REVIEW ARTICLE

The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms

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Abstract

Microbial communities play a pivotal role in the functioning of plants by influencing their physiology and development. While many members of the rhizosphere microbiome are beneficial to plant growth, also plant pathogenic microorganisms colonize the rhizosphere striving to break through the protective microbial shield and to overcome the innate plant defense mechanisms in order to cause disease. A third group of microorganisms that can be found in the rhizosphere are the true and opportunistic human pathogenic bacteria, which can be carried on or in plant tissue and may cause disease when introduced into debilitated humans. Although the importance of the rhizosphere microbiome for plant growth has been widely recognized, for the vast majority of rhizosphere microorganisms no knowledge exists. To enhance plant growth and health, it is essential to know which microorganism is present in the rhizosphere microbiome and what they are doing. Here, we review the main functions of rhizosphere microorganisms and how they impact on health and disease. We discuss the mechanisms involved in the multitrophic interactions and chemical dialogues that occur in the rhizosphere. Finally, we highlight several strategies to redirect or reshape the rhizosphere microbiome in favor of microorganisms that are beneficial to plant growth and health.

Introduction

Plants are colonized by an astounding number of (micro) organisms that can reach cell densities much greater than the number of plant cells (Fig. 1). Also, the number of microbial genes in the rhizosphere outnumbers by far the number of plant genes (Fig. 1). An overwhelming number of studies have revealed that many plant-associated microorganisms can have profound effects on seed germination, seedling vigor, plant growth and development, nutrition, diseases, and productivity (Fig. 2). Consistent with the terminology used for microorganisms colonizing the human body (Qin *et al.*, 2010; Zhao, 2010; Gevers *et al.*, 2012), the collective communities of plant-associated microorganisms are referred to as the plant microbiome or as the plants' other genome. In this context, plants can be viewed as superorganisms that rely in part on their microbiome for specific functions and traits. In return, plants deposit their photosynthetically fixed carbon into their direct surroundings, that is, spermosphere, phyllosphere, rhizosphere, and mycorrhizosphere (Nelson, 2004; Frey-Klett *et al.*, 2007; Raaijmakers *et al.*, 2009; Berendsen *et al.*, 2012; Vorholt, 2012), thereby feeding the microbial community and influencing their composition and activities. To date, the interplay between plants and microorganisms has been studied in depth for various leaf pathogens, symbiotic rhizobia, and mycorrhizal fungi. However, for the vast majority of plant-associated microorganisms, there is limited knowledge of their impact on plant growth, health, and disease. Hence, deciphering the plant microbiome is critical to identify microorganisms that can be exploited for improving plant growth and health.

The rhizosphere, that is, the narrow zone surrounding and influenced by plant roots, is a hot spot for numerous organisms and is considered as one of the most complex

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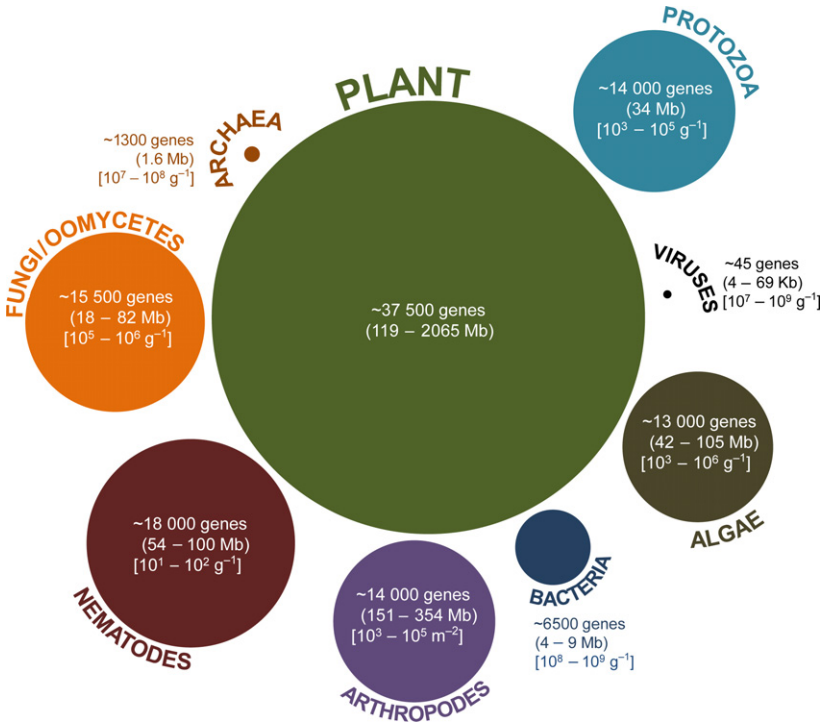

Fig. 1. Overview of (micro)organisms present in the rhizosphere zoo. The circle's size, except for VIRUSES, is a measure of the average number of genes in the genomes of representative species of each group of organisms; the size (or size range) of their respective genomes is indicated between parentheses. For each of these (micro)organisms, the approximate numbers for their abundance are indicated between square brackets (Alexander, 1977; Brady, 1974; Lynch, 1988; Meeting, 1992; Buée *et al.*, 2009). The endophytic microorganisms, including endosymbionts, are not included. The species selected to illustrate the composition of the rhizosphere microbiome and used to calculate the number of genes and genome sizes are: PLANT: *Glycine max, Populus trichocarpa, Zea mays, Oryza sativa, Arabidopsis thaliana*, and *Vitis vinifera*; PROTOZOA: *Dictyostelium discoideum*; VIRUSES: *Pseudomonas* phage 73, *Fusarium graminearum* dsRNA mycovirus-4, *Agrobacterium* phage 7-7-1, *Rhizoctonia solani* virus 717; ALGAE: *Chlorella variabilis* and *Chlamydomonas reinhardtii*; BACTERIA: *Pseudomonas fluorescens, Bradyrhizobium japonicum, Rhizobium leguminosarum, Bacillus cereus, Bacillus amyloliquefaciens, Burkholderia cenocepacia*, and *Streptomyces filamentosus*; ARTHROPODES: *Metaseiulus occidentalis, Acromyrmex echinatior,* and *Solenopsis invicta*; NEMATODES: *Caenorhabditis elegans* and *Meloidogyne hapla*; FUNGI/OOMYCETES: *Laccaria bicolor, Nectria haematococca, Piriformospora indica, Verticillium dahliae, Metarhizium anisopliae, Fusarium oxysporum, Sporisorium reilianum, Phytophthora sojae, Phytophthora parasitica, Aphanomyces euteiches, Phytophthora cinnamomi,* and *Pythium ultimum*; ARCHAEA: *Candidatus* Nitrosoarchaeum koreensis.

ecosystems on Earth (Hinsinger & Marschner, 2006; Pierret *et al.*, 2007; Jones & Hinsinger, 2008; Hinsinger *et al.*, 2009; Raaijmakers *et al.*, 2009). Organisms found in the rhizosphere include bacteria, fungi, oomycetes, nematodes, protozoa, algae, viruses, archaea, and arthropods (Fig. 1; Lynch, 1990; Meeting, 1992; Bonkowski *et al.*, 2009; Buée *et al.*, 2009; Raaijmakers *et al.*, 2009). Most members of the rhizosphere microbiome are part of a complex food web that utilizes the large amount of nutrients released by the plant. Given that these rhizodeposits (e.g. exudates, border cells, mucilage) are a major driving force in the regulation of microbial diversity and activity on plant roots, Cook *et al.* (1995) postulated that plants may modulate the rhizosphere microbiome to their benefit by selectively stimulating microorganisms with traits that are beneficial to plant growth and health. Others have argued that exudates are passively 'released' as overflow/waste products of the plant (Hartmann *et al.*, 2009; Jones *et al.*, 2009; Dennis *et al.*, 2010). So, whether plants are using exudates to 'cry for help' or are 'just crying' remains to be addressed.

Rhizosphere organisms that have been well studied for their beneficial effects on plant growth and health are the nitrogen-fixing bacteria, mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR), biocontrol microorganisms, mycoparasitic fungi, and protozoa. Rhizosphere organisms that are deleterious to plant growth and health include the pathogenic fungi, oomycetes, bacteria, and nematodes. A third group of microorganisms that can be found in the rhizosphere are the human pathogens. Over the past decade, there is an increasing number of reports describing the proliferation of human pathogenic bacteria

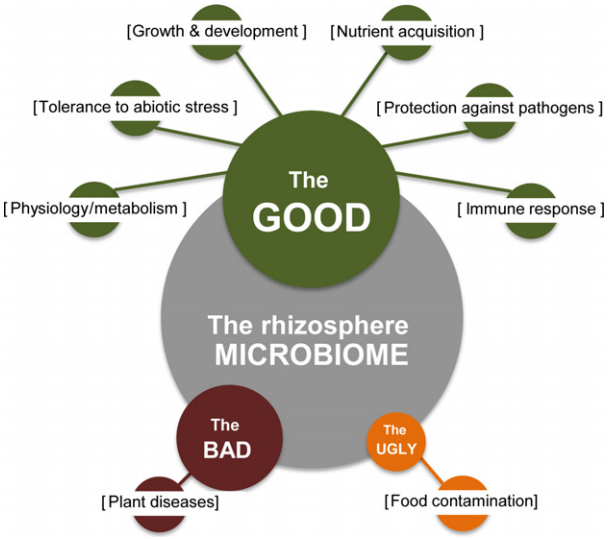

Fig. 2. Schematic overview of the functions and impact of plant beneficial ('the good'), plant pathogenic ('the bad'), and human pathogenic microorganisms ('the ugly') on the host plant. The terms 'the good', 'the bad', and 'the ugly' are arbitrary as microbial species may be beneficial or deleterious depending on its abundance (Maurhofer *et al.*, 1992). For example, also plant pathogenic and human pathogenic microorganisms may influence several of the functions depicted for the plant beneficial microorganisms. This anthropogenic terminology is merely used to facilitate the description of the complex rhizosphere microbiome environment.

in and on plant tissues (van Baarlen *et al.*, 2007; Tyler & Triplett, 2008; Holden *et al.*, 2009; Teplitski *et al.*, 2011; Kaestli *et al.*, 2012). Understanding the processes that shape and drive the composition and dynamics of the rhizosphere microbiome is therefore an essential step not only to safeguard plant productivity but also to safeguard human health. In this review, we will focus on the frequency, diversity, and activities of plant beneficial ('the good'), plant pathogenic ('the bad'), and human pathogenic ('the ugly') microorganisms in the rhizosphere and how they impact on health and disease. It should be emphasized that the use of the terms 'the good', 'the bad', and 'the ugly' is arbitrary as a specific microbial species may be beneficial or deleterious depending on its abundance (Maurhofer *et al.*, 1992). Hence, this anthropogenic terminology is merely used to facilitate the discussion of the complex rhizosphere microbiome environment. Specific attention is given to mechanisms involved in multitrophic interactions and chemical dialogues that occur in the rhizosphere. Finally, we will discuss strategies to redirect or reshape the rhizosphere microbiome in favor of those microorganisms that are beneficial to plant growth and health. Given the enormous number of publications in this multidisciplinary field of research, it was not possible to cover the entire literature. Instead, we decided to highlight several themes and, when necessary, refer to more comprehensive reviews on specific aspects of rhizosphere research.

The rhizosphere microbiome – who is there?

Culture-independent approaches have shown that microbial diversity of soil and rhizosphere microbiomes is highly underestimated. Next-generation sequencing technologies have demonstrated that only a minority (*c.* up to 5%) of bacteria have been cultured by current methodologies and that a significant proportion of the bacterial phyla detected by these technologies has no cultured representative yet. For example, the rarefaction curve built from 16S rRNA gene sequencing data obtained in a soil metagenome study failed to reach saturation and revealed that, of 150 000 sequencing reads obtained for a soil clone library, < 1% exhibited overlap with the sequencing reads of other independent soil clone libraries (Tringe *et al.*, 2005). In one of the first studies in this research field, Torsvik *et al.* (2002) estimated that the number of bacterial species in a gram of boreal forest soil was *c.* 10 000. Following the same strategy with substantial computational improvements, Gans *et al.* (2005) predicted that 1 g of soil can contain more than 1 million distinct bacterial genomes, exceeding previous estimates by several orders of magnitude. Two years later, Roesch *et al.* (2007) obtained 139 819 bacterial and 9340 crenarchaeotal rRNA gene sequences from four distinct soils and counted, based on diversity estimators, a maximum of 52 000 operational taxonomic units (OTUs). *Bacteroidetes*, *Betaproteobacteria*, and *Alphaproteobacteria* were the most abundant bacterial groups in the four soils investigated (Roesch *et al.*, 2007).

For the rhizosphere, most studies to date have focused on the number and diversity of bacterial taxa rather than on other rhizosphere inhabitants. Depending on the techniques used, numbers reported in rhizosphere studies range from < 100 to more than 55 000 OTUs (Table 1). For example, a meta-analysis of 19 clone libraries obtained from the rhizosphere of 14 plant species revealed more than 1200 distinguishable bacterial taxa from 35 different taxonomic orders, with the *Proteobacteria* as the most dominant phylum (Hawkes *et al.*, 2007). Based on 454 pyrosequencing, Uroz *et al.* (2010) detected 5619 OTUs in the rhizosphere of oak and showed that the bacterial community was dominated by the *Acidobacteria* and *Proteobacteria*. Their study also showed that the bacterial diversity was higher in the bulk soil than in the oak rhizosphere (Uroz *et al.*, 2010). Using the same approach, Uroz *et al.* (2012) demonstrated that also the ectomycorrhizospheres of *Xerocomus pruinatus* and *Scleroderma*

Table 1. Number of bacterial and archaeal taxa identified in the rhizosphere microbiome

Host	Approach*	Main findings related to rhizosphere microbiome composition	References
Erica andevalensis in a naturally metal-enriched and extremely acidic environment	16S rRNA gene clone library	Bacteria: of 101 sequenced clones, the majority was affiliated with the *Actinobacteria* (38 clones; 12 OTUs) followed by the *Acidobacteria* (21 clones; 10 OTUs), and *Proteobacteria* (18 clones; eight OTUs). Archaea: considering 27 clones, the community was composed by *Crenarchaeota* (21 clones; four OTUs) and *Euryarchaeota* (six clones; two OTUs)	Mirete *et al.* (2007)
Maize crop	*nif*H Cluster I clone library	*Azospirillum*, *Bradyrhizobium,* and *Ideonella* were the most abundant genera found in the rhizosphere, comprising c. 5%, 21% and 11% of the clones, respectively. The portion of unidentified bacteria was of 27%	Roesch *et al.* (2007)
Oat microcosms	16S rRNA gene microarray	A total of 1917 taxa were detected, and the community was dominated by *Proteobateria* and *Firmicutes*. Less expected rhizosphere-competent phyla were also detected, including *Actinobacteria*, *Verrucomicrobia*, and *Nitrospira*	DeAngelis *et al.* (2009)
Deschampsia antarctica and *Colobanthus quitensis* in the Arctic	16S rRNA gene pyrosequencing	*Firmicutes* was the most abundant group found, and *Acidobacteria* was rarely detected. The predominant genera found were *Bifidobacterium* (phylum *Actinobacteria*), *Arcobacter* (phylum *Proteobacteria*), and *Faecalibacterium* (phylum *Firmicutes*)	Teixeira *et al.* (2010)
Oak in a forest soil	16S rRNA gene pyrosequencing	In one of the rhizosphere samples, 5619 OTUs were identified in the bacterial community. The predominant phyla were *Proteobacteria* (38%), *Acidobacteria* (24%), and *Actinobacteria* (11%). A high proportion of unclassified bacteria (20%) were observed	Uroz *et al.* (2010)
Sugar beet in agricultural soil	16S rRNA gene microarray	A total of 33 346 bacterial and archaeal OTUs were detected, and the community was dominated by *Proteobacteria* (39%), *Firmicutes* (20%), and *Actinobacteria* (9%). The *Gamma-* and *Betaproteobacteria* and *Firmicutes* were identified as the most dynamic taxa associated with disease suppression	Mendes *et al.* (2011)
Potato in field soil	16S rRNA gene microarray	A total of 2432 OTUs were detected in at least one of the samples. The highest number of OTUs belonged to the *Proteobacteria* (46%), followed by *Firmicutes* (18%), *Actinobacteria* (11%), *Bacteroidetes* (7%), and *Acidobacteria* (3%).The bacterial families *Streptomycetaceae*, *Micromonosporaceae,* and *Pseudomonadaceae* showed the strongest response at the potato cultivar level	Weinert *et al.* (2011)
Rhizophora mangle and *Laguncularia racemosa* in mangroove	Archaeal 16S rRNA gene pyrosequencing	About 300 archaeal OTUs were identified. Four classes were found: *Halobacteria*, *Methanobacteria*, *Methanomicrobia*, and *Thermoprotei*	Pires *et al.* (2012)
Potato in field soil	Pyrosequencing	A total of 55 121 OTUs were found. *Actinobacteria* and *Alphaproteobacteria* were the most abundant groups, followed by *Gammaproteobacteria*, *Betaproteobacteria*, *Acidobacteria*, *Gemmatimonadetes*, *Firmicutes*, *Verrucomicrobia*, *Deltaproteobacteria*, *Cyanobacteria*, *Bacteriodetes*, and the TM7 group	Inceoglu *et al.* (2011)
Rhizophora mangle in mangroove	16S rRNA gene pyrosequencing	*Proteobacteria* was the most abundant phylum in all samples covering 36–40% of the total sequencing reads	Gomes *et al.* (2010)
Mannillaria carnea (cactus) in semi-arid environment	16S rRNA gene pyrosequencing	Dominant bacterial groups were *Acidobacteria*, *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes*	Torres-Cortes *et al.* (2012)
Arabidopsis thaliana in Cologne and Golm soils	16S rRNA gene pyrosequencing	About 1000 OTUs were estimated in the rhizosphere and 1000 OTUs in root compartments. The rhizosphere was dominated by *Acidobacteria*, *Proteobacteria*, *Planctomycetes*, and *Actinobacteria*. *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* were found as dominant phyla in root bacterial communities and significantly enriched compared with soil and rhizosphere	Bulgarelli *et al.* (2012)

Table 1. Continued

Host	Approach*	Main findings related to rhizosphere microbiome composition	References
Arabidopsis thaliana in Mason farm and Clayton soils	16S rRNA gene pyrosequencing	18 783 bacterial OTUs were firstly detected, and 778 measurable OTUs were used for analysis. The rhizosphere microbiome was dominated by *Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, and *Acidobacteria*. The endophytic compartment was dominated by *Actinobacteria*, *Proteobacteria*, and *Firmicutes* and was depleted of *Acidobacteria*, *Gemmatimonadetes*, and *Verrucomicrobia*	Lundberg *et al.* (2012)

OTUs, operational taxonomic units.

*Here, we focused on a select number of microarray and pyrosequencing studies; for more studies that used the clone library approach to access the dominant bacterial groups in the rhizosphere, we refer to Buée *et al.* (2009).

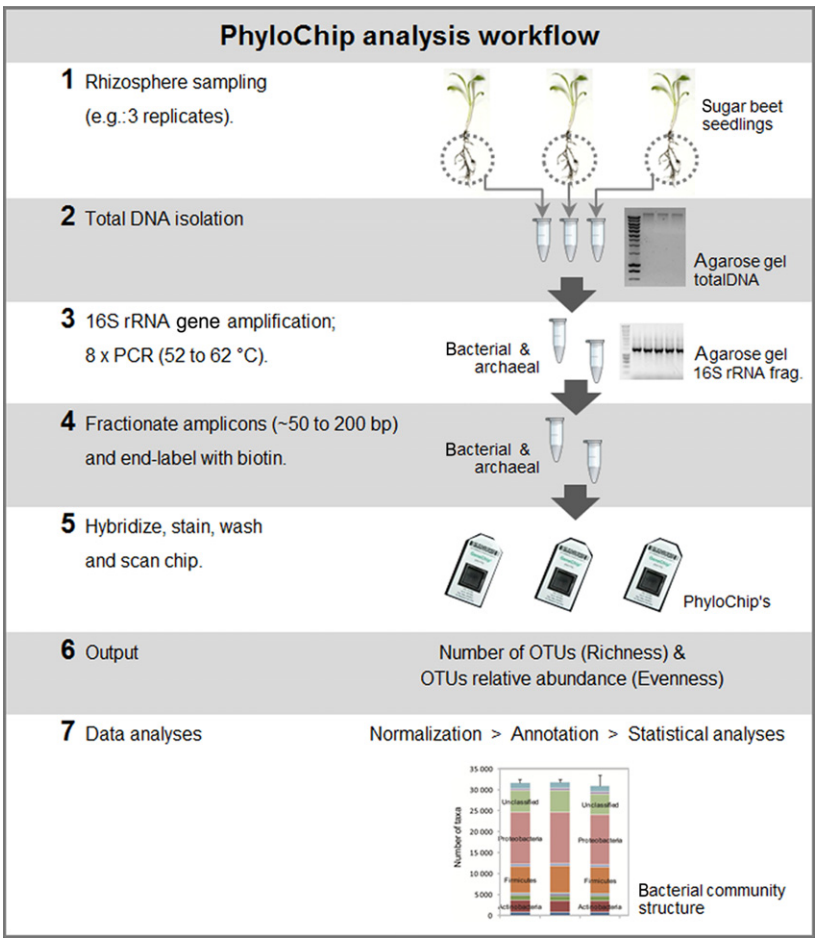

Fig. 3. Overall workflow of the PhyloChip technology to assess the diversity and abundance of the bacterial communities in the rhizosphere (adapted from Mendes *et al.*, 2011).

citrinum hosted significantly more *Alpha*-, *Beta*-, and *Gammaproteobacteria* than bulk soil. Despite the harsh abiotic conditions in Antarctic soils, up to 732 OTUs were detected in the rhizosphere of two vascular plants (Teixeira *et al.*, 2010). For most of the rhizosphere samples from the Antarctic, *Firmicutes* were the most abundant phylum, whereas in many other rhizosphere studies, the *Proteobacteria* are commonly more abundant. Using a high-density 16S rRNA gene oligonucleotide microarray, referred to as the PhyloChip (Fig. 3), DeAngelis *et al.* (2009) detected 2595 OTUs in the oat rhizosphere with 1917 OTUs consistently present in all three replicate samples. The dynamic subset (147 OTUs) responsive to root growth was dominated by the *Alphaproteobacteria*, *Firmicutes*, and *Actinobacteria* (DeAngelis *et al.*, 2009). PhyloChip analysis has also been used to access bacterial communities in the rhizosphere of other plant species, including potato and sugar beet. The work

by Weinert *et al.* (2011) showed that the number of OTUs found in the rhizosphere of three potato cultivars grown at two distant field sites ranged from 1444 to 2015. The dominant phylum detected was the *Proteobacteria* (46%), followed by *Firmicutes* (18%), *Actinobacteria* (11%), *Bacteroidetes* (7%), and *Acidobacteria* (3%). Interestingly, the relative abundance of the top 10 dominant phyla was similar for all three potato cultivars at both sites (Weinert *et al.*, 2011). With the increased capacity of the latest PhyloChip generation (G3), which includes *c.* 60 000 OTUs representing 147 phyla and 1123 classes of *Bacteria* and *Archaea* domains (Hazen *et al.*, 2010), over 33 000 OTUs were detected in the rhizosphere of sugar beet seedlings grown in soils from agricultural fields in the Netherlands (Mendes *et al.*, 2011). Similar to the results obtained by Roesch *et al.* (2007), the *Proteobacteria* was the most dominant phylum followed by the *Firmicutes*, *Actinobacteria*, and *Bacteroidetes*. The unclassified bacteria represented a relatively large group (16%) among the OTUs detected in the sugar beet rhizosphere (Mendes *et al.*, 2011). Recently, the taxonomic classification of the Greengenes database has been updated (McDonald *et al.*, 2012). By reevaluating the proportion of unclassified taxa found in the sugar beet rhizosphere using the updated database, the number of unclassified taxa in the sugar beet rhizosphere decreased to 7.5% (R. Mendes and J.M. Raaijmakers, unpublished data). Hence, expanding our basic taxonomic knowledge of microorganisms is essential to further improve the technological resolution and capabilities of next-generation sequencing to study the diversity and functional potential of plant and other microbiomes.

Consistent with the approaches and concepts in human microbiome studies, Lundberg *et al.* (2012) and Bulgarelli *et al.* (2012) recently investigated the spatial distribution of bacterial communities in the rhizosphere of different *Arabidopsis* accessions to determine the composition of the core microbiome. By pyrosequencing 16S rRNA gene segments of bacteria from bulk soil, rhizosphere, and endophytic root compartments of more than 600 *Arabidopsis* plants, Lundberg *et al.* (2012) showed a strong influence of the soil type on the bacterial communities in each of the compartments. Their results also showed that the endophytic root compartment was enriched with *Actinobacteria* and *Proteobacteria* and that the plant's developmental stage and genotype can drive differential recruitment and/or differential exclusion of bacterial communities (Lundberg *et al.*, 2012). Using different PCR primers, different computational pipelines and physicochemically different soils, similar findings were reported by Bulgarelli *et al.* (2012).

The discovery that *Archaea* represent an important group of ammonia oxidizers in soils (Leininger *et al.*, 2006) has led to an increasing number of studies on this microbial group. In a global survey of 146 soils, Bates *et al.* (2011) used a set of universal primers for nearly all bacterial and archaeal taxa and showed that the *Archaea* domain comprised an average of 2% of the total 16S rRNA gene sequences recovered from these soils and that their relative abundance was higher in soils with lower C : N ratios. For the rhizosphere, an earlier study by Chelius & Triplett (2001) identified six unique archaeal sequences associated with maize roots. In mangroves, about 300 archaeal OTUs distributed over four classes (*Halobacteria*, *Methanobacteria*, *Methanomicrobia,* and *Thermoprotei*) were recently identified in association with *Rhizophora mangle* and *Laguncularia racemosa* (Pires *et al.*, 2012). In the rhizosphere of sugar beet seedlings grown in agricultural soils, we detected 70 archaeal OTUs representing 0.21% of the total archaeal and bacterial community accessed by PhyloChip analysis (R. Mendes and J.M. Raaijmakers, unpublished data). Interestingly, we found a correlation between the composition of the Archaeal communities and the level of suppressiveness of soils to *Rhizoctonia* damping-off disease. Whether *Archaea* play a role in protection of plants against soilborne pathogens is not yet known.

The rhizosphere microbiome – what are they doing?

In addition to a comprehensive phylogenetic analysis of the rhizosphere microbiome, there is a strong need to go beyond cataloguing microbial communities ('collecting stamps') and to determine which microorganisms are active during the different developmental stages of plant/root growth and which functions and pathways are displayed in time and space. In the review by Barret *et al.* (2011), a variety of molecular approaches to study gene expression in the rhizosphere was discussed. From their detailed overview, it is apparent that most of our current knowledge of genes and functions expressed in the rhizosphere is still based on studies with reporter genes. Despite their limitations, reporter genes do enable the evaluation of how specific members of the rhizosphere microbiome perceive their habitat in terms of chemical, physical, and biological stimuli. An elegant promoter-trapping strategy, referred to as *in vivo* expression technology (IVET), was adopted to identify *Pseudomonas fluorescens* genes with elevated levels of expression in the rhizosphere (Rainey, 1999). Genes induced in *P. fluorescens* during rhizosphere colonization were genes involved in nutrient acquisition, stress response, and secretion (Rainey, 1999). In another study, the IVET technology revealed that proteins involved in environmental sensing, control of gene expression, metabolic reactions, and

membrane transport were specifically expressed in the pea-nodulating bacterium *Rhizobium leguminosarum* A34 during rhizosphere colonization (Barr *et al.*, 2008). Next to IVET, a number of studies have used a diverse panel of reporter genes to study specific processes in the rhizosphere, including responses of bacteria to carbon, nitrogen, phosphorus availability (Kragelund *et al.*, 1997; Jensen & Nybroe, 1999; Ramos *et al.*, 2000; Koch *et al.*, 2001; DeAngelis *et al.*, 2005), temperature, and water potential (Ullrich *et al.*, 2000; Axtell & Beatie, 2002; Herron *et al.*, 2010). Bioreporters were also successfully adopted to study bacterial communication in the rhizosphere (Andersen *et al.*, 2001; Steidle *et al.*, 2001; Withers *et al.*, 2001; Loh *et al.*, 2002; Steindler & Venturi, 2007; Ferluga & Venturi, 2009) as well as the *in situ* production of antimicrobial compounds (Hay *et al.*, 2000; Kulakova *et al.*, 2009; Rochat *et al.*, 2010). For more detailed information on the results of these and other reporter gene studies, we refer to Gage *et al.* (2008), Sorensen *et al.* (2009), and van der Meer & Belkin (2010).

To go beyond the 'one-gene-at-a-time' approach, Mark *et al.* (2005) used whole genome transcriptome profiling to evaluate the effects of root exudates from two sugar beet cultivars on gene expression in *Pseudomonas aeruginosa*. In addition to genes previously identified in plant–microbe interactions (i.e. metabolism, chemotaxis, type III secretion), Mark *et al.* (2005) showed that 104 genes were significantly altered in response to both root exudates and that the majority of these genes were regulated in response to only one of the two exudates. Recently, a whole genome microarray was also used to study endophytic colonization of rice by *Azoarcus* sp. BH72 (Shidore *et al.*, 2012). Among 3992 protein-coding genes analyzed, 2.4% was up-regulated and 2.0% was found down-regulated when exposed to root exudates. Subsequent mutational analysis indicated that genes encoding pilin PilX or signal transduction proteins with GGDEF domains and a serine–threonine kinase were important in colonization. The authors further suggested that strain BH72 is primed by root exudates for a lifestyle as endophyte, that is, microorganisms that live inside plant tissues without causing any immediate, overt negative effects (Shidore *et al.*, 2012). Microarrays have also been used to identify functional activities of multiple members within a complex microbial community. The functional gene array, termed GeoChip, contains more than 10 000 genes covering more than 150 functions involved in nitrogen, carbon, sulfur and phosphorus cycling, metal reduction and resistance, and organic contaminant degradation (He *et al.*, 2007). For example, the GeoChip 3.0 revealed that infection of citrus trees by the pathogen *Candidatus* Liberibacter asiaticus caused shifts in the composition and functional potential of rhizosphere microbial communities (Trivedi *et al.*, 2011).

'Omics' approaches that enable the identification of gene transcripts, proteins, or metabolites have been developed to provide a more detailed insight into the genes and functions expressed in the plant microbiome. A metaproteogenomic approach was first reported for bacterial communities in the phyllosphere of *Arabidopsis*, soybean, and clover plants (Delmotte *et al.*, 2009). For the rhizosphere, a recent metaproteomics study revealed complex interactions between plants and rhizosphere microorganisms in different cropping systems (Wang *et al.*, 2011). MALDI-TOF/TOF-MS resulted in the identification of 189 protein spots from rice rhizosphere samples and approximately one-third of the protein spots could not be identified (Wang *et al.*, 2011). The origin of each protein was determined, being from plants (107 proteins), fauna (10), fungi (29), or bacteria (43). Bacterial proteins were mostly linked to the *Proteobacteria* and *Actinobacteria*. They also found that 50% of the bacterial groups classified by proteomic analysis were not found in the genomic-based T-RFLP analysis and vice versa, highlighting the importance of combining different approaches to access the microbial community (Wang *et al.*, 2011). A similar approach was used to study the rhizosphere microbiome of the medicinal plant *Rehmannia glutinosa* (Wu *et al.*, 2011) and the phyllosphere plus rhizosphere microbiomes of rice (Knief *et al.*, 2011). The latter study resulted in the identification of about 4600 proteins and revealed the presence of one-carbon conversion processes, predominantly methanogenesis, in both rhizosphere and phyllosphere (Knief *et al.*, 2011).

Also, the development of stable isotope probing (SIP) to track plant-derived carbon into microbial nucleic acids has provided exciting new insights into the metabolically active rhizobacterial populations (Rangel-Castro *et al.*, 2005; Prosser *et al.*, 2006). Applying DNA-SIP to $^{13}CO_2$-exposed plants greatly helped to identify bacterial communities that actively assimilate root exudates in the rhizosphere of four plant species: wheat, maize, rape, and clover (Haichar *et al.*, 2008). Bacteria related to *Sphingobacteriales* and *Myxococcus* assimilated root exudates of all four plants, while *Sphingomonadales* were specific to monocotyledons (Haichar *et al.*, 2008). Analysis of fungal and bacterial biomarkers (phospholipid fatty acids) extracted from the rhizosphere of $^{13}CO_2$-exposed plants indicated that also fungi metabolized a significant amount of root exudates (Buée *et al.*, 2009). Hence, bacteria do not monopolize the rhizosphere and fungi can respond rapidly to the provision of easily degradable root exudates (Broeckling *et al.*, 2008; De Graaff *et al.*, 2010). Studying the community dynamics of saprotrophic fungi in the rhizosphere of six potato cultivars, Hannula *et al.* (2010)

indeed found that fungi make up a significant part of the rhizosphere microbial biomass especially during flowering and senescence. Based on DNA-SIP data, Drigo *et al.* (2010) provided a conceptual model in which plant-assimilated carbon is rapidly transferred to arbuscular mycorrhizal fungi (AMF), followed by a slower release from AMF to the active bacterial and fungal rhizosphere communities. Collectively, these studies exemplify that a combination of functional approaches provide powerful tools to infer physiological traits of microbial communities *in situ*.

Impact of the rhizosphere microbiome on plant growth, health, and disease

Rhizosphere microorganisms directly and indirectly influence the composition and productivity (i.e. biomass) of natural plant communities (van der Heijden *et al.*, 1998, 2006, 2008; Schnitzer *et al.*, 2011). Hence, microbial species richness belowground has been proposed as a predictor of aboveground plant diversity and productivity (De Deyn *et al.*, 2004; Hooper *et al.*, 2005; van der Heijden *et al.*, 2008; Lau & Lennon, 2011; Wagg *et al.*, 2011). Wagg *et al.* (2011) further suggested that belowground diversity may act as insurance for maintaining plant productivity under different environmental conditions. Due to their sensitivity to small changes in abiotic conditions, including environmental stress and perturbation, soil and rhizosphere microorganisms are considered as bioindicators of soil quality. Here, we will discuss which rhizosphere microorganisms impact on plant growth and health. We will focus on the plant beneficial ('the good'), plant pathogenic ('the bad'), and human pathogenic ('the ugly') microorganisms.

The good

Rhizosphere microorganisms promote plant growth and protect plants from pathogen attack by a range of mechanisms (Lugtenberg & Kamilova, 2009; Raaijmakers *et al.*, 2009). These involve biofertilization, stimulation of root growth, rhizoremediation, control of abiotic stress, and disease control. These mechanisms are well documented for rhizobacteria belonging to the *Proteobacteria* and *Firmicutes*, that is, *Pseudomonas* and *Bacillus*, as well as for fungi from the *Deuteromycetes*, that is, *Trichoderma* and *Gliocladium,* and from the *Sebacinales* order, that is, *Piriformospora* (Kogel *et al.*, 2006; Qiang *et al.*, 2012). Fortunately, more information is being obtained in the past years on the functions of other soil and rhizosphere inhabitants, including 'unusual' or 'rare' microbial genera such as the *Planctomycetes* (Hol *et al.*, 2010; Jogler *et al.*, 2012).

Effects of rhizosphere microorganisms on nutrient acquisition by plants

Members of the rhizosphere microbiome can significantly influence the nutrient status of plants (Fig. 2). Well-known examples are the nitrogen-fixing rhizobia and the mycorrhizal fungi that facilitate phosphorus uptake (Hawkins *et al.*, 2000; Richardson *et al.*, 2009; Miransari, 2011). The importance of symbionts such as mycorrhizal fungi for translocation of nutrients and minerals from soil to the plant (Gianinazzi *et al.*, 2010; Adeleke *et al.*, 2012; Johnson & Graham, 2013), for soil physical structuring and generating stable soil aggregates (Degens *et al.*, 1996; Miller & Jastrow, 2000), and for suppression of soilborne plant pathogens (Whipps, 2001; Pozo & Azcon-Aguilar, 2007) is well recognized and documented (Smith & Read, 1997; Varma & Hock, 1998; Kapulnik & Douds, 2000; Brundrett, 2002; van der Heijden & Sanders, 2002; Johnson *et al.*, 2012; Salvioli & Bonfante, 2013). Next to *Rhizobium* and *Bradyrhizobium,* various other nitrogen-fixing bacterial genera living in the rhizosphere have been identified (Zehr *et al.*, 2003; Gaby & Buckley, 2011). For example, analysis of the cowpea rhizosphere revealed a high genetic diversity of symbiotic rhizobial species in the western Amazon (Guimarães *et al.*, 2012). Based on glasshouse experiments and 16S rRNA gene sequencing, they indicated that *Bradyrhizobium*, *Rhizobium, Burkholderia,* and *Achromobacter* species were able to nodulate cowpea and were efficient in biological nitrogen fixation (Guimarães *et al.*, 2012). Despite extensive research on nitrogen fixation by rhizobia, the transfer of the legume-specific symbiosis to other agriculturally important plant species has not been achieved yet. In their recent review, Geurts *et al.* (2012) indicated that understanding the fundamental differences between the seemingly similar cellular responses induced by *Rhizobium* and mycorrhizal fungi will be necessary to achieve this 'old dream'.

Rhizosphere microorganisms can also facilitate the uptake of specific trace elements such as iron. Iron is abundant in soil but, under neutral to alkaline conditions, it exists primarily in the insoluble ferric oxide form, which is not available for microbial growth. Due to the scarcity of available iron in many microbial habitats as well as the toxicity of free iron at elevated concentrations, bacteria employ a variety of mechanisms to regulate intracellular iron concentrations by secretion of siderophores (Lindsay & Schwab, 1982; Andrews *et al.*, 2003; Buckling *et al.*, 2007; Hider & Kong, 2010). On the host side, plants respond to iron limitation by increasing the solubility of inorganic iron in the rhizosphere (strategy I) or by releasing phytosiderophores that are subsequently transported back into the root tissue by a specific uptake system (strategy II) (Walker & Connolly, 2008). In rice, iron can be

acquired by both strategies (Walker & Connolly, 2008). Various studies have proposed an additional strategy of iron acquisition by plants involving the use of iron chelated to microbial siderophores (Marschner & Römheld, 1994; Vansuyt *et al.*, 2007; Lemanceau *et al.*, 2009a, b). This was exemplified in studies with fluorescent pseudomonads, which promoted iron nutrition via siderophores not only for Graminaceous plants but also for dicotyledonous plant species (Vansuyt *et al.*, 2007; Shirley *et al.*, 2011). Also, rhizoferrin, a fungal siderophore produced by *Rhizopus arrhizus*, was found to be an efficient carrier of iron to plants with an efficiency that was comparable to that of synthetic chelates (Yehuda *et al.*, 2000). Rhizobacteria are also able to activate the plant's own iron acquisition machinery as was shown for *Bacillus subtilis* GB03 (Zhang *et al.*, 2009). In *Arabidopsis*, strain GB03 up-regulated transcription of the Fe-deficiency-induced transcription factor 1 (FIT1), thereby inducing the ferric reductase *FRO2* and the iron transporter *IRT1* (Zhang *et al.*, 2009). For more detailed overviews of the mechanisms by which rhizosphere microorganisms influence iron uptake by plants, we refer to Lemanceau *et al.* (2009a, b), and Marschner *et al.* (2011).

Most rhizobacterial species are organotrophs, that is, they obtain the energy from the assimilation of organic compounds. The availability and accessibility of degradable organic compounds are limited in most soils, and carbon availability is the most common limiting factor for soil bacteria growth (Alden *et al.*, 2001; Demoling *et al.*, 2007; Rousk & Baath, 2007). Bacterial communities play an essential role in releasing the nutritive cations from soil minerals required not only for their own nutrition but also for plant nutrition. Mineral weathering bacteria have been isolated from various environments, and particularly from rhizosphere and ectomycorrhizosphere (Puente *et al.*, 2004; Calvaruso *et al.*, 2007; Collignon *et al.*, 2011) and can contribute to plant growth in nutrient-poor soils (Leveau *et al.*, 2010; Mapelli *et al.*, 2012).

Supporting plant growth under biotic stress

The rhizosphere provides the frontline defense for plant roots against attack by soilborne pathogens (Cook *et al.*, 1995). Various members of the rhizosphere microbiome can antagonize soilborne pathogens before and during primary infection, and during secondary spread on and in root tissue (Fig. 2). The main mechanisms by which rhizosphere microorganisms ward off plant pathogens are antibiosis (Haas & Défago, 2005; Lugtenberg & Kamilova, 2009; Raaijmakers & Mazzola, 2012), competition for trace elements, nutrients and microsites (Duffy, 2001), parasitism (Druzhinina *et al.*, 2011; Mela *et al.*, 2011), interference with quorum sensing affecting virulence (Lin *et al.*, 2003; Uroz *et al.*, 2009; Chan *et al.*, 2011), and induced systemic resistance (Conrath, 2006; van Loon, 2007; Yang *et al.*, 2009; Pieterse, 2012; Schenk *et al.*, 2012).

Most, if not all, rhizobacteria produce metabolites that inhibit the growth or activity of competing microorganisms. Also, rhizosphere fungi are prolific producers of antibiotic metabolites (Hoffmeister & Keller, 2007; Brakhage & Schroeckh, 2011). Especially, *Trichoderma* species have received considerable attention for the production of antimicrobial compounds (Vyas & Mathus, 2002; Harman *et al.*, 2004; Mathivanan *et al.*, 2005; Elad *et al.*, 2008; Druzhinina *et al.*, 2011). Most fungal and bacterial biocontrol strains produce more than one antibiotic compound with overlapping or different degrees of antimicrobial activity. For example, bacteriocins such as agrocin 84 produced by *Agrobacterium radiobacter* (Reader *et al.*, 2005; Kim *et al.*, 2006) exhibit antibiotic activities against closely related genera, whereas many polyketide and nonribosomal peptide antibiotics exhibit broad-spectrum activities (Gross & Loper, 2009; Raaijmakers *et al.*, 2010). Interestingly, many antibiotic compounds have different effects on other microorganisms at subinhibitory concentrations, an observation which led to an exciting new direction in research on the natural functions of antibiotics. Recent studies have indeed shown that antibiotics function in a concentration-dependent manner, acting as growth inhibitors at high concentrations and as mediators of intercellular signaling at low concentrations (Davies *et al.*, 2006; Fajardo & Martinez, 2008; Romero *et al.*, 2011). Other natural functions attributed to antibiotics include a role in defense against predatory protozoa, motility, biofilm formation, and nutrition (Raaijmakers & Mazzola, 2012).

Among the metabolites produced by rhizosphere microorganisms, volatile organic compounds (VOCs) are receiving more attention over the past years. Some of them were shown to modulate plant growth and to mediate the intricate dialogues between microorganisms and plants (Bailly & Weisskopf, 2012; Effmert *et al.*, 2012). Although VOCs appear to represent a small proportion of the total number of metabolites produced by fungi and bacteria, their unique properties have been proposed to play essential functions in long-distance communication in the rhizosphere and in soil ecosystems. VOCs are small molecules (< 300 Da) with high vapor pressures able to diffuse through the water- and gas-filled pores in soil (Wheatley, 2002; Insam & Seewald, 2010). Various bacterial species including *Stenotrophomonas maltophilia*, *Serratia plymuthica*, *Pseudomonas trivialis*, *P. fluorescens*, *B. subtilis,* and *Burkholderia cepacia* produce VOCs that inhibit mycelial growth of fungal plant pathogens (Kai

et al., 2007, 2009; Vespermann *et al.*, 2007; Zou *et al.*, 2007; Jamalizadeh *et al.*, 2010). Most work on VOCs to date, however, is conducted *in vitro* on nutrient-rich media and may not be representative of the conditions that prevail in the rhizosphere. Effects of specific abiotic conditions on VOC production were shown by Weise *et al.* (2012), who reported a discrepancy in the number and spectrum of volatiles produced by a *Xanthomonas* species grown in broth culture and on solid agar media. Recent work showed that the spectrum of volatiles released by rhizobacteria can be influenced by the available pool of root exudates (P. Garbeva, unpublished data). For example, volatiles produced in soil amended with artificial root exudates without amino acids had strong antibacterial effects but mild antifungal effects, whereas volatiles produced from root exudates supplemented with amino acids had strong antifungal effects (P. Garbeva, unpublished data). Conversely, bacterial volatiles may promote growth of ectomycorrhizal fungi (Schrey *et al.*, 2005) and play important regulatory roles in mycorrhizal network establishment (Bonfante & Anca, 2009). They may also play a role in the tripartite interactions between bacteria, fungi, and nematodes. In this context, Son *et al.* (2009) showed that *Paenibacillus polymyxa* and *Paenibacillus lentimorbus* exhibited strong antifungal activities, thereby interfering with the interactions between *Meloidogyne incognita* and *Fusarium oxysporum* and concomitant nematode infestation of tomato plants. Recently, Chernin *et al.* (2011) reported that bacterial volatiles can also interfere with quorum sensing of phylogenetically different bacteria by suppressing the transcription of the *N*-acyl-homoserine lactone synthase genes. Dimethylsulfide was identified as one of the compounds that interfered with quorum sensing (Chernin *et al.*, 2011). Finally, VOCs can also induce systemic resistance in plants (Ryu *et al.*, 2003, 2004; Han *et al.*, 2006) and promote plant growth (Ryu *et al.*, 2003; Cho *et al.*, 2008; Blom *et al.*, 2011a, b; Bailly & Weisskopf, 2012).

Members of the rhizosphere microbiome can also modulate the plant immune system (De Vleesschauwer & Hofte, 2009; Pineda *et al.*, 2010; Berendsen *et al.*, 2012; Zamioudis & Pieterse, 2012). The systemic resistance response induced in plants by beneficial rhizobacteria is in many cases regulated by the phytohormones jasmonic acid (JA) and ethylene (ET) (Zamioudis & Pieterse, 2012). However, some bacterial strains do not induce systemic resistance via the JA/ET pathway but via the salicylic acid (SA)-pathway (Maurhofer *et al.*, 1994; De Meyer & Hofte, 1997; Maurhofer *et al.*, 1998; De Meyer *et al.*, 1999; Audenaert *et al.*, 2002; Barriuso *et al.*, 2008; van de Mortel *et al.*, 2012). Other rhizobacteria such as *Bacillus cereus* AR156 induce systemic resistance by activating both signaling pathways (Niu *et al.*, 2011). Furthermore, quorum-sensing molecules from rhizobacteria can provoke a range of plant responses, including the activation of various defense-related genes such as MPK3, MPK6, WRKY22, WRKY29, and Pdf1.2 (reviewed in Hartmann & Schikora, 2012). Over the past years, significant progress has been made in unraveling the transcriptional and metabolic changes induced in plants by rhizobacteria. For those bacterial strains that induce resistance via the JA/ET pathways, relatively few transcriptional changes were observed in *Arabidopsis* (Verhagen *et al.*, 2004; Cartieaux *et al.*, 2008;). However, for rhizobacterial strains that induce resistance in *Arabidopsis* via the SA pathway, substantial, transcriptional, and metabolic changes were observed (van de Mortel *et al.*, 2012). By integrating metabolic pathways and transcript profiles, Weston *et al.* (2012a, b) further showed that two distinct strains of *P. fluorescens* reduced the host plant's carbon gain, but provided a fitness benefit when the plants were challenged with the pathogen *Pseudomonas syringae*. These studies indicated that rhizobacteria can have diverse and profound effects on the immune response and physiology/metabolism of the host plant (Fig. 2), enhancing the production of known secondary metabolites but also inducing the biosynthesis of structurally unknown metabolites (van de Mortel *et al.*, 2012). Analysis of the identity and activities of 'cryptic' plant compounds induced by rhizobacteria should be pursued to resolve their putative functions in induced systemic resistance and other physiological processes.

Supporting plant growth under abiotic stress

It has been postulated that the rhizosphere microbiome contributes to the ability of some plant species to survive under extreme conditions (Jorquera *et al.*, 2012). For example, *Achromobacter piechaudii* ARV8, a soil isolate obtained from an arid and saline environment, significantly increased the biomass of tomato and pepper seedlings exposed to transient drought stress (Mayak *et al.*, 2004a, b). Also, under conditions of flooding, rhizobacteria were shown to support plant growth (Grichko & Glick, 2001). In diverse production systems, plant productivity can be strongly affected by soil salinity due to osmotic and drought stress. Halotolerant bacteria thrive under salt-stress conditions and in association with the host plant are able to express traits that promote plant growth. From the rhizosphere of wheat plants grown in a saline zone, Upadhyay *et al.* (2009) showed that of 130 rhizobacterial isolates, 24 were tolerant to relatively high levels (8%) of NaCl. All of the 24 salt-tolerant isolates produced indole-3-acetic acid, 10 isolates solubilized phosphorus, eight produced siderophores, six produced gibberellin, and two isolates contained the *nif*H gene,

indicating their potential for nitrogen fixation. The dominant bacterial genus isolated under these conditions was *Bacillus* (Upadhyay *et al.*, 2009). Halotolerant bacterial strains were also isolated from halophytic plant species found in coastal soils in Korea. Several of the obtained isolates enhanced plant growth under saline stress, and the reduction in ET production via ACC deaminase activity was proposed as the underlying mechanism of plant growth promotion (Siddikee *et al.*, 2010). New halotolerant diazotrophic bacteria harboring indole acetic acid production, phosphate solubilization, and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity were isolated from roots of the extreme halophyte *Salicornia brachiate* (Jha *et al.*, 2012). The isolates were identified as *Brachybacterium saurashtrense* sp. nov., *Zhihengliuella* sp., *Brevibacterium casei*, *Haererehalobacter* sp., *Halomonas* sp., *Vibrio* sp., *Cronobacter sakazakii*, *Pseudomonas* spp., *Rhizobium radiobacter*, and *Mesorhizobium* sp. (Jha *et al.*, 2012). For more comprehensive reviews on the beneficial effects of soil biota on plant responses to saline stress, we refer to reviews by Dodd & Pérez-Alfocea (2012) and Berg *et al.* (2013). In these reviews, several mechanisms are described by which microorganisms may alter plant physiological response under saline stress, including their effects on: (1) water homeostasis by osmolyte accumulation, (2) plant energetics by modulating the source-sink relationships, (3) root uptake of toxic ions and nutrients by altering host physiology, modifying physical barriers around the roots, or by directly reducing foliar accumulation of toxic ions, and (4) crop salt tolerance by altering hormonal root–shoot signaling.

Environments with low temperatures harbor microorganisms adapted to live under such conditions. It is interesting to note that despite the impact of low temperatures on nodule formation and nitrogen fixation, native legumes in the high arctic can nodulate and fix nitrogen at rates comparable to those reported for legumes in temperate climates (Bordeleau & Prévost, 1994). There is great interest in agriculture and horticulture for microbial inoculants that enhance growth of plants under cold conditions. For example, *Burkholderia phytofirmans* PsJN increased grapevine root growth and physiological activity at temperatures down to 4°C (Barka *et al.*, 2006). When coinoculated with *Bradyrhizobium japonicum*, *Serratia proteamaculans* stimulated soybean growth at 15°C, the temperature at which soybean nodule infection and nitrogen fixation are normally inhibited (Zhang *et al.*, 1995, 1996). To identify mechanisms involved in plant growth promotion at low temperatures, Katiyar & Goel (2003) selected cold-tolerant mutants of different *P. fluorescens* strains for their ability to solubilize phosphorus and to promote plant growth. They identified two cold-tolerant mutants that were more efficient in phosphorus solubilization at 10 °C than their respective wild types (Katiyar & Goel, 2003). Also, Trivedi & Sa (2008) found two mutants (of 115) that were more efficient than the wild-type strain *Pseudomonas corrugata* in phosphorus solubilization across a temperature range from 4 to 28 °C. In both studies, the identity of the genes associated with cold tolerance and phosphorus solubilization was not mentioned.

Other abiotic factors that may adversely affect plant growth are pH and high concentrations of toxic compounds. Soils with low pH or contaminated soils are major challenges in many production systems worldwide. In the case of pH stress, it was demonstrated that foliar lesions induced on corn growing in a low-pH soil were significantly reduced on plants treated with a 2,4-diacetylphloroglucinol (DAPG)-producing *P. fluorescens* strain. This was the first evidence that DAPG producers, in addition to their role in pathogen control, can also act to ameliorate abiotic stress factors (Raudales *et al.*, 2009). The presence of pollutants in soil has promoted the search for efficient bioremediation methods as an alternative for excavation and incineration. Rhizoremediation, a combination of phytoremediation and bioaugmentation (Kuiper *et al.*, 2004), is a promising strategy to clean polluted sites. During rhizoremediation, exudates of plants stimulate the survival and activity of rhizobacteria that degrade pollutants. A recent study, using a split-root model and a combination of T-RFLP, DGGE, and 16S rRNA gene pyrosequencing, showed that *Trifolium* and other legumes respond to polycyclic aromatic hydrocarbons contamination in a systemic manner (Kawasaki *et al.*, 2012). *Verrucomicrobia* and *Actinobacteria* were more abundant in the contaminated rhizospheres, and the *betaproteobacterium Denitratisoma* was substantially increased in the presence of the contaminant, suggesting that this genus may be important in the rhizoremediation process (Kawasaki *et al.*, 2012). Also, fungi are important players in rhizoremediation of hydrocarbons as was shown by inoculation of the endophytic fungus *Lewia* sp. in the rhizosphere of *Festuca arundinacea* (Cruz-Hernández *et al.*, 2012).

In conclusion, members of the rhizosphere microbiome can alleviate biotic and abiotic stresses on plants (Fig. 2), providing an environmentally sound alternative for genetic engineering and plant breeding. However, successful implementation of microbial inoculants is still in its infancy due to multiple constraints, including variable efficacy across environments and different plants species, limited shelf-life, and different registration procedures in different countries. To resolve several of these constraints, more fundamental knowledge is required on how beneficial rhizosphere microorganisms communicate with the host plant, which molecular and metabolic changes are

induced in plants, and how beneficial microorganisms affect the population dynamics and virulence of plant pathogenic microorganisms.

The bad

Soilborne plant pathogens cause major yield reductions in the production of food, feed, fiber, and fuel crops (Fig. 2). Two main groups of soilborne plant pathogens are the nematodes and the fungi, including the true fungi and the fungal-like oomycetes. In temperate climates, plant pathogenic fungi, oomycetes, and nematodes are agronomically more important than plant pathogenic bacteria, although some bacterial genera (i.e. *Pectobacterium, Ralstonia*) can cause substantial economic damage in some crops. For bacterial pathogens that infect plants via roots, *Agrobacterium tumefaciens*, *Ralstonia solanacearum, Dickeya dadanthi* and *Dickeya solani*, and *Pectobacterium carotovorum* and *Pectobacterium atrosepticum* are among the top 10 most notorious (Mansfield *et al.*, 2012). Also, viruses can infect plants via the roots but require vectors such as nematodes or zoosporic fungi to enter the root tissue (Campbell, 1996; Macfarlane, 2003). Compared with our understanding of the role of rhizodeposits in the communication between symbionts and plants, information on root exudates that activate and attract soilborne plant pathogens is more scarce and fragmented. Weston *et al.* (2012a, b) indicated that the limited knowledge of the communication between plants and root pathogens is largely due to a poor understanding of the complex physical–chemical conditions in soil and rhizosphere environments. Hence, expanding our analytical skills to elucidate the chemistry of rhizodeposits and their spatiotemporal production and distribution patterns, collectively termed 'ecometabolomics' (Sardans *et al.*, 2011; Weston *et al.*, 2012a, b), will be important to resolve the dialogues between pathogens and plant roots. Here, we will discuss which processes and chemical cues are important for soilborne pathogens to colonize the rhizosphere and to infect the root tissue. We will focus on few examples of fungi, oomycetes, and nematodes.

Fungi and oomycetes

For germination, growth and establishment in the rhizosphere, fungal, and oomycete pathogens depend on several different cues from the host plant. Dormancy of fungal spores can be triggered by a range of factors, including changes in abiotic conditions (i.e. pH) and root exudates. Wu *et al.* (2008a, b) found that phenolic compounds like *p*-hydroxybenzoic, gallic, coumaric, cinnamic, ferulic, salicylic, and sinamic acids in root exudates stimulated, at low concentrations, conidial germination of pathogenic fungi; when concentrations increased, an inhibitory effect was observed. Also, Zhang *et al.* (2012) found similar effects of four phenolic acids from cotton root exudates on germination of *Verticillium dahliae* spores. Also, alkaloids from roots of *Veratrum taliense* (*Liliaceae*) were shown to inhibit growth of *Phytophthora capsici* and *Rhizoctonia cerealis* (Zhou *et al.*, 2003). Interestingly, work by Joosten *et al.* (2009) showed that soil type and soil microorganisms greatly affected the composition of alkaloids in roots and shoots of *Jacobaea vulgaris*, in particular retrorsine and retrorsine N-oxide. Both alkaloids inhibit mycelium growth of several plant-associated fungi, including *F. oxysporum*, *Fusarium sambucinum*, and *Trichoderma* sp. (Hol & Van Veen, 2002). Based on these results, Joosten & van Veen (2011) postulated that the effect of microorganisms on the alkaloid composition of plants could have other ecological consequences as these changes may attract specialist herbivores aboveground while deterring generalists.

Saponins are probably the best examples of chemical constituents of roots that adversely affect plant pathogenic fungi. Saponins represent a structurally diverse group of glycosides with triterpene or steroid backbones. They form complexes with sterols causing pore formation and loss of membrane integrity in fungal pathogens (Gonzalez-Lamothe *et al.*, 2009; Osbourn *et al.*, 2011). Compelling evidence for a role of saponins in protection of plants against root-infecting fungi was provided by studies on avenacin (Bednarek & Osbourn, 2009; Gonzalez-Lamothe *et al.*, 2009; Osbourn *et al.*, 2011). Avenacin A-1 exhibits antifungal activity and is localized in the epidermal cells of root tips and emerging lateral roots of oats. The fungal root pathogen *Gaeumannomyces graminis* var *avenae* (*Gga*) can detoxify avenacin A-1 and infect oat roots, whereas *Gga*-mutants that lack the detoxifying hydrolase, designated avenacinase, were more sensitive to avenacin A-1 and were no longer able to infect. On the plant side, avenacin-deficient mutants showed compromised resistance to several pathogens. Recent studies further suggested that avenacin or avenacin intermediates may also elicit other processes in the plant such as callose deposition (Bednarek & Osbourn, 2009) which in turn strengthens the defense response. Other studies indicated that plant metabolites, like glucosinolates in cruciferous plants, are mobilized to pathogen infection sites where they are enzymatically converted into biologically active compounds only when they are released by disruption of the plant tissue (Bednarek & Osbourn, 2009). Pathways and mechanisms involved in the safe storage and exudation of secondary metabolites in plants were highlighted in recent reviews by Sardans *et al.* (2011) and Weston *et al.* (2012a, b).

In contrast to root-infecting fungi, oomycete pathogens produce motile zoospores that swim toward the plant

root to initiate infection. Next to the effects of specific compounds in seed and root exudates on zoospore behavior (Morris & Ward, 1992; Nelson, 2004; Hua *et al.*, 2008), the work by van West *et al.* (2002) pointed to electrotaxis as a key root-targeting mechanism for zoospores. Plant roots generate external electrical currents due to the flow of protons and other ions into and out of growing and wounded regions (van West *et al.*, 2002). In a series of experiments, van West *et al.* (2002) showed that the profile of endogenous electrical fields generated by plant roots coincided with the sites where electrotactic species of zoospores accumulated. They also showed that induced or imposed electrical fields were capable of overriding local chemical cues in the rhizosphere that either mediate attraction or repulsion. They further postulated that electrotaxis is an important cue for zoosporic pathogens to selectively colonize living rather than dead roots, thereby maximizing their survival rate. Whether electrotaxis also plays a role in the chemotactic responses of soilborne pathogenic fungi and bacteria is, to our knowledge, not known yet.

Nematodes

Most nematodes in soil are free living, but some feed on the root exterior (migratory ectoparasitic), some penetrate and move in the root interior (migratory endoparasitic), while others develop a feeding site in the root where they reproduce (sedentary endoparasites). For plant parasitic nematodes other than cyst or polyphagous root knot nematodes, it is critical to exploit chemical gradients to find their host plant (Rasmann *et al.*, 2012). Their sensory apparatus enables them to orientate, move, and locate nutrient sources. In the physico-chemically complex soil matrix, volatile as well as water-soluble compounds are important cues for nematode foraging. Volatile compounds have been suggested to play a major role in long-range chemotaxis, whereas water-soluble compounds were proposed to be more suitable for short-range chemotaxis (Rasmann *et al.*, 2012). Most studies to date have reported on plant-derived compounds that attract nematodes, but also nematode repellent compounds have been identified like α-terthienyl, inositol, and cucurbitacin A (Johnson & Nielsen, 2012; Rasmann *et al.*, 2012; Turlings *et al.*, 2012). Among the volatiles emitted by plant roots, CO_2 is the main so-called long-distance kairomone for root location by plant parasitic nematodes, with a theoretical action-radius of up to 1 m for a single root and more than 2 m for a complete root system (Johnson & Nielsen, 2012). Turlings *et al.* (2012) postulated that CO_2 most likely serves as a 'response activator' that alerts the entomopathogenic nematodes to the general presence of other organisms and may enhance their responsiveness to more specific cues. Besides CO_2, many other compounds from different chemical classes induce chemotaxis in nematodes such as 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), glutamic and ascorbic acid (Rasmann *et al.*, 2012). Knowledge of the chemical cues that attracts nematodes and other pathogens can and has been exploited to attract these pathogens to nonhost crops (Franco *et al.*, 1999). Classic examples of these trap crops are *Asparagus officinalis* and *Tagetes* species that attract a wide range of nematodes which, after being lured in, are killed by defensive compounds such as glycosides (Bilgrami, 1997; Rasmann *et al.*, 2012).

The ugly

In the last decade, disease outbreaks linked to human pathogen contamination of fresh plant produce are a growing concern worldwide (Berg *et al.*, 2005; van Baarlen *et al.*, 2007; Tyler & Triplett, 2008; Whipps *et al.* 2008; Holden *et al.*, 2009; Teplitski *et al.*, 2009; Critzer & Doyle, 2010). Salmonellosis is increasingly linked to contaminated horticultural products, including fruits, lettuce, cabbage, and other raw salad vegetables. Similarly, *Escherichia coli* O157:H7, the causal agent of the life-threatening hemorrhagic colitis and hemolytic uremic syndrome, has been isolated with increased frequency from fresh food products. A series of studies have clearly shown that human pathogenic bacteria can enter the food production chain not only after harvest and during handling of fresh food products, but also during the preharvest stages of crop production. Preharvest entry can occur via contaminated manure and irrigation water, animals, or seeds. Their ability to survive in soils and to colonize the plant exemplifies that human pathogenic bacteria are not solely adapted to propagate and survive in the animal gastrointestinal tracts. Instead, there appears to be a continuum of available microsites on different hosts that allows for cross-kingdom jumps by human pathogenic bacteria (van Baarlen *et al.*, 2007; Holden *et al.*, 2009; Kaestli *et al.*, 2012). In this context, Tyler & Triplett (2008) suggested that human pathogens may use plants '*as an alternative host to survive in the environment and as a vehicle to re-colonize animal hosts once ingested*'.

Opportunistic human pathogens in the rhizosphere

Next to the 'true' human pathogens such as *Salmonella enterica* serovar *Typhimurium* and *E. coli* O157:H7, the plant environment is a niche for pathogens that cause diseases only in debilitated or immunocompromised humans.

These so-called opportunistic or facultative human pathogens have been associated with significant case fatality ratios in patients in Europe and Northern America, and their impact on human health has increased substantially over the past two decades (Berg *et al.*, 2005; Teplitski *et al.*, 2011). Various wild and cultivated plant species have been reported to host opportunistic human pathogens in the rhizosphere (Fig. 2), in particular *B. (ceno)cepacia, P. aeruginosa,* and *S. maltophilia* (Berg *et al.*, 2005). However, also other bacterial species that cause skin, wound, and urinary tract infections (e.g. *B. cereus, Proteus vulgaris*) can be found in rhizosphere environments (Berg *et al.*, 2005). Although many studies have highlighted the presence of opportunistic human pathogens in the rhizosphere, relatively little is known about their virulence relative to their clinical counterparts. In a recent study on *P. aeruginosa* PaBP35, a strain isolated from the aerial shoots of black pepper plants grown in a remote rain forest in southern India, we used a panel of discriminatory genotyping methods such as *rec*N sequencing, multilocus sequence typing, and comparative genome hybridization to assess the strain's identity and to determine its genetic relatedness to *P. aeruginosa* strains that originated from clinical habitats (Kumar *et al.*, 2013). These polyphasic approaches showed that strain PaBP35 was a singleton among a large collection of *P. aeruginosa* strains, clustering distantly from the typical clinical isolates (Kumar *et al.*, 2013). However, subsequent analyses revealed that strain PaBP35 was resistant to multiple antibiotics, grew at temperatures up to 41°C, produced rhamnolipids, hydrogen cyanide, and phenazine antibiotics, displayed cytotoxicity on mammalian cells, and caused infection in an acute murine airway infection model (Kumar *et al.*, 2013). In contrast, Wu *et al.* (2011) found that plant-associated *P. aeruginosa* M18 was more susceptible to several antimicrobial agents and easier to be erased in a mouse acute lung infection model than clinical strain LESB58. These and other studies highlighted the versatile functional and adaptive behavior of *P. aeruginosa* and exemplified that *P. aeruginosa* strains originating from different environments can differ in accessory genome regions, genome expression profiles, virulence activities, and antibiotic resistance spectrum.

The occurrence of human pathogenic bacteria in the rhizosphere has been ascribed to several factors, including the high nutritional content, protection from UV radiation, and the availability of water films for dispersal and for preventing desiccation (Berg *et al.*, 2005; Tyler & Triplett, 2008). Others have argued that the abundant and highly diverse indigenous rhizosphere microbial communities provide a strong barrier against the invasion of human pathogens. This was exemplified in a study by Colley *et al.* (2003) where growth of *S. enterica* and *E. coli* O157:H7 on roots of *Arabidopsis thaliana* was strongly inhibited by a plant-associated strain of *Enterobacter asburiae*. Nevertheless, many of the human pathogenic bacteria can be highly competitive for nutrients and produce various antimicrobial metabolites allowing them to colonize and proliferate on plant surfaces in the presence of the indigenous microbial communities. For example, *P. aeruginosa* was shown to be an excellent colonizer of the wheat rhizosphere (Troxler *et al.*, 1997). Also, clinical and plant-associated *Stenotrophomonas* strains efficiently colonized the strawberry rhizosphere and even stimulated root growth and root hair development (Suckstorff & Berg, 2003). Interestingly, the mechanisms involved in rhizosphere colonization and antimicrobial activity of human pathogenic bacteria appear to be similar to the mechanisms involved in virulence and colonization of human tissues (Berg *et al.*, 2005; van Baarlen *et al.*, 2007; Holden *et al.*, 2009). For example, several of the *B. cepacia* strains that caused disease in a lung infection model were also virulent on alfalfa (Bernier *et al.*, 2003). For *S. enterica*, several pathogenicity genes as well as genes related to carbon utilization were differentially regulated in the presence of lettuce root exudates (Klerks *et al.*, 2007). Combined with the results of chemotaxis assays, Klerks *et al.* (2007) postulated that the root exudates trigger chemotaxis in *S. enterica* and switch on genes that play a role in adherence. Several other genes and traits have been identified to play a role in the attachment of human pathogens to plant surface, including fimbriae, adhesins, and capsule production. For more comprehensive reviews on this topic, we refer to van Baarlen *et al.* (2007), Tyler & Triplett (2008), Holden *et al.* (2009), and Teplitski *et al.* (2011).

Plant colonization by human pathogens

Following attachment, human pathogenic bacteria and in particular the *Enterobacteriaceae* can invade the root tissue. For a more extensive list of examples on internalization of human pathogens in plants, we refer to Warriner & Namvar (2010). In contrast to the invasion of animal hosts, enteric bacteria appear to reside mostly in the apoplastic spaces of plant hosts (Holden *et al.*, 2009). Various studies have indicated that human pathogenic bacteria enter the root tissue at sites of lateral root emergence. This was shown for *Salmonella* and *E. coli* O157:H7 on roots of *Arabidopsis* and lettuce, and for *Klebsiella pneumoniae* on multiple plant species (Tyler & Triplett, 2008). Endophytic and systemic colonization of barley by the foodborne pathogen *S. enterica* serovar *Typhimurium* was also demonstrated by Kutter *et al.* (2006). Also for opportunistic human pathogens, damaged roots provide an easy access point resulting in invasion and endophytic colonization. For example, *P. aeruginosa* PaBP35 was able

to colonize the shoots of black pepper stem cuttings at relatively high densities (> 10^5 CFU per gram of shoot segment) already after 8 min of root treatment (Kumar *et al.*, 2013). The invasive and endophytic behavior of strain PaBP35 was not limited to black pepper but was also demonstrated for tomato seedlings (Kumar *et al.*, 2013). Interestingly, strain PaBP35 established significantly higher population densities in the root and shoot of tomato seedlings than *P. aeruginosa* PA01 (Kumar *et al.*, 2013), suggesting some level of specificity in endophytic colonization.

Not only do the sites of lateral root emergence provide entry points, but damage caused by plant pathogens may also contribute to plant colonization and invasion by human pathogenic bacteria. To date, most studies have focused on the role of pathogen infection of edible plant produce on human pathogen colonization. For example, fruits and vegetables infected with soft rot pathogens led to significant increases in populations of *Salmonella* and *E. coli* O157:H7 (Teplitski *et al.*, 2011). Next to a loss of cell tissue integrity and a concomitant release of nutrients from infected plant tissue, degradation of plant tissue by macerating plant pathogens may also lead to an increase in pH that could be beneficial to enteric pathogens (Holden *et al.*, 2009; Teplitski *et al.*, 2011). Furthermore, plant pathogens may also suppress plant defenses that otherwise would have limited the invasion and endophytic colonization by human pathogens (Iniguez *et al.*, 2005). Teplitski *et al.* (2011) further postulated that controlling plant pathogens would reduce the predisposition of plant produce to colonization by human pathogens.

Soil health status and occurrence of potential human pathogens

In a first attempt to determine the effect of the soil and plant health status on the abundance and diversity of opportunistic human pathogenic bacteria in the rhizosphere, we analyzed the PhyloChip data obtained in the rhizosphere microbiome study conducted for sugar beet seedlings grown in soils that are suppressive or conducive to *Rhizoctonia* damping-off disease (Mendes *et al.*, 2011). In these disease-suppressive soils, the fungal pathogen *Rhizoctonia solani* did not cause disease or only very little as compared with the disease-conducive (nonsuppressive) soil. Disease suppressiveness was microbial in nature as it was eliminated by selective heat treatments or by γ-irradiation (Mendes *et al.*, 2011). For both the *Rhizoctonia*-suppressive and *Rhizoctonia*-conducive soils, we screened the PhyloChip data for the presence of 44 potentially human pathogenic bacteria reported previously by Berg *et al.* (2005) for the rhizosphere of other plant species. Based on these analyses, a total of 249 OTUs distributed over 29 bacterial species were detected in disease-conducive and disease-suppressive soils. However, most of these potentially human pathogenic bacterial OTUs were significantly more abundant in the conducive soil (158; 63.5%) than in the suppressive soil (91; 36.5%) (Fig. 4a). All *Firmicutes* (25 OTUs), with *B. cereus* as the dominant group (88%), were more abundant in the rhizosphere of sugar beet seedlings grown in the conducive soil. Considering the total abundance of each species, that is, the sum of the relative abundance of all OTUs within each species, nine potentially human pathogens were statistically more abundant in the nonsuppressive soil, including *Achromobacter xylosoxidans*, *Alcaligenes faecalis*, *Alcaligenes xylosoxidans*, *Janthinobacterium lividum*, *Enterobacter amnigenus*, *Serratia marcescens*, *B. cereus,* and *Staphylococcus aureus* (Fig. 4b). Conversely, *S. maltophilia* was significantly more abundant in suppressive than in conducive rhizosphere soil (Fig. 4b). These results suggest that the rhizosphere of sugar beet seedlings grown in a disease-conducive soil harbors more potentially human pathogenic bacteria than seedlings grown in a disease-suppressive soil. It should be noted that these preliminary data should be interpreted with caution as the PhyloChip-based 16S rRNA gene analysis does not allow accurate classification at the species level (Philippot *et al.*, 2010). Additional molecular markers, including virulence genes, should be used to further enhance the taxonomic resolution of these analyses and to support the hypothesis that root-infecting plant pathogens can lead to a substantial increase in the population densities of opportunistic human pathogens on and in root tissue.

Shaping the rhizosphere microbiome

From the previous sections, it is obvious that the rhizosphere microbiome is a dynamic blend of beneficial and pathogenic (plant, human) microorganisms. The composition, relative abundance, and spatiotemporal dynamics of these members of the rhizosphere microbiome will not only impact on plant growth but may also affect human health. Hence, there is a major interest to develop strategies that reshape the rhizosphere microbiome in favor of microorganisms that improve plant productivity and that prevent the proliferation of plant and human pathogens. Numerous studies conducted over the past three decades have clearly shown that the plant genotype and the soil type are two main drivers that shape the rhizosphere microbiome (Berg & Smalla, 2009; Bakker *et al.*, 2012). Plants are able to recruit specific members of the soil microbiome as was elegantly shown for malic-acid-mediated stimulation of beneficial *B. subtilis* (Rudrappa *et al.*, 2008). Recently, evidence was provided that beneficial *Pseudomonas putida* is not only tolerant but also attracted

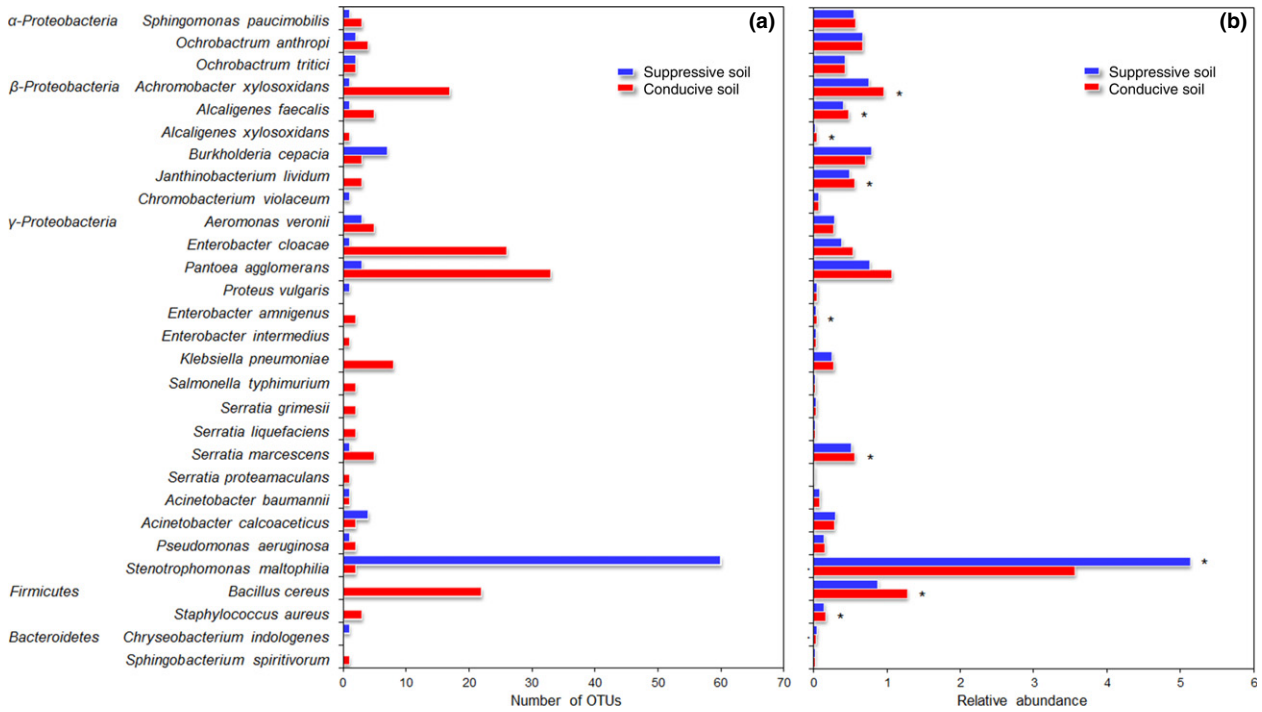

Fig. 4. Occurrence of putative opportunistic human pathogenic bacteria in the rhizosphere of sugar beet seedlings grown in soils suppressive or conducive to the fungal pathogen *Rhizoctonia solani*. Of more than 33 000 bacterial OTUs detected in the rhizosphere of sugar beet by PhyloChip analysis (Mendes *et al.*, 2011), 249 OTUs, distributed over 29 bacterial species, were detected in both soils and classified as potential human pathogens. (a) Number of OTUs: the bars indicate the number of opportunistic human pathogenic OTUs that are more abundant in suppressive or conducive soil. For example, all of the 23 OTUs classified as *Bacillus cereus* were more abundant in the conducive soil. (b) Relative abundance: the bars indicate the average ($N = 4$) of the total relative abundance of the putative human pathogenic OTUs. Asterisks indicate statistically significant differences ($P < 0.05$, Student's *t*-test).

to DIMBOA, the allelochemical that is exuded in relatively high quantities from roots of young maize seedlings (Neal *et al.*, 2012). However, several metabolites that act as chemoattractant for beneficial microorganisms may also trigger the germination and directional growth of plant pathogens. For example, isoflavones from soybean roots attract the symbiont *B. japonicum* but also the oomycete pathogen *Phytophthora sojae* (Morris *et al.*, 1998). Plant flavonoids also stimulate mycorrhizal spore germination and hyphal branching and can affect quorum sensing (Faure *et al.*, 2009; Guo *et al.*, 2011; Hassan & Mathesius, 2012). Similarly, volatiles released from plant roots attract both plant parasitic and entomopathogenic nematodes, and may also exhibit direct antimicrobial activities (Garbeva *et al.*, 2011a; Rasmann *et al.*, 2012; Turlings *et al.*, 2012).

The effects of soil type on the rhizosphere microbiome have been demonstrated for a variety of plant species worldwide (Berg & Smalla, 2009). Soils represent highly complex and heterogeneous environments, which in turn affect plant physiology, root exudation patterns, and concomitantly the rhizosphere microbiome. A key soil factor in this is pH. Fierer & Jackson (2006) collected 98 soil samples from across North and South America and showed that bacterial diversity was unrelated to site temperature, latitude, and other variables that typically predict plant and animal diversity. The diversity and richness of soil bacterial communities differed by ecosystem type and were largely explained by soil pH. They observed that bacterial diversity was highest in neutral soils and lower in acidic soils, with soils from the Peruvian Amazon as the most acidic and least diverse (Fierer & Jackson, 2006). Also, Lauber *et al.* (2009) found that the overall bacterial community composition in 88 different soils was significantly correlated with soil pH. This influence of pH on community composition was evident at a coarse level of taxonomic resolution with the relative abundance of certain bacterial phyla (e.g. *Actinobacteria*, *Bacterioidetes*, and *Acidobacteria*) changing in a constant manner across the soil pH gradient (Lauber *et al.*, 2009). When studying the abundance and diversity of the *amo*A gene in 47 well-characterized soils in the UK with pH ranges from 3.5 to 8.7, Gubry-Rangin *et al.* (2011) found evidence that also individual archaeal lineages were adapted to specific pH

ranges. The apparent influence of soil pH on microbiome structure has also been documented in several other studies (Baath & Anderson, 2003; Cookson *et al.*, 2007) and may be explained, in part, by the relatively narrow pH growth tolerance of bacterial taxa (Rousk *et al.*, 2010).

Redirecting the rhizosphere microbiome by plant breeding and genetic engineering

A number of strategies have been proposed to reshape the microbial composition of the rhizosphere and to redirect microbial activity. Considering the role of root exudates in the attraction of plant pathogens and the subsequent activation of virulence factors, changing the quantity and/or quality of root exudates via plant breeding or genetic modification is an obvious approach to redirect the rhizosphere microbiome. This strategy, also referred to as 'rhizosphere engineering' (Oger *et al.*, 2004; Ryan *et al.*, 2009; Bakker *et al.*, 2012), requires in-depth understanding of the chemical diversity of rhizodeposits and of the molecular communication in the rhizosphere.

Although our understanding of communications and interactions is progressing, there are still only a few examples of breeding programs that have considered rhizosphere-related traits and root exudation characteristics (Smith & Goodman, 1999; Smith *et al.*, 1999; Rengel, 2002; Wissuwa *et al.*, 2009). In this context, Bakker *et al.* (2012) stated that currently there is no known breeding program that evaluates plant lines for their broad interaction with the soil microbiome. Smith *et al.* (1999) provided one of the initial studies to investigate the genetic basis in plants for interactions with rhizobacteria that are antagonistic to plant pathogens. Using several inbred lines of tomato, they identified three quantitative trait loci (QTL) associated with disease suppression by a strain of *B. cereus*. They detected significant phenotypic variation among recombinant inbred lines of tomato and made an attempt to identify loci associated with resistance to *Pythium torulosum*, disease suppression by *B. cereus*, and with growth of *B. cereus* on the seed. Genetic analyses revealed that three QTL associated with disease suppression explained 38% of the phenotypic variation among the recombinant inbred lines. Their results indicated that genetic variation in host plant species can be exploited to enhance the beneficial associations between plants and rhizosphere microorganisms. Their work also suggested that modern plant breeding may have selected against plant traits that are essential for hosting and supporting beneficial microorganisms.

Genetic engineering is a promising alternative to traditional plant breeding but is time-consuming. Some of the genetic engineering has been performed to modify the rhizosphere pH (Gevaudant *et al.*, 2007; Yang *et al.*, 2007), to modulate organic anion efflux (Tesfaye *et al.*, 2001; Anoop *et al.*, 2003; Delhaize *et al.*, 2004; Sasaki *et al.*, 2004; Li *et al.*, 2005), or to facilitate citrate efflux (Furukawa *et al.*, 2007; Wang *et al.*, 2007). Results from experiments with transgenic plants manipulated to secrete specific signal molecules have also shown that plants communicate with microorganisms in the rhizosphere (Oger *et al.*, 1997, 2000). For example, plants release chemical compounds that interfere with bacterial quorum sensing (Gao *et al.*, 2003; Bauer & Mathesius, 2004). GM potato plants able to interfere with bacterial quorum sensing via expression of a lactonase gene, showed a higher level of resistance to the bacterial plant pathogen *P. carotovorum* (Dong *et al.*, 2001). Transgenic potato plants with increased production of 5-O-glucosyltransferase (Lorenc-Kukula *et al.*, 2005) and pectate lyase (Wegener, 2001) also showed increased resistance to *P. carotovorum*. To date, however, our knowledge of root exudation *in situ* is limited, and the composition of root exudates is mostly determined in hydroponic culture conditions. Hence, there are few specific targets available yet for plant breeding. Another bottleneck is the potentially high variability of root exudation across environments, soil types, and plant physiological conditions such as growth stage (Sandnes *et al.*, 2005; Dessureault-Rompre *et al.*, 2006, 2007; Phillips *et al.*, 2008; Shi *et al.*, 2011).

Redirecting the rhizosphere microbiome by introducing or stimulating microorganisms

Other strategies to redirect the rhizosphere microbiome are (1) to introduce beneficial microorganisms in soil, onto seeds, and planting materials, or (2) to stimulate resident beneficial rhizosphere microorganisms by soil or crop management. Many beneficial rhizobacterial and fungal strains with different traits have been introduced into soil or onto seeds or planting materials to boost plant performance (Bhattacharyya & Jha, 2012). Reshaping the rhizosphere microbiome by introducing beneficial microorganisms that protect the host plant against pathogen infections is in many ways comparable with the use of probiotics in humans. Probiotic bacteria, mainly *Lactobacillus* and *Bifidobacterium* species, have been extensively studied for prevention and treatment of diarrhea (Guandalini, 2011; Hempel *et al.*, 2012) and inflammatory bowel disease (Calafiore *et al.*, 2012). Related to plant pathogens, Fgaier & Eberl (2011) recently adopted a theoretical approach to investigate whether a probiotic strategy could eradicate a well-established pathogen by introducing a siderophore-producing bacterium. Their simulations indicated that a one-time or short-time exposure of the agricultural system to a control agent is not sufficient to eradicate the pathogen even if temporarily

very low cell counts of the pathogen can be achieved. If the treatment was stopped too early, the pathogen population can recover and reestablish thereby out-competing the biocontrol agent. Hence, effective beneficial microorganisms should proliferate and survive in the rhizosphere microbiome and attain cell densities above a specific threshold density at a time and place that is critical for pathogen infection. When introduced into new environments, however, many microbial strains do not survive or cannot establish densities in the rhizosphere that are necessary to control soilborne pathogens (Raaijmakers *et al.*, 2009). One approach to meet these criteria is to develop so-called designer probiotics, which are genetically engineered microbial strains (Paton *et al.*, 2006; Picard & Bosco, 2008; Picard *et al.*, 2008; Berlec, 2012). However, this approach has not been widely adopted due to public concerns about the use of recombinant microorganisms.

Instead of the 'one-microorganism' approach, the use of assemblages of different microorganisms with complementary or synergistic traits will probably provide a more effective and consistent effect. As indicated by Bakker *et al.* (2012), such consortia may serve to reduce the period of time required for the rhizosphere microbiome to achieve niche saturation and to competitively exclude pathogens. This concept of so-called concerted rhizosphere communities is gaining more and more momentum. However, to find or select the right players of a consortium is difficult due to problems with compatibility between the consortium members. In most of the biocontrol studies published to date, combinations of microorganisms usually consisted of strains (bacterial, fungal) that were effective on their own and/or controlled pathogens by different mechanisms (Raupach & Kloepper, 1998; Jetiyanon & Kloepper, 2002). Studies by Garbeva & de Boer (2009), however, showed that microorganisms that are not antagonistic on their own, can exhibit substantial antimicrobial activities when they are part of a microbial consortium. Subsequent transcriptome analyses further revealed that expression of specific genes involved in signal transduction and secondary metabolite production of one of the bacterial consortium members was strongly affected by the identity of other members (Garbeva *et al.*, 2011b). These results illustrated that rhizobacteria are able to distinguish among their neighbors and fine-tune the biosynthesis of antimicrobial metabolites. These studies also highlight the complexity of designing a microbial consortium for controlling soilborne plant pathogens.

Natural disease-suppressive soils probably provide the best framework to unravel the optimal composition of a microbial consortium that efficiently protects plants from soilborne pathogens. Using PhyloChip-based metagenomics, Mendes *et al.* (2011) detected more than 33 000 bacterial and archaeal species in the rhizosphere of sugar beet plants grown in a soil suppressive to *Rhizoctonia* damping-off disease. Based on the relative abundance of these bacterial taxa in the rhizosphere of sugar beet plants grown in soils with different levels of disease suppressiveness, they were able to pinpoint bacterial phyla that were consistently associated with disease suppression, including the *Proteobacteria*, *Firmicutes*, and *Actinobacteria*. For specific members of the *Gammaproteobacteria*, they demonstrated that the disease-suppressive activity was governed by the production of a chlorinated lipopeptide, designated thanamycin (Mendes *et al.*, 2011; Watrous *et al.*, 2012). For the other consortium members, it is not yet clear whether and how they contribute to disease suppressiveness. Also, the microarray-based analyses by Kyselková *et al.* (2009) of soils suppressive to black root rot of tobacco showed that multiple bacterial genera, including *Azospirillum, Gluconacetobacter, Burkholderia*, *Comamonas*, *Sphingomonadaceae*, and the fluorescent *Pseudomonas,* were more prevalent on roots of tobacco plants grown in disease suppressive than in conducive (nonsuppressive) soils. Recent studies by Rosenzweig *et al.* (2012) on a potato common scab-suppressive soil from Michigan (USA) revealed a higher number of *Lysobacter* and of *Acidobacteria* (groups 4 and 6) in the suppressive soil as compared with the conducive soil. Although the potential role of the identified bacterial communities in disease suppressiveness was not addressed in these two latter studies, their initial characterizations will help to target specific groups for functional analyses. Collectively, these studies indicated that suppressiveness of soils is not a matter of the exclusive presence of specific groups of antagonistic microorganisms but is largely determined by their relative abundance. Ramette *et al.* (2006) further hypothesized that suppressiveness may also be governed by differential effects of environmental factors on the expression of key biocontrol genes in rhizobacteria rather than by differences in their population structures. Collectively, these and other studies highlight the need for a community systems (CoSy) biology approach to resolve the interplay between individual community members, the host plant, and the soil environment. In this context, Zengler & Palsson (2012) indicated that top-down approaches such as metagenomics and bottom-up approaches targeting individual species or strains should be integrated and combined with modeling approaches to provide a comprehensive coverage and understanding of the microbial community as a whole. Zilber-Rosenberg & Rosenberg (2008) proposed the hologenome theory of evolution, where the hologenome is defined as the sum of the genetic information of the host and its microbiome. This proposition fits within the framework of the 'superorganism' (Wilson & Sober, 1989). In the case of animals,

Eberl (2010) described the immunity as the homeostasis of the superorganism, where the *immune system is not a killer, but rather a force that shapes homeostasis within the superorganism*. Extending this view to plants, we can assume that the intimate interaction between the host and its microbiome is a driving force for host development and functioning. Considering the adaptive behavior of pathogen populations to microbial antagonism (Duffy *et al.*, 2003), Kinkel *et al.* (2011) proposed a coevolutionary framework for inducing or managing natural disease suppressiveness of soils. They proposed, among others, to identify the nutrient conditions under which the microbial communities follow an antagonistic coevolutionary trajectory vs. a coevolutionary displacement trajectory. They also emphasized that '*effective antagonistic populations or phenotypes are likely to vary for different plant pathogens suggesting that distinct evolutionary and coevolutionary trajectories may be significant to disease suppression in different cropping systems*'. Top-down and bottom-up analyses of a number of different disease-suppressive soils will be required to determine whether this latter statement is actually true or whether a specific subset of microbial taxa contributes to suppressiveness of soils against multiple plant pathogens.

Conclusions and outlook

Although the importance of the rhizosphere microbiome in the functioning of plant ecosystems has been widely recognized, traditional approaches to unravel these functions are limited in their capacity and for the vast majority of rhizosphere organisms, no knowledge exists. Coupling traditional approaches with advanced next-generation sequencing techniques to assess organismal or community ecology and physiology will bring new insights to understand microbial life in the rhizosphere. Identification of the exudates, signals, and key players in the rhizosphere microbiome will provide chemical and microbial markers to elucidate whether and how plants recruit and stimulate beneficial (micro)organisms. Unraveling the rhizosphere microbiome also holds potential to improve crop protection and to uncover numerous yet unknown soil microorganisms, functions, and genes for diverse applications. Another challenge we face is how to prevent human pathogen proliferation in plant environments to critical doses causing human disease. Therefore, a better understanding of the factors and cues that enable human pathogens to find a suitable niche on plant surfaces is essential to safeguard human health.

To keep plant and human pathogens in check, different and complementary strategies should be developed that redirect the rhizosphere microbiome in favor of microorganisms that prevent pathogens to germinate, grow, attach, and invade the root tissue. One potential approach is to initiate plant breeding programs that are directed toward unraveling the molecular basis of interactions between plant lines and beneficial members of the rhizosphere microbiome. The initial studies by Smith *et al.* (1999) on QTL mapping of tomato lines for traits that support beneficial rhizobacteria provide an excellent framework for this. Combined with in-depth analysis of the rhizosphere microbiomes of wild relatives of economically important food crops, it should be feasible to resolve whether modern plant breeding can select for plant traits that are essential for hosting beneficial microorganisms. This approach of going 'back to the roots' will most likely also lead to the identification of new rhizosphere microorganisms, genes, and traits that can be exploited for other applications. To reduce the impact of plant diseases, we propose to design a 'core microbiome' that is effective against soilborne pathogens in different agro-ecosystems. Analogous to the concept of the core microbiome in human microbiology (Turnbaugh *et al.*, 2009; Huse *et al.*, 2012; Ursell *et al.*, 2012), we define the core rhizosphere microbiome in the context of plant health as the set of microorganisms that are needed to effectively protect plants from soilborne pathogens. How many microorganisms should be part of the core microbiome is not known, and also, the number of traits needed to effectively protect plants from pathogens remains elusive. Given that several antagonistic traits are shared by different rhizosphere microorganisms, there may be a certain level of functional redundancy among members of the core microbiome. In this respect, one could also design a 'minimal microbiome'. Analogous to the concept of the minimal genome (Gill *et al.*, 2006; Moya *et al.*, 2009; Juhas *et al.*, 2011), the minimal microbiome would comprise the minimal set of microbial traits needed to fulfill a specific ecosystem service, in this case protection of plants against soilborne diseases. One may argue that control of different pathogens on different crops requires a different subset of antagonistic microorganisms (Kinkel *et al.*, 2011). This is probably true for the different groups of soilborne plant pathogens, that is, bacteria, fungi, oomycetes, and nematodes. However, designing a core microbiome for each of these pathogen groups separately may be feasible. This assumption is based on several observations: studies on natural disease-suppressive soils have pointed to common players and identical mechanisms and genes in the suppressiveness of soils to different fungal pathogens; also, the onset of natural disease suppressiveness of soils follows a similar pattern for various fungal pathogens (Weller *et al.*, 2002), suggesting that similar processes, mechanisms, and microorganisms may be required for the transition of a soil from a conducive to a suppressive state. Knowledge of the shifts in

microbial community composition and activities during this transition phase will provide the basis to select potential candidate members of the core microbiome and to set their initial densities to jump start disease suppressiveness. A core microbiome also can be designed for the other functions listed in Fig. 2 that support and sustain plant growth and health. Following the work of Burke *et al.* (2011), we propose to assemble the core microbiomes more from a functional perspective than based on taxonomic classification only.

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