[1]Department of Microbiology, CCS Haryana Agricultural University, Hisar, India
[2]Institute of Microbiology, Friedrich Schiller University, Jena, Germany
[3]Department of Plant Breeding , CCS Haryana Agricultural University, Hisar, India

Role of root exudates in plant-microbe interactions

Neeru Narula[1], Erika Kothe[2], Rishi Kumar Behl[3]

Summary

The interactions in the rhizosphere are leading to a highly structured microbial community which, to a great deal, is influenced by the root exudates of plant origin. In this review, we have included the different types of interaction with special regard to the root exudates' function in such positive or negative interactions beween plants and both bacterial and fungal partners of the plant in the rhizosphere, including mycorrhiza, nitrogen-fixing symbionts, plant growth promoting rhizobacteria endophytes and biological control organisms as well as allelopathy, antimicrobial effects and effects on nematodes. The differences in root exudates induced by microbial associations, role of quorum sensing in structuring communitites and effect on biogeochemical cycles are reviewed. The focus is put on agricultural systems and implications for ecosystems on arable land are drawn.

Introduction

The soil, often considered as 'black box', furnishes a living environment to the extremely diverse communities of macro and microorganisms. Likewise, the rhizosphere is the zone of contact in soil surrounding a plant root where biological and chemical parameters of the soil are influenced by the roots. In these niches, complex biological and ecological processes occur. The spatial influences of the plant on such communities are exerted without any distinct edge (MORGAN et al., 2005). Rhizosphere is thus an area of intense activity (biological, chemical and physical) influenced by compounds exuded by roots and by microorganisms feeding on these compounds (KAMILOVA et al., 2006; KUMAR et al., 2007). This microenvironment is characterized by distinct conditions compared with the bulk soil, largely created by the plant roots and its various microbial associations (BENFEY and SCHERES, 2000). These associations include non-symbiotic, symbiotic and associative organisms such as bacteria and mycorrhizal fungi. Microbial population is one of the essential parts of the rhizosphere and it affects the rhizosphere soil by their various activities such as water and nutrient uptake, exudation, and all the biological transformations (WHITE, 2003).

Bacteria can be found nearly everywhere in nature and in many unique habitats, including in association with plants. Plants provide an important ecological niche for many different organisms not only above ground, but also below ground. In comparison to bare soil, the soil associated with plant roots contains significantly higher densities of microorganisms (PINTON et al., 2001). Many of these microbes live there as a part of a distinct community surrounding plant roots. Heterotrophic bacteria are able to use organic compounds excreted in root exudates (SORENSEN et al, 2001), whereas their metabolites can be used by other microbes, which in the end create a network of closely connected microorganisms. This phenomenon of highly active microorganisms in root-associated soil is known as the „rhizosphere effect" (WHIPPS, 1990). The expression „rhizosphere" was first used by HILTNER (1904). It described the zone in which plant roots (from Greek: rhiza) interact with the surrounding soil (sphere) or field of influence. The rhizosphere was originally defined as the important portion of soil near roots responsible for plant growth (by providing nutrients) or as source for plant diseases. Today its definition is much narrower, referring to the root with closely associated soil where microorganisms are influenced by the root. The rhizosphere is commonly subdivided spatially into the endo-rhizosphere (including root cortex, epiderma and root hairs) and the ecto-rhizosphere with root associated soil compartments up to a distance of 5 mm. It is an interesting area for investigating interactions between plants and microbes. The specific structure and diversity of the rhizosphere bacterial community varies between plant species and over time (BAUDOIN et al., 2002) and different root zones on the same plant can support distinctive bacterial communities, reflecting quantitative and qualitative differences in root exudation (YANG and CROWLEY, 2000). Plants alter the rhizobacterial community by releasing different substrates, which can vary from single sugar components to complex aromatic structures (KAMILOVA et al., 2006), and therefore selecting for increased numbers of certain taxa and/or functional groups of bacteria (KRAVCHENKO et al., 2003; NARULA et al., 2007).

1.   Root Functions

The main function of the root is to anchor and support the plant and to absorb and conduct water and minerals to the plant (ABBOT and MURPHY, 2003). In addition to tap root and lateral root system, plant roots produce root hairs on the epidermal cells (Fig. 1) which are specialized to absorb water and minerals from the soil. Although all these root functions have been known for a long time, the fate of the exudates in the rhizosphere and the exact nature of their reaction in the soil still remain obscure.
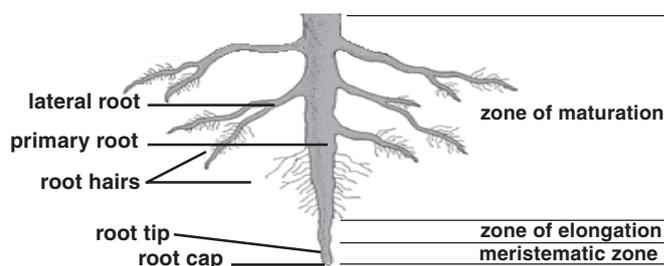

Fig. 1:   Root structure.

The rhizosphere supports diverse groups of bacteria that can stimulate growth of plants. Such plant growth promoting rhizobacteria (PGPR) operate by a wide variety of mechanisms including nitrogen fixation or phytohormone production (BAREA et al., 2005).

The present review therefore, describes advances made regarding the role of root exudates in interactions between plant roots and important dominating microbes present in the rhizosphere. Also the roles of root exudates taking part in the signaling events that initiate the execution of these interactions are assessed. Various positive and negative plant-microbe interactions are also described from the molecular to the ecosystem scale.

1.1   Root exudates

Plant root exudates are important factors that structure the rhizosphere bacterial community (WALKER et al., 2003) and are involved in important functions like providing defense against pathogenic (micro)organisms (ABBOT and MURPHY, 2003) and a basis for chemotaxis to attract and repel (particular) microbial species and populations (KUMAR et al., 2007), keeping the soil moist and wet, mobilizing nutrients, changing the chemical properties of the soil; stabilizing soil aggregates around the roots and inhibiting the growth of competitor plants.

Plant roots continuously exude compounds into the rhizosphere; this includes exudation or secretion of ions, free oxygen and water, enzymes, mucilage and a diverse array of carbon containing primary and secondary metabolites (NARDI et al., 2000). It is well established that root exudates provide nutrients leading to enhanced growth and higher prevalence of degrading strains of bacteria. On the other hand, numbers of certain bacteria are increasing by chemotactic response to root exudates. The resulting rhizosphere microflora can interact with root aggultinins present in the root exudates to form a rhizoplane community (KUMAR et al., 2007), directly attached to the root surface thus forming a subcompartment of the rhizosphere.

Root exudates are often divided into two different types of compounds:

1. Low molecular weight compounds such as amino acids, organic acids, sugars, phenolics and other secondary metabolites which account for much of the diversity of root exudates (ROUGIER, 1981).
2. High molecular weight exudates such as mucilage (polysaccharides) and proteins are less diverse but often comprise to a large proportion of the root exudates (ABBOT and MURPHY, 2003; WALKER et al., 2003).

The associated heterotrophic rhizobacteria of the rhizoplane and rhizosphere depend mostly on the carbohydrates exuded by the plant roots. BARBER and MARTIN (1976) determined that under sterile soil conditions between 5 to 10% of the net photosynthates of wheat may be released by the roots, whereas 12 to 18% is released in the non-sterile system. The later amount of carbon released would approximate 10 to 25% of the dry matter increase of the plants. Vesicular arbuscular mycorrhiza (VAM) forms a close and mutually beneficial relationship between plant root and mycorrhizal fungus. In order to meet each others needs, host plant and arbuscular mycorrhiza fungi (AMF) adjust through metabolic changes. Consequently, VAM induced root exudation will boost microbial communities as a whole

to grow in rhizosphere and acrue the beneficial effects on plant growth. On the other hand, root exudates are known to influence the proliferation of many pathogenic fungi such as *Rhizoctonia, Fusarium, Sclerotium, Aphanomyces, Pythium, Verticillium* and *Phytophthora*. These are shown to germinate as a result of stimulation and/or food source by root exudates of susceptible cultivars of host plants. Root exudates containing toxic substances such as glycosides and hydrocyanic acid may inhibit the growth of pathogens (RANGASWAMI, 1988). The compounds released by plant roots are diverse, and only a few have been shown to exert a direct effect on the growth of plants. We can conclude that root secretions and products are effective under the right set of conditions.

The specific rhizosphere community that is finally observed on mature roots may include symbionts which either can enter the root, like mycorrhizal fungi or rhizobia, or species that are found regularly on root surfaces (associative) but not inside the root. Aside from nutrient mobilization, the rhizoplane bacteria can provide protection from soil-borne pathogens thus also aiding plant growth.

Plants often benefit from the nitrogen compounds, either fixed or released from organic material by bacterial metabolism. For example, *A. vinelandii*, a free living nitrogen fixing bacterium, ultimately depends on carbon released by the plants, while the plants growing in soils with low nitrogen colonized by these bacteria benefit from the fixed nitrogen compounds. This is an example for mutually beneficial associations of free living nitrogen fixing bacteria with no direct contact (KUMAR et al., 2007).

Different types of interactions involving plants roots in the rhizosphere include root-root, root-insect, and root-microbe interactions. Chemical signaling between plant roots and other soil organisms, including the roots of neighbouring plants, is often based on chemicals exuded from the roots. The same chemical signals may elicit dissimilar responses from different recipients. An example of such divergent read-outs of a chemical signal is the secretion of isoflavones by soybean roots: It attracts a mutualist (*Bradyrhizobium japonicum*) and a pathogen (*Phytopthora sojae*) alike (BAIS et al., 2006).

2.   Plant root-microbal communication

Plant-microbe interaction is one of the important communications that characterizes the zone below-ground. Some of the compounds identified in root exudates that have shown to play an important role

Tab. 1: Analysis of root exudates obtained from control and inoculated plants

Plant variety	Inoculants	Sugars	Total sugars µg/ml	Amino acids	Organic acids
Cotton var. H1098 (American)	none	glucose	18.8	lysine, threonine	citric acid
	E 12	xylose	12.37	arginine, glutamate	succinic acid
	Ala 27	glucose	22.8	threonine	malonic acid
	HT 57	glucose	26.2	arginine	maleic acid
Cotton var. HD123 (Desi)	none	xylose, glucose	23	arginine	oxalic acid
	E 12	glucose	29.9	arginine, glutamate	succinic, malonic, maleic acid
	Ala 27	glucose	36.2	threonine	oxalic, succinic, malonic acid
	HT 57	glucose	30.7	arginine	malic, maleic acid
Wheat var. WH 711	none	glucose	33.6	arginine	succinic acid
	E 12	glucose, xylose	24.2	unidentified	oxalic acid
	Ala 27	fructose	106.3	arginine, threonine	malonic acid
	HT 57	sucrose, glucose	23.6	methionine	malonic acid

in root-microbe interactions include signals like flavonoids present in the root exudates of legumes that activate the *Rhizobium meliloti* genes responsible for the nodulation process. These compounds may also be responsible for colonization of VAM (BECARD et al., 1995). On the other hand, root cells are very delicate and are always prone to be attacked by pathogenic bacteria, but secretion of defense proteins like phytoalexins and other unknown chemicals protect them (FLORES et al., 1999). Still, the chemodiversity of root exudates is vast and one can always search for new compounds including antimicrobials. For example, recently identified rosmarinic acid in the root exudate of hairy root cultures of sweet basil elicited by fungal cell wall extracts from *Phytophthora cinnamoni* (BAIS et al., 2006). Similar studies by BRIGHAM et al. (1999) with *Lithospermum erythrorhizon* reported cell specific production of pigmented naphthoquinones; these findings suggest the importance of root exudates in defending the rhizosphere against pathogenic microorganisms.

Plant growth is positively influenced by microbe interactions through a variety of mechanisms, including biological nitrogen fixation by different classes of proteobacteria, increased biotic and abiotic stress tolerance imparted by the presence of endophytic microbes, and direct and indirect advantages rendered by plant growth-promoting rhizobacteria (PGPR) (BAREA et al. 2005;). Bacteria can also positively interact with plants by producing protective biofilms or antibiotics being used as biocontrols against plant pathogens, or by degradation by plant- and microbially produced compounds in the soil that would otherwise be allelopathic or even autotoxic. However, rhizospheric bacteria (YANG et al., 2001) can also have detrimental effects on plant health and survival through pathogenic or parasitic infection.

Root colonization is important as the first step of infection by soil-borne pathogens as well as for beneficial associations with micro-organisms. The „rhizosphere effect," as described by HILTNER (1904) assumes that many microorganisms are attracted to nutrients exuded by plant roots. He observed that the number and activity of micro-organisms always increased in the vicinity of plant roots. However, in addition to providing a carbon-rich environment through exudation, plant roots also initiate cross talk (WALKER et al., 2003) with soil microbes by producing signals that are recognized by the microbes. They, in turn, produce signals that initiate plant responses necessary for colonization. VAN WEST et al. (2002) described that motility is an important trait for competitive pathogenic and beneficial microbes, which enables them to colonize plant roots and to participate in this cross talk. Chemical attraction of soil microbes to plant roots, or chemotaxis, is a well-understood phenomenon involved between plant roots and microbes (KUMAR et al., 2007). Another, recently discovered mechanism involves the use of electric potentials in plant roots, produced by electrogenic ion transport at the root surface, to attract swimming zoospores of oomycete plant pathogens to plant root surfaces (BAIS et al., 2006). These data also suggest that the electrical signals may mask the chemical signals in mediating short-range responses of oomycete zoospores to root surfaces. It is still not known whether the perception of chemotactic or electrotactic signals may affect the likelihood of infection by soil microbes acting as pathogens or symbionts.

2.1 Positive Plant-Microbe Interactions

2.1.1 Mycorrhizae

Mycorrhizae refer to a mutualistic symbiotic relationship between plant roots and soil fungi. It is seen at the roots of the majority of terrestrial plants (MORGAN et al., 2005). Ecto- and endomycorrhiza are distinguished by their growth around or within root cells. Endo-mycorrhizal AMF are always found in association with the roots and hence considered as obligate parasites. They belong to the clade of glomeromycetes, related to zygomycetes. In contrast to AMF, ecto-mycorrhizal fungi belonging mostly to the basidiomycetes and rarely to asco- or zygomycetes, are not obligate biotrophs but can live saprophytic in soil. Ectomycorrhizal fungi in contact to their tree host form an extensive sheath around the root of the plant with penetration into the root between rhizodermic cells (AKIYAMA et al., 2005), whereas in VAM, the fungal mycelium infects root cells. Mycorrhizal fungi obtain their carbon from the root while taking up inorganic nutrients from the surrounding soil delivering those to the plant (Fig. 2). Beneficial effects of mycorrizal fungi (BEHL et al., 2007) can be best observed especially in poor soils and under stress conditions including, e.g., metal contamination.
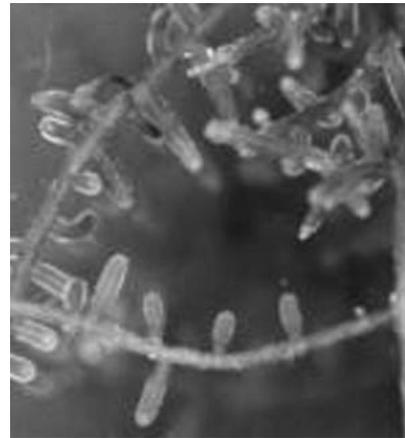
Fig. 2: Mutualistic mycorrhizal symbioses

Thus, mycorrhiza is one of the finest examples of plant-microbe mutual symbiosis in which both partners benefit: the mycorrhizal plant is better able to function physiologically and compete successfully in species rich plant communities, while the fungus benefits from a steady supply of organic nutrients (BAGO et al., 2003). Another advantage of this fungal association is the fungal property of phosphate solubilization to make phosphorous available to the plants. Thus, VAM is widely used as biofertilizer for various crops (BEHL et al., 2007; NEUMANN and GEORGE, 2004). Under stress conditions like drought, metal stress, or nutrient deficiency, VAM can provide a better and more continuous supply of water and nutrients and act as a biofilter for the uptake of heavy metals, thus aiding plant growth. In addition, AMF can supply phytohormones aiding plant growth.

Like rhizobia, mycorrhizal fungi recognize their compatible host through root exudates (NAGAHASHI and DOUDS, 2003). Hyphal branching ensures contact with the host root and hence the establishment of symbiosis (DECARVALHO et al., 2002). The branch inducing factor is a plant signaling molecule that triggers hyphal morphogenesis preceding successful colonization (BUEE et al., 2000). This branch inducing factor was present in all root exudates of every mycotrophic plant tested, but absent in those of non-host plants. Root exudates from phosphate limited plants are more active than those from plants with sufficient phoshor, suggesting that the production and/or the exudation of the branching factor in roots are regulated by phosphor availability (NAGAHASHI et al., 1999). AKIYAMA et al. (2005) identified sesquiterpenes which trigger hyphal branching in dormant mycorrhizal spores from exudates of *Lotus japonicus,* which could become helpful in establishing a new role for root exudates in plant-mycorrizal interaction. Defense processes, which are always triggered in response to microbial invasion, are modulated in mycorrhizal roots (GARCIA et al., 2002).

2.1.2 Nitrogen-fixing symbionts

Second most important and influential specific plant-microbe interactions are those of leguminous plants and Gram-negative nitrogen fixing bacteria (MORGAN et al., 2005). Several agricultural industries revolve around leguminous crops and their ability to grow without nitrogen fertilizer; this saves farmers millions of dollars yearly the fertilizer costs. *Rhizobium, Bradyrhizobium, Sinorhizobium, Mesorhizobium, Azorhizobium and Photorhizobium* are rod shaped proteobacteria that can grow in a free living state in soil or can infect legume plants and establish a symbiotic relationship (BLOEMBERG and LUGTENBERG, 2001; MADIGAN and MARTINKO, 2006). Root infection with appropriate species of one of these rhizobia leads to the formation of root nodules (Fig. 3; HEIDSTRA and BISSELING, 1996). Therefore, it is being used as biofertilizer for most of the leguminous crops worldwide (DEAKER et al., 2004).

Fig. 3: Legume with nodules

Attachment of a bacterium to the plant in legume-rhizobium symbiosis is the first step in the formation of nodules (SAWADA et al., 2003). The penetration of rhizobia is preceded by root hair curling which is induced by a bacterial substance, the nod factor (PERRET et al., 2000). Following root hair curling the bacteria enters the root hair and induces formation by the plant of a cellulosic tube called the infection thread which spreads down the root hairs. Root cells adjacent to the root hairs subsequently become infected by rhizobia and *nod factors* help in stimulating plant cell division and continued plant cell division leads to nodule formation associated with formation of bacteroids of flexible shape. These differenciated cells perform nitrogen fixation however; they do not multiply anymore.

The host specificity is determined by at least two steps in the mutual signal exchange between the plants and microsymbionts. First, bacterial nodulation (*nod*) genes are activated in response to plant-secreted signal molecules such as flavonoids (LOON and BAKKER, 2004) resulting in biosynthesis and secretion of nod factors by the rhizobium. Flavonoids and isoflavonoids exuded from legume roots that activate *nod* genes are flavones (luteolin, apigenin), flavanones (naringenin, hespertin) and isoflavones (daidzein, genestein) (PERRET et al., 2000). In the second step, the Nod factors trigger the infection process and elicit nodule formation on the host plant roots.

After a phase of effective dinitrogen fixation, bacteria and host cell degenerate (PERRET et al., 2000). Thus, the development of the nitrogen fixation symbiosis depends upon an extensive exchange of chemical signals between the symbiotic partners.

A second nitrogen fixing association is found with tree roots and the Gram-positive, filamentous actinobacterial genus *Frankia* forming intracellular nitrogen fixing symbiosis with over 200 angiosperm species belonging to 8 families (DANIEL et al., 2007). The rate of nitrogen fixation is in the same range as many nodulated legumes, i.e., 40-350 kg ha^{-1} year^{-1}. The broad range, and the worldwide distribution of the host plants (ranging from arctic to tropical habitats) makes actinorhizae to major contributors to geochemical nitrogen cycling. The best known association of Frankia is with *Alnus* (DANIEL et al., 2007).

2.1.3 Plant growth promoting rhizobacteria (PGPR)

In recent years, a new group of microorganisms have gained much attention because of their effect on enhancement and health of crops (BLOEMBERG and LUGTENBERG, 2001). These microorganisms can influence plant growth by producing one or more substances that act as growth stimulators and are referred as plant growth promoting bacteria/rhizobacteria (PGPB or PGPR). As they are also inhibitory to the growth of plant pathogenic organisms they have been described as biological control agents (KLOEPPER, 1993). Several asymbiotic, associative associations have been cited between microbes and plant roots, for example *Azospirillum* with grass family crops like barley, sorghum, wheat and barley, *Azotobacter paspali* with a perennial grass, *Campylobacter* with spartina, a grass common in marshes, *Acetobacter* with sugarcane or sweet potato, *Achromobacter* with rice (DOBEREINER, 1988). These beneficial microorganisms are included in management practices in sustainable agriculture. A variety of bacterial traits and specific genes contribute to these processes, but only a few have been identified on a molecular level. These include motility, chemotaxis towards seed and root exudates, protein secretion and quorum sensing. An interesting report is by JAEGER et al. (1999) which shows mapping of sugar and amino acid availability in the root exudate of *Avena barbata*. The studies show the availability of tryptophan mainly near the root tip region. Tryptophan is the precursor for indole acetic acid (IAA), an auxin phytohormone (COOKE et al., 2002), suggesting that PGPR could exploit the root exudate pools for precursors of plant growth regulators.

Indirectly, plant growth and yield is enhanced via supression of phytopathogens. The competitive mechanisms suppressing pathogens include the ability to produce siderophores (PAREZ-MIRANDA et al., 2007), iron chelators, that render iron unavailable to pathogens, the synthesis of antifungal metabolites, cell wall lysing enzymes, or hydrogen cyanide which suppress the growth of fungal pathogens. They also show the ability to compete with pathogens for nutrients, or specific niches on the root, and the ability to induce systemic resistance.

Among direct mechanisms are fixation of atmospheric nitrogen that is transferred to plants, production of siderophores (PAGE, 1987; GUAN and KAMINO, 2001), solubilization of phosphorous, and synthesis of phytohormones. There are few reports (SINGH et al., 2007) on the increase of mineral uptake at the root surface by inoculation with PGPR. Bacteria are likely to locate roots through some signals from the roots and it is observed that carbohydrates and amino acids stimulate PGPB chemotaxis towards roots (KUMAR et al., 2007). Flagellar motility in some rhizobacteria is influenced by root exudates (LUGTENBERG et al., 2002). This could be shown using *cheA* mutants defective in flagella driven chemotaxis in four strains of *Pseudomonas fluorescence*, a known PGPB. Chemotaxis is an important parameter for competitive colonization. Outer membrane proteins of bacteria also play an important role in early host recognition. These proteins from *Azospirillum brasiliense* bind to membrane immobilized root extracts from several plant species with different affinities. This *Azospirillum* showed stronger adhesion

to extracts of cereals as compared to the extracts of legumes and tomatoes (BASHAN and LEVANONY, 1991).

2.1.4 Endophytes

Some of the soil bacteria are reported to produce growth hormones which affect plant growth. For example, gibberellic acid and cyto-kinin production has been reported for *Azospirillum* (UMALI-GARCIA et al., 1980), *Arthrobacter* (CACCCIARI et al., 1989) and *Azotobacter* (PATHAK et al., 1995). DOBBELAERE et al. (1999) suggested that plant growth promoting substances are one of the key factors observed in plant growth promotion. The bacteria are known to change root morphology and increase their biomass thus enabling the roots to take up more soil nutrients. Treatment with auxins has been shown to increase the colonization of roots by soil bacteria e.g., *Azospirillum* (KENNEDY and TCHAN, 1992).

Most of the soil bacteria tested were able to produce IAA, and stimulated a lateral root development and colonization by addition of 2,4-D and IAA. Formation of paranodules on roots as a result of crack entry invasion was observed with 2,4-D as well as with IAA (Plate 1-4, NARULA et al., 2006).

YOST et al. (1998) reported that methyl-accepting chemotaxis proteins (MCPs) play important roles in the chemotactic response of many bacteria. In this investigation oligonucleotide primers designed to amplify the conserved signaling domain of MCPs by PCR were used to identify potential MCP-encoding genes in *Rhizobium leguminosarum*. The results overall suggested that *R. leguminosarum* possessed *mcp*-like genes, and that at least some of these play a role in early steps of the plant-microbe interaction.

2.1.5 Biological control

The ability to supress plant diseases by some natural and rhizosphere soils has been attributed to the indigenous beneficial rhizosphere microorganisms, as already discussed above (KLOEPPER et al., 1993). Especially mycorrhizal symbiosis can lead to reduction in symptoms and lower susceptability of the plant to pathogenic microorganims. One example was investigated by CHHABRA et al. (1996), who studied the role of a VAM fungus (*Glomus mosseae*) in biological control of flag smut (*U. agropyri*) of wheat. They reported that VAM inoculation suppressed flag smut incidence from 48.2% to 23% in double inocu-lation with *Glomus* and the pathogen. Dual inoculation also resulted in increased dry weight of roots and shoots, as well as yield.

Several bacterial genera are known to be capable of providing disease conrol, among them *Streptomyces, Agrobacterium, Enterobacter, Erwinia, Bacillus, Serratia, Azotobacter* and fluorescent *Pseudo-monas* strains. The nature of biological control by bacterial strains is difficult to determine. This can be either in the form of direct killing or suppression of the pathogenic organisms, or by indirect compe-tition for nutrients or inhibiting the establishment of pathogens by increasing the competence and ecological fitness of the biocontrol agent.

2.2   Negative Effects of Root Exudates

2.2.1 Root exudates and their allelopathy activity

The application of allelopathy in biological pest and weed control mostly aims at plant protection and improvement of plant resistance to diseases. The growth and development of plants in natural or
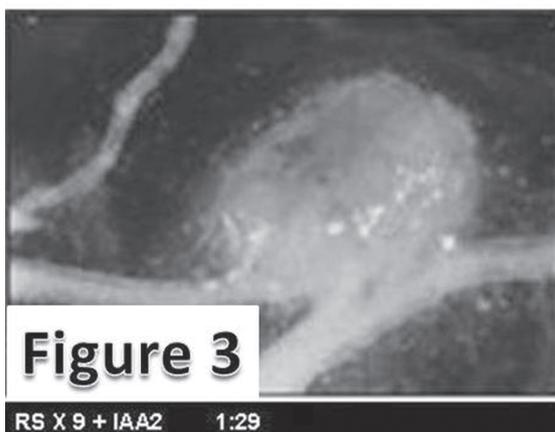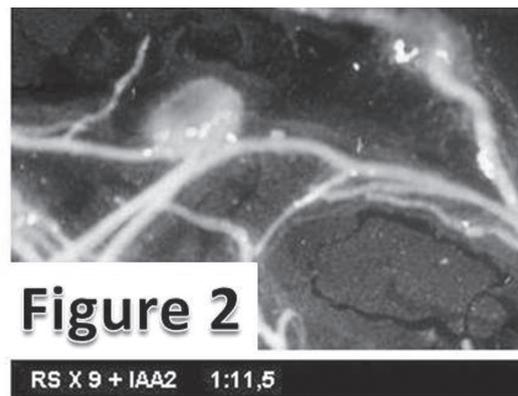
Fig. 4: Fig. 1-4: Zoom microscopic photographs of wheat roots in *Azotobacter* inoculation + hormone treatments. Fig. 1: Swollen roots – MSX9 + 2,4-D; Fig. 2: Paranodule formation – MSX9 + IAA; Fig. 3: Paranodule formation – MSX9 + IAA; Fig. 4: Reisolate from paranodule-tested

agricultural/horticultural ecosystems is frequently modified by physical and chemical processes due to influence of neighbouring plants. The dominance of certain species in the field may be explained by their strong allelopathic potential against neighboring species (LESZCZYNSKA et al., 2004). Allelopathic compounds produced as root exudates generally enter the rhizosphere soon after their release (INDERJIT, 2001), these compounds may be released in large amounts but are subjected to sorption (physical), metal oxidation (chemical) and microbial degradation (biological) with in the rhizosphere (HUANG et al., 1999). In addition to chemical breakdown, microbial degradation can limit the persistence of many secondary metabolites of plant origin in the soil.

2.2.3 Root exudate's effects on nematodes

Root exudates are known to be a carbon source for soil microbes leading to abundant population in the rhizosphere. ROVIRA et al. (1974) reported that out of large microbial popuation in the rhizosphere, bacteria occupy < 10% of the root surface and the fungal hyphal densities are only 12-14 mm m^{-2} roots. Under these conditions, nematodes can select uncolonized sections of the root for feeding. If a good colonization is observed, microbes may interfere with the plant pathogenic nematodes. Various beneficial rhizobacteria like *Azotobacter* and *Gluconacetobacter* have been evaluated for their antagonistic effect on a variety of plant parasitic nematodes including *Meloidogyne incognita*. An antibiosis effect causing decreased nematode infestation in the soil ecosystem has been observed as a consequence of microbial colonization and active growth (BANSAL et al., 2005). Among the volatile metabolites of rhizosphere bacteria, ammonium ions have been shown to repel *M. incognita* juveniles and acetic acid inhibited egg hatching and movement of infective juveniles (BANSAL and BAJAJ, 2003). However, other nematodes graze on the microbial population and take advantage of the dense microbial populations as a food source. Environmental conditions and plant species-specific exudates greatly affect the quality and quantity of carbon and nitrogen sources secreted into the rhizosphere. However, the specific influence of these factors on microbe-nematode interactions is still unknown. There are few reports on interactions among plant roots, microbes and nematodes. Soil dwelling nematodes may mediate the interaction of plant roots and rhizobia leading to enhanced nodulation. *Medicago truncatula* releases volatiles that attract these nematodes indicating an important role in multitrophic interactions for these volatile compounds. Various fatty acids are known to be toxic to various developmental stages of plant parasitic nematodes (BANSAL and BAJAJ, 2003). Acetic acid and caprylic acid reduced hatching most effectively and irreversibly by impairing embryogenesis of *Meloidogyne incognita* eggs.

2.3 Role of Quorum Sensing in Root-Microbe Interactions

Quorum sensing is the ability of bacteria to communicate and coordinate behavior via signaling molecules and it is a regulatory process by which bacteria monitor their population density. During growth, bacteria produce and subsequently percept diffusible signal molecules (XUESONG et al., 2003).

Many bacteria regulate diverse physiological processes in concert with their population size (WEST et al., 2006). The population as a whole is thus able to modify its behaviour as a single unit. Both groups of Gram positive and Gram negative bacteria including plant pathogenic bacteria like *Erwinia, Pseudomonas* spp. and *Agrobacterium* possess quorum sensing system that control the expression of several genes required for pathogenicity (FRAY, 2002). Amongst Gram-negative bacteria (VISIK and RUBY, 1999), the quorum sensing signals most commonly used are *N*-acylhomoserine lactones (AHLs).

Bacteria which use quorum sensing produce and secrete autoinducers. It binds to its receptor and activates transcription of certain genes, including those for inducer synthesis. The chemical signals differ between Gram-positive and Gram-negative, with homoserine lactones in Gram-negative and peptide autoinducers in endospore forming content Gram-positives. Streptomycetes, Gram-positives with high-G+C-content, however, have been shown to regulate spore formation as well as antibiotic production by a quorum sensing signal called A-factor.

In the nodulating rhizobium *R. leguminosarum* the quorum sensors are arranged in hierarchical network that coordinate conjugal transfer gene transfer on symbiotic plasmid rhizospheric specific gene expression and other as yet unidentified functions. This can also influence different aspects of interactions with the host, ranging from the modulatory to direct roles during nodulation (DANIELS et al., 2002). It is speculated that quorum sensing affects population dynamics in association with host plants.

Both siderophores and HSLs have been suggested to play roles as chemical signals for interspecies communication between bacteria (GUAN et al., 2001). However, little is known on interspecies communication in the natural microbial ecosystem. MATHESIUS et al. (2003) reported increased secretion of AHL mimics in exudates of *M. truculata*.

The chemical nature of such active quorum sensing mimicking secondary metabolites is currently unknown and still requires further clarification (TEPLITSKI et al., 2000; CHEN et al., 2002). In addition to signal mimics, also quorum quenching by, e.g., enzymatic degradation of the signaling molecules, has been described.

3.1 Role of exudates in remediation of heavy metal / agrochemical contamination

There are certain soils contaminated with heavy metals due to application of fertilizers (rock phosphate, e.g., usually contains uranium) or some pesticides containing metals, or application of sewage sludge/industrial waste. The search for inexpensive remediation technologies for contaminated soil and ground water has led to great interest in bioremediation and plant-based remediation (or phytoremediation). Vegetation can also enhance *in situ* bioremediation by taking advantage of natural attenuation processes in many applications. However, since the rhizosphere is an environment of high microbial activity, the influence of microorganisms on the processes involved in mobilization/immobilization or degradation of organic containing contaminants has to be taken into account (KOTHE et al., 2005). Microbial transformations occur in soil and water external to plant roots. Some of the organic pollutants can be enzymatically attacked and degraded microbiologically, while many other compounds do not naturally occur and may be therefore resistant to biological degradation. These substances are called „recalcitrant". For example, 2,4-dichlorophenoxyacetic acid can be degraded with in four weeks, whereas DDT can be persists in the soil for more than 15 years. Bioremediation is environment friendly and a cost-effective method for cleaning up pollutant, in this case, this would imply introduction of a strain capable of attacking a recalcitrant substance.

With respect to heavy metal contamination, any bioremediation approach has to take into account the survival of rhizobacteria under high metal loads (BÜCHEL et al., 2005). Thus, a screening for heavy metal resistant soil microbes can provide strains applicable in microbially stimulated phytoextraction or also for biostabilization protecting the water path from metal seepage (HAFERBURG and KOTHE, 2007). Therefore, microbes able to accumulate high levels of metals are interesting (HAFERBURG et al., 2006, 2007; SCHMIDT et al., 2008). Evidences for copper, cadmium, and nickel bioaccumulation have been investigated with special emphasis on streptomycetes, a group ot Gram-positive bacteria dominating, especially,

poor soils with high metal loads (Albarracin et al., 2008; Schmidt et al., 2005; Sineriz et al., 2008). In addition, the capacity of fungi including ectomycorrhizal fungi for bioaccumulation of heavy metals has been tested (Merten et al., 2004). This might be coupled to uptake of phosphate as heavy metals can be stored in the vacuole of fungal cells as phosphate salts (Kothe et al., 2002; Terpitz and Kothe, 2006).

4. Plant-microbe interactions for agricultural ecosystems

Plant microbe interactions are responsible for a number of transformation in the rhizospere such as carbon sequestration, ecosystem functioning and nutrient cycling. Type and quantity of microbes present in the soil influence the ability of a plant to obtain nitrogen and other nutrients. Plants can influence these ecosystems changes through deposition of secondary metabolites into the rhizosphere which help to attract or inhibit the microorganisms. Rhizodeposition is made up of small molecular weight metabolites, amino acids, secreted enzymes, mucilage, and cell lysate can range from less than 10% of the net carbon assimilation by the plant to as higher as 44% of nutrient stressed plant's total carbon. Soil microbes utilize this abundant carbon source, whereas secretion of other compounds might inhibit pathogenic associations.

In addition, there is a need to know how diazotrophs may benefit the plant. Investigations on the production of phytohormones and the action of siderophores produced by *Azotobacter* strains might help to understand this aspect of interactions. A consideration of the factors that might play a role in interactions of bacteria and hosts has to be extended to the mechanisms likely to be involved in stable colonization of distinct microhabitats of the rhizosphere. Only then, application of the results seems possible in agriculture which may benefit the ecosystem if less mineral fertilizers have to be used in the future.

Free living and associative diazotrophs are more numerous in the rhizosphere than in bulk soils, indicating their dependence on organic compounds exuded by roots in the rhizosphere (Gransee and Wittenmeyer, 2000). Various nitrogen fixing microorganisms have been found to be present in the rhizosphere of agricultural plants, but the contribution of fixed nitrogen to plant nutrition is controversial. Diazotrophs found in the soil or associated with roots include *Azotobacter chroococcum*, *Azospirillum brasiliense* and *Gluconacetobacter diazotrophicus* (formerly *Acetobacter diazotrophicus*) and the positive responses of plants to inoculation with these bacteria are attributed to N_2 fixation, but in addition due to several other factors like phytohormone and/or ammonium production, etc. (Okon, 1985).

References

Abbott, L., Murphy, D., 2003: Soil biology fertility: A key to sustainable land use in agriculture. Kluwer Academic Publishers, 187-203.

Akiyama, K., Matsuzaki, K., Hayashi, H., 2005: Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435, 824-827.

Albarracín, V.H., Winik, B., Kothe, E., Amoroso, M.J., Abate, C.M., 2008: Copper bioaccumulation by the actinobacterium *Amycolatopsis* sp. AB0. J. Basic Microbiol. 48, 323-330.

Bago, N.B., Pfeffer, P.E., Abubakar, J., Jun, J., Allen, J.W., 2003: Carbon export from arbuscular mycorrizal roots involves the translocation of carbohydrate as well as lipid. Plant Physiol. 13, 1496-1507.

Bais, H.P., Tiffony, L., Weir, L.T., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006: The role of root exudates in rhizosphere interactions with plant and other organisms. Annu. Rev. Plant Biol. 57, 233-266.

Bansal, R.K., Bajaj, A., 2003: Effect of volatile fatty acids on embryogenesis and hatching of *Meloidogyne incognita* eggs. Nematol. Medit. 31, 135-140.

Bansal, R.K., Dahiya, R.S., Narula, N., Jain, R.K., 2005: Management of *Meloidogyne incognita* in cotton, using strains of bacterium *Gluconacetobacter diazotrophicus*. Nematol. Medit. 33, 103-105.

Barber, D.A., Martin, J.K., 1976: The release of organic substances by cereal roots into soil. New Phytol. 76, 69-80.

Barea, J.M., Pozo, M.J., Azcon, R., Azcon-Aguilar, C., 2005: Microbial cooperation in the rhizosphere. J. Exp. Bot. 56, 1761-1778.

Bashan, Y., Levanony, H., 1991. Alterations in membrane potential and in proton efflux in plant roots induced by *Azosprillum brasilense*. Plant Soil 137, 99-103.

Baudoin, E., Benizri, E., Guckert, A.V., 2002: Impact of growth stage on the bacterial community structure along maize roots, as determined by metabolic and genetic fingerprinting. Appl. Soil. Ecol. 19, 135-145.

Becard, G., Taylor, L.P., Douds, D.D., Pfeffer, P.E., Doner, L.W., 1995: Flavonoids are not necessary plant signal compounds in arbuscular mycorrhizal symbiosis. Mol. Plant-Microbe Interact. 8, 252-258.

Behl, R.K., Ruppel, S., Kothe, E., Narula, N., 2007: Wheat x Azotobacter x VA mycorrhiza interactions towards plant nutrition and growth – a review. J. Appl. Bot. Food Qual. 81, 95-109.

Benfey, P.N., Scheres, B., 2000: Root development. Curr. Biol. 16, 813-815.

Bloemberg, G.V., Lugtenberg, B.J., 2001: Molecular basis of plant growth promotion and biocontrol by rhizobacteria. Curr. Opin. Plant Biol. 4, 343-350.

Brigham, L.A., Michaels, P.J., Flores, H.E., 1999: Cell-specific production and antimicrobial activity of naphthoquinones in roots of *Lithospermum erythrorhizon*. Plant Physiol. 119, 417-428.

Büchel, G., Bergmann, H., Ebenå, G., Kothe, E., 2005: Geomicrobiology in remediation of mine waste. Chem. Erde 65S1, 1-5.

Buee, M., Rossignol, M., Januneau, A., Ranjeva, R., Becard, G., 2000: The pre-symbiotic growth of arbuscular mycorrhizal fungi is induced by a branching factor partially purified from the plant root exudates. Mol. Plant-Microbe Interact. 13, 693-698.

Cacciari, D., Lippi, D., Pietrosanti, T., Petrosanti, W., 1989: Phytohormone-like substances produced by single and mixed diazotrophic cultures of *Azospirillum* and *Arthrobacter*. Plant Soil 115, 151-153.

Chen, X., Schauder, S., Potier, N., van Drosselaer, A., Pelczer, I., 2002: Structural identification of a bacterial quorum-sensing signal containing boron. Nature 415, 545-549.

Chhabra, M.L., Beniwal, M.S., Karwasra, S.S., Chand, H., Jalali, B.L., 1996: VAM: A biological tool for control of flag smut of wheat under field conditions. Proc. Natl Symp. „Molecular Approaches in Plant Disease Management", Shimla, India.

Cooke, T.J., Poli, D.E., Sztein, A.E., Colin, J.D., 2002: Evolutionary patterns in auxin action. Plant Mol. Biol. 49, 319-338.

Daniel, G., Jaffre, T., Prin, Y., 2007: Abundance of *Frankia* from *Gymnostoma* spp. in the rhizosphere of *Alphitonia neocaledonica*, a non-nodulated Rhamnaceae endemicto New Caledonia. Europ. J. Soil Biol. 36, 169-175.

Daniels, R., De Vos, D.E., Desair, J., Raedshelders, G., Luyten, V., Rosemeyer, C., Veereth, E., Shoeters, J., Vanderleyden, J., Michiels, J., 2002: Quorum sensing in *Rhizobium etli* CNPAF512 affects growth and symbiotic nitrogen fixation. J. Biol. Chem. 277, 462-468.

De Carvalho-Niebel, F., Timmers, A.C., Chabaud, M., Defaux P., Abarkar, D.G., 2002: The nod factor-elicited annexin MtAnn1 is preferentially localized at the nuclear periphery in symbiotically activated root tissues of *Medicago truncatula*. Plant J. 32, 343-352.

Deaker, R., Roughley, R.J., Kennedy, I.R., 2004: Legume seed inoculation technology – a review. Soil Biol. Biochem. 36, 1275-1288.

Dobbelaere, S., Croonenborghs, A., Thys, A., Broek, A.V., Vanderleyden, J., 1999: Phytostimulatory effect of *A. brasiense* wild type and mutant strains altered in IAA production on wheat. Plant Soil 212, 155-164.

Doebereiner, J., 1988: Isolation and identification of root associated

diazotrophs. Plant Soil 110, 207-212.

FLORES, H.E., VIVANCO, J.M., LOYOLA-VARGAS, V.M., 1999: „Radicle" biochemistry: the biology of root-specific metabolism. Trends Plant Sci. 4, 220-226.

FRAY, R.G., 2002: Altering plant microbe interaction through artificially manipulating bacterial quorum sensing. Ann. Bot. 89, 245-253.

GARCIA-GARRIDO, J.M., OCAMPO, J.A., 2002: Regulation of plant defense response in arbuscular mycorrizal symbiosis. J. Expt. Bot. 53, 1377-1386.

GRANSEE, A., WITTENMEYER, L., 2000: Qualitative and quantitative analysis of water soluble root exudates in relation to plant species and development. J. Plant Nutr. Soil Sci. 163, 381-385.

GUAN, L.L., KAMINO, K., 2001: Bacterial response to siderophore and quorum sensing chemical signals in the seawater microbial community. BMC Microbiol. 1, 27.

GUAN, L.L., KANOH, K., KAMINO, K., 2001: Effect of exogenous siderophores on iron uptake activity of marine bacteria under iron limited conditions. Appl. Env. Microbiol. 67, 1710-1717.

HAFERBURG, G., KOTHE, E., 2007: Microbes and metals: interactions in the environment. J. Basic Microbiol. 47, 453-367.

HAFERBURG, G., MERTEN, D., BÜCHEL, G., KOTHE, E., 2007: Biosorption of metal and salt tolerant microbial isolates from a former uranium mining area. Their impact on changes in rare earth element patterns in acid mine drainage. J. Basic Microbiol. 47, 474-484.

HAFERBURG, G., REINICKE, M., MERTEN, D., BÜCHEL, G., KOTHE, E., 2006: Microbes adapted to acid mine drainage as source for strains active in retention of aluminum or uranium. J. Geochem. Explor. 92, 196-204.

HEIDSTRA, R., BISSELING, T., 1996: Nod factor induced host responses and mechanisms of Nod factor perception. New Phytol. 133, 25-43.

HILTNER, L., 1904: Über neue Erfarungen und Probleme auf dem Gebiete der Bodenbakteriologie. Arbeiten der Deutschen landwirtschaftl. Gesellschaft 98, 59-78.

HUANG, P.M., WANG, M.C., WANG, M.K., 1999: Catalytic transformation of phenolic compounds in the soil. In: Inderjit, Dakshini, K.M.M., Foy, C.L. (eds.), Principles and practices in plant ecology: allelochemical interactions, 287-306. CRC Press, Boca Raton.

INDERJIT, 2001: Soil: environmental effect on allelochemical activity. Agron. J. 93, 79-84.

JAEGER, J.H., LINDOW, S.E., MILLER, S., CLARK, E., FIRESTONE, M.K., 1999: Mapping of sugar and amino acid availability in soil around roots with bacterial sensors of sucrose and tryptophan. Appl. Environ. Microbiol. 65, 2685-2690.

KAMILOVA, F., KRAVCHENKO, L.V., SHAPOSHINKOV, A.I., AZAROVA, T., MAKAROVA, N., LUGTENBERG, B., 2006: Organic acids, sugars and L-tryptophan in exudates of vegetables growing on stonewool and their effects on activities of rhizospere bacteria. Mol. Plant-Microbe Interact. 19, 250-256.

KENNEDY, I.R., TCHAN, Y.T., 1992: Biological nitrogen fixation in non-leguminous field crops. Rec. Adv. Plant Soil 141, 93-118.

KLOEPPER, J.W., 1993: Plant growth promoting rhizobacteria as biological control agents. In: Metting, F.B. Jr. (ed.), Soil Microbial Ecology: Application in Agricultural and Environmental Management, 255-274. Marcel Dekker Inc., New York, USA.

KOTHE, E., BERGMANN, H., BÜCHEL, G., 2005: Molecular mechanisms in bio-geo-interactions. Chem. Erde. 65S1, 7-27.

KOTHE, E., MÜLLER, D., KRAUSE, K., 2002: Different high affinity phosphate uptake systems of ectomycorrhizal Tricholoma species in relation to substrate specificity. J. Appl. Bot. 76, 127-131.

KRAVCHENKO, L.V., AZAROVA, T.S., DOSTANKO, O.Y., 2003: Effect of exometabolites of wheat with different genome ploidy on growth of Azospirillum brasilense. Microbiol. U.S.S.R. 62, 517-520.

KUMAR, R., BHATIA, R., KUKREJA, K., BEHL, R.K., DUDEJA, S.S., NARULA, N., 2007: Establishment of Azotobacter on plant roots: chemotactic response, development and analysis of root exudates of cotton (G. hirusitum L.) and wheat (T. aestivum L.). J. Basic Microbiol. 47, 436-439.

LESZCZYNSKA, D., STOCHMAL, A., OLESZEK, W., 2004: Cereal root exudates and their allelopathic activity, 409-415. 2nd Allelopathy Symposium „Allelopathy – from understanding to application. 50.

LOON, L.C., VAN BAKKER., P.A.H.M., 2004: Signalling in rhizobacteria-plant interactions. In: Kroon, H., de Visser, E.J.W. (eds.), Root ecology (Ecological studies 168). Springer, 297-330.

LUGTENBERG, B.J., CHIN-A-WOENG, T.F., BLOEMBERG, G.V., 2002: Microbe plant interactions: principle and mechanisms. Antonie van Leeuwenhoek 81, 373-383.

MADIGAN, M.T., MARTINKO, J.M., 2006:Brock: Biology of Microorganisms, 655-667. Pearson Prentice Hall, New Jersey.

MATHESIUS, U., MULDERS, S., GAO, M., TEPLITSKI, M., CAETANO-ANOLLES, G., ROLFE, B.G., 2003: Extensive and specific responses of a eukaryote to bacterial quorum-sensing signals. Proc. Natl. Acad. Sci. U.S.A. 100, 1444-1449.

MERTEN, D., KOTHE, E., BÜCHEL, G., 2004: Studies on microbial heavy metal retention from uranium mine drainage water with special emphasis on rare earth elements. Mine Water and the Environm. 23, 34-43.

MORGAN, J.A., BENDING, W., WHITE, P.J., 2005: Biological costs and benefits to plant microbe interactions in the rhizosphere. J. Exp. Bot. 56, 1729-1739.

NAGAHASHI, G., DOUDS, D.D. Jr., 1999: A rapid and sensitive bioassay with practical application for studies on interactions between root exudate and arbuscular mycorrhizal fungi. Biotechnol. Tech. 13, 893-897.

NAGAHASHI, G., DOUDS, D.D. Jr., 2003: Action spectrum for the induction of hyphal branches of an arbuscular mycorrhizal fungus: exposure sites versus branching site. Mycol. Res. 107, 1075-1082.

NARDI, S., CONCHERI, G., PIZZEGHELLO, D., STURARO, A., RELLA, R., PARVOLI, G., 2000: Soil organic matter mobilization by root exudates. Chemosphere 5, 653-658.

NARULA, N., REMUS, R.A., DEUBEL, A.A., GRANSE, A., DUDEJA, S.S., BEHL, R.K., MERBACH, W., 2007: Comparison of the effectiveness of wheat root colonization by Azotobacter chroococcum and Pantoea agglomerans using serological techniques. Plant Soil Env. 53, 167-176.

NARULA, N., DEUBLE, W., GANJ, A., BEHL, R.K., MERBACH, W., 2006: Colonization and induction of paranodules of wheat roots by phytohormone producing soil bacteria. Plant Soil Env. 52, 119-129.

NEUMANN, E., GEORGE, E., 2004: Colonization with the arbuscular mycorrhizal fungus Glomus mosseae (Nicole and Gerd.) enhanced phosphorous uptake from dry soil in Sorghum bicolor (L.). Plant Soil 261, 245-255.

OKON, Y., 1985: Azospirillum as a potential inoculant for agriculture. Trends Biotechnol. 3, 223-228.

PAGE, W.J., 1987: Iron dependent production of hydroxamate by sodium dependent Azotobacter chroococcum. Appl. Environ. Microbiol, 53, 1418-1424.

PAREZ-MIRANDA, S., CABIROL, N., GEORGE-TELLEZ, R., ZAMUDIO-RIVERA, L.S., FERNANDEZ, F.J., 2007: O-CAS, a fast and universal method for siderophore detection. J. Microbial Methods 70, 127-131.

PATHAK, D.V., LAKSHMINARAYANA, K.L., NARULA, N., 1995: Analogue resistant mutants of A. chroococcum affecting growth parameters in sunflower (Helianthus annus L.) under pot culture conditions. Proc. Natl. Acad. Sci. (India). 18, 203-206.

PERRET, X., STAEHELIN C., BROUGHTON, W.J., 2000: Molecular basis of symbiotic promiscuity. Microbiol. Mol. Biol. Rev. 64, 180-201.

PINTON, R., VARANINI, Z., NANNIPIERI, P. (eds.), 2001: The rhizosphere: biochemistry and organic substances at the soil-plant interface, 850-874. Marcel Dekker, New York.

RANGASWAMI, G., 1988: Soil plant microbe interrelationships. Ind. Phytopath. 41, 165-172.

ROUGIER, M., 1981: Secretory activity at the root cap. In: Tanner, W., Loews, FA. (eds.), Encyclopidia of Plant Physiology. Vol. 13 B Plant carbohydrates II. 542-574. Springer Verlag, Berlin.

ROVIRA, A.D., NEWMAN, E.L., BOWEN, H.J., CAMPBELL, R., 1974: Quantitative assessment of the rhizosphere microflora by direct microscopy. Soil Bio-

chem. 6, 211-216.

SAWADA, H., KUYKENDALL, L.D., YOUNG, J.M., 2003: Changing concepts in the systematics of bacterial nitrogen fixing legume symbionts. J. Gen. Microbiol. 49, 155-179.

SCHMIDT, A., HAFERBURG, G., MERTEN, D., GHERGEL, F., BÜCHEL, G., KOTHE, E., 2008: Heavy metal resistance *Streptomyces* strains from a former uranium mining area. Chem. Erde, in press.

SCHMIDT, A., HAFERBURG, G., SINERIZ, M., MERTEN, D., BÜCHEL, G., KOTHE, E., 2005: Heavy metal resistance mechanisms in actinobacteria for survival in AMD contaminated soils. Chem. Erde 65S1, 131-144.

SINERIZ, M.L., KOTHE, E., ABATE, C.M., 2008: Cadmium biosorption by *Streptomyces* sp. F4 isolated from former uranium mine. J. Basic Microbiol., in press.

SINGH, R., BEHL, R.K., JAIN, P., NARULA, N., SINGH, K.P., 2007: Performance and gene effects for root characters and micronutrients uptake in wheat under inoculation of arbuscular mycorrhiza fungi and *Azotobacter chroococcum*. Acta Hungarica Agronomica. 55, 325-330.

SORENSEN, J., JENSEN, L.E., NYBROE, O., 2001: Soil and rhizospere as habitats for *Pseudomonas* inoculants: New knowledge on distribution, activity and physiological state derived from micro-scale and single cell studies. Plant Soil 232, 97-108.

TEPLITSKI, M., ROBINSON, J.B., BAUER, W.D., 2000: Plant secreted substances that mimic bacterial N-acyl homoserine lactone signal activities and affect population density-dependent behaviors in associated bacteria. Mol. Plant-Microbe Interact. 13, 637-648.

TERPITZ, U., KOTHE, E., 2006: Diversity and adaptation of soil fungi in an ecosystem with contamination originating from a phosphate fertilizer plant. J. Appl. Bot. Food Qual. 80, 187-193.

UMALI GARCIA, M., HUBBELL, D.H., GASKINS, M.H., DAZO, F.B., 1980: Association of *Azospirillum* with grass roots. Appl. Envir. Microbiol. 39, 219-226.

van WEST, P., MORRIS, B.M., REID, B., APPIAH, A.A., OSBORNE, M.C., 2002: Oomycetes plant pathogens use electric fields to target roots. Mol. Plant-MicrobeInteract. 15, 790-798.

VISIK, K.L., RUBY, E.G., 1999: The emergent properties of quorum sensing: consequences to bacteria of autoinducer signalling in their natural environment, In: Dunny, D.M., Winnas, S.C. (eds.), Cell-cell signalling of bacteria, 333-352. American Society Microbiology, Washington.

WALKER, T.S., BAIS, H.P., GROTEWOLD, E., VIVANCO, J.M., 2003: Root exudation and rhizosphere biology. Plant Physiol. 132, 44-51.

WEST, S.A., GRIFFIN, A.S., GARDNER, A., DIGGLE, J.P., 2006: Social evolution theory for microorganisms. Nat. Rev. Microbiol. 4, 597-607.

WHIPPS, J.M., 1990: Microbial interactions and biocontrol in the rhizosphere. J. Expt. Bot. 5, 487-511.

WHITE, P.J., 2003: Ion transport. In: Thomas, B., Murphy, D.J, Murray, D.J. (eds.), Encyclopedia of Applied Plant Sciences, 625-634. Academic press, London.

XUESONG, H., WILLIAMS, C., DEANNE, L.P., LAURA, O.S, WAGNER, J., CLAY, F., 2003: Quorum sensing in *Rhizobium* sp. strain NGR234 regulates conjugal transfer (*tra*) gene expression and influences growth rate. J. Bacteriol. 185, 809-822.

YANG, C.H., CROWLEY, D.E., 2000: Rhizosphere microbial community structure in relation to root location and plant iron nutritional status. Appl. Environ. Microbiol. 66, 345-351.

YANG, C.H., CROWLEY, D.E., MENGE, J.A., 2001: 16S rDNA fingerprinting of rhizosphere bacterial communities associated with healthy and *Phytophthora* infected avocado roots. FEMS Microbiol. Ecol. 35, 129-136.

YOST, C.K., ROCHEPEAU, P., HYNES, M.F., 1998: *Rhizobium leguminosarum* contains a group of genes that appear to code for methyl-accepting chemotaxis proteins. Microbiology-Reading. 144, 1945-1956.

Address of the author:
Prof. Dr. E. Kothe, Friedrich-Schiller-Universität, Institut für Mikrobiologie, Neugasse 25, D-07743 Jena
E-mail: erika.kothe@uni-jena.de