Plant Soil (2009) 321:235–257
DOI 10.1007/s11104-008-9814-y

REVIEW ARTICLE

Plant-driven selection of microbes

Anton Hartmann · Michael Schmid · Diederik van Tuinen · Gabriele Berg

Received: 1 July 2008 / Accepted: 20 October 2008 / Published online: 15 November 2008
© Springer Science + Business Media B.V. 2008

Abstract The rhizodeposition of plants dramatically influence the surrounding soil and its microflora. Root exudates have pronounced selective and promoting effects on specific microbial populations which are able to respond with chemotaxis and fast growth responses, such that only a rather small subset of the whole soil microbial diversity is finally colonizing roots successfully. The exudates carbon compounds provide readily available nutrient and energy sources for heterotrophic organisms but also contribute e.g. complexing agents, such as carboxylates, phenols or siderophores for the mobilization and acquisition of rather insoluble minerals. Root exudation can also quite dramatically alter the pH- and redox-milieu in the rhizosphere. In addition, not only specific stimulatory compounds, but also antimicrobials have considerable discriminatory effect on the rhizosphere microflora. In the "biased rhizosphere" concept, specific root associated microbial populations are favored based on modification of the root exudation profile. Rhizosphere microbes may exert specific plant growth promoting or biocontrol effects, which could be of great advantage for the plant host. Since most of the plant roots have symbiotic fungi, either arbuscular or ectomycorrhizal fungi, the impact of plants towards the rhizosphere extends also to the mycorrhizosphere. The selective effect of the roots towards the selection of microbes also extends towards the root associated and symbiotic fungi. While microbes are known to colonize plant roots endophytically, also mycorrhiza are now known to harbor closely associated bacterial populations even within their hyphae.

The general part of the manuscript is followed by the more detailed presentation of specific examples for the selection and interaction of roots and microbes, such as in the rhizosphere of strawberry, potato and oilseed rape, where the soil-borne plant pathogen *Verticillium dahliae* can cause high yield losses; the potential of biocontrol by specific constituents of the rhizosphere microbial community is demonstrated. Furthermore, plant cultivar specificity of microbial communities is described in different

Responsible editor: Philippe Lemanceau.

A. Hartmann (✉) · M. Schmid
Department Microbe-Plant Interactions,
Helmholtz Zentrum München,
German Research Center for Environmental Health (GmbH),
Ingolstaedter Landstrasse 1,
D-85764 Neuherberg, Germany
e-mail: anton.hartmann@helmholtz-muenchen.de

D. v. Tuinen
UMR INRA Université de Bourgogne,
Plante-Microbe-Environnement CMSE-INRA,
17 rue Sully, BP 86510, Dijon Cedex F-21065, France

G. Berg
Institute for Environmental Biotechnology,
Graz University of Technology,
Petersgasse 12,
A-8010 Graz, Austria

potato lines including the case of transgenic lines. Finally, also the specific selective effect of different *Medicago* species on the selection of several arbuscular mycorrhizal taxa is presented.

Keywords Root exudation · Rhizodeposition · Microbial diversity · Rhizosphere bacteria · Mycorrhizal fungi · Arbuscular mycorrhiza · Ectomycorrhiza · Antimicrobials · Signalling compounds · Plant growth promotion · Biological control · "Biased rhizosphere concept"

Introduction

The rhizosphere, an unique environment for microbial colonization

According to the general view of the rhizosphere, it includes plant roots and the surrounding soil. This is a wide and wise definition, already coined more than hundred years ago by Lorenz Hiltner, as documented in detail by Hartmann et al. (2008). In the rhizosphere, a biologically and chemically highly diverse, complex and dynamic interaction occurs between plant roots, soil (micro) biota and the physico-chemical conditions of the soil. The autotrophic plant partner is providing substrate and energy flow into the rhizosphere and gets in return essentials for its development and growth: nutrients, minerals and water. Heterotrophic soil biota usually are limited in the supply of carbon and energy and thus a complex sequence of responses are initiated, which in due course also influence the plants. Soil biota (bacteria, fungi, micro-fauna and the plant root) are themselves embedded in food webs and thus interactions with consumers or predators in the microbial as well as micro- and mesofaunal world are important to understand rhizosphere processes.

From the viewpoint of the plant, the rhizosphere is characterized by the investment of the plant into an effective development of the root architecture and the return of mineral nutrients and water from the soil. In the root system, sloughing off of root cells (in particular at the root tip), root death (root hair cells and epidermis cells in older root parts) and the exudation of carbon compounds are processes which support soil biota and select a specific rhizosphere community according to their composition (see below). Already in the initial phases of the evolution of terrestrial plants, the necessity and opportunity appeared to integrate the abilities of soil microbes to explore the soil for nutrients and water into the development of plants. Vice versa a high number of soil microbes attained properties enabling them to interact more efficiently with roots and withstand the quite challenging conditions of rhizosphere life (see below). This process can be regarded as an ongoing process of micro-evolution in low-nutrient environments, which are quite common in natural ecosystems (Schloter et al. 2000). For example, the interaction with soil fungi lead to the development of mycorrhiza which explore the soil for phosphate, nitrogen and other nutrients and micronutrients much beyond the physical expansion of the root system. The bacteria with their impressive metabolic versatility and originality - expanding much beyond the oxygen-dependent spheres - were also taken on board to gain e. g. better access and even independence from the often most limiting nitrogen supply. The size and dynamic of the plants investment into the rhizosphere is dependent from the aboveground part of the plant and differs by ecosystem type, plant species and growth stage of the plant. In grasslands, the ratio of shoot to root (S:R) development is roughly 1:1 and is much different to forests, where far more photosynthate is allocated into the aboveground parts. Far more carbon is accumulating in the rhizospheres of e. g. arctic tundra, where the turnover is very slow and the range of S:R can be found as low as 0.1 (Farrar et al. 2003; Moore et al. 2007).

From the viewpoint of soil microbiota which are mostly heterotrophic organisms depending on exogenous supply of carbon substrates as energy as well as nutrient sources for growth and development, roots are providing almost all, what is lacking in soil. While in pathogens or root grazers complete utilization and destruction is one extreme version of this interaction with plant roots, the balance of utilization of the resource and coexistence or even symbiosis is reached in many other rhizosphere colonizing microbiota. Surely, the plant is restricting or directing the development of the attracted organisms in a way to keep control of these guests by excreting quite selective mixtures of substances which provide selective conditions for rhizosphere organisms. Furthermore, the rhizosphere is a quite heavily populated microhabitat which is characterized by competition and even predation among the inhabitants. Therefore,

soil organisms do experience the rhizosphere environment as micro-habitat of great opportunities but also of big challenges. Rhizospheres can only be successfully colonized with the appropriate tools of efficient substrate acquisition, resistance mechanisms as well as competitive traits. Thus, evolution shaped soil biota to fit into these specific niche conditions which are also characterized by specificities based on the diversity of plants and soil environments. Furthermore, the colonization of the interior of plant roots by microbial endophytes appears as most attractive goal, because there plant nutrient resources can be explored even more effectively without the tough competition with the high number of other microbes colonizing the root surface and environment (Rosenblueth and Martinez-Romero 2006; Schulz et al. 2006). However, in this case the efficient interaction with the plant host gets even more important.

In this review, we follow the original hypothesis of Lorenz Hiltner in 1904, that plant roots set the stage for the development of a unique rhizosphere microbial community and we extend this by including mycorrhizal fungi and their associated bacteria as well as root endophytic microbes. The present state of the art based on modern and molecular methods is presented in four major chapters: (i) Plant traits shaping the conditions for microbial colonization, (ii) Microbial responses to specific rhizosphere conditions, (iii) The mycorrhizosphere and its specific traits and interactions with other rhizosphere constitutents and (iv) Selected examples for the specific selection and interaction of roots and microbes. The influence of the soil on the composition of rhizosphere microbial communities is not treated in this chapter, because it is obvious, that the rhizosphere microflora is recruited in most part from the given soil microflora (which is certainly different in different soils).

Plant traits shaping the conditions for microbial colonization

Soluble carbon compounds and other rhizodepositions

Plants exude a variety of organic compounds (e.g. carbohydrates, carboxylic acids, phenolics, amino acids) as well as inorganic ions (protons and other ions) into the rhizosphere to change the chemistry and biology of the root microenvironment. This exudation is plant specific and generally accepted to reflect the evolution and/or specific physiological adaptation to particular soil habitat conditions (Crowley and Rengel 1999). In order to withstand challenges like deficiencies of various macro- and micro-nutrients, like iron (Marschner and Römheld 1994) zinc, manganese or phosphate, plants have different strategies to cope with (see below) (Rengel 1999). The type of root exudates is crucial for the ecosystem distribution and niche-specificity of certain plants (Dakora and Phillips 2002). For example, a so called “calcifuge” plant does not tolerate alkaline (basic) soil. The word is derived from the Latin 'to flee from chalk'. These plants are also described as ericaceous, as the prototypical calcifuge is the genus *Erica* (heaths). It is not the presence of carbonate or hydroxide ions per se that these plants cannot tolerate, but the fact that under alkaline conditions, iron becomes less soluble (see below). There are many horticultural plants which are calcifuges, most of which require an 'ericaceous' compost with a low pH, composed principally of Sphagnum moss peat. These include heathers, Camellias, Rhododendrons, Azaleas, and most carnivorous plants. In contrast, “calcicole” plants can cope very well with alkaline soil conditions.

While so called “calcicole“ plants exude mostly di- and tricarboxylic acids, the ”calcifuge” plants exude mostly monocarboxylic acids. While the former plants efficiently complex phosphate and ferric iron ions, the latter complex only poorly phosphate and iron from alkaline soils. The capacity of plants to respond to environmental conditions of nutrient deprivation can be separated into three major processes: (1) the signaling, (2) a powerful biosynthetic capacity, and (3) specific membrane transporter processes to foster the transfer of effective organic compounds into the rhizosphere.

Roots products and rhizodepositions may probably consist of every type of plant compound, except specific compounds involved in photosynthesis. Most root products are regular plant compounds which became available as substrate of rhizosphere colonizing microbes, including specific compounds typical of the secondary metabolism of each plant species. This is especially true, when root hairs are decaying or the rhizodermis is partially degraded in older root parts. Root products with a certain biological activity may also be actively secreted. These secretions can be

classified as allelochemicals, phytotoxins, phytoalexins, phytohormons and ectoenzymes—they are discussed in more detail below.

The amounts of exudates (also as proportions of photosynthate) vary considerably in different plants, plant growth cycle and root segments and the methodological and ecological implications were reviewed extensively (Jones et al. 2004; van Veen et al. 2007). To be able to realistically evaluate the relevance of certain excreted compounds and their individual fluxes (excretion and uptake), the exudation / uptake rate per unit root length per hour may be important to know and to be specified for a particular root segment (e.g. root cap or elongation zone). The types and amounts of root products excreted or secreted into the root environment is in detail reviewed by Uren (2007). In general, the fate of the more or less diffusible exudates or secretions in the rhizosphere is determined by their physicochemical properties and nutrient quality. The rhizosphere can be regarded as a gradient system, where free diffusible compounds spread into the root surroundings (Fig. 1). The longer the distance of diffusion is the more binding to soil mineral or humic compounds as well as microbial degradation is going to occur. Thus, the immediate surface of the root, the rhizoplane, is certainly exposed to the highest rates and concentrations of beneficial and harmful exudation / secretion products. With distance and time, the organic carbon compounds are progressively metabolized to carbon dioxide or into recalcitrant or colloidal bound forms of humic carbon compounds. Therefore, the molecular scenario a root creates is most complex and variable also due to the soil conditions. The selective effects on the rhizosphere microflora is to be expected very complex and only at the right set of conditions, an targeted effect on the behavior of a certain microbial subpopulation, e.g. an introduced inoculum, which is supposed to get established and interactive with the plant root is possible.

pH- and redox-modulating factors

Both protons and electrons are secreted as C-compounds in the form of undissociated acids or compounds with reducing abilities. In addition, plasma membrane enzymatic processes are the main sites of proton or electron transport processes (Bérczi and Møller 2000; Yan et al. 2002). The origin and adaptation to changing environmental conditions of root mediated pH-changes have been recently been reviewed by Hinsinger et al. (2003). The reducing power is a long observed property of plant roots and was demonstrated in several different approaches, such as the reduction of insoluble manganese oxide by roots (Uren 1981). Although other biogenic acids can affect soil acidification and weathering dissolution, root uptake of nutrient ions, organic acid production, redox-cycling of electron-deficient metals and the carbonic acid system are major contributors to

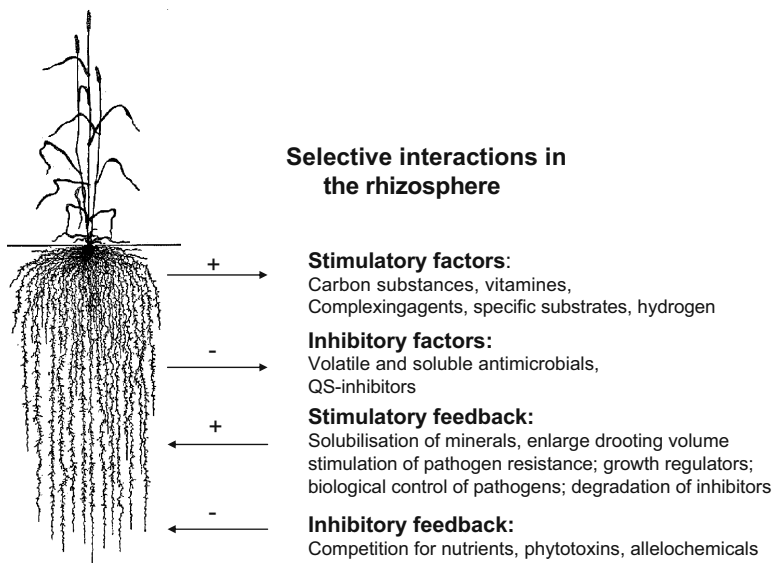


Fig. 1 Stimulatory and inhibitory factors on rhizosphere microbial communities and the different quality of feedback effects of microbes and plants

rhizosphere acid production and soil formation (Richter et al. 2007). Rhizosphere acidification, which may be as much as two pH units, can result from the "excess cation uptake" by plant roots leaving behind protons in the rhizosphere soil, since the overall plant nutrient uptake process is regarded as electro-neutral. Since oxygen is very actively consumed in the rhizosphere due to high rates of microbial decomposition and root respiration, steep redox gradients can develop between the root environment and the surrounding bulk soil. In contrast, roots are providing the rhizosphere with oxygen in waterlogged soils and sediments. As a consequence, iron-oxidizing bacteria precipitate Fe plaque as oxidized coatings at root surfaces (Uren 2007). Finally, carbonic acid weathering involves all three phases of the soil system: CO_2 in the gas phase, carbonic acid and associated ions in the liquid phase and mineral surfaces and structures in the solid phase. Since partial pressures of CO_2 increases with soil depth, B- and C-horizons are subject to this type of acidification process. The detailed estimation of the sources and sinks of CO_2 in the rhizosphere was recently reviewed by Kuzyakov (2005).

Complexing agents: siderophores, phenols and carboxylates

Together with the excretion of protons and carboxylates, siderophores and phenols play significant roles in mineral weathering. Roots are most active in the excretion of these compounds to overcome nutrient limitation and join in soil microbes to overcome these limitations too. Thus, rhizosphere conditions assist microbes and microbes assist roots in this most important interaction with soil minerals and nutrient mineral solubilization.

Iron deficiency

Under conditions of iron deficiency, plants employ two basic mechanisms. Strategy I involves the stimulation of proton extrusion, enhanced exudation of reductants and chelators (carboxylates and phenolics) and an enhanced activity of plasma-membrane-bound Fe-(III)-reductase (Marschner 1991; Marschner and Römheld 1994; Rengel 1999). In strategy II, which is restricted to *Gramineae*, the biosynthesis and excretion of phytosiderophores like mugineic acid is specifically induced under iron-limited conditions. The amount of phytosiderophore release is different between plant species. Relative efficiency of phytosiderophore exudation decreases in the order barley, maize, sorghum, and correlates with Fe-deficiency tolerance. Interestingly, also Zn-deficiency leads to increased phytosiderophore exudation. In maize, the particular Fe-deficiency-sensitive yellow-stripe mutant (*ys1*) shows a comparable rate of phytosiderophore release, but it has a defect in the uptake system for the phytosiderophore (von Wiren et al. 1994). It could be demonstrated that e. g. Alice maize has a high affinity iron uptake component (von Wiren et al. 1995). In the rhizosphere, also microorganisms excrete siderophores under iron limited conditions which prevail in aerobic soils, when iron is present in mostly insoluble Fe-(III)-oxide / hydroxide complexes. It could be demonstrated, that plants profit from the Fe-(III)-solubilizing activity of microbes as well as microbes can take advantage from phytosiderophores after ligand exchange or using heterologeous siderophores (Marschner and Crowley 1998). Since the acquisition of the highly insoluble ferric iron complexes is an essential component of rhizosphere competence and fitness, it is usually well developed in rhizosphere microorganisms. However, important differences in the iron uptake capabilities occur at the strain level in bacteria (Hartmann 1988) and this trait appears essential to be regarded in selecting successful rhizosphere colonizing plant growth promoting or biocontrol inoculant strains (Moenne-Loccoz et al. 1996).

Phosphate deficiency

In many plants, phosphate deficiency enhances the production and exudation of phenolic compounds (Chishaki and Horiguchi 1997) (see Fig. 1). Phenolic biosynthesis can be regarded as a metabolic bypass reaction or response of P-starved cells to solubilize inorganic P_i from soil. Since certain phenolic compounds have antibiotic properties, this component of exudates could be relevant in counteracting infectious root pathogens, but may also prevent fast microbial breakdown of exudates. On the other hand, root exudation of metal-chelating carboxylates (e.g. citrate, malate, malonate, and oxalate) in sufficient amounts to mediate P mobilization in soils can comprise up to 25% of the assimilated carbon (Dinkelaker et al. 1995). This is comparable to the carbon investment

for mycorrhizal associations. Cluster rooted plant species (Neumann and Martinoia 2002), characterized by the highest P-deficiency induced carboxylate (mostly citrate) exudation are mostly nonmycorrhizal plants and cluster roots are regarded as alternate strategy for nutrient acquisition (Skene 2000).

Exudation of antimicrobials

Most plant species are resistant to most potential pathogens. However, it is not known in a comprehensive manner, why most plant-microbe interactions do not lead to disease, although many resistance mechanisms are known and the disease resistance is certainly a multi-factorial response (Thordal-Christensen 2003). A very widely found mechanism of local defense is the generation of reactive oxygen species and the subsequent stress on the colonizing microbes or neighboring roots. Thus, antioxidant enzymes, like catalase, laccase, superoxide dismutase (SOD) and the glutathione system are important in order to face this challenge in the root environment. However, ROS and also activated nitrogen species (like NO) are known as part of the innate immunity system of plants posing selective pressure on the rhizosphere microflora (Apel and Hirt 2004; Zeidler et al. 2004). When analyzing the response in gene expression of root colonizing *Pseudomonas putida* (Matilla et al. 2007) it appeared that also bacterial antioxidant enzymes are important to face the challenge of the root environment.

While in the case of leave pathogens, several specific resistance mechanisms have been developed by plants, the investment into the antagonistic potential within the rhizosphere microbial community appears to be an important part of biological control of pathogens in roots (Cook et al. 1995). In addition, the exudation of specific root derived antimicrobial metabolites is certainly a major mechanism, as has been shown for many plant species (Bais et al. 2006). Plant secondary metabolites such as butanoic acid, cinnamic acid, o- and p-coumaric acid, vanillic acid or p-hydroxybenzamide were shown to occur in the rhizosphere of Arabidopsis plants when challenged with the Gram-negative bacterial pathogen *Pseudomonas syringae* pv. tomato (Bais et al. 2005). Most interestingly, bacteria can effectively modify this antimicrobial plant response, because the strains which are partly resistant to these compounds are able to block the exudation of antimicrobials using a mechanism based on the type III secretory system (Bais et al. 2005). Therefore, overcoming host response is not only due to a resistance towards exuded antimicrobial compounds but in a second step also in the blockage of further production of antimicrobials. Most interesting, volatile substances with antimicrobial activity have also been identified (Ryu et al. 2004) which could play an important role in selecting the plant associated microflora.

Another most interesting group of plant derived compounds are quorum sensing inhibitors. Many Gram-negative rhizosphere bacteria, including pathogens, use auto-inducer signaling compounds in order to coordinate their activity when colonizing the rhizoplane (Fuqua et al. 2001; Gantner et al. 2006). This density dependent response is called “quorum sensing” (QS), since it becomes effective only in high density cell populations. More recently it was suggested, that the auto-inducers, e.g. of the N-acylhomoserine lactone type, have even a more general relevance in sensing the quality of the micro-environment for its diffusion characteristics and to acquire the important information whether it is economically sound to initiate the expensive biosynthesis of exoenzymes, termed efficiency sensing (Hense et al. 2007). Thus, auto-inducer signaling is very common in bacteria, and plants are facing these compounds regularly. The interference with bacterial signaling by excreting QS-mimic or -inhibitory substances would have the advantage to disturb the coordination of the bacterial attack - especially in the case of pathogens. It has been indeed found in several plants, that QS-inhibitors are produced (Bauer and Mathesius 2004; Degrassi et al. 2007; Hentzer et al. 2002; Rasmussen et al. 2005; Teplitski et al. 2000). On the other hand, it was demonstrated that mostly leguminous plants are able to degrade bacterial N-acyl homoserine lactone (AHL) autoinducers by excreting lactonases or AHL-hydrolases (d'Angelo-Picard et al. 2005; Delalande et al. 2005). In other plants it was shown (Götz et al. 2007; von Rad et al. 2008), that the short side chain C4-, C6- and C8-AHLs are taken up by plants and they could be found also in the shoots (Götz et al. 2007; von Rad et al. 2008). A quite wide range of responses of plants were shown to be triggered by the exposition to bacterial AHL-compounds. In tomato plants, C6-and C8-AHLs induced a systemic resistance response (Schuhegger et al. 2006) with stimulated induction of the PR1-protein and chitinase. On the other hand, *Arabidopsis thaliana* responded by altered phytohormone levels (increased

auxin/cytokinin-ratio) in roots and stimulated root growth (von Rad et al. 2008). Thus, plant roots are responding to the presence of bacteria and their signaling compounds and their selective effect on the rhizosphere microflora has to be regarded as a dynamic one which is modulated by the "history" of the rhizosphere colonization events.

Exudation of specific stimulatory compounds

In contrast to inhibitory compounds which are present in root exudates of plants under particular conditions, many root exudates, like sugar, organic acids or amino acids, stimulate a positive chemotactic response of bacteria (Somers et al. 2004) (see Fig. 1). Thus, a flagellum-driven chemotaxis towards roots and their exudates is an important trait for root colonization in many root-bacteria interactions (de Weert et al. 2002). Certain compounds have even specific sites of exudation. It has been shown that tryptophan, the precursor of bacterial indole acetic acid (IAA) production, is mainly exuded near the root tip in *Avena barbata* (Jaeger et al. 1999). Since rhizobacterial IAA-production by root associated bacteria is a major mechanism of plant growth promotion this has important implication for the development of the root system under the influence of rhizosphere microbes. The *ipdC*-gene, coding for indole pyruvate decarboxylase, in the major route of IAA-biosynthesis of the plant growth promoting rhizobacterium *Azospirillum brasilense* was shown to be induced in rhizoplane colonizing bacteria (Rothballer et al. 2005). On the other hand, a high diversity of rhizosphere bacteria have recently been characterized to be able to use indole acetic acid as carbon source for growth (Leveau and Gerards 2008).

Since exudation is a major driving force for microbial root colonization, plant root exudation could be specifically engineered to selectively stimulate specific microbial colonization. Oger at al. (1997) has demonstrated that genetically engineered plants which produce opines have an altered rhizosphere community. In transgenic *Lotus* plants producing two opines, mannopine and nopaline, specific microbial rhizosphere communities were stimulated by the modified root exudation. Opine-utilizing microbes represented a large community in the rhizosphere of opine-producing *Lotus* plants and opine utilizes were found to belong to the Gram-positive as well as Gram-negative bacteria (Oger et al. 1997). The natural example of opine production is provided by the genetic colonization of plant roots by *Agrobacterium tumefaciens* and its T_i plasmid in order to divert assimilate flow from the plant specifically to support the growth of the bacterium which is equipped with opine degrading enzymes. This strategy, termed "biased rhizosphere", could be successfully used to engineer "artificial symbioses" (O'Connell et al. 1996) and was successfully applied to engineer e. g. transgenic tobacco plants capable of releasing substantial amounts of opine compounds in the rhizosphere (Oger et al. 2004).

A different quality of specific stimulatory rhizosphere effect can be found in leguminous roots, where nitrogen fixing nodules release substantial amounts of molecular hydrogen (Dong et al. 2003). The generation of hydrogen is an unavoidable side reaction in the nitrogenase reaction (Simpson and Burris 1984). Since rhizobia and legumes harbor hydrogen uptake activities to different degrees, an escape of hydrogen is present in certain leguminous species. It could be shown that this hydrogen release from nodules has a substantial effect on both the general microbial activity and the bacterial numbers as well as on the activity level of the bacteria (Stein et al. 2005). In addition, a shift in the bacterial community composition was shown which was most pronounced in the group of Betaproteobacteria and *Cytophaga/Flavobacteria*. Interestingly, beyond a certain threshold level of hydrogen flux, an onset of carbon dioxide fixation was observed to occur in these communities (Dong et al. 2003; Stein et al. 2005), which was also indicated by the demonstration of mRNA of bacterial ribulose bisphosphate carboxylase (*cbbL*) in these communities (Rohe and Hartmann, unpublished results). Thus, under these specific rhizosphere conditions of hydrogen releasing legumes, carbon dioxide fixation occurs in a wide variety of soil and rhizosphere bacteria harboring the *cbbL*-genes (Selesi et al. 2005).

Shaping specific habitat conditions by physicochemical forces

The rhizosphere is the critical interface between biota and geologic environments. Growing roots and their mycorrhizal hyphae follow pores and channels that are usually not less than their own diameter. When perennial roots (e.g. tree roots) grow, they expand in volume radially and exert enormous pressures on the

surrounding soil (Richter et al. 2007). Even unweathered rocks are susceptible to these physical effects of roots. Mechanical weathering is stimulated by these root forces, accelerating chemical weathering by increasing minerals surface area that is contacted by microbes, organic compounds, electrons and protons. In B-horizons, root growth results in a significant increase in bulk densities of soils, creating reduced porosity, hydraulic conductivity and aeration. Thus biogeochemical processes and the activity of soil microbes may well be affected by this phenomenon, which is quite less studied. A higher degree of permanently water-filled pores my favor anaerobic microbial processes which may lead to increased denitrification (possibly NO and N_2O production) or other microaerobic or anaerobic microbial processes. This steep spatial redox gradients and dynamics may have considerable consequences for the microbial degradation of complex xenobiotic organic substances, because aerobic and anaerobic conditions may foster very different metabolic potentials in different microbial clades leading to more complete removal of xenobiotic compounds.

Microbial responses to specific rhizosphere conditions

The unique rhizosphere conditions are the basis for the sustainable fertility of soils providing soil biota specific support for their continuous activity in nutrient cycling and provision of nutrients for plants and they are fundamentally important for pedogenetic processes. Due to the high diversity of chemical influences in the rhizosphere of different plants, roots drive specific selections of microbes out of the almost indefinite pool of soil microbial diversity. In addition to the selection of pre-existing diversity, also microevolution towards most properly adapted microbial life forms (Schloter et al. 2000) is supported in the well nourished rhizosphere environment, because e. g. of the possibility of genetic exchange employing horizontal gene transfer (van Elsas et al. 2003) and/or creation and selection of spontaneous mutants, transconjugants and transformants with improved properties for specific selective rhizosphere conditions. Thus, engineering root exudation towards the production of two novel carbon compounds leads to the selection of distinct microbial populations in the rhizosphere (Oger et al. 2004; Savka et al. 2002). This concept of "artificial symbiosis" provides an interesting concept for engineering specific microbe-plant interactions. The impact of this modification of root exudation has been studied extensively as model system of the impact of engineered plants on soil ecosystem (Bruinsma et al. 2003; Kowalchuk et al. 2003).

There are many independent evidences using microbiological and molecular techniques that roots stimulate selectively soil microbial communities creating unique rhizosphere communities (Duineveld et al. 1998; Marschner et al. 2001; Rengel and Marschner 2005) (see also below for specific examples). However, only with the availability of the Stable Isotope Probing (SIP) technique (Radajewski et al. 2000) the utilization and fate of plant carbon substrates in the rhizosphere by associated microbes and the dynamic feature of this process in the microbial food web could be investigated in detail (Prosser et al. 2006). There are two major rather independent approaches concerning the molecular markers for carbon assimilation: the analysis of (i) the phospholipids fatty acids (PLFA) (Butler et al. 2004; Butler et al. 2003; Paterson et al. 2007; Treonis et al. 2004) and (ii) the ribosomal genes or ribosomal RNA (Lu and Conrad 2005; Lu et al. 2006; Prosser et al. 2006; Rangel-Castro et al. 2005) (see separate chapter).

Microbial traits important for the performance in the rhizosphere

Microorganisms living in the rhizosphere can have a neutral, pathogenic or beneficial interaction with their host plant (Raaijmakers et al. 2008; Whipps 2001). This reaction depends on the balance of the plant-microbe interaction. Interestingly, the colonization strategy of microbes is highly similar independent of their effect on host. Steps of colonization include recognition, adherence, invasion (only endophytes and pathogens), colonization and growth, and several strategies to establish interaction. The importance to recognize and adhere to plant roots for all plant-associated microorganisms is underlined in many studies. Factors that contribute to recognition include the ability to sense and use root exudates composed of small organic molecules like carbonic acids, amino acids or sugars etc. Chemotaxis especially to plant root exudates is an important trait for colonization of the rhizosphere: this was shown for pathogenic and

symbiotic plant-associated bacteria, e.g. *Ralstonia solanacearum* (Yao and Allen 2006) as well as *Rhizobium leguminosarum* (Miller et al. 2007). Interestingly, chemotaxis experiments of cyanobacteria with host plants like *Gunnera* and *Blasia* and non-host plants like *Arabidopsis* showed the possibility to attract cyanobacteria may be widespread in plants. Using comparative transcriptome analysis of *Pseudomonas aeruginosa*, root exudates of sugar beet altered gene expression of genes involved in chemotaxis (Mark et al. 2005). An early step in the establishment of a plant-bacterium interaction is attachment of cells to plant roots, in which for example fimbriae and cell-surface proteins are involved. For the colonization of *Pseudomonas* of plant roots, flagella, pili, O-antigen of lipopolysaccharides (LPS), the growth rate and the ability to grow on root exudates are important (Lugtenberg and Dekkers 1999). Attachment also is an initial step for the formation of microbial biofilms on plant roots as reviewed by Rodríguez-Navarro et al. (2007). The same authors explain mechanisms of attachment of rhizobia on legumes: the first phase of attachment, which is a weak, reversible, and unspecific binding of plant lectins, a Ca^{2+}-binding bacterial protein (rhicadhesin), and bacterial surface polysaccharide and a second attachment step, which requires the synthesis of bacterial cellulose fibrils that cause a tight and irreversible binding of the bacteria to the roots. In *Agrobacterium*, cyclic glucans, capsular polysaccharide, and cellulose fibrils also appear to be involved in the attachment of to plant cells while in *Azospirillum brasilense* the attachment to cereals roots also can be divided into two different steps (Rodriguez-Navarro et al. 2007). Not only bacteria but also fungi attach to the root surface. Fungal adhesion to plants is a key step for establishment of interaction (Tucker and Talbot 2001). Some plant-microbe interaction have evolved complex signal exchange mechanisms that allow a specific bacterial species to induce its host plant to form invasion structures through which the bacteria can enter the plant root, e. g. *Sinorhizobium* (Jones et al. 2007). For the grass endophyte *Azoarcus*, the putative type IV pilus retraction protein PilT is not essential for the bacterial colonization of the plant surface, but twitching motility is necessary for invasion of and establishment inside the plant (Bohm et al. 2007). Plant-associated bacteria used quorum-sensing signals and two-component regulatory systems to coordinate, in a cell density-dependent manner or in response to changing environmental conditions, the expression of important factors for host colonization and invasion (Soto et al. 2006). The success of invasion and survival within the host also requires that bacteria overcome plant defense responses triggered after microbial recognition, a process in which surface polysaccharides, antioxidant systems, ethylene biosynthesis inhibitors and virulence genes are involved (Soto et al. 2006).

There are microbial species, which can colonize only a few or single plant species. This fact is well-known for the beneficial interactions, e.g. *Rhizobium* - legumes, as well as for many plant pathogens. On the other side, some microbial species such as *Pseudomonas* and *Trichoderma* occur ubiquitous and more or less on each plant species. However, it was shown for *Pseudomonas fluorescens/putida* group as well as for *Serratia* that plant specific genotypes exists (Berg et al. 2006; Berg et al. 2002). Theoretically, the composition of microbes, which colonize the rhizosphere, can be a result of a positive or negative selection procedure or both. However, little is known about this important issue, and there are only a few examples for both ways. *Stenotrophomonas maltophilia* is a member of the rhizobacterial populations of cruciferous plants, which produce particularly high levels of sulphur-containing compounds, f. e. amino acids like methionine (Debette and Blondeau 1980). *Stenotrophomonas maltophilia* requires methionine (Ikemoto et al. 1980). These results can base on a positive relationship between both partners. Due to the fact that root exudates are highly plant species specific the use of specific compounds can explain plant specificity of microbial communities. Interestingly, flavonoids, a diverse class of polyphenolic compounds secreted by plants, often serve as signals in plant-microbe interactions (Shaw et al. 2006). On the other hand, plants produce and secrete a variety of secondary metabolites, which can be toxic to microorganisms. Those plants, which are known for their high production of toxins, e. g. walnut (*Juglans regia* L.) are colonized by specific microbial population which can degrade or detoxify metabolites via specific hydrolases (Rettenmaier and Lingens 1985). Another strategy to survive despite the occurrence of toxins are efflux pumps, which pump toxic components outside the body. In addition, production of toxins can be very effective in maintaining microbial diversity (Czárán et al. 2002). A global analysis of *Pseudomonas putida* gene expression during their interaction with maize roots showed the importance

of two selective forces of *Pseudomonas* cells to colonize the rhizosphere: stress adaptation and availability of particular nutrients (Matilla et al. 2007). More in detail, genes involved in nutrition (amino acid uptake and metabolism of aromatic compounds) and adaptation (induction of efflux pumps and enzymes for glutathione metabolism) were preferentially expressed in the rhizosphere.

Many plant-associated bacteria, especially root endophytic bacteria, intimately interact with plant metabolism. Fascinating examples are endophytic methylobacteria, which use C1 bodies from the plant for their energy production (Zabetakis 1997). The chemical compound hydroxypropanol is given back to the plant and works as precursor of the flavor compounds mesifuran und 2,5-dimethyl-4-hydroxy-2H-furan (DMHF). The latter posses additional antifungal activity and can be responsible for pathogens defense. These bacteria show also a strong plant growth promoting effect. Interestingly, a recent report provided evidence that hormone-producing methylobacteria are essential for germination and development of protonema of *Funaria hygrometrica* (Hornschuh et al. 2002).

The mycorhizosphere: specific traits and interactions with other rhizosphere constituents

Mycorrhizal symbioses - mutualistic root-fungus associations - are present in almost all land plants and are essential biological constituents of the rhizosphere. Mycorrhizae are grouped in two main categories: endomycorrhizae such as arbuscular (AM), ericoid and orchid mycorrhiza and ectomycorrhiza (EM). The arbuscular mycorrhizal symbiosis represents the most widespread and ancient plant symbiosis. From molecular data and information from fossils in the Devonian, a period during which plant started to colonize land, a close interaction between plant roots and soil born fungi has been established about 450 millions years ago (Remy et al. 1994). These fungi have recently been grouped, on the basis of molecular data, in a new phylum the *Glomeromycota* (Schüßler et al. 2001). In the ectomycorrhizae thousands of *Asco-* and *Basidiomycota* species are known as being mycorrhizal. Nowadays, more than 80% of surveyed plant species and 92% of plant families, present in most ecosystems are mycorrhizal (Wang and Qiu 2006), and mycorrhizal fungi are, on a biomass basis, the largest fungal group in soils (Olsson et al. 1999). In a single cubic centimeter of soil, the mycorrhizal fungal network can represent up to 20 meters (Pearson et al. 1993). For these reasons, the rhizosphere concept has been extended to include the fungal component of this symbiosis, resulting in the mycorrhizosphere (Rambelli 1973). This term includes the physical zone influenced by the root, but also by the mycorrhizal fungus mycelium or hyphosphere. Mycorrhizae are regarded at least as tripartite symbioses since they commonly interact with bacteria and other soil organisms producing beneficial effects on plant nutrition and health as well as on soil structure and stability (Frey-Klett et al. 2007). The fungal and bacterial communities associated with roots vary at different developmental stages, e.g. in *Medicago truncatula* (Mougel et al. 2006). The diversity of arbuscular mycorrhizal communities and their relation with bacteria on grass roots and in grassland ecosystems is documented (Oehl et al. 2003; Singh et al. 2008). The mycorrhizal fungus through the mycelium network increases by several orders of magnitude the soil volume which can be explored. This is achieved by the extension of the mycelium network, but also as the size of the fungal hyphae, which are thinner than the roots, and therefore can enter soil particles in a more efficient than the roots. The strongly reduced mobility of P_i and the rapid uptake of P_i by the plant root generates P_i depleted zones around the plant root hairs followed by a decline in the Pi uptake by the plant (Marschner and Dell 1994; Roose and Fowler 2004). In non-mycorrhizal roots, the P_i depletion zone is closely related to the extension of the root system, whereas in a mycorrhizal root system the P_i depletion zone exceeds greatly the root cylinder (Harley and Smith 1983). The fine fungal mycelia can explore soil particles and then translocate P_i from the soil to root cells, improving the phosphate nutrition. In AM-symbioses, the transfer of the phosphate from the fungus to the plant occurs mainly at the level of the arbuscule, symbiotic organ formed by the fungal hyphae penetrating cortex cells, and forming a arbuscule like structure (Smith and Read 1997). In EM-symbioses the fungal hyphae forming the Hartig net surrounding root cortical cells are the structures of nutrient exchange from root to the fungus. These structures are essential for active symbioses and the development of extraradical mycelium (Smith and

Read 1997). In return, the plant transfers carbon to the fungus. The amount of photosynthates transferred from the plant to the fungus can be has high as 20% (Johnson et al. 2002). This carbon is essential for these fungi, which relies on the plant for their growth, but part of it is transferred through the fungal mycelium to the soil and the atmosphere. Johnson et al. (2002) showed that under field conditions a large amount of carbon, provided under the form of CO_2 was released with a peak 9 – 14 h after labeling by the mycorrhizal fungus. The colonization of roots by AM-fungi was also shown to decrease root exudation (Jones et al. 2004). It has also been shown, that mycorrhization also has a qualitative effect of plant exudation which affects the associated microflora and the soil adjacent to the roots (Jones et al. 2004) resulting in changing the bacterial community composition in the rhizosphere (Marschner and Baumann 2003).

The extension of mycorrhizal fungi into the soil and thus their effect on rhizosphere processes is very dependent on the fungal taxa. Hart and Reader (2002) showed that fungi belonging to the *Glomus* or *Acaulospora* genus had a mean extraradical hyphal length of 1 m to 2 m per cm^{-3}, whereas the fungi belonging to the *Gigaspora* or *Scutellospora* genus had an average hyphal length in the soil of 6 to 9 m per cm^{-3}. The colonization rate was also very dependent on the fungal taxa. *Glomus* species colonized the first plant roots in their conditions after 1 week, whereas *Gigaspora* or the *Scutellopsora* colonized the first roots after 4 to 6 weeks. It has been shown (van Tuinen et al. 1998), that colonization efficiency of *Glomus* and *Gigaspora* fungi, were not identical if these fungi were inoculated alone or in a mixed community. *Gig. rosea* colonized pea or onion roots more efficiently when other mycorrhizal fungi, mainly from the genus *Glomus* where present, suggesting a synergetic behavior of these fungi. These important differences in the colonization pattern could be a reason for the predominant present of *Glomus* species in field collected mycorrhizal roots. (Hempel et al. 2007; Mathimaran et al. 2005; Pivato et al. 2007; Turnau et al. 2001; Vandenkoornhuyse et al. 2003) The differences in colonization speed and mycelium extension observed between the different arbuscular mycorrhizal fungi emphasizes the dynamics of the mycorrhizosphere in time and space. Among the ectomycorrhizae, four different "exploration types" with respect to their ecologically important contact area with the soil substrate were characterized: contact, short, medium and long distance types (Agerer 2001). The long distance type reaches out far into the soil and is also able to bridge different root systems. The mycorrhizal fungal community in a soil is evolving over the season, the mycorrhizosphere impacts also the soil components and the other microorganisms in a temporal way.

In the interaction of mycorrhizal fungi and roots specific signaling factors are known. Root exudates of *Lotus japonicum* contain a "branching factor" which was recently identified as a strigolactone, 5-deoxy-strigol (Akiyama et al. 2005). At very low concentrations, this sesquiterpene induces an extensive branching Gigaspora at very low concentrations. On the other hand, the AM fungal partners release diffusible molecules (socalled Myc factor) perceived by the host root in the absence of direct physical contact. In addition, fungal auxins play a key role in ectomycorrhizal development, root morphology and branching of ectomycorrhizae. Events in the early development and ethylene production by *P. microcarpus* are presumably triggered by the production of indole acetic acid. The influences of the mycorrhizal fungi on soil structure and quality are due to the physical presence of the fungal mycelium, and also to the secretion of glomalin by hyphae of *Glomeromycota*. The extensive extrametrical mycelium of the EM-fungi is ideally placed for nutrient acquisition in the top 10 cm of soils, where most of the local nutrient pools are present.

Although little detailed information is available on the direct impact and interaction of bacteria on mycorrhizal fungi, it has been shown that the germination of mycorrhizal spores, can be affected by the presence of some bacteria (Daniels and Trappe 1980; Mayo et al. 1986; Mosse 1959). In a similar way, the establishment of an active symbiosis has an impact on the rhizospheric bacteria population. It has been shown that mycorrhizal symbiosis does not have a significant influence on the number of cultivable bacteria in the mycorrhizosphere (Andrade et al. 1997; Mansfeld-Giese et al. 2002), but on the contrary has a qualitative effect. When plant roots were colonized by a mycorrhizal fungus, *Paenibacillus* spp. were preferentially isolated from the mycorrhizosphere when compared to non-mycorrhizal plant roots (Artursson et al. 2005; Mansfeld-Giese et al. 2002). This suggests a close relation between mycorrhizal fungi and soil bacteria. By using root organ cultures

Toljander and collaborators (Toljander et al. 2007), showed that mycorrhizal fungi through their exudates had a direct impact on the soil bacterial community. This observation could explain the differential influence different taxa of arbuscular mycorrhizal fungi of on associated bacteria (Rillig et al. 2006). Some of the bacteria associated with arbuscular mycorrhiza fungi, can improve the mycorrhizal colonization (Barea et al. 1998; Budi et al. 1999), improve root branching (Gamalero et al. 2002), or present antifungal properties (Budi et al. 1999). From the mycorhizosphere of sorghum, a bacterial strain, *Paenibacillus* sp B2, has been isolated (Budi et al. 1999). This bacteria beside stimulating mycorrhizal colonization (Budi et al. 1999) produces a molecule with biopesticide properties. This molecule which has been characterized, has a structure with some similarities to polymyxin B (Selim et al. 2005), has a very broad inhibitory spectrum against positive or negative bacteria, but also fungi such as *Fusarium accuminatum* or *F. solani* (Selim et al. 2005). Nevertheless this molecule is compatible with the growth of mycorrhizal fungi (Budi et al. 1999). The influences of mycorrhizal fungi on the bacterial diversity, and through them on some soil characteristics such as soil aggregation (Rillig et al. 2005), reveals some of the links between the plant, the mycorrhizal fungus and soil bacteria at the diversity and functional level.

Concerning ectomycorrhiza, mycorrhizal helper bacteria are also known (Frey-Klett et al. 2007; Garbaye 1994). The mycorrhizal mantle and the emanating hyphae are densely colonized by a biofilm-like structure of diverse bacterial community. Using the direct fluorescence *in situ* hybridization (FISH) approach, Mogge et al. (2000) could demonstrate that Betaproteobacteria commonly are found to colonize the *Laccaria subdulcis* / beech mycorrhizosphere although they could not be cultured from this mycorrhiza. In addition, *Acidobacteria* were also shown to be very frequent colonizers of different ectomycorrhizas (C. Kellermann, R. Agerer, A. Hartmann, unpublished results) by 16S rDNA clone bank and FISH-studies, although their cultivation in pure culture was not possible up to date. Depending on the mycorrhizal type and environmental conditions, more than 10.000 bacteria per mm^2 could be counted. While most of the bacteria are usually found to colonize the surface of mycorrhizal fungi, some bacteria were also found to enter the fungal hyphae, such as *Paenibacillus* sp. 101 in cultures of the ectomycorrhizal fungus *Laccaria bicolour* S238N (Bertaux et al. 2003). In contrast, in the natural environment the fungus was colonized intracellularly by Alphaproteobacteria mostly (Bertaux et al. 2005). Also a *Streptomyces* strain (GB 4−2), belonging to the *Actinomycetales* (Gram-positive organisms with high DNA G+C DNA content) was characterized as effective colonizer of the ectomycorrhizosphere of Norway spruce (Lehr et al. 2007). Most interestingly, this bacterium caused a systemic response in the spruce plants resulting in inhibition of the phytopathogenic fungus *Heterobasidium abietinum*. This bacterium also increased the general photosynthetic yield and peroxidase activity in the needles leading to decreased infection by *Botrytis cinerea*. Another mycorrhizal helper bacterium, *Streptomyces* AcH 505, from the mycorrhizosphere of fly agaric produces the antibiotic auxofuran, which causes changes of microbial communities in the mycorrhizosphere and additionally stimulates plant growth (Riedlinger et al. 2006). Thus the interaction of mycorrhiza with bacteria can alter the function of plants and rhizosphere communities considerably.

Selected examples for the specific selection and interaction of roots and microbes

After the separate discussion of plant traits shaping microbial communities, of microbial responses towards rhizosphere conditions and the mycorrhizosphere, this chapter finally presents selected case studies, demonstrating the interaction of plant and microbial activities in the rhizosphere to result in plant specificity of rhizosphere microbial communities. This plant specificity has e. g. great relevance for the development of biological control of phytopathogens (case study of the biological control of the soil-borne plant pathogen *Verticillium*), the influence of roots of genetically engineered plants on the rhizosphere microflora (case study of transgenic modified potato lines) and the selection of mycorrhizal microdiversity (case study of arbuscular mycorrhiza in different *Medicago* lines).

Plant specificity of microbial communities in the rhizosphere of Verticillium

Although several studies using cultivation-dependent techniques found indications for plant specificity in the rhizosphere (Germida et al. 1998; Grayston et al. 1998;

Kremer et al. 1990; Miller et al. 1989), Smalla et al. (2001) showed for the first time that roots of each model plant species are colonized by its own bacterial communities using cultivation-independent methods. Three phylogenetically different and economically important crops - strawberry (*Fragaria x ananassa* (Duchense) Decaisne and Naudin [*Rosaceae*]; potato (*Solanum tuberosum* L. [*Solanaceae*]; and oilseed rape *Brassica napus* L. [*Brassicaceae*] - were analyzed in this study. All species belong to the broad host range of the soil-borne fungal pathogen *Verticillium dahliae* Kleb., which cause high yield losses world-wide (Tjamos et al. 2000). Besides the analysis of whole bacterial community structures in rhizospheres, the functional group of antagonists was another indicator to analyze differences and similarities between the three plants. Antagonists are naturally occurring micro-organisms that express traits that enable them to interfere with pathogen growth, survival, and infection. They form the antagonistic potential against plant pathogens interacting by diverse mechanisms with pathogens and host plants (Cook et al. 1995).

It was possible to differentiate plant species on the basis of the rhizosphere microbial communities using denaturing gradient gel electrophoresis (DGGE) in a randomized field trial (Smalla et al. 2001). The DGGE fingerprints showed plant-dependent shifts in the relative abundance of bacterial populations in the rhizosphere which became more pronounced in the second year. Interestingly, all rhizospheres showed some bands in common but also specific bands, e.g. *Nocardia* populations were identified as strawberry-specific bands. The proportion and composition of bacterial antagonists of potato, oilseed rape and strawberry towards *V. dahliae* was also shown to be influenced by the plant species (Berg et al. 2002). Furthermore, plant specific genotypes of 34 *Pseudomonas putida* A isolates were observed, suggesting that these bacteria were specifically enriched in each rhizosphere. When the field experiment with the three *Verticillium* host plants was performed at different sites (Rostock, Berlin, Braunschweig in Germany) plant specificity of rhizosphere communities was detected again while also different bulk soil community fingerprints were revealed for each sampling site (Costa et al. 2006a). Universal and group-specific (Alphaproteobacteria, Betaproteobacteria and *Actinobacteria* primers were used to PCR-amplify 16S rRNA gene fragments of bacterial and 18S rRNA amplificates for the fungal communities prior to DGGE analysis. The plant species was the determinant factor in shaping similar Actinobacterial communities in the strawberry rhizosphere from different sites in both years. The rhizosphere effect on the antagonistic bacterial community was demonstrated by an enhanced proportion of antagonistic isolates, by enrichment of specific ARDRA types, species and genotypes as evidenced by BOX-PCR, and by a reduced diversity of antagonistic bacteria in the rhizosphere in comparison to bulk soil (Berg et al. 2006). Since bacteria of the genus *Pseudomonas* are prominent root-associated bacteria (Haas and Défago 2005) they were investigated by culture dependent and independent techniques. Based on the data of this field trial, the factors sampling site, plant species and year-to-year variation were shown to significantly influence the community structure of *Pseudomonas* in rhizosphere soils (Costa et al. 2006b). The composition of *Pseudomonas* 16S rRNA gene fragments in the rhizosphere differed from that in the adjacent bulk soil and the rhizosphere effect tended to be plant-specific. The clone sequences of most dominant bands analyzed belonged to the *Pseudomonas fluorescens* lineage and showed closest similarity to culturable *Pseudomonas* known for displaying antagonistic properties. In addition, *Pseudomonas*-specific *gac*A fingerprints of total-community rhizosphere DNA were surprisingly diverse, plant-specific and differed markedly from those of the corresponding bulk soils (Costa et al. 2007). By combining multiple culture-dependent and independent surveys, a group of *Pseudomonas* isolates antagonistic towards *V. dahliae* was shown to be genotypically conserved, to carry the *phl*D biosynthetic locus (involved in the biosynthesis of 2,4-diacetylphloroglucinol − 2,4-DAPG) (Costa et al. 2007). This group of *Pseudomonas* isolates corresponded to a highly frequent *Pseudomonas* population in the rhizosphere of field-grown strawberries planted at three sites in Germany which have different land use histories. It belongs to the *Pseudomonas fluorescens* phylogenetic lineage and showed closest relatedness to *P. fluorescens* strain F113 (97% *gac*A gene sequence identity in 492-bp sequences), a biocontrol agent and 2,4-DAPG producer. Partial *gac*A gene sequences derived from isolates, clones of the strawberry rhizosphere and DGGE bands retrieved in this study represent previously unknown *Pseudomonas gacA*

gene clusters as revealed by phylogenetic analysis (Costa et al. 2007).

Concerning fungal rhizosphere communities, a plant-specific composition could also be detected, but not in all cases (Costa et al. 2006a). Higher heterogeneity of DGGE profiles within soil and rhizosphere replicates was observed for the fungi than for bacteria. A high proportion of fungi antagonistic towards the pathogen *V. dahliae* were found for bulk and rhizosphere soil at all sites (Berg et al. 2005). A plant- and site-dependent specificity of the composition of antagonistic morphotypes and their genotypic diversity was found. *Trichoderma* strains displayed high diversity in all soils, and a high degree of plant specificity could be shown by BOX-PCR fingerprints. The diversity of rhizosphere-associated antagonists was lower than that of antagonists in bulk soil, suggesting that some fungi were specifically enriched in each rhizosphere. In Fig. 2, a model for the rhizosphere effect of bacterial and fungal antagonists was developed. Altogether, the rhizosphere effect for fungal antagonists was lower pronounced than for bacteria. Altogether, these results obtained in these six-year field studies proofed a clear influence of plant species on the structure and function of rhizosphere bacterial communities. Although there are several contrasting reports in the literature indicating plant or soil type as dominant factor (Girvan et al. 2003; Grayston et al. 1998; Nunan et al. 2005) in more or less all studies the influence of plant species is clearly visible [rev. in (Berg and Smalla 2008; Garbeva et al. 2004)]. Extend of plant specificity is influenced by the selected plant species, applied methods as well as by the experimental design. Exemplarily, Fig. 3 corroborates the plant specific selection of rhizosphere microbial communities since it was clearly demonstrated that different herbaceous plants select a very different bacterial community from the very same soil (Dohrmann and Tebbe 2005).

Cultivar specificity of microbial communities in the rhizosphere of different potatoes (*Solanum tuberosum* L.) including transgenic lines

Rhizosphere microbial communities are not only influenced at the plant species level, but also at the cultivar level (Germida and Siciliano 2001). Genetically modified plants with altered root exudates are interesting model systems to study cultivar-specific effects, which were found in several studies for root-associated bacterial as well as fungal communities (Mansouri et al. 2002; Oger et al. 1997; Oger et al. 2004; Oliver et al. 2008). T4 lysozyme potatoes are a well-studied model system to investigate the potential risk of pathogen resistant plants (Düring et al. 1993). For example, in a 6-year field release of T4 lysozyme producing potatoes cv. Désirée the changes in structure and function of plant-associated bacterial populations were monitored by a polyphasic approach. However, in both microenvironments (rhizosphere and geocaulosphere) no statistically significant

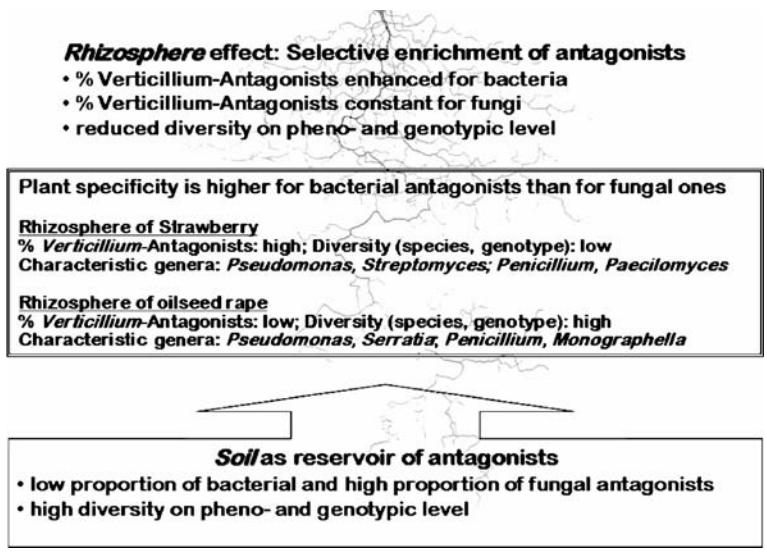


Fig. 2 Selective enrichments of antagonistic populations in the rhizosphere according to results obtained in a six-year field trial with Verticillium host plants (Berg et al. 2002, 2005, 2006)

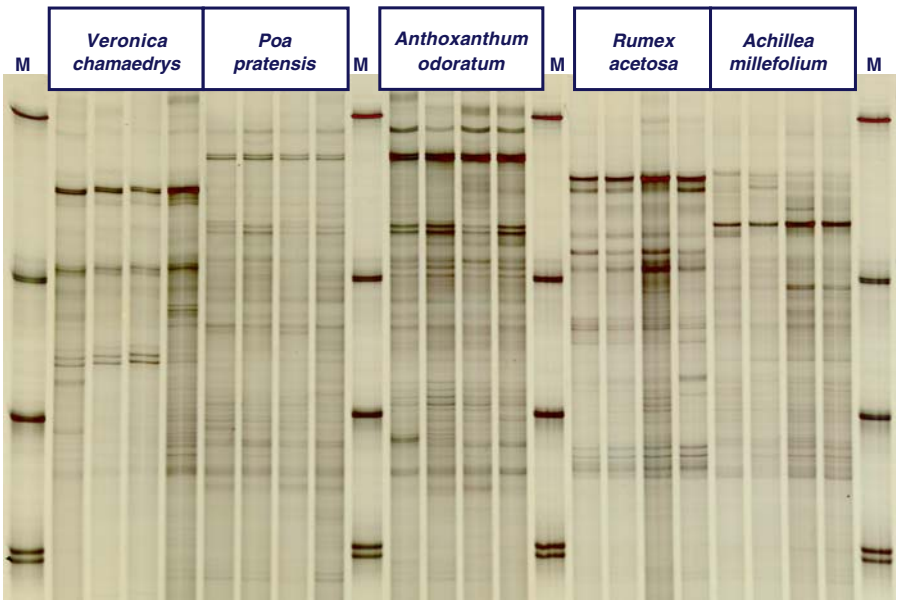


Fig. 3 Plant driven selection of bacterial communities in the rhizosphere of different herbaceous plants. Six different herbaceous plants were cultivated in the same soil and the rhizosphere bacterial communities were analyzed using the SSCP-profiling technique (according to Dohrmann and Tebbe (2005))

differences between transgenic and non transgenic plants were found in the following parameters: (i) the abundances of bacteria, (ii) the percentage of auxin-producing bacteria, (iii) the percentage of antagonistic bacteria, and (iv) on the diversity of bacterial antagonists on genotypic and phenotypic level (Lottmann and Berg 2001; Lottmann et al. 1999; Lottmann et al. 2000). In an additional approach, rifampicin resistant mutants of two antagonistic plant-associated bacteria were used for seed tuber inoculation of transgenic and non-transgenic potato lines. During flowering of plants, significantly more colony counts of the lysozyme tolerant *Pseudomonas putida* QC14-3-8 were recovered from the transgenic T4 lysozyme plant than from the non-transgenic control and the parental line. Furthermore, using a root hair - *Bacillus subtilis* model, roots from potato lines expressing the T4 lysozyme gene always showed significantly (1.5- to 3.5-fold) higher killing (Ahrenholtz et al. 2000). However, using cultivation-independent methods the influence of environmental factors on potato associated bacteria was much higher than of the transgene (Heuer et al. 2002). Altogether, an influence of transgenic T4 lyzozyme on bacterial strains and community was to be seen in special experiments. In field trials, the influence was negligible compared to other environmental factors.

To assess potential effects of T4 lysozyme on culturable plant-associated fungi in the rhizosphere, the abundances of colony forming units, the percentage of antagonistic fungi and their diversity were investigated (Berg, unpublished results). The results from this study suggest that transgenic plants producing T4 lysozyme did not affect the fungal communities and the abundance and composition of fungi with antagonistic activity. Furthermore, the composition and relative abundance of endophytic fungi in roots of T4-lysozyme producing potatoes and the parental line were assessed by classical isolation from root segments and cultivation-independent techniques to test the hypothesis that endophytic fungi are affected by T4-lysozyme (Götz et al. 2006). Fungi were isolated from the majority of root segments of both lines and at least 63 morphological groups were obtained with *Verticillium dahliae, Cylindrocarpon destructans, Colletotrichum coccodes* and *Plectosporium tabacinum* as the most frequently isolated species. Dominant bands in the fungal fingerprints obtained by denaturing gradient gel electrophoresis analysis of 18S rRNA gene fragments amplified from total community DNA corresponded to the electrophoretic mobility of the 18S rRNA gene fragments of the three most abundant fungal isolates, *V. dahliae, C. destructans* and *Col. coccodes*, but not to *P. tabacinum*. The assignment of the bands to these isolates was confirmed for *V. dahliae* and *Col. coccodes* by sequencing of clones. *Verticillium dahliae* was the most abundant endophytic fungus in the roots of healthy potato plants. Differences in the relative abundance of endophytic fungi colonizing the roots of T4-lysozyme producing potatoes and the parental line could be detected by both methods.

These results obtained for T4-lysozyme potato were confirmed in greenhouse experiments (Rasche et al. 2006) and in other studies analyzing transgenic plants (Bruinsma et al. 2003). There was only a minor, and in comparison to other environmental factors, negligible influence on the structure and function of microbial communities to be seen. In another approach comparing zeaxanthine producing potatoes with different potato cultivars, the effect of cultivar was much higher than of the transgene (Schloter, pers. communication).

Impact of *Medicago* species on arbuscular mycorrhizal fungi

A relationship of the diversity of arbuscular mycorrhizal fungi and plant diversity has been documented several times under field conditions (Gollotte et al. 2004; Husband et al. 2002; Oehl et al. 2005; van der Heijden et al. 1998; Vandenkoornhuyse et al. 2003; Wolfe et al. 2007). These knowledge has been obtained by analyzing the root-associated mycorrhizal community on the basis of spore counting (Husband et al. 2002; Oehl et al. 2005; Vandenkoornhuyse et al. 2003; Wolfe et al. 2007), PCR-RFLP analysis of the small ribosomal sub-unit (Husband et al. 2002; Scheublin et al. 2004; Vandenkoornhuyse et al. 2003) or by sequencing of the large ribosomal subunit of the fungi (Gollotte et al. 2004). More recently, Real-Time PCR has been used to quantify mycorrhizal fungi in plant roots inoculated with a single (Filion et al. 2003) or two fungal isolates (Alkan et al. 2004; Alkan et al. 2006). This method opens the possibility of quantifying the fungal ribosomal operon in the soil or plant roots, by a very refined and sensitive method, and has been used to estimate the fungal community in the roots, by monitoring several arbuscular mycorrhizal taxa, in closely related *Medicago* species (Pivato et al. 2007). As it is known that the plant used to trap arbuscular mycorrhizal has a great influence on the species detected (Jansa et al. 2002), a preliminary experiment was carried out to identify the indigenous arbuscular mycorrhizal fungi present in the soil. This was performed on a low fertility soil from the Mediterranean basin, corresponding to the naturally growing zone of annual medics. The arbuscular mycorrhizal fungi were identified by sequencing the large ribosomal subunit (LSU), directly amplifying from soil extracted DNA. By using *Glomeromycota* specific primers, targeting the 5' end of the LSU (Gollotte et al. 2004; van Tuinen et al. 1998), Pivato and co-workers (2007) were enabled to group, after a phylogenetic analysis, the 246 obtained sequences in 12 *Glomus* species, or OTU, belonging to the *Glomus* A group (Schwarzott et al. 2001; van Tuinen et al. 1998). From these 12 OTU, only two could be identified on the basis of their homology with well-identified *Glomus* species, whose sequences are available in the databases, namely *G. mosseae* and *G. intraradices*. No *Acaulosporaceae* nor *Gigasporaceae* were detected, although the *Glomeromycota* specific primers used were also able to positively amplify the former taxa (Gollotte et al. 2004). Primers specifically amplifying 4 of the 12 identified *Glomus* OTU, were then designed, and used to quantify by Real-Time PCR, the presence of the corresponding OTU in bare soil or in roots of 4 closely related *Medicago* species, namely *Medicago laciniata* L., *M. murex* Wild., *M. polymorpha* L. and *M. truncatula* Gaertn, grown for 34 days in the same soil. For each OTU specific primer the primer binding site was fully conserved within the sequences of the corresponding OTU, this was important as it is well known that different ribosomal operons are harbored in the same single *Glomeromycota* spore. This approach enabled to show that the amount of the four selected OTU varied between bare soil and the plants, but also between the *Medicago* species. No statistical differences were found in the roots of *M. laciniata* and *M. murex*, whereas statistical differences were observed between *M. polymorpha* and *M. truncatula* for 2 of the selected OTU. Interestingly one of the OTU was present in the same amount in all 4 root systems. This approach demonstrated a subtle modification in the arbuscular mycorrhizal fungi community composition between closely related plants grown in their native soil environment. These measurements were performed at a single time point, and it is possible that the community structure varies over time. Thus, this technique offers the possibility to accurately monitor the selective impact of plants on arbuscular mycorrhizal fungi associated with their roots or their mycorhizospheres.

Summary and conclusions

Ample evidences exist which clearly demonstrate the selection of microbes by roots of plants. Due to many

usually overlapping and interfering mechanisms, the roots provide a specific microhabitat for the proliferation of a specific subset of soil microbes. Usually, new interactions amongst colonizing microbes arise in the quite densely colonized rhizosphere. For example, specific mycorrhiza-bacteria interactions lead to a stimulation of symbiosis and other microbe-microbe interactions result in the biological control of phytopathogenic microbes by plant beneficial root colonizers. Vice versa, the plant is profiting manifold from microbial activities in the rhizosphere and is additionally influenced by root colonizing microbes through signaling pathways, leading to potentially improved plant fitness. It is probably not the mere utilization of available carbon sources which selects the rhizosphere community but rather the presence of selective and inhibitory interactions which creates the bias into root-associated microbial populations.

To get deeper insight into key rhizosphere processes and the major steering factors involved, a combination of stable isotope probing (through e. g. ^{13}C-CO_2 labeling of plant assimilates) with molecular biological techniques of community characterization will certainly gain even more importance in future. Since m-RNA can be retrieved from soil with more confidence now, studies on functional gene expression of specific bacterial genes and even rhizosphere transcriptome analysis are feasible. These studies should be combined with metagenome, proteome and metabolome studies to get a complete picture. However, to be able to cope with the complexity and amount of data, bioinformatics and mathematical modeling will have to be included in these endeavors. Finally, on site field studies of rhizosphere research should be performed more intensively to be able to proof the experience of more or less laboratory model studies to the field and forest setting. Climatic or environmental simulation chambers will help to reduce the unpredictable climatic factors to well designed factorial analyses while keeping the complexity of a realistic ecosystem setting. This will allow studying the influence of extreme climatic conditions on plant performance and how plants influence rhizosphere communities and processes under these conditions.

Rhizosphere driven selection of microbes has high potential to improve the development and health of plants. Although some promising products are in applications, this route needs to be much more developed and applied for the sake of sustainable agriculture, silviculture and horticulture. In future, both the plant side and the microbial side should be included in concerted biotechnological development and breeding programs.

References

Agerer R (2001) Exploration types of ectomycorrhizal mycelial systems: A proposal to classify mycorrhizal mycelial systems with respect to their ecologically important contact area with the substrate. Mycorrhiza 11:107–114. doi:10.1007/s005720100108

Ahrenholtz I, Harms K, de Vries J, Wackernagel W (2000) Increased killing of *Bacillus subtilis* on the hair roots of transgenic T4 lysozyme-producing potatoes. Appl Environ Microbiol 66:1862–1865. doi:10.1128/AEM.66.5.1862-1865.2000

Akiyama K, Matsuzaki K-i, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435:824–827. doi:10.1038/nature03608

Alkan N, Gadkar V, Coburn J, Yarden O, Kapulnik Y (2004) Quantification of the arbuscular mycorrhizal fungus *Glomus intraradices* in host tissue using real-time polymerase chain reaction. New Phytol 161:877–885. doi:10.1046/j.1469-8137.2004.00975.x

Alkan N, Gadkar V, Yarden O, Kapulnik Y (2006) Analysis of quantitative interactions between two species of arbuscular mycorrhizal fungi, *Glomus mosseae* and *G. intraradices*, by Real-Time PCR. Appl Environ Microbiol 72:4192–4199. doi:10.1128/AEM.02889-05

Andrade G, Mihara KL, Linderman RG, Bethlenfalvay GJ (1997) Bacteria from the rhizosphere and hyphoshere soils of different arbuscular-mycorrhizal fungi. Plant Soil 192:71–79. doi:10.1023/A:1004249629643

Apel K, Hirt H (2004) Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399. doi:10.1146/annurev.arplant.55.031903.141701

Artursson V, Finlay RD, Jansson JK (2005) Combined bromodeoxyuridine immunocapture and terminal-restriction fragment length polymorphism analysis highlights differences in the active soil bacterial metagenome due to *Glomus mosseae* inoculation or plant species. Environ Microbio l7:1952–1966. doi:10.1111/j.1462-2920.2005.00868.x

Bais HP, Prithiviraj B, Jha AK, Ausubel FM, Vivanco JM (2005) Mediation of pathogen resistance by exudation of antimicrobials from roots. Nature 434:217–221. doi:10.1038/nature03356

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266. doi:10.1146/annurev.arplant.57.032905.105159

Barea JM, Andrade G, Bianciotto V, Dowling D, Lohrke S, Bonfante P, O'Gara F, Azcon-Aguilar C (1998) Impact on arbuscular mycorrhiza formation of *Pseudomonas* strains used as inoculants for biocontrol of soil-borne fungal plant pathogens. Appl Environ Microbiol 64:2304–2307

Bauer WD, Mathesius U (2004) Plant responses to bacterial quorum sensing signals. Curr Opin Plant Biol 7:429–433. doi:10.1016/j.pbi.2004.05.008

Bérczi A, Møller IM (2000) Redox enzymes in the plant plasma membrane and their possible roles. Plant Cell Environ 23:1287–1302. doi:10.1046/j.1365-3040.2000.00644.x

Berg G, Smalla K (2008) Plant species versus soil type: which factors influence the structure and function of the microbial communities in the rhizosphere? FEMS Microbiol Ecol (submitted)

Berg G, Roskot N, Steidle A, Eberl L, Zock A, Smalla K (2002) Plant-dependent genotypic and phenotypic diversity of antagonistic rhizobacteria isolated from different *Verticillium* host plants. Appl Environ Microbiol 68:3328–3338. doi:10.1128/AEM.68.7.3328-3338.2002

Berg G, Zachow C, Lottmann J, Gotz M, Costa R, Smalla K (2005) Impact of plant species and site on rhizosphere-associated fungi antagonistic to *Verticillium dahliae* Kleb. Appl Environ Microbiol 71:4203–4213. doi:10.1128/AEM.71.8.4203-4213.2005

Berg G, Opelt K, Zachow C, Lottmann J, Gotz M, Costa R, Smalla K (2006) The rhizosphere effect on bacteria antagonistic towards the pathogenic fungus *Verticillium* differs depending on plant species and site. FEMS Microbiol Ecol 56:250–261. doi:10.1111/j.1574-6941.2005.00025.x

Bertaux J, Schmid M, Prevost-Boure NC, Churin JL, Hartmann A, Garbaye J, Frey-Klett P (2003) In situ identification of intracellular bacteria related to *Paenibacillus* spp. in the mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. Appl Environ Microbiol 69:4243–4248. doi:10.1128/AEM.69.7.4243-4248.2003

Bertaux J, Schmid M, Hutzler P, Hartmann A, Garbaye J, Frey-Klett P (2005) Occurrence and distribution of endobacteria in the plant-associated mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. Environ Microbio l7:1786–1795. doi:10.1111/j.1462-2920.2005.00867.x

Bohm M, Hurek T, Reinhold-Hurek B (2007) Twitching motility is essential for endophytic rice colonization by the N_2-fixing endophyte *Azoarcus* sp. Strain BH72. Mol Plant Microbe Interact 20:526–533. doi:10.1094/MPMI-20-5-0526

Bruinsma M, Kowalchuk GA, van Veen JA (2003) Effects of genetically modified plants on microbial communities and processes in soil. Biol Fertil Soils 37:329–337

Budi SW, van Tuinen D, Martinotti G, Gianinazzi S (1999) Isolation from the *Sorghum bicolor* mycorrhizosphere of a bacterium compatible with arbuscular mycorrhiza development and antagonistic towards soilborne fungal pathogens. Appl Environ Microbiol 65:5148–5150

Butler JL, Williams MA, Bottomley PJ, Myrold DD (2003) Microbial community dynamics associated with rhizosphere carbon flow. Appl Environ Microbiol 69:6793–6800. doi:10.1128/AEM.69.11.6793-6800.2003

Butler JL, Bottomley PJ, Griffith SM, Myrold DD (2004) Distribution and turnover of recently fixed photosynthate in ryegrass rhizospheres. Soil Biol Biochem 36:371–382. doi:10.1016/j.soilbio.2003.10.011

Chishaki N, Horiguchi T (1997) Responses of secondary metabolism in plants to nutrient deficiency. Soil Sci Plant Nutr 43:987–991

Cook RJ, Thomashow LS, Weller DM, Fujimoto D, Mazzola M, Bangera G, Kim D (1995) Molecular mechanisms of defense by rhizobacteria against root disease. Proc Natl Acad Sci U S A 92:4197–4201. doi:10.1073/pnas.92.10.4197

Costa R, Gotz M, Mrotzek N, Lottmann J, Berg G, Smalla K (2006a) Effects of site and plant species on rhizosphere community structure as revealed by molecular analysis of microbial guilds. FEMS Microbiol Ecol 56:236–249. doi:10.1111/j.1574-6941.2005.00026.x

Costa R, Salles JF, Berg G, Smalla K (2006b) Cultivation-independent analysis of *Pseudomonas* species in soil and in the rhizosphere of field-grown *Verticillium dahliae* host plants. Environ Microbiol 8:2136–2149. doi:10.1111/j.1462-2920.2006.01096.x

Costa R, Gomes NCM, Krogerrecklenfort E, Opelt K, Berg G, Smalla K (2007) *Pseudomonas* community structure and antagonistic potential in the rhizosphere: insights gained by combining phylogenetic and functional gene-based analyses. Environ Microbiol 9:2260–2273. doi:10.1111/j.1462-2920.2007.01340.x

Crowley DE, Rengel Z (1999) Biology and chemistry of rhizosphere influencing nutrient availability. In: Rengel Z (ed) Mineral nutrition of crops: Fundamental mechanisms and implications. The Haworth Press, New York, pp 1–40

Czárán TL, Hoekstra RF, Pagie L (2002) Chemical warfare between microbes promotes biodiversity. Proc Natl Acad Sci U S A 99:786–790. doi:10.1073/pnas.012399899

Dakora FD, Phillips DA (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 13:35–47

d'Angelo-Picard C, Faure D, Penot I, Dessaux Y (2005) Diversity of N-acyl homoserine lactone-producing and -degrading bacteria in soil and tobacco rhizosphere. Environ Microbiol l7:1796–1808

Daniels BA, Trappe JM (1980) Factors affecting spore germination of the vesicular-arbusuclar mycorrhizal fungus *Glomus epigaeus.* Mycologia 72:457–471

Debette J, Blondeau R (1980) Présence de *Pseudomonas maltophilia* dans la rhizosphère de quelque plantes cultivée. Can J Microbiol 26:460–463

Degrassi G, Devescovi G, Solis R, Steindler L, Venturi V (2007) *Oryza sativa* rice plants contain molecules that activate different quorum-sensing N-acyl homoserine lactone biosensors and are sensitive to the specific AiiA lactonase. FEMS Microbiol Lett 269:213–220

Delalande L, Faure D, Raffoux A, Uroz S, D'Angelo-Picard C, Elasri M, Carlier A, Berruyer R, Petit A, Williams P, Dessaux Y (2005) N-hexanoyl-l-homoserine lactone, a mediator of bacterial quorum-sensing regulation, exhibits plant-dependent stability and may be inactivated by germinating *Lotus corniculatu*s seedlings. FEMS Microbiol Ecol 52:13–20

de Weert S, Vermeiren H, Mulders IHM, Kuiper I, Hendrickx N, Bloemberg GV, Vanderleyden J, De Mot R, Lugtenberg BJJ (2002) Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by *Pseudomonas fluorescens* Mol Plant Microbe Interact 15:1173–1180

Dinkelaker B, Hengeler C, Marschner H (1995) Distribution and function of proteoid roots and other root clusters. Bot Acta 108:183–200

Dohrmann AB, Tebbe CC (2005) Effect of elevated tropospheric ozone on the structure of bacterial communities inhabiting the rhizosphere of herbaceous plants native to Germany. Appl Environ Microbiol 71:7750–7758

Dong Z, Wu L, Kettlewell B, Caldwell CD, Layzell DB (2003) Hydrogen fertilization of soils - is this a benefit of legumes in rotation? Plant Cell Environ 261:875–1879

Duineveld BM, Rosado AS, van Elsas JD, van Veen JA (1998) Analysis of the dynamics of bacterial communities in the rhizosphere of the *Chrysanthemum* via denaturing gradient gel electrophoresis and substrate utilization patterns. Appl Environ Microbiol 64:4950–4957

Düring K, Porsch P, Fladung M, Lörz H (1993) Transgenic potato plants resistant to the phytopathogenic bacterium *Erwinia carotovora* Plant J 3:587–598

Farrar J, Hawes M, Jones D, Lindow S (2003) How roots control the flux of carbon to the rhizosphere. Ecology 84:827–837

Filion M, St-Arnaud M, Jabaji-Hare SH (2003) Direct quantification of fungal DNA from soil substrate using real-time PCR. J Microbiol Meth 53:67–76

Frey-Klett P, Garbaye J, Tarkka M (2007) The mycorrhiza helper bacteria revisited. New Phytol 176:22–36

Fuqua C, Parsek MR, Greenberg EP (2001) Regulation of gene expression by cell-to-cell communication: Acyl-homoserine lactone quorum sensing. Annu Rev Genet 35:439–468

Gamalero E, Martinotti MG, Trotta A, Lemanceau P, Berta G (2002) Morphogenetic modifications induced by *Pseudomonas fluorescens* A6RI and *Glomus mosseae* BEG12in the root system of tomato differ according to the plant growth conditions. New Phytol 155:293–300

Gantner S, Schmid M, Duerr C, Schuhegger R, Steidle A, Hutzler P, Langebartels C, Eberl L, Hartmann A, Dazzo FB (2006) In situ quantitation of the spatial scale of calling distances and population density-independent N-acylhomoserine lactone-mediated communication by rhizobacteria colonized on plant roots. FEMS Microbiol Ecol 56:188–194

Garbaye J (1994) Helper bacteria: A new dimension to the mycorrhizal symbiosis. New Phytol 128:197–210

Garbeva P, van Veen JA, van Elsas JD (2004) Microbial diversity in soil: Selection of Microbial Populations by Plant and Soil Type and Implications for Disease Suppressiveness. Annu Rev Phytopathol 42:243–270

Germida JJ, Siciliano SD (2001)Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. Biol Fert Soils 33:410–415

Germida JJ, Siciliano SD, Renato de Freitas J, Seib AM (1998) Diversity of root-associated bacteria associated with field-grown canola (*Brassica napus* L.) and wheat (*Triticum aestivum* L.). FEMS Microbiol Ecol 26:43–50

Girvan MS, Bullimore J, Pretty JN, Osborn AM, Ball AS (2003) Soil type is the primary determinant of the composition of the total and active bacterial communities in arable soils. Appl Environ Microbiol 69:1800–1809

Gollotte A, van Tuinen D, Atkinson D (2004) Diversity of arbuscular mycorrhizal fungi colonising roots of the grass species *Agrostis capillaris* and *Lolium perenne* in a field experiment. Mycorrhiza 14:111–117

Götz C, Fekete A, Gebefuegi I, Forczek S, Fuksová K, Li X, Englmann M, Gryndler M, Hartmann A, Matucha M, Schmitt-Kopplin P, Schröder P (2007) Uptake, degradation and chiral discrimination of N-acyl-D/L -homoserine lactones by barley (*Hordeum vulgare*) and yam bean (*Pachyrhizus erosus*) plants. Anal Bioanal Chem 389: 1447–1457

Götz M, Nirenberg H, Krause S, Wolters H, Draeger S, Buchner A, Lottmann J, Berg G, Smalla K (2006) Fungal endophytes in potato roots studied by traditional isolation and cultivation-independent DNA-based methods. FEMS Microbiol Ecol 58:404–413

Grayston SJ, Wang S, Campbell CD, Edwards AC (1998) Selective influence of plant species on microbial diversity in the rhizosphere. Soil Biol Biochem 30:369–378

Haas D, Défago G (2005) Biological control of soil-borne pathogens by fluorescent pseudomonads. Nat Rev Microbiol 3:307–319

Harley JL, Smith SE (1983) Mycorrhizal Symbioses. Academic Press Inc., London, New York, pp 483

Hart MM, Reader RJ (2002) Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytol 153:335–344

Hartmann A (1988) Ecophysiological aspects of growth and nitrogen fixation in *Azospirillum* spp. Plant Soil 110:225–238

Hartmann A, Rothballer M, Schmid M (2008) Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil 312:7–14

Hempel S, Renker C, Buscot F (2007) Differences in the species composition of arbuscular mycorrhizal fungi in spore, root and soil communities in a grassland ecosystem. Environ Microbiol 9:1930–1938

Hense BA, Kuttler C, Müller J, Rothballer M, Hartmann A, Kreft J-U (2007) Does efficiency sensing unify diffusion and quorum sensing? Nat Rev Microbiol 5:230–239

Hentzer M, Riedel K, Rasmussen TB, Heydorn A, Andersen JB, Parsek MR, Rice SA, Eberl L, Molin S, Hoiby N, Kjelleberg S, Givskov M (2002) Inhibition of quorum sensing in *Pseudomonas aeruginosa* biofilm bacteria by a halogenated furanone compound. Microbiol 148:87–102

Heuer H, Kroppenstedt RM, Lottmann J, Berg G, Smalla K (2002) Effects of T4 lysozyme release from transgenic potato roots on bacterial rhizosphere communities are negligible relative to natural factors. Appl Environ Microbiol 68:1325–1335

Hinsinger P, Plassard C, Tang C, Jaillard B (2003) Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. Plant Soil 248:43–59

Hornschuh M, Grotha R, Kutschera U (2002) Epiphytic bacteria associated with the bryophyte *Funaria hygrometrica*: Effect of *Methylobacterium* strains on protonema development. Plant Biol 4:682–682

Husband R, Herre EA, Young JPW (2002) Temporal variation in the arbuscular mycorrhizal communities colonising seedlings in a tropical forest. FEMS Microbiol Ecol 42:131–136

Ikemoto S, Suzuki K, Kaneko T, Komagata K (1980) Characterization of strains of *Pseudomonas maltophilia* which do not require methionine. Int J Syst Bacteriol 30:437–447

Jaeger CHIII, Lindow SE, Miller W, Clark E, Firestone MK (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

Jansa J, Mozafar A, Anken T, Ruh R, Sanders I, Frossard E (2002) Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12: 225–234

Johnson D, Leake JR, Ostle N, Ineson P, Read DJ (2002) In situ $^{13}CO_2$ pulse-labelling of upland grassland demonstrates a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. New Phytol 153:327–334

Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol 163:459–480

Jones KM, Kobayashi H, Davies BW, Taga ME, Walker GC (2007) How rhizobial symbionts invade plants: the *Sinorhizobium-Medicago* model. Nat Rev Microbiol 5:619–633

Kowalchuk GA, Bruinsma M, van Veen JA (2003) Assessing responses of soil microorganisms to GM plants. Trends Ecol Evol 18:403–410

Kremer RJ, Begonia MFT, Stanley L, Lanham ET (1990) Characterization of rhizobacteria associated with weed seedlings. Appl Environ Microbiol 56:1649–1655

Kuzyakov Y, Bol R (2005) Three sources of CO_2 efflux from soil partitioned by ^{13}C natural abundance in an incubation study. Rapid Commun Mass Spectrom 19:1417–1423

Lehr NA, Schrey SD, Bauer R, Hampp R, Tarkka MT (2007) Suppression of plant defence response by a mycorrhiza helper bacterium. New Phytol 174:892–903

Leveau JH, Gerards S (2008) Discovery of a bacterial gene cluster for catabolism of the plant hormone indole 3-acetic acid. FEMS Microbiol Ecol 65:238–250

Lottmann J, Berg G (2001) Phenotypic and genotypic characterization of antagonistic bacteria associated with roots of transgenic and non-transgenic potato plants. Microbiol Res 156:75–82

Lottmann J, Heuer H, Smalla K, Berg G (1999) Influence of transgenic T4-lysozyme-producing potato plants on potentially beneficial plant-associated bacteria. FEMS Microbiol Ecol 29:365–377

Lottmann J, Heuer H, Vries J, Mahn A, During K, Wackernagel W, Smalla K, Berg G (2000) Establishment of introduced antagonistic bacteria in the rhizosphere of transgenic potatoes and their effect on the bacterial community. FEMS Microbiol Ecol 33:41–49

Lu Y, Conrad R (2005) In situ stable isotope probing of methanogenic *Archaea* in the rice rhizosphere. Science 309:1088–1090

Lu Y, Rosencrantz D, Liesack W, Conrad R (2006) Structure and activity of bacterial community inhabiting rice roots and the rhizosphere. Environ Microbiol 8(8):1351–1360

Lugtenberg BJJ, Dekkers LC (1999) What makes *Pseudomonas* bacteria rhizosphere competent? Environ Microbiol 1: 9–13

Mansfeld-Giese K, Larsen J, Bodker L (2002) Bacterial populations associated with mycelium of the arbuscular mycorrhizal fungus *Glomus intraradices*. FEMS Microbiol Ecol 41:133–140

Mansouri H, Petit A, Oger P, Dessaux Y (2002) Engineered rhizosphere: the trophic bias generated by opine-producing plants is independent of the opine type, the soil origin, and the plant species. Appl Environ Microbiol 68:2562–2566

MarkG L, Dow JM, Kiely PD, Higgins H, Haynes J, Baysse C, Abbas A, Foley T, Franks A, Morrissey J, O, Gara F (2005) Transcriptome profiling of bacterial responses to root exudates identifies genes involved in microbe-plant interactions. Proc Natl Acad Sci U S A 102:17454–17459

Marschner H (1991) Root-induced changes in the availability of micronutrients in the rhizosphere. In: Waise lY, Eshel A, Kakafi U (eds) Plant Roots: The Hidden Half, Marcel Dekker, New York, U S A, p. 503

Marschner H, Dell B (1994) Nutrient uptake in mycorrhizal symbiosis. Plant Soil 159:89–102

Marschner H, Römheld V (1994) Strategies of plants for acquisition of iron. Plant Soil 165:261–274

Marschner P, Crowley DE (1998) Phytosiderophores decrease iron stress and pyoverdine production of *Pseudomonas fluorescens* PF-5 (PVD-INAZ). Soil Biol Biochem 30: 1275–1280

Marschner P, Baumann K (2003) Changes in bacterial community structure induced by mycorrhizal colonisation in split-root maize. Plant Soil 251:279–289

Marschner P, Yang CH, Lieberei R, Crowley DE (2001) Soil and plant specific effects on bacterial community composition in the rhizosphere. Soil Biol Biochem 33:1437–1445

Mathimaran N, Ruh R, Vullioud P, Frossard E, Jansa J (2005) *Glomus intraradices* dominates arbuscular mycorrhizal communities in a heavy textured agricultural soil. Mycorrhiza 16:61–66

Matilla M, Espinosa-Urgel M, Rodriguez-Herva J, Ramos J, Ramos-Gonzalez M (2007) Genomic analysis reveals the major driving forces of bacterial life in the rhizosphere. Genome Biol 8:R179

Mayo K, Davies RE, Motta J (1986) Stimulation of germination of spores of *Glomus versiforme* by spore associated bacteria. Mycologia 78:426–431

Miller HJ, Henken G, van Veen JA (1989) Variation and composition of bacterial populations in the rhizospheres of maize, wheat and grass cultivars. Can J Microbiol 35: 656–660

Miller LD, Yost CK, Hynes MF, Alexandre G (2007) The major chemotaxis gene cluster of *Rhizobium leguminosarum* bv. *viciae* is essential for competitive nodulation. Mol Microbiol 63:348–362

Moenne-Loccoz Y, McHugh B, Stephens PM, McConnell FI, Glennon JD, Dowling DN, O'Gara F (1996) Rhizosphere competence of fluorescent *Pseudomonas* spB24 genetically modified to utilise additional ferric siderophores. FEMS Microbiol Ecol 19:215–225

Mogge B, Loferer C, Agerer R, Hutzler P, Hartmann A (2000) Bacterial community structure and colonization patterns of *Fagus sylvatica* L. ectomycorrhizospheres as determined by fluorescence *in situ* hybridization (FISH) and confocal laser scanning microscopy (CLSM). Mycorrhiza 9:272–278

Moore JC, McCann K, de Ruiter PC (2007) Soil rhizosphere food webs, their stability, and implications for soil processes in ecosystems. In: Cardon ZG, Whitbeck JL (eds) The rhizosphere: An ecological perspective. Academic Press Inc., London, New York, pp 101–125

Mosse B (1959) The regular germination of resting spores and some observations on the growth requirements of an

Endogone sp. causing vesicular-arbuscular mycorrhiza. Trans Br Mycol Soc 42:273–286

Mougel C, Offre P, Ranjard L, Corberand T, Gamalero E, Robin C, Lemanceau P (2006) Dynamic of the genetic structure of bacterial and fungal communities at different developmental stages of *Medicago truncatula* Gaertn. cv. Jemalong line J5. New Phytol 170:165–175

Neumann G, Martinoia E (2002) Cluster roots - an underground adaptation for survival in extreme environments. Trends Plant Sci 7:162–167

Nunan N, Daniell TJ, Singh BK, Papert A, McNicol JW, Prosser JI (2005) Links between Plant and Rhizoplane Bacterial Communities in Grassland Soils, Characterized Using Molecular Techniques. Appl Environ Microbiol 71:6784–6792

O'Connell KP, Goodman RM, Handelsman J (1996) Engineering the rhizosphere: expressing a bias. Trends Biotechnol 14:83–88

Oehl F, Sieverding E, Ineichen K, Mader P, Boller T, Wiemken A (2003) Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of central europe. Appl Environ Microbiol 69:2816–2824

Oehl F, Sieverding E, Ineichen K, RisE-A, Boller T, Wiemken A (2005) Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. New Phytol 165:273–283

Oger P, Petit A, Dessaux Y (1997) Genetically engineered plants producing opines alter their biological environment. Nat Biotechnol 15:369–372

Oger PM, Mansouri H, Nesme X, Dessaux Y (2004) Engineering root exudation of *Lotus* toward the production of two novel carbon compounds leads to the selection of distinct microbial populations in the rhizosphere. Microb Ecol 47:96–103

Oliver KL, Hamelin RC, Hintz WE (2008) Effects of transgenic hybrid aspen over-expressing P 1 olyphenol oxidase on rhizosphere diversity. Appl Environ Microbiol. doi:10.1128/AEM.02836-02807

Olsson PA, Thingstrup I, Jakobsen I, Baath F (1999) Estimation of the biomass of arbuscular mycorrhizal fungi in a linseed field. Soil Biol Biochem 31:1879–1887

Paterson E, Gebbing T, Abel C, Sim A, Telfer G (2007) Rhizodeposition shapes rhizosphere microbial community structure in organic soil. New Phytol 173:600–610

Pearson JN, Abbott LK, Jasper DA (1993) Mediation of competition between two colonizing VA mycorrhizal fungi by host plants. New Phytol 123:93–98

Pivato B, Mazurier S, Lemanceau P, Siblot S, Berta G, Mougel C, van Tuinen D (2007) *Medicago* species affect the community composition of arbuscular mycorrhizal fungi associated with roots. New Phytol 176:197–210

Prosser JI, Rangel-Castro JI, Killham K (2006) Studying plant-microbe interactions using stable isotope technologies. Curr Opin Biotechnol 17:98–102

Raaijmakers JM, Paulitz CT, Steinberg C, Alabouvette C, Moenne-Loccoz Y (2008) The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil. doi:10.1007/s11104-11008-19568-11106

Radajewski S, Ineson P, Parekh NR, Murrell JC (2000) Stable-isotope probing as a tool in microbial ecology. Nature 403:646–649

Rambelli A (1973) The Rhizosphere of mycorrhizae. In: Mg L, Koslowski TT (eds) Ectomycorrhizae. Academic Press, New York, pp 299–343

Rangel-Castro JI, Killham K, Ostle N, Nicol GW, Anderson IC, Scrimgeour CM, Ineson P, Meharg A, Prosser JI (2005) Stable isotope probing analysis of the influence of liming on root exudate utilization by soil microorganisms. Environ Microbiol 7:828–838

Rasche F, Hodl V, Poll C, Kandeler E, Gerzabek MH, van Elsas JD, Sessitsch A (2006) Rhizosphere bacteria affected by transgenic potatoes with antibacterial activities compared with the effects of soil, wild-type potatoes, vegetation stage and pathogen exposure. FEMS Microbiol Ecol 56:219–235

Rasmussen TB, Bjarnsholt T, Skindersoe ME, Hentzer M, Kristoffersen P, Kote M, Nielsen J, Eberl L, Givskov M (2005) Screening for quorum-sensing inhibitors (QSI) by use of a novel genetic system, the QSI selector. J Bacteriol 187:1799–1814

Remy W, Taylor TN, Hass H, Kerp H (1994) Four hundred-million-year-old vesicular arbuscular mycorrhizae. Proc Natl Acad Sci U S A 91:11841–11843

Rengel Z (1999) Physiological mechanisms underlying differential nutrient efficiency of crop genotypes. In: Rengel Z (ed) Mineral nutrition of crops: Mechanisms and implications, The Haworth Press, New York, U S A, pp 227–265

Rengel Z, Marschner P (2005) Nutrient availability and management in the rhizosphere: exploiting genotypic differences. New Phytol 168:305–312

Rettenmaier H, Lingens F (1985) Purification and some properties of two isofunctional juglone hydroxylases from *Pseudomonas putida* J1. Biol Chem Hoppe Seyler 366 (7):637–646

Richter DD, OhN-H, Fimmen R, Jackson J (2007) The rhizosphere and soil formation. In: Cardon ZG, Whitbeck JL (eds) The rhizosphere: An ecological perspective. Elsevier Academic Press, Burlington, U S A, pp 179–200

Riedlinger J, Schrey SD, Tarkka MT, Hampp R, Kapur M, Fiedler H-P (2006) Auxofuran, a novel metabolite that stimulates the growth of fly agaric, is produced by the mycorrhiza helper bacterium *Streptomyces* strain AcH 505. Appl Environ Microbiol 72:3550–3557

Rillig MC, Lutgen ER, Ramsey PW, Klironomos JN, Gannon JE (2005) Microbiota accompagning different arbuscular mycorrhizal fungal isolates influence soil aggregation. Pedobiologia 49:251–259

Rillig MC, Mummey DL, Ramsey PW, Klironomos JN, Gannon JE (2006) Phylogeny of arbuscular mycorrhizal fungi predicts community composition of symbiosis-associated bacteria. FEMS Microbiol Ecol 57:389–395

Rodriguez-Navarro DN, Dardanelli MS, Ruiz-Sainz JE (2007) Attachment of bacteria to the roots of higher plants. FEMS Microbiol Lett 272:127–136

Roose T, Fowler AC (2004) A mathematical model for water and nutrient uptake by plant root systems. J Theor Biol 228:173–184

Rosenblueth M, Martinez-Romero E (2006) Bacterial endophytes and their interactions with hosts. Mol Plant Microbe Interact 19:827–837

Rothballer M, Schmid M, Fekete A, Hartmann A (2005) Comparative in situ analysis of *ipd*C-gfpmut3 promoter

fusions of *Azospirillum brasilense* strains Sp7 and Sp245. Environ Microbio l7:1839–1846

Ryu C-M, Farag MA, Hu C-H, Reddy MS, Kloepper JW, Pare PW (2004) Bacterial volatiles induce systemic resistance in *Arabidopsis.* Plant Physiol 134:1017–1026

Savka MA, Dessaux Y, Oger P, Rossbach S (2002) Engineering bacterial competitiveness and persistence in the phytosphere. Mol Plant Microbe Interact 15:866–874

Scheublin TR, Ridgway KP, Young JPW, van der Heijden MGA (2004) Nonlegumes, legumes, and root nodules harbor different arbuscular mycorrhizal fungal communities. Appl Environ Microbiol 70:6240–6246

Schloter M, Lebuhn M, Heulin T, Hartmann A (2000) Ecology and evolution of bacterial microdiversity. FEMS Microbiol Rev 24:647–660

Schuhegger R, Ihring A, Gantner S, Bahnweg G, Knappe C, Vogg G, Hutzler P, Schmid M, van Breusegem F, Eberl L, Hartmann A, Langebartels C (2006) Induction of systemic resistance in tomato by N-acylhomoserine lactone-producing rhizosphere bacteria. Plant Cell and Environment 29: 909–918

Schulz B, Boyle C, Sieber N (2006) Microbial root endophytes. Springer VerlagBerlin, Heidelberg, New York

Schüßler A, Schwarzott D, Walker C (2001) A new fungal phylum, the *Glomeromycota*: Phylogeny and evolution. Mycol Res 105:1413–1421

Schwarzott D, Walker C, Schuler A (2001)*Glomus*, the largest genus of the arbuscular mycorrhizal fungi (*Glomales*), is non monophyletic. Mol Phylogenet Evol 21:190–197

Selesi D, Schmid M, Hartmann A (2005) Diversity of green-like and red-like ribulose−1,5-bisphosphate carboxylase/oxygenase large-subunit genes (*cbb*L) in differently managed agricultural soils. Appl Environ Microbiol 71:175–184

Selim S, Negrel J, Govaerts C, Gianinazzi S, van Tuinen D 92005) Isolation and partial characterization of antagonistic peptides produced by *Paenibacillus* spstrain B2 isolated from the *Sorghum* mycorrhizosphere. Appl Environ Microbiol 71:6501–6507

Shaw LJ, Morris P, Hooker JE (2006) Perception and modification of plant flavonoid signals by rhizosphere microorganisms. Environ Microbiol 8:1867–1880

Simpson FB, Burris RH (1984) A nitrogen pressure of 50 atmospheres does not prevent evolution of hydrogen by nitrogenase. Science 224:1095–1097

Singh BK, Nunan N, Ridgway KP, McNicol J, Young JPW, Daniell TJ, Prosser JI, Millard P (2008) Relationship between assemblages of mycorrhizal fungi and bacteria on grass roots. Environ Microbiol 10:534–541

Skene KR (2000) Pattern formation in cluster roots: Some developmental and evolutionary considerations. Ann Bot 85:901–908

Smalla K, Wieland G, Buchner A, Zock A, Parzy J, Kaiser S, Roskot N, Heuer H, Berg G (2001)Bulk and rhizosphere soil bacterial communities studied by denaturing gradient gel electrophoresis: Plant-dependent enrichment and seasonal shifts revealed. Appl Environ Microbiol 67:4742–4751

Smith SE, Read DJ (1997) Mycorrhizal Symbiosis. Academic Press, London

Somers E, Vanderleyden J, Srinivasan M (2004)Rhizosphere bacterial signalling: A love parade beneath our feet. Crit Rev Microbiol 304:205–240

Soto MJ, Sanjuan J, Olivares J (2006) Rhizobia and plant-pathogenic bacteria: common infection weapons. Microbiol 152:3167–3174

Stein S, Selesi D, Schilling R, Pattis I, Schmid M, Hartmann A (2005) Microbial activity and bacterial composition of H_2-treated soils with net CO_2 fixation. Soil Biol Biochem 37:1938–1945

Teplitski M, Robinson JB, Bauer WD (2000) Plants secrete 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

Thordal-Christensen H (2003) Fresh insights into processes of nonhost resistance. Curr Opin Plant Biol 6:351–357

Tjamos EC, Rowe RC, Heale JB, Fravel DR (2000) Advances in *Verticillium* research and disease managementAPS Press. The American Phytopathological Society, Minnesota, USA, 357

Toljander JF, Lindahl BD, Paul LR, Elfstrand M, Finlay RD (2007) Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. FEMS Microbiol Ecol 61:295–304

Treonis AM, Ostle NJ, Stott AW, Primrose R, Grayston SJ, Ineson P (2004) Identification of groups of metabolically-active rhizosphere microorganisms by stable isotope probing of PLFAs. Soil Biol Biochem 36:533–537

Tucker SL, Talbot NJ (2001) Surface attachment and pre-penetration stage development by plant pathogenic fungi. Annu Rev Phytopathol 39:385–417

Turnau K, Ryszka P, Gianinazzi-Pearson V, van Tuinen D (2001)Identification of arbuscular mycorrhizal fungi in soils and roots of plants colonizing zinc wastes in southern Poland. Mycorrhiza 10:169–174

Uren NC (1981) Chemical reduction of an insoluble higher oxide of manganese by plant roots. J Plant Nutr Soil Sci 4:65–71

Uren NC (2007) Types, amounts and possible functions of compounds released into the rhizosphere by soil-grown plants. In: Pinto RZ, Varanini PN (eds) The Rhizosphere: Biochemistry and organic substances at the soil-plant interface. CRC Press, Boca Raton, Florida, USA, pp 1–21

van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

van Elsas JD, Turner S, Bailey MJ (2003) Horizontal gene transfer in the phytosphere. New Phytol 157:525–537

van Tuinen D, Jacquot E, Zhao B, Gollotte A, Gianinazzi-Pearson V (1998) Characterization of root colonization profiles by a microcosm community of arbuscular mycorrhizal fungi using 25S rDNA-targeted nested PCR. Mol Ecol 7:879–887

van Veen JA, Morgan JAW, Whipps JM (2007) Methodological approaches to the study of carbon flow and the associated microbial population dynamics in the rhizospherePintoRZ, VaraniniPNThe Rhizosphere: Biochemistry and organic substances at the soil-plant interface. CRC Press , Boca Raton, Florida, USA, 371–399

Vandenkoornhuyse P, Ridgway KP, Watson IJ, Fitter AH, Young JPW (2003) Co-existing grass species have

distinctive arbuscular mycorrhizal communities. Mol Ecol 12:3085–3095

von Rad U, Klein I, Dobrev PI, Kottova J, Zazimalova E, Fekete A, Hartmann A, Schmitt-Kopplin P, Durner J (2008) Response of *Arabidopsis thaliana* to N-hexanoyl-DL-homoserinelactone, a bacterial quorum sensing molecule produced in the rhizosphere. Planta. doi:10.1007/s00425-008-0811-4

von Wiren N, Marschner H, Römheld V (1995) Uptake kinetics of iron-phytosiderophores in two maize genotypes differing in iron efficiency. Physiol Plant 93:611–616

von Wiren N, Mori S, Marschner H, Römheld V (1994) Iron inefficiency in maize mutant ys1 (*Zea mays* Lcv Yellow-Stripe) is caused by a defect in uptake of iron phytosiderophores. Plant Physiol 106:71–77

Wang B, Qiu YL (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299

Whipps JM (2001) Microbial interactions and biocontrol in the rhizosphere. J Exp Bot 52:487–511

Wolfe B, Mummey D, Rillig M, Klironomos J (2007) Small-scale spatial heterogeneity of arbuscular mycorrhizal fungal abundance and community composition in a wetland plant community. Mycorrhiza 17:175–183

Yan F, Zhu Y, Muller C, Zorb C, Schubert S (2002) Adaptation of H^+-pumping and plasma membrane H^+ ATPase activity in proteoid roots of white Lupin under phosphate deficiency. Plant Physiol 129:50–63

Yao J, Allen C (2006) Chemotaxis is required for virulence and competitive fitness of the bacterial wilt pathogen *Ralstonia solanacearum.* J Bacteriol 188:3697–3708

Zabetakis I (1997) Enhancement of flavour biosynthesis from strawberry (*Fragaria ananassa*) callus cultures by *Methylobacterium* species. Plant Cell Tissue Organ Cult 50:179–183

Zeidler D, Zahringer U, Gerber I, Dubery I, Hartung T, BorsW, Hutzler P, Durner J (2004) From The Cover: Innate immunity in *Arabidopsis thaliana*: Lipopolysaccharides activate nitric oxide synthase (NOS) and induce defense genes. Proc Natl Acad Sci U S A 101:15811–15816