MINIREVIEW

Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere

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Abstract

The rhizosphere is of central importance not only for plant nutrition, health and quality but also for microorganism-driven carbon sequestration, ecosystem functioning and nutrient cycling in terrestrial ecosystems. A multitude of biotic and abiotic factors are assumed to influence the structural and functional diversity of microbial communities in the rhizosphere. In this review, recent studies on the influence of the two factors, plant species and soil type, on rhizosphere-associated microbial communities are discussed. Root exudates and the response of microorganisms to the latter as well as to root morphology were shown to shape rhizosphere microbial communities. All studies revealed that soil is the main reservoir for rhizosphere microorganisms. Many secrets of microbial life in the rhizosphere were recently uncovered due to the enormous progress in molecular and microscopic tools. Physiological and molecular data on the factors that drive selection processes in the rhizosphere are presented here. Furthermore, implications for agriculture, nature conservation and biotechnology will also be discussed.

Introduction

The term 'rhizosphere' was coined by Hiltner in 1904 to describe the portion of soil where microorganism-mediated processes are under the influence of the root system. Functions of the rhizosphere are of central importance for plant nutrition, health and quality. The well-studied rhizosphere effect describes the phenomenon that, in comparison with bulk soil, the biomass and activity of microorganisms is enhanced as a result of exudation of compounds by the root (Sørensen, 1997; Raaijmakers *et al.*, 2009). Because of the enormous importance of plant–microorganism interactions in the rhizosphere for carbon sequestration, ecosystem functioning and nutrient cycling in natural ecosystems as well as in agricultural and forest systems (Singh *et al.*, 2004), it is crucial to understand the factors influencing the microbial communities in this habitat.

The use of polyphasic approaches combining novel cultivation-independent and more traditional techniques to study microbial communities led to a significantly better understanding of community structure and function in the rhizosphere in the last decade. Several biotic and abiotic factors influencing the structural and functional diversity of bacterial communities (Fig. 1), for example, climate and season, grazers and animals, pesticide treatments, soil type and structure and plant health and developmental stage, were investigated (Lemanceau *et al.*, 1995; Siciliano *et al.*, 2001; Graner *et al.*, 2003; reviewed in Garbeva *et al.*, 2004; Jousset *et al.*, 2006; Rasche *et al.*, 2006b). Different soil types are assumed to harbour specific microbial communities, as recently shown in a continental-scale study of soil bacterial communities (Fierer & Jackson, 2006). In contrast to what we know about the biodiversity of macroorganisms, the microbial biogeography is controlled primarily by edaphic variables, especially by pH (Fierer & Jackson, 2006). Furthermore, the bacterial community composition changed with age of soil that developed over *c.* 77 000 years of intermittent aeolian deposition, and the overall diversity, richness and evenness of the communities increased (Tarlera *et al.*, 2008). Plants affect these indigenous microbial populations in soil; each plant species is thought to select specific microbial populations. Root exudates are a driving force in this process, but researchers are only beginning to understand the role of single compounds in mediating

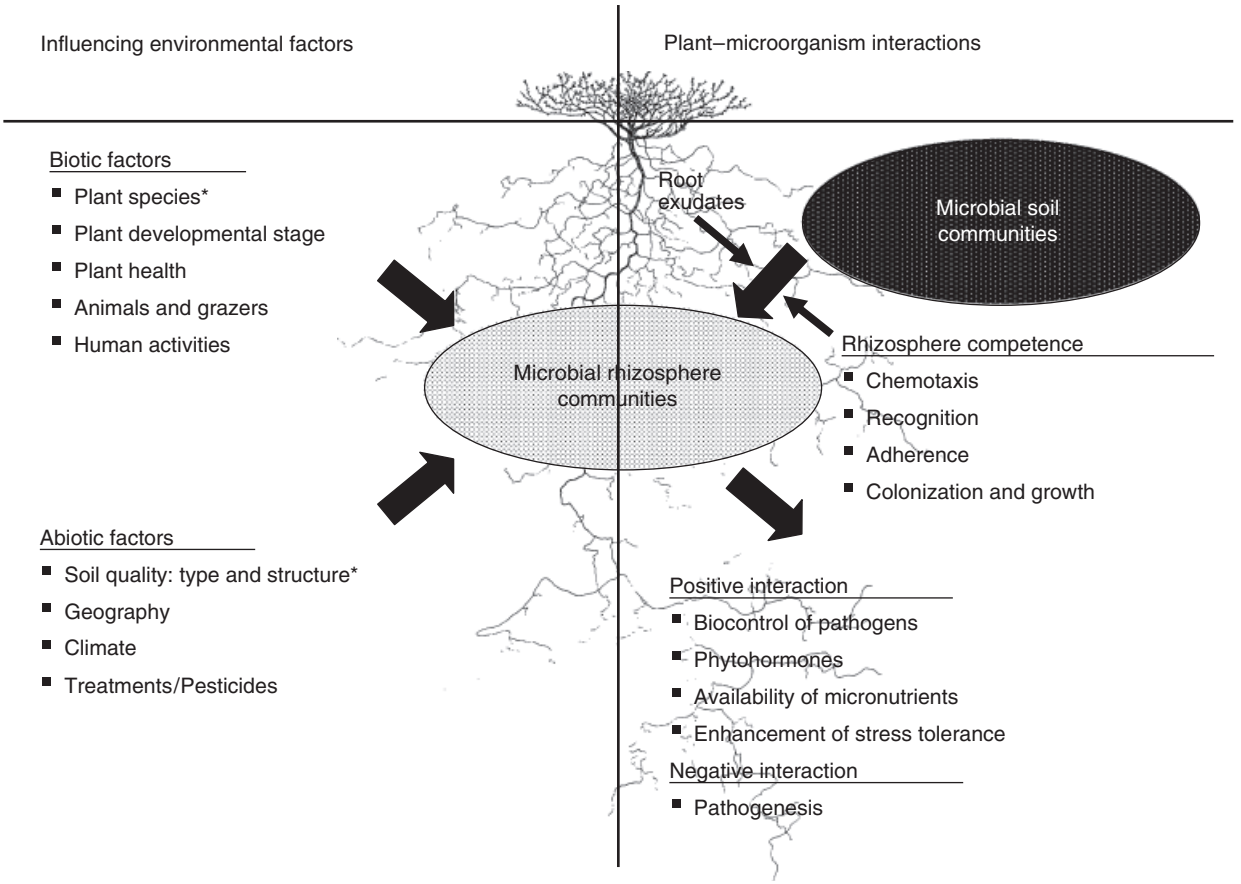

Fig. 1. Influencing factors of rhizosphere microbial communities and model how microbial communities were selected from soil: by root exudates and their rhizosphere competence. *Factors that are analysed in the review.

belowground interactions (reviewed in Bais *et al.*, 2006; Haichar *et al.*, 2008). The composition of root exudates varies from plant to plant and affects the relative abundance of microorganisms in the vicinity of the root (Somers *et al.*, 2004). Plants not only provide nutrients for microorganisms, but some plant species also contain unique antimicrobial metabolites in their exudates. Many of them are used as medical plants, for example camomile, thyme and eucalyptus. The existing huge diversity of plant species with an estimated range from 310 000 to 422 000 species (Pitman & Jörgensen, 2002) and corresponding secondary metabolites of plants (Buchanan *et al.*, 2000) affects below-ground diversity. Interestingly, invasive plants can have major effects on microbial communities in soil (Van der Putten *et al.*, 2007). There is no doubt that both factors, soil properties as well as plant species, influence the structure and function of microbial communities. However, the extent to which both factors contribute to microbial communities is not fully understood.

There are several contrasting reports in the literature indicating plant or soil type as dominant factor (Grayston *et al.*, 1998; Girvan *et al.*, 2003; Nunan *et al.*, 2005). This review will present historical and more recent findings about plant specificity of rhizosphere communities and will analyse the background for this phenomenon on the basis of examples and physiological data. Furthermore, conclusions for agriculture, nature conservation and biotechnology will be discussed.

Each plant species is colonized by specific microbial populations

History and overview of plant specificity

Many phytopathogenic organisms, bacteria as well as fungi, have coevolved with plants and show a high degree of host specificity (Raaijmakers *et al.*, 2009). However, up till now, the molecular basis of this host specificity is only partially understood. Another well-studied example is rhizobia–legume interactions, which are highly specific (Long, 2001). Studies on the basis of cultivation-dependent methods gave first hints of different composition of the bacterial community on plants (Kremer *et al.*, 1990; Lemanceau *et al.*, 1995;

Maloney *et al*., 1997; Germida *et al*., 1998). In a study by Germida & Siciliano (2001), the evolutionary relationship in plant–microorganism interactions was revealed: old wheat cultivars were colonized by phylogenetically diverse rhizobacteria, whereas the rhizosphere of modern cultivars was dominated by fast-growing *Proteobacteria*. Cultivar specificity was also reported for oilseed rape (Graner *et al*., 2003). A plant species-dependent composition of bacterial and fungal rhizosphere isolates with *in vitro* antagonistic activity towards the plant-pathogenic fungus *Verticillium dahliae* Kleb. was shown by Berg *et al*. (2002, 2005b, c, 2006). There is currently an ongoing debate about the pros and cons of cultivation-dependent and -independent techniques (Nichols, 2007; Ritz, 2007), but it is clear that both methods have their limitations and not all microorganisms can be investigated (Bent & Forney, 2008). Cultivation-based methods address only the culturable bacteria, which are thought to represent only a small proportion (0.1–10%) of the total bacteria present in soil and in the rhizosphere (Amann *et al*., 1995).

The analysis of nucleic acids directly extracted from rhizosphere soils provided an opportunity to study a much broader spectrum of microorganisms residing in the rhizosphere. Most frequently rRNA gene fragments are amplified from total community DNA and subsequently analysed by fingerprinting techniques. Cultivation-independent fingerprinting methods clearly showed the influence of the plant species on the structure of the microbial community. Marschner *et al*. (2001) concluded that the bacterial community composition in the rhizosphere is affected by a complex interaction between soil type, plant species and root zone location. They analysed three plant species (chickpea, rape and Sudan grass) grown in intact cores of three Californian soils (sandy soil, sandy loam and clay) by PCR-denaturing gradient gel electrophoresis (DGGE) of 16S rRNA gene fragments. Other studies indicated plant species (Wieland *et al*., 2001; Kowalchuk *et al*., 2002) or soil type (Da Silva *et al*., 2003; Salles *et al*., 2004) as the dominant factor influencing the composition of the rhizosphere microbial community. However, in the latter studies plant specificity was also found, but to a lesser degree. Soil type instead of maize cultivar type was the overriding determinative factor that influenced the community structures of the *Paenibacillus* communities in the rhizosphere investigated by Da Silva *et al*. (2003). Salles *et al*. (2004) found using genus-specific DGGE that plant species affected *Burkholderia* community structure to a lesser extent than did land use history. However, canonical correspondence analysis demonstrated plant specificity of *Burkholderia* in maize, grass, barley and oat. The majority of studies, especially those performed in the field or in native vegetation, clearly demonstrate a high degree of plant specificity. In Canyonlands National Park (Utah), bacterial communities associated with the rhizospheres of the native bunchgrasses *Stipa hymenoides* and *Hilaria jamesii*, the invading annual grass *Bromus tectorum* and the interspaces colonized by cyanobacterial soil crusts were compared using terminal restriction fragment length polymorphism (T-RFLP; Kuske *et al*., 2002). Major differences were observed in the rhizospheres of the three plant species and they were most apparent with analysis of the *Acidobacterium* division. In another study analysing eight herbaceous plants, native to Germany, in the greenhouse experiment, clear plant-specific single strand conformation polymorphism profiles for bacteria, *Alphaproteobacteria*, *Actinobacteria* and *Pseudomonas* were found (Dohrmann & Tebbe, 2005). In an experiment to test the hypothesis that plant species are a major driver of bacterial rhizoplane community composition, further evidence for the complexity of bacterial communities in grassland soils and resultant difficulties in distinguishing plant-mediated effects was provided. Nunan *et al*. (2005) analysed field-grown root-associated communities of *Agrostis capillaris*, *Agrostis vinealis*, *Deschampsia cespitosa*, *Festuca rubra* and *Poa pratensis* by analysis of the plastid tRNA leucine (*trnL*) UAA gene intron, and plant-related bacterial communities using T-RFLP and DGGE. Although microbial fingerprints show high similarity between the grass species, statistical analysis of data generated by different fingerprinting techniques demonstrated an influence of plant community composition on bacterial communities and also indicated the significant influence of other factors (topography and uncharacterized, environmental factors). Additionally, studies on sugar beet-associated microorganisms in different European countries clearly showed an influence of soil type and geographical region on specific communities (Zachow *et al*., 2008b).

Using cultivation-independent methods, evidence for the impact of plant species was not only found for the structure of rhizosphere communities but also for the function. Briones *et al*. (2002) found cultivar-specific differences for ammonia-oxidizing bacteria (AOB) in rice rhizospheres by a multiphasic approach, including DGGE of the *amoA* gene, analysis of libraries of cloned *amoA*, fluorescently tagged oligonucleotide probes targeting the 16S rRNA gene of AOBs as well as metabolism rates obtained by the ^{15}N dilution technique. Impact of plant species on the composition of *nirK*-type denitrifier communities in eight nonleguminous grassland plant species was shown by Bremer *et al*. (2007). In this 2-year microcosm study, denitrifier community composition was analysed by T-RFLP of PCR-amplified *nirK* gene fragments coding for the copper-containing nitrite reductase. Especially less-abundant T-RFs occurred in relation to several plant species. Interestingly, statistical analysis revealed that the plants affected the *nirK*-type denitrifier community composition directly, for example, through root exudates.

The majority of studies analysed plant specificity on the bacterial communities; the structure and function on rhizosphere fungi is only poorly understood. In a study using ^{13}C labelling and phospholipid fatty acid (PLFA) analysis to examine the microbial dynamics associated with rhizosphere C cycling, the fungi were the most highly labelled and active group (Butler *et al.*, 2003). Broeckling *et al.* (2008) showed that two model plant species (*Arabidopsis thaliana* and *Medicago truncatula*) are able to maintain resident soil fungal populations, but unable to maintain nonresident soil fungal populations. In a hierarchical set of greenhouse experiments, the key role of root exudates for this process was identified. On Tenerife Island, a natural laboratory to study terrestrial biodiversity, a high similarity at a correspondence analysis biplot between fungal and plant populations was found (Zachow *et al.*, 2008a).

Extensive studies related to the question of plant specificity of bacterial as well as fungal community were carried out for host plants of the phytopathogenic fungus *V. dahliae* Kleb. These studies will be explained in more detail in the following section.

Example: Plant specificity of microbial communities in the rhizosphere of *Verticillium* host plants

In order to test the hypothesis that each plant species selects their own specific microbial community, three phylogenetically different and economically important crops – strawberry, potato and oilseed rape – were grown under field conditions in a randomized plot design. All three plant species are hosts of the soil-borne fungal pathogen *V. dahliae* Kleb. that causes high yield losses world wide (Tjamos *et al.*, 2000). In a first 2-year study, rhizosphere samples taken at different plant growth stages from one field site (Braunschweig, Germany) were analysed by cultivation-dependent and -independent methods. DGGE analysis of 16S rRNA gene fragments amplified from total community DNA revealed plant species-dependent pattern (Smalla *et al.*, 2001). DGGE patterns of oilseed rape and potato rhizosphere communities were more similar to each other than to the strawberry patterns. Interestingly, all rhizospheres showed some bands in common but also specific bands, for example *Nocardia* populations were identified as strawberry-specific bands. The proportion and composition of bacteria with *in vitro* antagonistic activity towards *V. dahliae* was also shown to be influenced by the plant species (Berg *et al.*, 2002). In addition, plant-specific genotypes of 34 *Pseudomonas putida* A isolates were observed, suggesting that these bacteria were specifically enriched in each rhizosphere.

The extent to which this plant specificity can be observed at different sites was still unclear. Therefore, in a second trial, *Verticillium* host plants oilseed rape and strawberry were analysed at different sites in Germany (Rostock, Berlin, Braunschweig). Again, plant specificity was detected in the rhizosphere by bacterial and group-specific (*Alphaproteobacteria*, *Betaproteobacteria* and *Actinobacteria*) DGGE profiles (Costa *et al.*, 2006a). The plant species was a determinant factor in shaping similar actinobacterial communities in the strawberry rhizosphere from different bulk soil communities in both years. Cloning and sequencing of 16S rRNA gene fragments obtained from dominant DGGE bands detected in the bacterial profiles of the Rostock site revealed that *Streptomyces* sp. and *Rhizobium* sp. were among the dominant ribotypes in the strawberry rhizosphere, while sequences from *Arthrobacter* sp. corresponded to dominant bands from oilseed rape bacterial fingerprints. The rhizosphere effect on the bacterial antagonists was shown by their enhanced proportion, by enrichment of specific species and genotypes as evidenced by BOX-PCR, and by a reduced diversity of antagonistic bacteria in the rhizosphere in comparison with bulk soil (Berg *et al.*, 2006). This effect was influenced by both the plant species and the site of its cultivation. Bacteria of the genus *Pseudomonas*, which is an important and often dominant plant-associated genus known for its beneficial interaction with the host plant (Haas & Défago, 2005) were studied in more detail. Also in the rhizosphere of *Verticillium* host plants, the majority of bacterial isolates with antagonistic activity towards *V. dahliae* belonged to *Pseudomonas* (Berg *et al.*, 2002, 2006). 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, 2007). A dominant band in the *gacA* fingerprints, which was detected in the strawberry rhizosphere profiles of all three sites had the same sequences as *Pseudomonas* isolates antagonistic towards *V. dahliae* that carried the *phl*D biosynthetic locus. The sequences determined for the isolates and the reamplified band showed closest relatedness to *Pseudomonas fluorescens* strain F113 (97% *gac*A gene sequence identity in 492 bp sequences), a biocontrol agent and 2,4-DAPG producer.

The results for bacterial communities raised the hypothesis that a plant-dependent rhizosphere effect might also be seen for fungal communities. To address this idea, the fungal communities of *Verticillium* host plants were also analysed for their structures and antagonistic functions. Using cultivation-independent techniques, plant-specific composition of fungal communities in the rhizosphere 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. In contrast to bacteria, the proportion of fungal isolates with antagonistic activity toward *V. dahliae* was similar for both bulk and rhizosphere soil (Berg *et al.*,

2005c). However, 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, but a high degree of plant specificity was shown by BOX-PCR fingerprints.

Summarizing all results, an influence of plant species on the structure (microbial fingerprints) and function (microorganisms with antagonistic activity) of rhizosphere communities was shown in each case, but the extent of the plant-dependent rhizosphere effect differed for the taxa studied and method used. The effect of plant species for fungal communities was less pronounced than for bacteria.

Cultivar specificity of microbial communities in the rhizosphere

In several studies, an influence not only of plant species but also of the cultivars on the rhizosphere microbial communities was shown (Germida & Siciliano, 2001; Briones *et al*., 2002; Graner *et al*., 2003; Milling *et al*., 2004). 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; Castaldini *et al*., 2005; Oliver *et al*., 2008). T4-lysozyme potato plants (Düring *et al*., 1993) are one of the best-investigated models. 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. Bacteria and group-specific DGGE fingerprints revealed an influence of the transgene on potato-associated bacteria, but the influence of environmental factors was much stronger (Heuer *et al*., 2002). No statistically significant differences between transgenic and nontransgenic plants were found for cultivated bacteria (Lottmann *et al*., 1999). In contrast, in an additional experiment analysing colonization of bacteria, the lysozyme-tolerant strain *P. putida* QC14-3-8 was recovered from the transgenic T4 lysozyme plant in higher abundances than from the control lines (Lottmann *et al*., 2000). Furthermore, using a root hair *Bacillus subtilis* model, roots from potato lines expressing the T4 lysozyme gene always showed significantly (1.5–3.5-fold) higher killing (Ahrenholtz *et al*., 2000). Differences in the relative abundance of endophytic fungi colonizing the roots of T4-lysozyme-producing potatoes and the parental line could also be detected (Götz *et al*., 2006). While an influence of transgenic T4 lysozyme on microbial strains was shown in *in vitro* experiments, the influence was negligible in field trials, compared with other environmental factors. These results obtained for T4-lysozyme potatoes were confirmed in greenhouse experiments (Rasche *et al*., 2006a, b) and in other studies analysing transgenic plants (Bruinsma *et al*., 2002). Interestingly, in another approach comparing zeaxanthine-producing potatoes with different potato cultivars, the effect of cultivar was apparent and much higher than that of the transgene (Schloter M, pers. commun.).

Impact of methods and techniques on rhizosphere research

The multitude of studies on the effect of the soil type, the plant species and the cultivar on rhizosphere microbial communities and the findings reported are often difficult to compare, and thus it is even more difficult to come up with some general conclusion. The reason for this dilemma is manifold, and thus we felt that a discussion of the general challenges to sample the rhizosphere and to analyse the microorganisms residing in the rhizosphere might be useful for the reader of this minireview. In most studies, the rhizosphere is defined as the soil that is closely adhering to the root (Smalla *et al*., 2001; Sanguin *et al*., 2006). Thus, plants carefully dug out of the soil were vigorously shaken and the remaining root-attached soil is treated as the rhizosphere. Clearly, the type of soil and its moisture influences the amount of root-adhering soil. Therefore, in other studies root washes or other cleaning procedures were performed before obtaining the microbial fraction from the surface of the root (Briones *et al*., 2002; Bremer *et al*., 2007). Sometimes this special microenvironment is differentiated from the rhizosphere and called rhizoplane (Nunan *et al*., 2005). Another critical point is which part of the root system should be sampled. Microscopic studies of *gfp*-tagged inoculants revealed highly heterogeneous colonization patterns (Götz *et al*., 2006). Exemplarily, different colonization patterns are shown for *Pseudomonas trivialis*: on lettuce roots a dense colonization in lines was found while on sugar beet cell clusters were observed (Fig. 2). A great variability of the colonization patterns among roots, even of the same age, is problematic for the subsequent analysis. The use of subsamples of the whole root system and, depending on the size of the plant, composite samples might contribute to overcome this variability. However, the representative picture of the kind and abundance of microorganisms in the rhizosphere obtained when analysing composite samples is certainly an underestimate of the existing diversity. As root exudation changes during plant growth development, the sampling time might be another critical factor in the experimental design. Studies which aimed to explore the extent to which plant species and the soil determine the microbial diversity have been performed at different levels of complexity, which again might have influenced the findings reported. The systems used range from very simple, often axenic or hydroponic systems, to more complex microcosm or mesocosm studies performed under growth chamber or

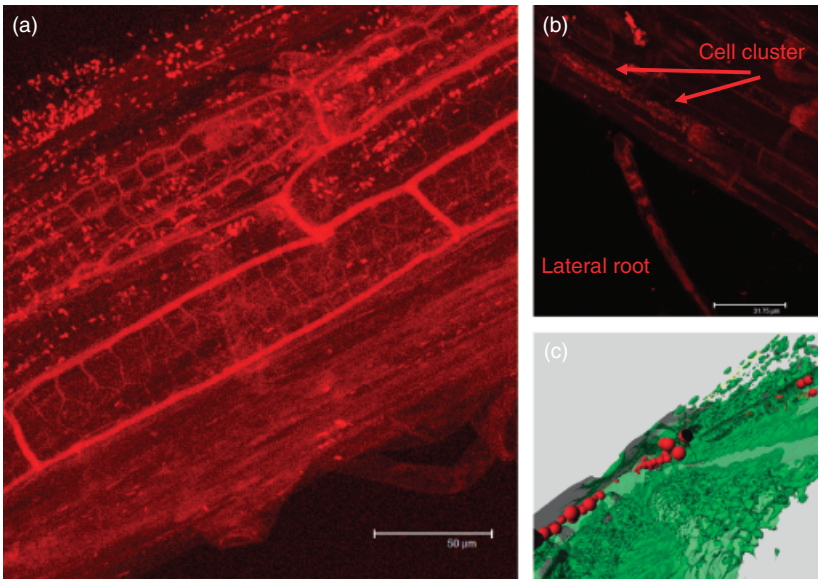

Fig. 2. Confocal laser scanning microscopy of 3-week-old roots colonized by DsRed2-labeled bacteria: (a) *Pseudomonas trivialis* on lettuce and (b) on sugar beet. (c) Three-dimensional reconstruction of a cross section of an area densely colonized by *P. trivialis* RE*1-1-14 with Imaris® 6.0 (Bitplane AG, Zürich, Switzerland) clearly shows that the bacterial cells also colonized endophytic parts of the sugar beet root.

greenhouse conditions to field tests. Although each system has its benefit, it is difficult to extrapolate *in vitro* results to natural conditions if the experimental design does not allow for the natural rhizosphere development. This factor is often neglected in plant ecology, or even in agricultural experiments. Last but not least, the resolution of the methods used to analyse the microbial community might be decisive for the findings reported. While the cultivation-dependent methods usually focus on the small proportion of culturable aerobic bacteria and in some cases on particular taxa such as *Pseudomonas*, the analysis of total nucleic acids or PLFA directly extracted from the rhizosphere soil or the use of microscopic methods in combination with FISH should provide a much broader spectrum of the rhizosphere microbial community. Altogether, multiphasic approaches yielded in comprehensive pictures of rhizosphere communities. New techniques have a great impact on our understanding; this was shown for example for transcriptome profiling (Mark *et al.*, 2005; Yuan *et al.*, 2008), microarrays (Sanguin *et al.*, 2006), *in vivo* expression technology and differential fluorescence induction promoter traps as tools for exploring niche-specific gene expression (Rediers *et al.*, 2005), new methods for the *in situ* analysis of antifungal gene expression using flow cytometry combined with green fluorescent protein-based reporter fusions (De Werra *et al.*, 2008), and ultradeep sequencing (Velicer *et al.*, 2006). Stable isotope probing used to determine bacterial communities assimilating each carbon source in the rhizosphere of four plant species resulted in plant species-specific pattern (Haichar *et al.*, 2008). Also metagenomic approaches are established to analyse the plant–soil interface (Erkel *et al.*, 2006; reviewed in Leveau, 2007).

In most studies, the effect of the plant and the soil type on the relative abundance of the numerically dominant bacteria and fungi was analysed. Thus, very little is known about how these factors affect less common colonizers of the rhizosphere – a general problem in microbial ecology recently termed 'the tragedy of the uncommon', which was formulated by Bent & Forney (2008). With this multitude of factors in mind, the often contrasting findings among studies on the factors shaping rhizosphere might not be too surprising.

Mechanisms contributing to plant specificity and specific beneficial plant–microorganism interactions in the rhizosphere

The rhizosphere represents a highly dynamic and complex interface for chemical, physical and biological interactions. Plant roots continuously produce and excrete compounds into the rhizosphere (Uren, 2000; Rovira, 2005). Root exudates are a key factor for the enrichment of specific microbial populations in the rhizosphere; they consist of ions, free oxygen and water, enzymes, mucilage and a diverse array of carbon-containing primary and secondary metabolites (Uren, 2000). From 10% up to 44% of the photosynthetically fixed carbon is excreted by the root (Bais *et al.*, 2006). Organic acids, sugars, amino acids, lipids, coumarins, flavonoids, proteins, enzymes, aliphatics and aromatics are

examples of the primary substances found at the soil–root interface. Among them, the organic acids have received considerable attention owing to their role in providing substrates for microbial metabolism and for serving as intermediates for biogeochemical reactions in soil. The amount and composition is specific for each plant family or species. Especially, plants growing in low-nutrient environments also employ root exudates in ways other than as symbiotic signals to soil microorganisms involved in nutrient acquisition (reviewed by Dakora & Phillips, 2002): extracellular enzymes release P from organic compounds, and several types of molecules increase iron availability through chelation, and organic acids from root exudates can solubilize unavailable soil Ca, Fe and Al phosphates. A transgenic tobacco overexpressing ferritin (P6) was shown to accumulate more iron than the wild type, leading to a reduced availability of iron in the rhizosphere and shifts in the pseudomonad community (Robin *et al*., 2006, 2007). Theoretically, the composition of microorganisms that colonize the rhizosphere can be a result of a positive or negative selection procedure, or both. However, little is known about this important and complex issue. *Stenotrophomonas maltophilia* is a member of the rhizobacterial populations of cruciferous plants, which produce particularly high levels of sulphur-containing compounds, for example amino acids such as methionine (Debette & Blondeau, 1980). *Stenotrophomonas maltophilia* requires methionine (Ikemoto *et al*., 1980). Because of 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–microorganism interactions (Shaw *et al*., 2006). For example, the secretion of isoflavones in soybean roots attracts the beneficial bacterium *Bradyrhizobium japonicum* as well as the pathogen *Phytophthora sojae* (Morris *et al*., 1998). Flavonoids isolated from white lupin roots additionally mobilized inorganic phosphorus and decreased soil microbial respiration, citrate mineralization and soil phosphohydrolase (Tomasi *et al*., 2008), which indicates their central importance for plant–microorganism interaction as well as soil quality. 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, for example walnut (*Juglans regia* L.) for the production of juglone are colonized by specific microbial populations that can degrade or detoxify metabolites via specific hydrolases (Rettenmaier & Lingens, 1985). Another strategy to survive despite the occurrence of toxins is with the help of efflux pumps, which pump toxic components outside the bacterial cell. In addition, production of toxins can force diversification of microbial communities (Czárán *et al*., 2002). A whole genome analysis of gene expression of *P. putida* during 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*., 2008). Specifically, 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.

There are microbial species that are typically associated with only a few or a single plant species. This fact is well known for pathogens as well as beneficial interactions, for example *Rhizobium*–legumes. *Sinorhizobium meliloti* effectively colonize plant genera of *Medicago*, *Melilotus* and *Trigonella*, whereas *Rhizobium leguminosarum* induce nodules in *Pisum vicea*, *Lens* and *Lathyrus* plants (Bais *et al*., 2006). Other microbial species such as *Pseudomonas* and the fungus *Trichoderma* are ubiquitous. However, it was shown even for ubiquitous species such as *P. fluorescens/putida* that plant-specific (Lemanceau *et al*., 1995; Berg *et al*., 2002, 2006; Weller *et al*., 2002; Picard & Bosco, 2008) and soil-specific (Latour *et al*., 1996, 1999) genotypes exist. Not only the plant but also the microbial metabolism has an essential influence on colonization of the rhizosphere. However, it is still possible to detect new taxonomic groups in the rhizosphere such as nonthermophilic members belonging to the archaeal division *Crenarchaeota* (Sliwinski & Goodman, 2004; Simon *et al*., 2005). Also for crenarchaeal consortia, a high degree of plant specificity was shown in a study analysing native terrestrial plant groups, including bryophytes (mosses), lycopods (club mosses), pteridophytes (ferns), gymnosperms (conifers) and angiosperms (seed plants) (Sliwinski & Goodman, 2004).

Competitive colonization of the rhizosphere and establishment in the root zone is important for successful functioning of rhizosphere organisms (Weller, 1988; Lugtenberg *et al*., 2002; reviewed in Compant *et al*., 2005). Steps of colonization include recognition, adherence, invasion (only endophytes and pathogens), colonization and growth, and several strategies to establish interaction. Plant roots initiate cross talk with soil microorganisms by producing signals that are recognized by the microorganisms, which in turn produce signals that initiate colonization (Bais *et al*., 2006). To participate and react in this cross talk, motile organisms are preferred (Lugtenberg *et al*., 2002). For example, swarming of *Serratia liquefaciens* appeared to be specifically induced by exudates of *Pisum sativum* (Eberl *et al*., 1999). Phenotypes of *P. fluorescens* F113 with enhanced motility were selected during rhizosphere colonization of alfalfa (Martinez-Granero *et al*., 2006). Under gnotobiotic conditions, several of these highly motile variants were more competitive than the wild-type strain, displacing it from the root tip within 2 weeks. 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 such as 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, for example *Ralstonia solanacearum* (Yao & Allen, 2007) as well as *R. leguminosarum* (Miller *et al.*, 2007). Interestingly, chemotaxis experiments of cyanobacteria with host plants such as *Gunnera* and *Blasia* and nonhost plants such as *Arabidopsis* showed that the capability to attract cyanobacteria might be widespread in plants (Nilsson *et al.*, 2006). 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* on plant roots, flagella, pili, O-antigen of lipopolysaccharides, the growth rate and the ability to grow on root exudates are important (Dekkers *et al.*, 1998; Lugtenberg & Dekkers, 1999). Attachment also is an initial step for the formation of microbial biofilms on plant roots as reviewed in Rodríguez-Navarro *et al.* (2007). The same authors explain mechanisms of rhizobial attachment to legumes: the first phase of attachment, which is a weak, reversible and unspecific binding of plant lectins, a Ca^{2+}-binding bacterial protein, 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 to plant cells (Rodríguez-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 & Talbot, 2001). It was also shown for fungi that root exudates play a key role in this process (Broeckling *et al.*, 2008). Another study established that the *Nectria haematococca* PDA1-CD chromosome carries a gene(s) for the utilization of homoserine, a compound found in large amounts in pea root exudates (Rodriguez-Carres *et al.*, 2008). Competition studies demonstrated that an isolate that lacks the cluster containing genes for pea pathogenicity, but carries a portion of the CD chromosome that includes the homoserine utilization gene(s) is more competitive in the pea rhizosphere than an isolate without the CD chromosome. Interestingly, besides chemical signals the electric potential produced by electrogenic ion transport on the root also is able to attract microorganisms, for example oomycete zoospores (Van West *et al.*, 2002). Some plant–microorganism interactions 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, for example *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 (Böhm *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). Using a highly sensitive biosensor increased AHL availability in intact rhizosphere microbial communities compared with that in bulk soil was shown by De Angelis *et al.* (2007). The success of invasion and survival within the host also requires that bacteria overcome plant defence 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). However, not only is the plant–microorganism interaction important for the composition of microbial communities in the rhizosphere, but the microorganisms can influence or select each other. This was shown for the influence of pathogens (Rasche *et al.*, 2006b), introduction of beneficial microorganisms in the rhizosphere (Scherwinski *et al.*, 2008) as well as specific interactions such as those between *Bacillus cereus* and bacteria of the *Cytophaga–Flavobacterium* group (Peterson *et al.*, 2006).

Conclusions

Plant species, as well as the soil type, have a substantial influence on the structure and function of rhizosphere-associated microbial populations. As shown in many studies, there is no general decision about the key player: both factors can dominate depending on biotic and abiotic conditions. The rhizosphere is a unique microenvironment in terrestrial ecosystems and integrated in a complex microbial and macrobial network and food chains. However, the influence of the plant species themselves was clearly shown in almost all the studies discussed. Also the experimental design and applied methods influenced the findings. For example, community fingerprints of PCR products obtained with group-specific primers have a higher resolution than those generated with universal primers. Furthermore, the plant species and their phylogenetic positions and life style can have an influence on the results; for example, monocotyledonous grass species showed highly similar rhizosphere communities in diverse studies.

The finding of plant specificity might have implications for different areas. For agricultural applications, it is important to consider the crop species in the context with their associated microorganisms, because they fulfil important functions for plant growth, health and quality. Each crop selects its specific antagonistic microorganisms. This fact should be exploited in breeding strategies as it is already carried out with the resistance against phytopathogenic microorganisms (reviewed in Smith *et al.*, 1999). Furthermore, the plant-dependent composition of antagonists has to be considered in crop rotations, mixed cropping strategies and soil treatments. Plant specificity is important for applications in biocontrol. However, the question of whether allochthonous or autochthonous bicontrol agents are more successful has to be solved in scientific studies. Also for issues of nature conservation, it is important to recognize that plant-specific microorganisms exist. Although the total number of plants worldwide remains unknown, Pitman & Jörgensen (2002) found that between 22% and 47% of the world's plants are endangered. If plants become extinct an unknown microbial diversity might be affected as well. An improved knowledge of specific plant–microorganism interactions in the rhizosphere could also be important for reforestation projects in which forests and woodlands that have been depleted should be replanted with native tree stock. Also, for invasive plants, the microorganism–plant interactions are an important issue influencing their competition within the native flora. Furthermore, the impact of climate change on plant–microorganism interaction, for example on plant pathogens, is important to predict.

Because of the fact that a high proportion of root-associated bacteria and fungi possess an antagonistic potential against other microorganisms, rhizosphere microorganisms are an important bioresource for bioactive substances, i.e. antibiotics, biosurfactants, enzymes and osmoprotective substances. In this respect, an enormous untapped pool of biological resources might be harboured in hot spots of plant diversity, such as Mediterranean heath lands or tropical rainforests. Interestingly, the rhizosphere is also a reservoir for opportunistic pathogens that have an increasing importance for human health (Berg *et al.*, 2005a). To understand the ecological behaviour and factors of pathogenicity of these emerging pathogens is an important issue in the fight against diseases. One way could be to find new plant-derived metabolites to inhibit their colonization or regulation of pathogenicity. There are many open questions in rhizosphere microbial ecology, for example, to understand the enrichment process in the rhizosphere and the mechanisms involved in specificity (recognition, adherence). All of our knowledge is mainly based on agricultural or model systems and crops, but it is a major task for future research to expand these studies to native plants in natural ecosystems.

Plant–microorganism interaction might have contributed to plant evolution: to what extent did rhizosphere communities contribute to the exorbitant evolutionary diversity of $>$ 420 000 plants? More comparative, biogeographic studies are needed to assess a possible role of microbial communities as selective constraints for the diversification of plant populations and vice versa.

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References

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.

Amann RI, Ludwig W & Schleifer KH (1995) Phylogenetic identification and *in situ* detection of individual microbial cells without cultivation. *Microbiol Rev* **59**: 143–169.

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**: 234–266.

Bent SJ & Forney LJ (2008) The tragedy of the uncommon: understanding limitations in the analysis of microbial diversity. *ISME J* **2**: 689–695.

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.

Berg G, Eberl L & Hartmann A (2005a) The rhizosphere as a reservoir for opportunistic human pathogenic bacteria. *Environ Microbiol* **71**: 4203–4213.

Berg G, Krechel A, Ditz M, Faupel A, Ulrich A & Hallmann J (2005b) Endophytic and ectophytic potato-associated bacterial communities differ in structure and antagonistic function against plant pathogenic fungi. *FEMS Microbiol Ecol* **51**: 215–229.

Berg G, Zachow C, Lottmann J, Götz M, Costa R & Smalla K (2005c) Impact of plant species and site on rhizosphere-associated fungi antagonistic to *Verticillium dahliae* Kleb. *Appl Environ Microbiol* **171**: 4203–4213.

Berg G, Opelt K, Zachow C, Lottmann J, Götz 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.

Böhm M, Hurek T & Reinhold-Hurek B (2007) Twitching motility is essential for endophytic rice colonization by the N2-fixing endophyte *Azoarcus* sp. strain BH72. *Mol Plant Microbe Interact* **20**: 526–533.

Bremer C, Braker G, Matthies D, Reuter A, Engels C & Conrad R (2007) Impact of plant functional group, plant species, and sampling time on the composition of nirK-type denitrifier communities in soil. *Appl Environ Microbiol* **73**: 6876–6884.

Briones AM, Okabe S, Umemiya Y, Ramsing N, Reichardt W & Okuyama H (2002) Influence of different cultivars on populations of ammonia-oxidizing bacteria in the root environment of rice. *Appl Environ Microbiol* **68**: 3067–3075.

Broeckling CD, Broz AK, Bergelson J, Manter DK & Vivanco JM (2008) Root exudates regulate soil fungal community composition and diversity. *Appl Environ Microbiol* **74**: 738–744.

Bruinsma M, Kowalchuk GA & Veen JA (2002) *Effects of Genetically Modified Plants on Soil Ecosystem*. Ponsen and Looyen BV, Wageningen, the Netherlands.

Buchanan BB, Gruissem W & Jones RL (2000) *Biochemistry and Molecular Biology of Plants*. American Society of Plant Physiologists, Rockville, MA.

Butler JL, Williams MA, Bottomley PJ & Myrold DD (2003) Microbial community dynamics associated with rhizosphere carbon flow. *Appl Environ Microbiol* **69**: 6793–6800.

Castaldini M, Turrini A, Sbrana C *et al.* (2005) Impact of Bt corn on rhizospheric and soil eubacterial communities and on beneficial mycorrhizal symbiosis in experimental microcosms. *Appl Environ Microbiol* **71**: 6719–6729.

Compant S, Duffy B, Nowak J, Clement C & Barka EA (2005) Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Appl Environ Microbiol* **71**: 4951–4959.

Costa R, Götz 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.

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.

Costa R, Gomes NC, Krögerrecklenfort 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.

Czárán TL, Hoekstra RF & Pagie L (2002) Chemical warfare between microbes promotes biodiversity. *P Natl Acad Sci USA* **99**: 786–790.

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

Da Silva KRS, Salles JF, Seldin L & van Elsas JD (2003) Application of a novel *Paenibacillus*-specific PCR-DGGE method and sequence analysis to assess the diversity of *Paenibacillus* spp. in the maize rhizosphere. *J Microbiol Meth* **54**: 213–231.

De Angelis KM, Firestone MK & Lindow SE (2007) Sensitive whole-cell biosensor suitable for detecting a variety of *N*-acyl homoserine lactones in intact rhizosphere microbial communities. *Appl Environ Microbiol* **73**: 3724–3727.

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

Dekkers LC, van der Bij AJ, Mulders IHM, Phoelich CC, Wentwoord RAR, Glandorf DCM & Lugtenberg BJJ (1998) Role of the O-antigen of lipopolysaccharide, and possible roles of growth rate and NADH: ubiquinone oxidoreductase (nuo) in competitive tomato root-tip colonization by *Pseudomonas fluorescens* WCS365. *Mol Plant Microbe Interact* **11**: 763–771.

De Werra P, Baehler E, Huser A, Keel C & Maurhofer M (2008) Detection of plant-modulated alterations in antifungal gene expression in *Pseudomonas fluorescens* CHA0 on roots by flow cytometry. *Appl Environ Microbiol* **74**: 1339–1349.

Dohrmann A & 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.

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

Eberl L, Molin S & Giskov M (1999) Surface motility of *Serratia liquefaciens* MG1. *J Bacteriol* **181**: 1703–1712.

Erkel C, Kube M, Reinhardt R & Liesack W (2006) Genome of rice cluster I archaea – the key methane producers in the rice rhizosphere. *Science* **313**: 370–372.

Fierer N & Jackson RB (2006) The diversity and biogeography of soil bacterial communities. *P Natl Acad Sci USA* **103**: 626–631.

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 Microb 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 total and active bacterial communities in arable soils. *Appl Environ Microbiol* **69**: 1800–1809.

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.

Graner G, Persson P, Meijer J & Alstrom S (2003) A study on microbial diversity in different cultivars of *Brassica napus* in

relation to its wilt pathogen, *Verticillium longisporum*. *FEMS Microbiol Lett* **29**: 269–276.

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.

Haichar FE, Marol C, Berge O, Rangel-Castro JI, Prosser JI, Balesdent J, Heulin T & Achouak W (2008) Plant host habitat and root exudates shape soil bacterial community structure. *ISME J* **2**: 1221–1230.

Heuer H, Kroppenstadt R, Lottmann J, Berg G & Smalla K (2002) No detectable effects of T4 lysozyme release from transgenic potato roots on bacterial rhizosphere consortia in a 3-year field experiment, but variability due to natural factors. *Appl Environ Microbiol* **68**: 1325–1335.

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.

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.

Jousset A, Lara E, Wall LG & Valverde C (2006) Secondary metabolites help biocontrol strain *Pseudomonas fluorescens* CHA0 to escape protozoan grazing. *Appl Environ Microbiol* **72**: 7083–7090.

Kowalchuk GA, Buma DS, De Boer W, Klinkhammer PGL & van Veen H (2002) Effects of above-ground plant species composition and diversity on the diversity of soil-borne microorganisms. *A van Leeuw J Microb* **81**: 509–520.

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

Kuske CR, Ticknor LO, Miller ME, Dunbar JM, Davis JA, Barns SM & Belnap J (2002) Comparison of soil bacterial communities in rhizospheres of three plant species and the interspaces in an arid grassland. *Appl Environ Microbiol* **68**: 1854–1863.

Latour X, Corberand T, Laguerre G, Allard F & Lemanceau P (1996) The composition of fluorescent pseudomonad populations associated with roots is influenced by plant and soil type. *Appl Environ Microbiol* **62**: 2449–2456.

Latour X, Philippot L, Corberand T & Lemanceau P (1999) The establishment of an introduced community of fluorescent pseudomonads in the soil and in the rhizosphere is affected by the soil type. *FEMS Microbiol Ecol* **30**: 163–170.

Lemanceau P, Corberand T, Gardan L, Latour X, Laguerre G, Boeufgras JM & Alabouvette C (1995) Effect of two plant species, flax (*Linum usitatissinum* L.) and tomato (*Lycopersicon esculentum* Mill.), on the diversity of soilborne populations of fluorescent pseudomonads. *Appl Environ Microbiol* **61**: 1004–1012.

Leveau JHJ (2007) The magic and menace of metagenomics: prospects for the study of plant growth-promoting rhizobacteria. *Eur J Plant Pathol* **119**: 279–300.

Long SR (2001) Genes and signals in rhizobium–legume symbiosis. *Plant Physiol* **125**: 69–72.

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

Lottmann J, Heuer H, Smalla K & Berg G (2000) Establishment of introduced antagonistic bacteria in the rhizosphere of transgenic potatoes and their effect on the bacterial community. *FEMS Microb Ecol* **33**: 41–49.

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

Lugtenberg BJJ, Chin-A-Woeng TFC & Bloemberg GV (2002) Microbe–plant interactions: principles and mechanisms. *Antonie van Leewenhoek* **81**: 373–383.

Maloney PE, van Bruggen AHC & Hu S (1997) Bacterial community structure in relation to the carbon environments in lettuce and tomato rhizospheres and in bulk soil. *Microb Ecol* **34**: 109–117.

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

Mark GL, Dow JM, Kiely PD *et al.* (2005) Transcriptome profiling of bacterial responses to root exudates identifies genes involved in microbe–plant interactions. *P Natl Acad Sci USA* **102**: 17454–17459.

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.

Martinez-Granero F, Rivilla R & Martin M (2006) Rhizosphere selection of highly motile phenotypic *Pseudomonas fluorescens* with enhanced colonization ability. *Appl Environ Microbiol* **72**: 3429–3434.

Matilla MA, Espinosa-Urgel M, Rodriguez-Herva JJ, Ramos JL & Ramos-Gonzalez MI (2008) Genomic analysis reveals the major driving forces of bacterial life in the rhizosphere. *Genome Biol* **8**: R179 . Epub ahead of print.

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.

Milling A, Smalla K, Xaver F, Maidl K, Schloter M & Munch JC (2004) Effects of transgenic potatoes with an altered starch composition on the diversity of soil and rhizosphere bacteria and fungi. *Plant Soil* **266**: 23–39.

Morris PF, Bone E & Tyler BM (1998) Chemotrophic and contact response of *Phytophthora sojae* hyphae to soybean isoflavonoids and artificial substrates. *Plant Physiol* **117**: 1171–1178.

Nichols D (2007) Cultivation gives context to the microbial ecologist. *FEMS Microbiol Ecol* **60**: 351–357.

Nilsson M, Rasmussen U & Bergman B (2006) Cyanobacterial chemotaxis to extracts of host and nonhost plants. *FEMS Microbiol Ecol* **55**: 382–390.

Nunan N, Daniell TJ, Singh BK, Papert A, Mc Nicol JW & Prosser JI (2005) Links between plant and rhizoplane bacterial communities in grassland soils, characterized using molecular techniques. *Appl Environ Microbiol* **71**: 6784–6792.

Oliver KL, Hamelin RC & Hintz WE (2008) Effects of transgenic hybrid aspen over-expressing P 1 olyphenol oxidase on rhizosphere diversity. *Appl Environ Microb* **74**: 5340–5348.

Peterson SB, Dunn AK, Klimowicz AK & Handelsman J (2006) Peptidoglycan from *Bacillus cereus* mediates commensalism with rhizosphere bacteria from the *Cytophaga–Flavobacterium* group. *Appl Environ Microbiol* **72**: 5421–5427.

Picard C & Bosco M (2008) Genotypic and phenotypic diversity in populations of plant-probiotic *Pseudomonas* spp. colonizing roots. *Naturwissenschaften* **95**: 1–16.

Pitman NCA & Jörgensen PM (2002) Estimating the size of the threatened world flora. *Science* **298**: 989.

Raaijmakers JM, Paulitz CT, Steinberg C, Alabouvette C & Moënne-Loccoz Y (2009) The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. *Plant Soil* DOI: 10.1007/s11104-008-9568-6.

Rasche F, Hodl V, Poll C, Kandeler E, Gerzabek MH, van Elsas JD & Sessitsch A (2006a) 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.

Rasche F, Velvis H, Zachow C, Berg G, van Elsas JD & Sessitsch A (2006b) Impact of transgenic potatoes expressing antibacterial agents on bacterial endophytes is comparable to effects of soil, wildtype potatoes, vegetation stage and pathogen exposure. *Can J Microbiol* **43**: 555–566.

Rediers H, Rainey PB, Vanderleyden J & De Mot R (2005) Unraveling the secret lives of bacteria: use of *in vivo* expression technology and differential fluorescence induction promoter traps as tools for exploring niche-specific gene expression. *Microbiol Mol Rev* **69**: 217–261.

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

Ritz K (2007) The plate debate: cultivable communities have no utility in contemporary environmental microbial ecology. *FEMS Microbiol Ecol* **60**: 358–362.

Robin A, Mougel C, Siblot S, Vansuyt G, Mazurier S & Lemanceau P (2006) Effect of ferritin overexpression in tobacco on the structure of bacterial and pseudomonad communities associated with the roots. *FEMS Microbiol Ecol* **58**: 492–502.

Robin A, Mazurier S, Mougel C, Vansuyt G, Corberand T, Meyer JM & Lemanceau P (2007) Diversity of root-associated fluorescent pseudomonads as affected by ferritin overexpression in tobacco. *Environ Microbiol* **9**: 1724–1737.

Rodriguez-Carres M, White G, Tsuchiya D, Taga M & van Etten HD (2008) The supernumerary chromosome of *Nectria haematococca* that carries pea-pathogenicity-related genes also carries a trait for pea rhizosphere competitiveness. *Appl Environ Microbiol* **74**: 3849–3856.

Rodríguez-Navarro DN, Dardanelli MS & Ruíz-Saínz JE (2007) Attachment of bacteria to the roots of higher plants. *FEMS Microbiol Lett* **272**: 127–136.

Rovira AD (2005) Plant root excretions in relation to the rhizosphere effect. *Plant Soil* **7**: 178–194.

Salles JF, van Veen JA & van Elsas JD (2004) Multivariate analyses of *Burkholderia* species in soil: effect of crop and land use history. *Appl Environ Microbiol* **70**: 4012–4020.

Sanguin H, Remenant B, Dechesne A, Thioulouse J, Vogel TM, Nesme X, Moënne-Loccoz Y & Grundmann GL (2006) Potential of a 16S rRNA-based taxonomic microarray for analyzing the rhizosphere effects of maize on *Agrobacterium* spp. and bacterial communities. *Appl Environ Microbiol* **72**: 4302–4312.

Scherwinski K, Grosch R & Berg G (2008) Effect of bacterial antagonists on lettuce: active biocontrol of *Rhizoctonia solani* and negligible, short-term effect on non-target microbes. *FEMS Microb Ecol* **64**: 106–116.

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

Siciliano DS, Forin N, Mihoc A *et al.* (2001) Selection of specific endophytic bacterial genotypes by plant in response to soil contamination. *Appl Environ Microbiol* **67**: 2469–2475.

Simon HM, Jahn CE, Bergerud LT, Sliwinski MK & Weimer PJ (2005) Cultivation of mesophilic soil *Crenarchaeotes* in enrichment cultures from plant roots. *Appl Environ Microbiol* **71**: 4751–4760.

Singh BK, Milard P, Whitely AS & Murrell JC (2004) Unravelling rhizosphere-microbial interactions: opportunities and limitations. *Trends Microbiol* **12**: 386–393.

Sliwinski MK & Goodman RM (2004) Comparison of crenarchaeal consortia inhabiting the rhizosphere of diverse terrestrial plants with those in bulk soil in native environments. *Appl Environ Microbiol* **70**: 1821–1826.

Smalla K, Wieland G, Buchner A, Zock A, Parzy J, 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. *Appl Environ Microbiol* **67**: 4742–4751.

Smith KP, Handelsman J & Godman RM (1999) Genetic basis in plants for interactions with disease-suppressive bacteria. *P Natl Acad Sci USA* **9**: 4786–4790.

Somers E, Vanderleyden J & Srinivisam M (2004) Rhizosphere bacterial signaling: a love parade beneath our feet. *Crit Rev Microbiol* **30**: 205–240.

Sørensen J (1997) The rhizosphere as a habitat for soil microorganisms. *Modern Soil Microbiology* (Van Elsas JD, Trevors JT & Wellington EMH, eds), pp. 21–45. Marcel Dekker Inc., New York.

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

Tarlera S, Jangid K, Ivester AH, Whitman WB & Williams MA (2008) Microbial community succession and bacterial diversity in soils during 77 000 years of ecosystem development. *FEMS Microbiol Ecol* **64**: 129–140.

Tjamos EC, Rowe RC, Heale JB & Fravel DR (2000) *Advances in Verticillium Research and Disease Management*. The American Phytopathological Society (APS) Press, St Paul, MN, 357pp.

Tomasi N, Weisskopf L, Renella G, Landi L, Pinton R, Varanini Z, Nannipieri P, Torrent J, Martinoia E & Cesco S (2008) Flavonoids of white lupin participate in phosphorous mobilization in soil. *Soil Biol Biochem* **40**: 1971–1974.

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

Uren NC (2000) Types, amounts and possible functions of compounds released into the rhizosphere by soil grown plants. *The Rhizosphere: Biochemistry, and Organic Substances at the Soil Interface* (Pinton R, Varani Z & Nanniperi P, eds), pp. 19–40. Marcel Dekker Inc., New York.

Van der Putten WH, Klironomos JN & Wardle DA (2007) Microbial ecology of biological invasions. *ISME J* **1**: 28–37.

Van West P, Morris BM, Reid B, Appiah AA & Osborne MC (2002) Oomycete plant pathogens use electric fields to target roots. *Mol Plant Microbe Interact* **15**: 790–798.

Velicer GJ, Raddatz G, Keller H, Deiss S, Lanz C, Dinkelacker I & Schuster SC (2006) Comprehensive mutation identification in an evolved bacterial cooperator and its cheating ancestor. *P Natl Acad Sci USA* **103**: 8107–8112.

Weller DM (1988) Biological control of soilborne plant pathogens in the rhizosphere with bacteria. *Ann Rev Phytopathol* **26**: 379–407.

Weller DM, Raaijmakers JM, Gardener BB & Thomashow LS (2002) Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu Rev Phytopathol* **40**: 309–348.

Wieland G, Neumann R & Backhaus H (2001) Variation of microbial communities in soil, rhizosphere, and rhizoplane in response to crop species, soil type, and crop development. *Appl Environ Microbiol* **67**: 5849–5854.

Yao J & Allen C (2007) Chemotaxis is required for virulence and competitive fitness of the bacterial wilt pathogen *Ralstonia solanacearum*. *J Bacteriol* **188**: 3697–3708.

Yuan Z, Liu P, Saenkham P, Kerr K & Nester EW (2008) Transcriptome profiling and functional analysis of *Agrobacterium tumefaciens* reveals a general conserved response to acidic conditions (pH 5.5) and a complex acid-mediated signaling involved in *Agrobacterium*–plant interactions. *J Bacteriol* **190**: 494–507.

Zachow C, Berg C, Müller H, Meincke R, Komon-Zelazowska M, Druzhinina IS, Kubicek C & Berg G (2008a) Fungal biodiversity in the soils/rhizospheres of Tenerife (Canary Islands): relationship to vegetation zones and environmental factors. *ISME J* **3**: 79–92.

Zachow C, Tilcher R & Berg G (2008b) Sugar beet-associated bacterial and fungal communities show a high indigenous antagonistic potential against plant pathogens. *Microb Ecol* **55**: 119–129.