglieri L, Orlando J, Rodriguez MI, Chulze S, Etcheverry M. Biocontrol of Bacillus subtilis against Fusarium verticillioides in vitro and at the maize root level. Res Microbiol, 2005;156:748–754.*
17. Shidore T, Dinse T, Öhrlein T, Becker A, Reinhold-Hurek B. Transcriptomic analysis of responses to exudates reveal genes required for rhizosphere competence of the endophyte *Azoarcus* sp. strain BH72. Environ. Microbiol, 2012;14:2775-2787.
18. Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. The role of root exudates in rhizosphere interactions with plants and other organisms. Annual review of Plant Biology, 2006;57:233-266.
19. Lugtenberg BJ, Dekkers L, Bloemberg GV. Molecular determinants of rhizosphere colonization by *Pseudomonas*. Annu Rev Phytopathol, 2001;39:461-90.
20. Bacilio-Jiménez M, Aguilar-Flores S, Ventura-Zapata E, Pérez-Campos ES. Bouquelet S, Zenteno E. Chemical characterization of root exudates from rice (*Oryza sativa*) and their effects on the chemotactic response of endophytic bacteria. Plant Soil, 2003;249:271-277.
21. Coombs JT, Franco CMM. Visualization of an endophytic *Streptomyces* species in wheat seed. Appl Environ Microbiol, 2003b;69:4260-4262.
22. Rosenblueth M, Martinez Romero E. *Rhizobium etli* maize populations and their competitiveness for root colonization. Arch. Microbiol, 2004;181:337-344.
23. Bais HP, Fall R, Vivanco JM. Biocontrol of *Bacillus subtilis* against infection of Arabidopsis roots by *Pseudomonas syringae* is facilitated by biofilm formation and surfactin production. Plant Physiol, 2004a;134:307.
24. Bais HP, Park SW, Weir TL, Callaway RM, Vivanco JM. How plants communicate using the underground information superhighway. Trends Plant Sci, 2004b;9:26.
25. Walker TS, Bais HP, Grotewold E, Vivanco JM. Root exudation and rhizosphere biology. Plant Physiol, 2003;1320:44.
26. Uren NC. 2000. Types, amounts and possible functions of compounds released into the rhizosphere by soil grown plants. In: Pinton R, Varanini Z, Nannipieri P (eds) The rhizosphere: biochemistry and organic substances at the soil interface. Dekker, New York, pp 19–40.

27. Cai Z, Kastell A, Knorr D, Smetanska I. Exudation: An expanding technique for continuous production and release of secondary metabolites from plant cell suspension and hairy root cultures. Plant cell reports, 2012;3:461-477.
28. Carvalhais LC, Dennis PG, Fan B, Fedoseyenko D, Kierul K, Becker A, Von Wiren N, Borriss R. Linking plant nutritional status to plant-microbe interactions. PLoS One, 2013;8:e68555.
29. Cai T, Cai W, Zhang J, Zheng H, Tsou AM, Xiao L, Zhong Z, Zhu J. Host legume-exuded antimetabolites optimize the symbiotic rhizosphere. Mol Microbiol, 2009;73:507-517.
30. Guttman D, McHardy AC, Schulze-Lefert P. Microbial genome-enabled insights into plant-microorganism interactions. Nat Rev Genet, 2014;15:797-813.
31. Bergsma-Vlami M, Prins ME, Raaijmakers JM. Influence of plant species on population dynamics, genotypic diversity and antibiotic production in the rhizosphere by indigenous *Pseudomonas* spp. FEMS Microbiol Ecol, 2005;52:59-69.
32. Aira M, Gómez-Brandón M, Lazcano C, Baath E, Domínguez J. Plant genotype strongly modifies the structure and growth of maize rhizosphere microbial communities. Soil Biol Biochem, 2010;42:2276-2281.
33. Ramachandran VK, East AK, Karunakaran R, Downie JA, Poole PS. Adaptation of *Rhizobium leguminosarum* to pea, alfalfa and sugar beet rhizospheres investigated by comparative transcriptomics. Genome Biol, 2011;12:R106.
34. Moulin L, Munive A, Dreyfus B, Boivin-Masson C. Nodulation of legumes by members of the beta-subclass of Proteobacteria. Nature, 2001;411:948.
35. Schardl CL, Leuchtmann A, Spiering MJ. Symbioses of grasses with seedborne fungal endophytes. Annu Rev Plant Biol, 2004;55:315.
36. Gray EJ, Smith DL. Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes. Soil Biol Biochem, 2005;37:395.
37. Bais HP, Broeckling CD, Vivanco JM. 2008. Root Exudates Modulate Plant—Microbe Interactions in the Rhizosphere. In: Karlovsky P. (eds) Secondary Metabolites in Soil Ecology. *Soil Biology,* 14. Springer, Berlin, Heidelberg, pp. 241-252.
38. Le´vy J, Bres C, Geurts R, Chalhoub B, Kulikova O, Duc G, Journet EP, Ane´ JM, Lauber E, Bisseling T, De´narie´ J, Rosenberg C, Debelle´ F. A putative Ca^{2+} and

calmodulin dependent protein kinase required for bacterial and fungal symbioses. Science, 2004;303:1361–1364.

39. Nagahashi G, Douds DD. Rapid and sensitive bioassay to study signals between root exudates and arbuscular mycorrhizal fungi. Biotechnol Tech, 1999;13:893–897.
40. Tamasloukht MB, Sejalon-Delmas N, Kluever A, Jauneau A, Roux C, Becard G, Franken P. Root factors induce mitochondrial-related gene expression and fungal respiration during the developmental switch from asymbiosis to pre-symbiosis in the arbuscular mycorrhizal fungus Gigaspora rosea. Plant Physiol, 2003;131:1468–1478.
41. Akiyama K, Ki M, Hayashi H. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature, 2005;435:824–827.
42. Harrison MJ. Signaling in the arbuscular mycorrhizal symbiosis. Annu Rev Microbiol, 2005;59:19–42.
43. Karandashov V, Bucher M. Symbiotic phosphate transport in arbuscular mycorrhizas. Trends Plant Sci, 2005;10:22–29.
44. Paszkowski U. Mutualism and parasitism: the yin and yang of plant symbioses. Curr Opin Plant Biol, 2006;9:364–370.
45. Gherbi H, Markmann K, Svistoonoff S, Estevan J, Autran D, Giczey G, Auguy F, Pe´ret B, Laplaze L, Franche C, Parniske M, Bogusz D. SymRK defines a common genetic basis for plant root endosymbioses with arbuscular mycorrhiza fungi, rhizobia, and Frankia bacteria. Proc Natl Acad Sci USA, 2008;105:4928–4932.
46. Lugtenberg B, Kamilova F. Plant-growth-promoting rhizobacteria. Annu. Rev. Microbiol, 2009;63:541–556.
47. Bodhankar S, Grover M, Hemanth S, Reddy G, Rasul S, Yadav SK, Desi S, Mallappa M, Mandapaka M, Srinivasarao C. Maize seed endophytic bacteria: dominance of antagonistic, lytic enzyme-producing *Bacillus* spp. 3 Biotech, 2017;7(4):232.
48. Werra P, Huser A, Tabacchi R, Keel C, Maurhofer M. Plant- and Microbe-Derived Compounds Affect the Expression of Genes Encoding Antifungal Compounds in a Pseudomonad with Biocontrol Activity. Applied and Environmental Microbiology, 2011;77(8):2807–2812.
49. Cazorla FM, Mercado-Blanco J. Biological control of tree and woody plant diseases: an impossible task? Bio Control, 2016;61(3):233-242.
50. Aziz NH, El-Fouly El, El-Essawy AA, Khalaf MA. Influence of bean seedling root exudates on the rhizosphere colonization by *Trichoderma lignorum* for the control of *Rhizoctonia solani*. Bot. Bull. Acad. Sin., 1997;38: 33-39.

51. Yi Y, Jong A, Elrike Frenzel E, Kuipers OP. Comparative transcriptomics of *Bacillus mycoides* Strains in Response to Potato-Root Exudates Reveals Different Genetic Adaptation of Endophytic and Soil Isolates. Front. Microbiol, 2017;8:1487.
52. Schreiter S, Babin D, Kornelia S, Rita G. Rhizosphere Competence and Biocontrol Effect of *Pseudomonas* sp. RU47 Independent from Plant Species and Soil Type at the Field Scale. Front. Microbiol, 2018;9:97.
53. Wang N, Wang L, Zhu K, Hou S, Chen L, Mi D, Gui Y, Qi Y, Jiang C, Guo J. Plant Root Exudates Are Involved in *Bacillus cereus* AR156 Mediated Biocontrol Against *Ralstonia solanacearum*. Front. Microbiol, 2019;10:98.
54. Badri DV, Vivanco JM. Regulation and function of root exudates. Plant Cell Environ, 2009;32:666–681.
55. Weston LA, Ryan PR, Watt M. Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. J. Exp. Bot., 2012;63:3445–3454. doi:10.1093/jxb/ers054. PMID:22378954.
56. Badri DV, Loyola-Vargas VM, Broeckling CD, De-la-Peña C, Jasinski M, Santelia D, Martinoia E, Sumner LW, Banta LM, Stermitz F, Vivanco JM. Altered profile of secondary metabolites in the root exudates of Arabidopsis ATP-binding cassette transporter mutants. Plant Physiol, 2008;146(2):762–771. doi:10.1104/pp.107.109587. PMID:18065561.
57. Badri DV, Quintana N, El Kassis EG, Kim HK, Choi YH, Sugiyama A, Verpoorte R, Martinoia E, Manter DK, Vivanco JM. An ABC transporter mutation alters root exudation of phytochemicals that provoke an overhaul of natural soil microbiota. Plant Physiol, 2009a;151(4):2006–2017. doi: 10.1104/pp.109.147462. PMID:19854857.
58. Loyola-Vargas V, Broeckling C, Badri D, Vivanco J. Effect of transporters on the secretion of phytochemicals by the roots of *Arabidopsis thaliana*. Planta, 2007;225(2): 301–310. doi:10.1007/s00425-006-0349-2. PMID:16868775
59. Yazaki K. Transporters of secondary metabolites. Curr. Opin. Plant Biol, 2005;8(3):301–307. doi:10.1016/j.pbi.2005.03.011. PMID:15860427.
60. Reddy VS, Shlykov MA, Castillo R, Sun EI, Saier MH. The major facilitator superfamily (MFS) revisited. FEBS J, 2012;279(11):2022–2035. doi:10.1111/ j.1742-4658.2012.08588.x. PMID:22458847.

61. Broeckling CD, Broz AK, Bergelson J, Manter DK, Vivanco JM. Root exudates regulate soil fungal community composition and diversity. Appl. Environ. Microbiol, 2008;74(3):738–744. doi:10.1128/AEM.02188-07.
62. Doornbos R, Loon L, Bakker PHM. Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. Agron. Sust. Dev, 2012;32(1):227–243. doi:10.1007/s13593-011-0028-y.
63. Chaparro JM, Badri DV, Bakker MG, Sugiyama A, Manter DK, Vivanco JM. Root exudation of phytochemicals in Arabidopsis follows specific patterns that are developmentally programmed and correlate with soil microbial functions. PloS ONE, 2013a;8(2):e55731. doi:10.1371/journal.pone. 0055731. PMID:23383346.
64. Chaparro JM, Badri DV, Vivanco JM. Rhizosphere microbiome assemblage is affected by plant development. ISME J, 2013b;8(4):790–803. doi:10. 1038/ismej.2013.196.
65. Micallef SA, Channer S, Shiaris MP, Colón-Carmona A. Plant age and genotype impact the progression of bacterial community succession in the Arabidopsis rhizosphere. Plant Signal. Behav, 2009a;4(8):777–780. doi:10.4161/ psb.4.8.9229. PMID:19820328.
66. Mercado-Blanco J, Bakker P. Interactions between plants and beneficial *Pseudomonas* spp.: exploiting bacterial traits for crop protection. Antonie van Leeuwenhoek, 2007;92(4):367–389. doi:10.1007/s10482-007-9167-1.
67. Raaijmakers J, Paulitz T, Steinberg C, Alabouvette C, Moënne-Loccoz Y. The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil, 2009;321(1–2): 341–361. doi:10.1007/ s11104-008-9568-6.
68. Newton AC, Fitt BDL, Atkins SD, Walters DR, Daniell TJ. Pathogenesis, parasitism and mutualism in the trophic space of microbe– plant interactions. Trends Microbiol, 2010;18(8):365–373. doi:10.1016/j.tim.2010.06. 002. PMID:20598545.
69. Davidson IA, Robson MJ. Effect of contrasting patterns of nitrate application on the nitrate uptake, N2-fixation, nodulation and growth of white clover. Ann. Bot, 1986;57(3):331–338.
70. Zahran HH. Rhizobium–legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. Microbiol. Mol. Biol. Rev. 1999;63(4):968–989. PMID:10585971.

71. Coronado C, Zuanazzi J, Sallaud C, Quirion JC, Esnault R, Husson HP, Kondorosi A, Ratet P. Alfalfa root flavonoid production is nitrogen regulated. Plant Physiol, 1995;108(2): 533–542. doi:10.1104/pp.108.2.533. PMID:12228491.
72. Zhang J, Subramanian S, Stacey G, Yu O. Flavones and flavonols play distinct critical roles during nodulation of Medicago truncatula by *Sinorhizobium meliloti*. Plant J, 2009;57(1):171–183. doi:10.1111/j.1365-313X.2008. 03676.x. PMID:18786000.
73. Jones DL, Hodge A, Kuzyakov Y. Plant and mycorrhizal regulation of rhizodeposition. New Phytol, 2004;163:459e480.
74. Vranova V, Rejsek K, Formanek P. Aliphatic, cyclic, and aromatic organic acids, vitamins, and carbohydrates in soil. Sci. World J, 2013;15:524239, http://dx.doi.org/10.1155/2013/524239.
75. Neumann G, Romheld V. 2000. The release of root exudates as affected by the plant's physiological status. In The Rhizosphere, Biochemistry and Organic Substances at the Soil–Plant Interface (eds. R.Pinton, Z.Varanini & P.Nannipieri), pp. 41–93. Marcel Dekker, New York, NY, USA.
76. Sanders D, Bethke P. 2000. Membrane transport. In Biochemistry and Molecular Biology of Plants (eds. B.B. Buchanan, W. Gruisham & R.L. Jones), pp. 110–158. ASPP, Rockville, MD, USA.
77. Guern J, Renaudin JP, Brown SC. 1987. The compartmentation of secondary metabolites in plant cell cultures. In Cell Culture and Somatic Cell Genetics of Plants (eds. F.Constabel & I.K.Vasil), pp. 43–76. Academic Press, San Diego, CA, USA.
78. Marschner H. 1995. Mineral Nutrition of Higher Plants. Academic Press, London, UK.
79. Samuel AL, Fernando M, Glass ADM. Immunofluorescent localization of plasma membrane H^+-ATPase in barley roots and effects of K nutrition. Plant Physiology, 1992;99:1509-1514.
80. Jones DL, Darrah PR. Influx and efflux of organic acids across the soil–root interface of *Zea mays* L. and its implications in rhizosphere C flow. Plant and Soil, 1995;173:103–109.
81. Ryan PR, Delhaize E, Randall PJ. Characterization of Al-stimulated efflux of malate from the apices of Al-tolerant wheat roots. Planta, 1995;196:103–110.

82. Zheng SJ, Ma JF, Matsumoto H. High aluminum resistance in buckwheat. Aluminum-induced specific secretion of oxalic acid from root tips. Plant Physiology, 1998;117:745–751.
83. Neumann G, Massonneau A, Martinoia E, Romheld V. Physiological adaptation to phosphorus deficiency during proteoid root development in white lupin. Planta, 1999;208:373–382.
84. Williams LE, Pittman JK, Hall JL. Emerging mechanisms for heavy metal transport in plants. Biochimica et Biophysica Acta, 2000;1465:104–126.
85. Hussain D, Haydon MJ, Wang Y, Wong E, Sherson SM, Young J, Camakaris J, Harper JF, Cobbett CS. P-type ATPase heavy metal transporters with roles in essential zinc homeostasis in *Arabidopsis*. The Plant Cell, 2004;16:1327–1339.
86. Colangelo EP, Guerinot ML. Put the metal to the petal: metal uptake and transport throughout plants. Current Opinion in Plant Biology, 2006;9,322–330.
87. Hirner A, Ladwig F, Stransky H, Okumoto S, Keinath M, Harms A, Frommer WB. Koch W. *Arabidopsis* LHT1 is a high-affinity transporter for cellular amino acid uptake in both root epidermis and leaf mesophyll. The Plant Cell, 2006;18:1931–1946.
88. Hoekenga OA, Maron LG, Piñeros MA, Cançado GMA, Shaff J, Kobayashi Y, Ryan PR, Dong B, Delhaize E, Sasaki T, Matsumoto H, Yamamoto Y, Koyama H, Kochian LV. AtALMT1, which encodes a malate transporter, is identified as one of several genes critical for aluminum tolerance in *Arabidopsis*. Proceedings of the National Academy of Sciences of the United States of America, 2006;103:9749–9750.
89. Grabov A. Plant KT/KUP/HAK potassium transporters: a single family – multiple functions. Annals of Botany, 2007;99:1035–1041.
90. Lee YH, Foster J, Chen J, Voll LM, Weber AP, Tegeder M. AAP1 transports uncharged amino acids into roots of *Arabidopsis*. The Plant Journal, 2007;50:305–319.
91. Hayden MJ, Cobbett CS. Transporters of ligands for essential metal ions in plants. New Phytologist, 2007;174:499–506.
92. Curie C, Panaviene Z, Loulergue C, Dellaporte SL, Briat JF, Walker EL. Maize yellow stripe1 encodes a membrane protein directly involved in Fe(III) uptake. Nature, 2001;409:346–349.

93. Curie C, Briat JF. Iron transport and signaling in plants. Annual Review of Plant Biology, 2003;54:183–206.
94. Ma JF, Yamaji N, Mitani N, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M. An efflux transporter of silicon in rice. Nature, 2007;448:209–212.
95. Ma JF, Yamaji N. Functions and transport of silicon in plants. Cellular and Molecular Life Sciences, 2008;65:3049–3057.
96. Kobayashi Y, Hoekenga OA, Itoh H, Nakashima M, Saito S, Shaff JE, Maron LG, Pineros MA, Kochian LV, Koyama H. Characterization of AtALMT1 expression in aluminum-inducible malate release and its role for rhizotoxic stress tolerance in *Arabidopsis*. Plant Physiology, 2007;145:843–852.
97. Klepek YS, Geiger D, Stadler R, Klebl F, Landour-Arsivaud L, Lemoine R, Hedrich R, Sauer N. *Arabidopsis* POLYOL TRANSPORTERS, a new member of the monosaccharide transporter-like superfamily, mediates H^+-symport of numerous substrates including myo-inositol, glycerol and ribose. The Plant Cell, 2005;17:204–218.
98. Buttner M. The monosaccharide transporter (-like) gene family in *Arabidopsis*. FEBS Letters, 2007;581:2318–2324.
99. Battey NH, Blackbourn HD. The control of exocitosis in plant cells. New Phytologist, 1993;125:307–308.
100. Field B, Jordan F, Osbourn A. First encounters – deployment of defence-related natural products by plants. New Phytologist, 2006;172:193–207.
101. Lin Y, Irani NG, Grotewold E. Sub-cellular trafficking of phytochemicals explored using auto-fluorescent compounds in maize cells. BMC Plant Biology, 2003;3:e10.
102. Snyder BA, Nicholson RL. Synthesis of phytoalexins in sorghum as a site-specific response to fungal ingress. Science, 1990;248:1637–1639.
103. Snyder BA, Leite B, Hipskind J, Butler LG, Nicholson RL. Accumulation of sorghum phytoalexins induced by *Colletotrichum graminicola* at the infection site. Physiological and Molecular Plant Pathology, 1991;39:463–470.
104. Tabata M. The mechanism of shikonin biosynthesis in cell *Lithospermum* cultures. Plant Tissue Culture Letters, 1996;13:117–125.
105. Yazaki K, Kunihisa M, Fujisaki T, Sato F. Geranyl diphosphate: 4-hydroxybenzoate geranyl transferase from *Lithospermum erythrorhizon*. Journal of Biological Chemistry, 2002;277:6240–6246.

106. Yazaki K, Matsuoka H, Shimomura K, Bechthold A, Sato F. A novel dark-inducible protein LeDI-2 and its involvement in root-specific secondary metabolism in *Lithospermum erythrorhizon*. Plant Physiology, 2001;125:1831–1841.

107. Leslie WA, Peter R, Ryan Michelle W. Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. Journal of Experimental Botany, 2012;63(9):3445–3454, https://doi.org/10.1093/jxb/ers054

108. Martinoia E, Klein M, Geisler M, Bovet L, Forestier C, Kolukisaoglu U, Muller R, Schulz B. Multifunctionality of plant ABC transporters – more than just detoxifiers. Planta, 2002;214:345-355.

109. Noh B, Murphy AS, Spalding EP. Multidrug resistance-like genes of Arabidopsis required for auxin transport and auxin-mediated development. Plant Cell, 2001;13:2441-2454.

110. Geisler M, Murphy A. The ABC of auxin transport: the role of P-glycoproteins in plant development. FEBS Letters, 2006;580:1094-1102.

111. Jasinski M, Stukkens Y, Degand H, Purnelle B, Marchand Brynaert J, Boutry MA. Plant plasma membrane ATP binding cassette-type transporter is involved in antifungal terpenoid secretion. Plant Cell, 2001;13:1095-1107.

112. Sugiyama A, Shitan N, Yazaki K. Involvement of a soybean ATP-binding cassette-type transporter in the secretion of genistein, a signal flavonoid in legume–Rhizobium symbiosis. Plant Physiology, 2007;144:2000-2008.

113. Geibel M. Sensitivity of the fungus *Cytospora persoonii* to the flavonoids of *Prunus cerasus*. *Phytochemistry*, 1994;38:599-601.

114. Stein M, Dittgen J, Sanchez-Rodrıguez C, Hou BH, Molina A, Schulze-Lefert P, Lipka V, Shauna S. Arabidopsis PEN3/PDR8, an ATP binding cassette transporter, contributes to nonhost resistance to inappropriate pathogens that enter by direct penetration. Plant Cell, 2006;18:731-746.

115. Kim DY, Bovet L, Maeshima M, Martinoia E, Lee Y. The ABC transporter AtPDR8 is a cadmium extrusion pump conferring heavy metal resistance. The Plant Journal, 2007;50:207-218.

116. Krattinger SG, Lagudah ES, Spielmeyer W, Singh RP, Huerta Espino J, McFadden H, Bossolini E, Selter LL, Keller B. Putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. Science, 2009;323:1360-1363.

117. Hvorup RN, Winnen B, Chang AB, Jiang Y, Zhou XF, Saier MH. The multidrug/oligosaccharidyl-lipid/polysaccharide (MOP) exporter superfamily. European Journal of Biochemistry, 2003;270:799-813.

118. Magalhaes JV. How a microbial drug transporter became essential for crop cultivation on acid soils: aluminium tolerance conferred by the multidrug and toxic compound extrusion (MATE) family. Annals of Botany, 2010;106:199-203.

119. Li L, He Z, Pandey GK, Tsuchiya T, Luan S. Functional cloning and characterization of a plant efflux carrier for multidrug and heavy metal detoxification. Journal of Biological Chemistry, 2002;277:5360-5368.

120. Furukawa J, Yamaji N, Wang H, Mitani N, Murata Y, Sato K, Katsuhara M, Takeda K, Ma JF. An aluminum-activated citrate transporter in barley. Plant and Cell Physiology, 2007;48:1081-1091.

121. Liu JP, Magalhaes JV, Shaff J, Kochian LV. Aluminum-activated citrate and malate transporters from the MATE and ALMT families function independently to confer Arabidopsis aluminum tolerance. The Plant Journal, 2009;57:389-399.

122. Ma JF, Ryan PR, Delhaize E. Aluminium tolerance in plants and the complexing role of organic acids. Trends in Plant Science, 2001;6:273-278.

123. Delhaize E, Gruber BD, Ryan PR. The roles of organic anion permeases in aluminium tolerance and mineral nutrition. FEBS Letters, 2007;581:2255-2262.

124. Ishimaru Y, Kakei Y, Shimo H, Bashir K, Sato Y, Sato Y, Uozumi N, Nakanishi H, Nishizawa NK. A rice phenolic efflux transporter is essential for solubilizing precipitated apoplasmic iron in the plant stele. Journal of Biological Chemistry, 2011;286:24649-24655.

125. Marschner H, Romheld V, Kissel M. Localization of phyto siderophore release and of iron uptake along intact barley roots. Physiology Plant, 1987;71:157-162.

126. Kim SA, Guerinot ML. Mining iron: Iron uptake and transport in plants. FEBS Letters, 2007;581:2273-2280.