4 Plant Rhizosphere Microbial Communities

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Introduction

Plants have evolved in a microbial world. Thus, plant-microbe interactions may be inherent to plants' adaptation to their environment. On the other hand, plants are the major source of organic nutrients in the soil, the driving force for microbial activity. The soil microflora interacts with plant roots and can even modulate the plant's response to both biotic and abiotic stresses. Here, we describe the rhizosphere as an organized unit, composed of the root and its associated microbiome. This interaction occurs in the limited soil region directly influenced by the living plant root. The presence and activities of the root affect the surrounding soil chemically, physically, and biologically. Thus, numerous processes occur in parallel in the rhizosphere, creating a unique and active niche. The chemical processes involve passive and active deposition of a multitude of compounds, mostly labile organic matter from the plant root and sloughed-off plant cells and tissues. The deposits discharged from the roots into the surrounding soil include different amino acids and proteins, organic acids, carbohydrates and sugars, vitamins, and the mucilage, accounting for a large proportion of the plant's fixed carbon. These, of course, are the driving force for alterations in the activity, function, abundance, composition and structure of the soil microbial community. The rhizosphere community will, in turn, affect root health and development.

Is it possible to consider the plant-rhizobacteria complex as a "holobiont" composed of the plant and its accompanying microbiome, acting as a consortium, a unit of selection in evolution (Rosenberg et al. 2007; Zilber-Rosenberg and Rosenberg 2008; Rosenberg and Zilberg-Rosenberg 2011)? Rosenberg and Zilberg-Rosenberg (2011) suggested four criteria for the hologenome theory. These criteria can be examined with regard to the rhizosphere: (1) the rhizosphere contains abundant and diverse microorganisms acquiring a nutrient-rich environment from the plant, (2) the rhizobacteria affect the plant's fitness, and (3) variation in the hologenome can be brought about by changes in either the plant genome or the microbial population genomes. The fourth criterion of the hologenome theory suggests the ability to transmit genetic variation from one generation to the next. In the case of the rhizosphere, this is not straightforward. However, the genetic variation in the soil microbiota is enormous: 1 g of soil can contain millions of bacterial cells belonging to more than 10,000 unique taxa (Fierer et al. 2007). It may be suggested that roots grown in such a soil will enrich the required functional, rather than phylogenetic group, to support its development under the given conditions. The high degree of coadaptation between plants and soil microorganisms is manifested by the high diversity of root-associated and endophytic species (Manter et al. 2010; Uroz et al. 2010) and

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the concomitant high frequency of plant-growth-promotion-related traits in soil and rhizosphere bacteria (De Brito Alvarez et al. 1995; Cattelan et al. 1999; Berg et al. 2002, 2006; Ahmad et al. 2008; Garbeva et al. 2008; Zachow et al. 2008; Sato et al. 2009; Fürnkranz et al. 2009; Çakmakçi et al. 2010).

In this chapter, we describe the rhizosphere and its microbiome, focusing on data and theories describing general natural rhizospheric microbial ecology in health and disease. We discuss the anthropogenic and global warming impacts on rhizosphere microbiome, and the effects of mycorrhiza. We describe the structure and function of the microbial community at the rhizosphere, and the great impact recent developments in molecular techniques has and will continue to have in the near future in this field. We do not, however, discuss specific symbiotic/pathogenic interactions and mechanisms.

The Rhizosphere: Definitions, Compartments, and Spatial and Temporal Scales

Plant roots are linear units that can be divided into compartments that differ in their degree of development and differentiation, as well as in their functional, physiological, and biochemical characteristics. Plant root systems also exhibit high physiological and biochemical plasticity (Waisel and Eshel 2002), which is manifested by changes in root properties and activities (Neumann and Römheld 2002). Moreover, within a single root system, different types of roots are formed, even when grown under homogeneous aeroponic conditions (Waisel and Eshel 2002). These root types may differ in their structure; rates of water and nutrient uptake; growth and accumulation of ions; responses to salinity, hypoxia, and nutrient deprivation; and expression and activity of important enzymes. The life span of roots ranges from days to over a year, depending on the plant species and root type, as influenced by abiotic and biotic factors. Roots elongate continuously. The different compartments formed along the growing root axis include the root cap, root tip, elongation zone, root-hair zone, and mature zone. Each compartment represents a different level of differentiation and performs distinctive functions. Roots also produce lateral roots, whose sites of emergence constitute yet another root compartment. Finally, wounds caused by friction with soil particles, as well as by grazers and pathogens, and mycorrhiza also contribute to the array of compartments within the root system.

A rhizosphere is created around each root as it grows and the root's activity changes the chemical, physical, and biological properties of the soil in its immediate vicinity. Thus, the rhizosphere is defined by its function rather than its "geometry" and can vary greatly in its spatial and temporal dimensions, even under transient or minute modulation of any one of its components. The radial dimensions of the rhizosphere may span several millimeters in diameter for soluble nutrients (such as nitrate) or volatiles, but is much more restricted (<1 mm) for sparingly soluble minerals (such as P and Fe) (Neumann and Römheld 2002). Root compounds released into the soil may directly facilitate the plant's acquisition of mineral nutrients. These include excreted and secreted compounds (carbon dioxide, bicarbonates, protons, electrons, etc.) that affect the soil pH and redox potentials. Other secreted compounds, such as phytosiderophores, target specific nutrients and directly increase their availability to the plant. Rates of release of these compounds are highly affected by nutrient limitations. Although inorganic compounds can directly modify the biogeochemistry of the surrounding soil (Hinsinger 2001; Cheng et al. 2004; Vetterlein and Reinhold 2004; Hinsinger et al. 2009), the dramatic rhizosphere effect is mainly attributed to the release of large amounts of organic compounds.

Many factors affect the quantity and composition of root-released organic carbon: plant species (Hütsch et al. 2002; Jones et al. 2009), environmental factors (light, temperature), nutritional balance, stresses (including herbivores), and biological interactions, including mycorrhiza and prokaryotes, which act as strong sinks (Neumann and Römheld 2002; Jones et al. 2004). Concentrations of organic root depositions are inversely related to the distance from the root surface (Cheng et al. 1996; Kuzyakov et al. 2003; Gao et al. 2011). The main components of organic root depositions are thought to be root debris, which includes cell lysates, sloughed-off root cap cells (border cells), and senescent tissue (Uren 2001). Therefore, the composition of root depositions includes the entire array of root products. Root exudates, defined as compounds released from intact root cells by either diffusion or secretion, account for a smaller fraction of root depositions, but can have a direct and immediate function in rhizospheric processes (Neumann and Römheld 2002). Many types of low-molecular-weight organic compounds diffuse from intact cells into the soil. The most abundant diffusates are the principal cytoplasm compounds (e.g., sugars, organic acids, and amino acids) that move out of the cells due to the dramatic gradient in their concentration between the root and its environment. These sharp gradients are maintained by the rapid consumption of such compounds by soil microorganisms.

Carbon Flow in the Rhizosphere and Microbial Responses

Root deposition of carbon (C) in the soil is of major importance in regulating ecosystem functioning. However, it is clear that C flow in the rhizosphere is an extremely complex process, varying spatially and temporally along the root and affected by myriad interactions between the plant root and biotic and abiotic environmental factors (Jones et al. 2004). Experiments conducted using pulse-labeling with ^{14}C and ^{13}C isotopes have enabled a description of the flow of plant-assimilated C into the soil microbial biomass. Roughly, half of the biological activity in soils is supported by recent (hours to a few days) photosynthesis-assimilated C (Högberg and Read 2006). On average, 17% of the total C assimilated by photosynthesis is released into the soil (Nguyen 2003). However, the actual percentage may vary greatly among plant species, and usually decreases with plant age (Gransee and Wittenmayer 2000; Nguyen 2003). While most of the released C is rapidly respired by the root and soil

microorganisms, about a third resides in the soil incorporated in the microbial biomass or in the soil organic matter (Kuzyakov and Domanski 2000; Nguyen 2003; Jones et al. 2009). Assimilation of newly photosynthesized organic compounds into soil microbial biomass occurs rapidly—within hours for different grass species (Rattray et al. 1995; Domanski et al. 2001; Kuzyakov and Domanski 2002; Rangel-Castro et al. 2005a) and after 2 days for Scots pine trees (Högberg et al. 2008). Rapid incorporation of assimilates into bacterial RNA (Rangel-Castro et al. 2005b; Vandenkoornhuyse et al. 2007) and membrane fatty acids (Treonis et al. 2004) has also been confirmed. In grassland soil, microbial RNA turnover was estimated to be 5 days with a mean residence time of 15–20 days (Ostle et al. 2003). RNA stable isotope probing, combined with community profiling methods, revealed that the most active bacterial populations residing in the rhizosphere utilize recently fixed C (Rangel-Castro et al. 2005b; Vandenkoornhuyse et al. 2007). However, the degree of labeling of different populations was uneven, indicating differences in rates of assimilation and C turnover, as well as reliance on other sources of organic C, including soil organic matter or remnant dead roots (Rangel-Castro 2005b; Vandenkoornhuyse et al. 2007).

Several studies have demonstrated interrelations between plant deposits and the microbial community. In rice rhizosphere, following a labeling period of 7 days, the assimilation of root-derived compounds by microorganisms was inversely related to distance from the root (Lu et al. 2007). This is consistent with rhizosphere dogma. Rhizosphere bacteria respond to changes in root exudation rates and composition. For example, Liljeroth et al. (1990) used ^{14}C labeling of wheat to demonstrate that at higher N, exudation, as well as bacterial numbers, increase. A mutation in an ABC transporter of *Arabidopsis thaliana* involved in the secretion of phytochemicals resulted in a shift in composition of root exudates and a concomitant shift in the rhizosphere-associated bacterial community (Bardi et al. 2009). It was also confirmed that plant root exudation is influenced by association with bacteria. For *Lolium perenne* plants grown under sterile conditions, metabolites produced by *Pseudomonas aeruginosa* significantly increased root exudation (Meharg and Killham 1995). In contrast, inoculation of sterile-grown maize plants with P-solubilizing, growth-promoting *Pantoea agglomerans* led to a significant decrease in root exudation (Laheurte and Berthelin 1988).

It is important to note here that C flow in the rhizosphere is bidirectional: roots take up organic compounds from the soil, which can be later transferred to the shoot (Jones et al. 2009). Of high importance is the uptake of sugars and amino acids, that is mediated by membrane transporters. However, a growing body of evidence indicates that uptake of large molecules, including proteins and DNA which can sustain plant growth as sole sources of N and P, respectively, probably occurs via endocytosis (Paungfoo-Lonhienne et al. 2008, 2010a). Furthermore, recent evidence has shown that intact *Escherichia coli* as well as *Saccharomyces cerevisiae* cells are taken up and consumed by roots of *Arabidopsis thaliana* and tomato plants, respectively, and that the consumed microbial-derived N is incorporated in the leaves (Paungfoo-Lonhienne et al. 2010b).

Spatial Distribution of Root-Associated Microbial Communities

As we have seen, the spatial-temporal heterogeneity of the rhizosphere is enormous. Although well-recognized, a relatively small proportion of rhizosphere studies have addressed the issue of spatial distribution of bacterial populations on roots and in the rhizosphere. Naturally, such topological studies require in situ visualization of root-adhering bacteria with minimal physical disruption of the samples. Accordingly, the main technical arsenal includes different microscopy technologies (light and fluorescence microscopy, confocal laser-scanning microscopy, transmission and/or scanning electron microscopy) coupled (or not) with suitable reporting systems (such as fluorescence-labeled probes or antibodies, general stains, and reporter genes). As a result, the studies are laborious and the number of samples that can be thoroughly processed is limited. Furthermore, most of the knowledge obtained is related to studies examining the root- or seed-colonization pattern of a specific inoculated bacterial species, many times under gnotobiotic conditions. Nevertheless, the basic and applied knowledge culled has been very valuable.

Several studies have demonstrated colonization of roots by either indigenous soil communities or inoculated strains. These studies have outlined several basic aspects of root colonization topology.

1. The major part of the root surface is bacteria-free. Early scanning electron microscopy (SEM) observations of wheat, ryegrass, and clover roots revealed that only a small fraction of the root surface is occupied by bacteria (Campbell and Rovira 1973; Rovira and Campbell 1974). Using light microscopy (LM) and cell staining, rhizoplane coverage by indigenous bacteria was estimated to be between 5% and 10% for eight different grasses and perennials grown in soil (Rovira et al. 1974). In the rhizoplane of pine (*Pinus radiata*) inoculated with *Pseudomonas* sp. or *Bacillus* sp. isolates, microbial coverage ranged between 10% and 20% of the surface area (Bowen and Theodorou 1979). SEM and LM examination of rice seedlings gave estimates of 1–9% coverage (Asanuma et al. 1979). More recent studies have also shown low relative coverage of the root surface (Hansen et al. 1997) or seed surface (Hood et al. 1998), but without providing numerical estimates. However, Watt et al. (2006) estimated that bacteria attached to wheat roots grown in natural soil cover between 12% and 15% of the root surface area.
2. Microorganisms are not randomly distributed on roots: they tend to aggregate. The relative scarcity of root-surface colonization by microorganisms has led to the hypothesis that root colonization is not random and that a few sites on the root are favorable. Newman and Bowen (1974) used a statistical approach to pattern analysis of bacterial rhizoplane colonization in different plant species. They confirmed variance in bacterial densities not only on a small scale (fields 100 μM apart), but also on larger scales, that is, along a single root and between different roots of the same root system.

Nonrandom aggregation of bacteria on root surfaces was again demonstrated for tomato roots inoculated with *Pseudomonas fluorescens* under gnotobiotic conditions using a geostatistical model (Dandurand et al. 1997) and for wheat roots grown in natural soil (Watt et al. 2006). While in both cases, nonrandom distribution was conclusive, the different authors pointed out the difficulty in establishing the causes underlying the pattern of root colonization, due to high variance between samples. Patchy distribution was also confirmed for Euryarchaeota colonizing rice roots (Grosskopf et al. 1998).

An explanation for the large variance may relate to the mode of root infection. Although the number of bacteria in a grain of soil may be huge, they occupy only a minute fraction of the grain's surface area (Young and Crawford 2004; Young et al. 2008) and are preferentially associated with organic debris (including particular organic matter and plant residues). Therefore, spatial variance in root colonization may, in part, stem from the low probability of a physical encounter. Indeed, sites of contact between dead root remnants and live roots have been shown to be bacterial colonization hot spots in wheat roots (Watt et al. 2006).

One important aspect is the distance between neighboring bacterial microcolonies on the root surface, and between microcolonies in the rhizosphere soil. Since much of microbe-microbe communication relies on volatile and diffusible chemical compounds, the distance between microcolonies will determine the degree of interaction between populations. For wheat roots grown in natural soil, the average distance between bacterial microcolonies was 84 μm (Watt et al. 2006). Quorum-sensing signals of *Pseudomonas putida* were efficient at eliciting a response in populations as far apart as 37 μm in the root tip/elongation zone and 78 μm in the root-hair zone (Gantner et al. 2006).

Bacteria are thought to colonize favorable microsites, including junctions between adjacent cells, cells and regions of increased rates of root exudation (root cap, root hair, sites of lateral root emergence), and sites of lysed rhizodermal cells. Aggregation of bacteria at such sites was corroborated in a series of experiments tracking root colonization by inoculated beneficial bacterial strains. In general, the colonization pattern of inoculants showed a preference for different root features. Most studies found aggregation of bacteria at junctions between rhizodermal cells, in agreement with early (Rovira and Campbell 1974; Asanuma et al. 1979) and more recent (Lübeck et al. 2000; Watt et al. 2006; Ofek et al. 2011) observations of native rhizosphere communities. Foster and Bowen (1982) proposed that this pattern results from higher rates of exudation at the junctions. Surface roughness, which often affects microbial aggregation on surfaces (Riedewald 2006), was suggested as an alternative explanation (Dandurand et al. 1997). Surface properties, rather than shifts in exudation, were also suggested as an explanation for abrupt changes in root-colonization patterns observed on cucumber seedling roots between the root-hair zone and the tips of emerging lateral roots in that same zone (Ofek et al. 2011).

Preferential colonization of root segments at different developmental stages has also been frequently observed in inoculation studies. For example, *Azospirillum brasilense* could be found attached to all types of root surfaces of wheat and several non-cereal crops, but was most abundant in the root-hair zone, on root-hair cells, in the elongation zone, and at sites of lateral root emergence (Bashan et al. 1991; Assmus et al. 1995; Guerrero-Molina et al. 2011). *Bacillus megaterium* colonizing *Morus alba* (Ji et al. 2010), and *Burkholderia cepacia* colonizing maize and rice (Liu et al. 2006), were also found preferentially in the root-hair zone and sites of lateral root emergence, through which these bacteria had penetrated the root cortex to reside as endophytes. Favored colonization of sites of lateral root emergence and the root-elongation zone en route to endophytic colonization appears to be common for root endophytes (Senthilkumar et al. 2011). Root colonization by many plant-growth-promoting *Pseudomonas* spp. was highest at the root base and markedly decreased toward the root tip (Hansen et al. 1997; Dekkers et al. 2000; Lübeck et al. 2000). This pattern of colonization was suggested to be related to the method of inoculation (seed or young axenic seedling inoculation, rather than soil inoculation) (Benizri et al. 2001). However, investigation of wheat-root colonization by indigenous soil *Pseudomonas* populations revealed that the pattern of distribution is affected by mechanical impedance of the soil, which dictates the rate of root elongation (Watt et al. 2003): in loose soil, wheat roots grew rapidly, and accumulation of native *Pseudomonas* was positively related to the distance from the root tip. In compact soil, root growth was slow and *Pseudomonas* accumulation was similar along the entire length of the root. Nevertheless, heterogeneity in the composition of bacterial colonization of different root compartments has been demonstrated in community-level studies (Schallmach et al. 2000; Marschner et al. 2001b; Baudoin et al. 2002; Marschner et al. 2004).

Examination of differences in community-level densities between different root compartments has produced contradictory results. Rovira and Campbel (1974) and Asanuma et al. (1979) concluded that microbial colonization initiates in the root-hair zone. In contrast, bacterial numbers were highest in the root cap zone of wheat plants grown in soil, and the elongation zone was the least colonized (Watt et al. 2006). Bacterial densities were high on the root tip and in mature root compartments of young cucumber seedlings, while the root-hair zone was sparingly colonized, if at all (Ofek et al. 2011). These discrepancies most probably result from differences between the plant-soil systems examined. Altogether, accumulated evidence suggests that nonrandom distribution of bacteria on the root is the outcome of variations in the soil, root, and microbiome characteristics and their interactions.

3. A significant proportion of the root is coated by gels of root or microbial origin, collectively termed mucilage (Foster 1986). Typically, the mucilaginous material will cover the root cap and extend from the root tip to the region of root-hair senescence. In more mature root parts, the mucilage is usually absent due to microbial degradation (Foster 1986).

Bacteria have been shown to have an effect on the mucilage, increasing its amount on the root surface (Bashan et al. 1991). Bacteria have been found embedded in the mucilage and attached to the roots below it (Rovira and Campbell 1975; Werker and Kislev 1978; Chin-A-Woeng et al. 1997; Bacilio-Jiménez et al. 2001; Puente et al. 2004; Poonguzhali et al. 2008). Beyond its role as a nutrient source for the microorganisms (Mary et al. 1993; Knee et al. 2001; Puente et al. 2004), the mucilage has been suggested to have protective value against stressors such as desiccation (Watt et al. 1994). Additionally, it was demonstrated that bacteria embedded in wheat root mucilage could even resist chloroform fumigation (Martin and Foster 1985).

Complexity of the Rhizosphere Microbial Community

The complexity of biological communities is described by their taxonomic richness and the relative abundance distribution of these taxa, collectively termed diversity. Several factors determine the successful estimation of community diversity: the adequacy of the sampling effort, the technique used, and the estimation model. Determination of adequate sample size is deemed a critical stage in ecological surveys. This is particularly true for the determination of prokaryotic diversity in soil habitats, as both the numbers of individuals and the numbers of distinct taxa are exceptionally high (Torsvik et al. 1996; Øvreås and Torsvik 1998; Whitman et al. 1998; Gans et al. 2005; Roesch et al. 2007; Fierer et al. 2007 AEM).

Based on major inconsistencies between plate counts and direct microscopy quantifications, our ability to describe the prokaryotic diversity of the rhizosphere using culture media was acknowledged to be poor long before molecular tools were introduced into microbial ecology studies (Rovira 1965; Rovira et al. 1974). For nearly 30 years now, analysis of rhizosphere bacterial community composition has been based primarily on analyses of molecular markers, mostly ribosomal (r) RNA gene sequences and their transcripts, amplified directly from DNA/RNA extracted from intact samples (Kowalchuk et al. 2010). Methods such as PCR-denaturing gradient gel electrophoresis (DGGE), 16S rRNA gene-clone libraries, ribosomal intergenic spacer analysis (RISA), and terminal restriction length polymorphism (T-RFLP) have allowed us to make a giant leap in understanding rhizosphere microbial ecology. However, these techniques have not provided us with anything more than a better characterization of the numerically dominant populations. Indeed, the percentage of shared taxa detected simultaneously in, for example, clone libraries compared to cultivation is very low for samples of rhizospheric soil communities (Dunbar et al. 1999), or rhizoplane communities (Kaiser et al. 2001), indicating that we are still far from a census of rhizospheric bacterial diversity (Donachie et al. 2007; Dunbar et al. 2002). Novel high-throughput sequencing technologies have, in essence, lifted the barrier to adequately sampling complex microbial communities (Schloss and Handelsman 2006), at least with respect to molecular markers such as rRNA genes. Although still relatively few in number, published studies utilizing high-throughput sequencing for description of root-associated bacterial communities have vastly improved estimates of diversity (Bardi et al. 2009; Lauber et al. 2009; Manter et al. 2010; Navarro-Noya et al. 2010; Teixeira et al. 2010; Uroz et al. 2010; Gardner et al. 2011; Gomes et al. 2010; Gottel et al. 2011; Inceoğlu et al. 2011; Kolton et al. 2011; Ofek et al. 2011; Somenahally et al. 2011). *Table 4.1* provides examples of different diversity estimates derived from studies employing isolation, clone libraries, and high-throughput sequencing strategies.

Root-associated populations represent a subset of the bulk soil community (Normander and Prosser 2000; Weinert et al. 2008). Increasing selective pressure with proximity to the root, due to the root's presence and activity, is therefore expected to result in a gradual decrease in species richness, and a shift in composition and in relative abundance distribution patterns (expressed by rank-abundance patterns or evenness/dominance indices). Reductions in complexity from bulk to rhizosphere soil, rhizoplane, and endorhiza have been reported for different wild and cultivated plant species (Germida et al. 1998; Marilley et al. 1998; Dunbar et al. 1999; Kielak et al. 2008; Ofek et al. 2009). Reduced complexity in rhizosphere soil compared to bulk soil can also be manifested by an increased level of dominance, without reduction in species richness (Navarro-Noya et al. 2010). Uroz et al. (2010) reported a 15% decrease in species richness between the bulk and rhizosphere soils of oak trees, from 7,070 to 6,018 operational taxonomic units (OTUs) classified at 97% sequence similarity threshold. Being a soil compartment, it is not surprising that species richness in the rhizosphere soil was of the same order of magnitude as that in the bulk soil. Similarly, PhyloChip analysis of the rhizosphere of wild oats (*Avena fatua*) revealed a significant change in relative abundance for only 7% of the rhizosphere microbial community members (DeAngelis et al. 2009). The rhizosphere effect on bacterial community complexity is much more pronounced in the rhizoplane and endorhiza (Marilley et al. 1998; Normander and Prosser 2000; Green et al. 2006; Belcom and Crowley 2009; Ofek et al. 2009; Han et al. 2011), where species richness may be one to two orders of magnitude lower than that of the bulk soil or rhizosphere soil communities (Gottel et al. 2011; Ofek et al. 2011). Still, hundreds to thousands of species may coexist in these niches.

The complexity of the rhizosphere microbial community may increase with plant age for some plant species (Gomes et al. 2001; Ibekwe and Grieve 2004), and may vary between cultivars within species, as has been demonstrated for potato (Inceoğlu et al. 2011). However, the opposite trend has also been reported (Ibekwe et al. 2010). Selective enrichment of different microbial consortia at different root locations (Schallmach et al. 2000; Marschner et al. 2001b; Baudoin et al. 2002; Marschner et al. 2004), by different root types (Marschnner et al. 2002; Ofek et al. 2007; Weisskopf et al. 2008) or different states of mycorrhization (Marschner and Baumann 2003; Söderberg et al. 2002) also contribute to the overall complexity of the rhizosphere's microbial community.

Table 4.1
Examples of published diversity estimates of root associated and soil bacterial communities

Sample	Method	Sample size[a]	Diversity estimates		
			OTUs[b]	Chao1[c]	H′[d]
Endorhiza					
Saccharum officinarum[e,1]	Isolation	44	23		
Oryza sativa[e,2]	Clone library	192	52		
Populus deltoides[f,3]	Pyrosequencing	1,170	86		
Solanum tuberosum[e,4]	Pyrosequencing	12,000	477	1,265	
Rhizoplane					
Trifolium repens[e,5]	Clone library	29	15		0.99
Lycopersicon esculentum[e,6]	Isolation	316	96		
Hordeum vulgare[e,7]	Clone library	466	152		
Cucumis sativus[g,8]	Pyrosequencing	2,379	472	689	
Rhizosphere soil					
Trifolium repens[e,5]	Clone library	29	23		1.31
Pinyon pine[e,9]	Isolation	37	14		3.25
Saccharum officinarum [e,1]	Isolation	61	25		
Saccharum officinarum [g,10]	Clone library	78	64	217	4.09
Pinyon pine[e,9]	Clone library	212	161		7.09
Colobanthus quitensis[f,11]	Pyrosequencing	2,709	649	1,363	4.15
Populus deltoides[f,3]	Pyrosequencing	4,778	1,319		
Sweet pepper[e,12]	Pyrosequencing	5,035	1,660		
Quercus sp.[f,13]	Pyrosequencing	37,000	6,018	12,308	
Solanum tuberosum[e,14]	PhyloChip		2,432		
Bulk soil					
Trifolium repens[e,5]	Clone library	29	27		1.42
Pinyon pine[e,9]	Isolation	46	8		2.41
Pinyon pine[e,9]	Clone library	196	154		7.07
Quercus sp.[f,13]	pyrosequencing	37,000	7,070	16,272	
80 different soils[f,15]	Pyrosequencing	1,501	1,017		

[a]Number of individual isolates/clones/amplicons examined
[b]Operational taxonomic units
[c]Chao1 nonparametric estimate of species richness
[d]Shannon-Weiner index of diversity
[e]Based on the sum of all individuals examined
[f]Averages across all samples examined are presented
[g]One example from the presented data is presented
[1]Mendes et al. 2007; [2] Sun et al. 2008; [3]Gottel et al. 2011; [4]Manter et al. 2010; [5]Marilley et al. 1998; [6]Shiomi et al. 1999; [7]Buddrus-Schiemann et al. 2010; [8]Ofek et al. 2011; [9]Dunbar et al. 1999; [10] Pisa et al. 2011; [11]Teixeira et al. 2010; [12]Kolton et al. 2011; [13]Uroz et al. 2010; [14]Weinert et al. 2011; [15]Lauber et al. 2009

Rhizosphere Microbial Community Composition

Cultivable Root-Associates

The many limitation of cultivation strategies in microbial ecology were repeatedly acknowledged and emphasized by many authors (Torsvik et al. 1996; Rondon et al. 1999; Amann and Lodwig 2000; Van Elsas and Bersma 2011). Biased as it may be, this fraction includes some of the most important plant symbionts, pathogens, and plant-growth-promoting species. In many respects, cultivation is irreplaceable even today as the advantages of high-throughput sequencing technologies become available to a growing part of the scientific community. Most importantly, physiology and function of populations can be inferred from genetic data only in cases where homology to genetic data obtained from cultivated species or strains (Giovannoni and Stingl 2007; Nichols 2007).

Over a century of investigation on rhizosphere prokaryotic communities has relied mostly on cultivation of the

microorganisms on defined media, thus primarily described the cultivable aerobic (as well as facultative anaerobic) heterotrophic fraction of root-associated prokaryotes, but also specific groups of autotrophs (e.g., denitrifying bacteria and archaea) and anaerobes (methanogenic bacteria and archaea). One basic hypothesis of rhizosphere microbial ecology states that the activity and numbers of fast-growing opportunistic species (r-strategists or copiotrophs, as opposed to k-strategists or oligotrophs) and symbionts will increase with proximity to the root, due to availability of labile organic carbon or specific signaling molecules. Where representatives of these specific groups were targeted, specifically *Pseudomonas*, *Burkholderia*, and *Rhizobium*, the hypothesis was readily supported by cultivation assays (Thies et al. 1995; Schortemeyer et al. 1996; Grayston et al. 1998b; Miller et al. 2002; Van Elsas et al. 2002; Berg et al. 2006; Garbeva et al. 2008). However, with respect to general enrichment of copiotrophs, the picture was more complex. De Leij et al. (1993) have proposed that the concept of copiotrophs to oligotrophs (C:O) ratios could be examined by cultivation using defined media, and recording of colony appearance over long incubation periods. In that study, C:O distribution that characterized the bulk soil and mature washed roots of wheat was even, but in roots of young plants copiotrophs dominated. Using the same method, a shift from copiotrophs domination to more even C:O distribution during plant maturation was also reported for maize rhizosphere (Chiarini et al. 1998; Kozdrój et al. 2004) and wheat roots (De Leij et al. 1995). In another study, even C:O distribution in the bulk soil and in maize rhizosphere soil was found regardless of plant age (Brusetti et al. 2004). Along roots of lettuce (Maloney et al. 1997) and cucumber (Folman et al. 2001), the C:O ratio decreased toward the root base. However, in tomato, the ratio was constant among all root locations (Maloney et al. 1997). Decrease in C:O ratio tip to base characterized young but not mature chrysanthemum plants (Duineveld and van Veen 1999). Although concentrations of labile organic carbon increase with proximity to the root, Sarathchandra et al. (1997) found that the proportion of copiotrophs was lower in the rhizoplane compared to rhizosphere soil for *Lolium perenne* and *Trifolium repens* growing in pasture soil. Furthermore, these authors reported a significant difference in C:O ratios between the two plant species. Differences in C:O proportions were also reported for the rhizosphere of a single maize cultivar planted in different soils (Chiarini et al. 1998).

Cultivation strategies have been used in order to assess the composition or rhizosphere and root colonizing bacteria with defined plant-growth-promoting and pathogens antagonistic properties. Those include phosphorous solubilization, nitrogen fixation, siderophores production, plant hormones production, chitinases, and antibiotic substances. The relative abundance of bacteria showing (in vitro) plant-growth-promotion-related traits is frequently higher in the rhizosphere compared to bulk soil. For instance, in the rhizosphere of strawberry and oilseed rape, the relative abundance of *Verticillium* antagonists was two to three times higher compared to the bulk soil (Berg et al. 2002, 2006). Among those *Verticillium* antagonistic isolates, the incidence of concomitant antagonism toward other phytopathogenic fungi, as well as production of secondary metabolites and indole-acetic acid was highly frequent (Berg et al. 2002). Similarly, relative abundance of *Rhizoctonia solani* bacterial antagonists was higher in the rhizosphere of maize, oat, barley, and *Lolium* spp. compared to the bulk soil (Garbeva et al. 2008). In some studies, conducted in temperate European agricultural soils, Gram-negative bacteria and particularly *Pseudomonas* spp. were most dominant among antagonists of fungal plant pathogens (Berg et al. 2002, 2006; Krechel et al. 2002; van Overbeek and van Elsas 2008; Zachow et al. 2008). Furthermore, the occurrence and frequency of antibiotics-producing pseudomonads was related to the natural development of take-all suppressive soils (Raaijmakers et al. 1997; de Souza et al. 2003). This has motivated studies dedicated to exploration of the diversity of antagonistic rhizosphere pseudomonads in different crops and sites (Picard et al. 2000; Mazzola and Gu 2002; Garbeva et al. 2004; Bergsma-Vlami et al. 2005; Costa et al. 2006). However, the diversity of cultivated fungal antagonists includes representatives of many other Gram-negative as well as Gram-positive genera. Interestingly, in studies performed under warm climate conditions, Gram-positive bacteria and particularly *Bacillus* dominated the fungal-antagonistic cultivated population (Yang et al. 2008; Köberl et al. 2011). Examples of the dominant taxonomic groups isolated in surveys for single or multiple plant-growth-promoting traits are listed in *Table 4.2*.

The Contribution of Cultivation-Independent Methods

The dominant rhizosphere bacterial community generally includes members of Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes, and Acidobacteria. The same groups are dominant in soils (Roesch et al. 2007; He et al. 2010; Uroz et al. 2010; Will et al. 2010). Therefore, at such gross level of resolution, the transition from culture-dependent to high-throughput culture-independent strategy has little revolutionized our view of taxonomy of rhizosphere bacterial community (*Table 4.3*). One striking exception is predominance of Acidobacteria in the rhizosphere. Members of this group were recognized as a novel division rather recently (Kuske et al. 1997) and are poorly represented in standard culture media used for cultivation and isolation of soil and rhizosphere bacteria. Cultivation-independent analyses revealed dominance of Acidobacteria in the rhizosphere of Lodgepole pine (Chow et al. 2002), *Thlaspi caerulescens* (Gremion et al. 2003), and Oak (Uroz et al. 2010). Remarkable dominance of Acidobacteria (>50%) was described in the rhizosphere of chestnut tree (*Castanea crenata*) in both DNA- and RNA- derived 16S rRNA clone libraries (Lee et al. 2008). Singh et al. (2007) had reported a strong rhizosphere effect on Acidobacteria for different grass species, with high relative abundance in the rhizosphere soil (29–55%), while in the respective bulk soils relative abundance was 10% on average. Similar trend was previously observed for

Table 4.2

Examples of dominant bacterial genera retrieved in cultivation-based surveys of plant-growth-promoting bacteria

Functional group	Dominant taxa
Fungal/bacterial pathogens antagonists	[5]*Arthrobacter*, [1]*Azotobacter*, [1,3,5,13,21]*Bacillus*, [11]*Brevundimonas*, [21]*Burkholderia*, [13]*Chryseobacterium*, [13]*Enterobacter*, [20]*Flavobacterium*, [13,20]*Lysobacter*, [5]*Micrococcus*, [13]*Paenibacillus*, [13]*Pantoea*, [1,3,4,5,6,9,13,20]*Pseudomonas*, [4,5,13]*Serratia*, [5,13,16,20]*Streptomyces*
Chitin/glucan degrading enzymes	[5]*Arthrobacter*, [5,7]*Bacillus*, [5]*Micrococcus*, [28]*Micromonospora*, [6]*Pantoea*, [5,7,27]*Pseudomonas*, [6,28]*Serratia*, [27]*Stenotrophomonas*; [5,28]*Streptomyces*
Nematocidal activity	[26]*Agrobacterium*, [26,27]*Bacillus*, [24]*Burkholderia*, [24]*Corybacterium*, [22,23,25,27]*Pseudomonas*, [22]*Rhizobium*, [27]*Stenotrophomonas*, [25]*Streptomyces*
Siderophores production	[8]*Achromobacter*, [10]*Agrobacteirum*, [5]*Arthrobacter*, [1]*Azotobacter*, [1,5,8,15]*Bacillus*, [2]*Bradyrhizobium*, [8]*Brevundimonas*, [15]*Chryseomonas*, [8]*Ensifer*, [7]*Flavobacterium*, [14]*Methylobacterium*, [8,10]*Microbacterium*, [5]*Micrococcus*, [8]*Ochrobacterium*, [14]*Okibacterium*, [1,5,7,10]*Pseudomonas*, [10]*Ralstonia*, [2]*Rhizobium*, [14]*Rhodococcus*, [8, 10,15]*Serratia*, [8]*Sinorhizobium*, [5,16]*Streptomyces*
Phytohormones production	[8]*Achromobacter*, [12]*Acinetobacter*, [10]*Agrobacterium*, [10,12]*Alcaligenes*, [10]*Arthrobacter*, [1]*Azotobacter*, [1,8,12,15]*Bacillus*, [2]*Bradyrhizobium*, [8,11]*Brevundimonas*, [11]*Burkholderia*, [1,6,10,11,12]*Pseudomonas*, [1]*Mesorhizobium*, [2]*Rhizobium*, [8,10]*Microbacterium*, [11,15]*Chryseomonas*, [12]*Enterobacter*, [8]*Ochrobacterium*, [12]*Pantoea*, [10]*Ralstonia*, [10,15]*Serratia*, [8,10]*Sinorhizobium*, [11]*Sphingomonas*, [11,15]*Stenotrophomonas*, [16]*Streptomyces*
Associative nitrogen fixation	[19]*Alcaligenes*, [17,19] *Azospirillum*, [17]*Azoarcus*, [7]*Bacillus*, [7,11]*Burkholderia*, [11,15]*Chryseomonas*, [19]*Enterobacter*, [7]*Flavobacterium*, [19]*Klebsiella*, [19]*Pantoea*, [11]*Pseudomonas*, [11]*Sphingomonas*, [19]*Xanthobacter*, [17]*Zoogloea*
Phosphate solubilization	[7]*Acinetobacter*, [1]*Azotobacter*, [1,15,18]*Bacillus*, [2]*Bradyrhizobium*, [18]*Burkholderia*, [1]*Mesorhizobium*, [18]*Pantoea*, [1,7]*Pseudomonas*, [2]*Rhizobium*, [15]*Serratia*, [15]*Stenotrophomonas*, [18]*Streptomyces*
1-Aminocyclopropane-1-carboxylic acid degradation	[8]*Achromobacter*, [10]*Alcaligenes*, [7,8]*Bacillus*, [8]*Ensifer*, [14]*Methylobacterium*, [8]*Microbacterium*, [8]*Ochrobacterium*, [14]*Okibacterium*, [7,10]*Pseudomonas*, [8]*Sinorhizobium*

[1]Ahmad et al. 2008; [2]Antoun et al. 1998; [3]Aranda et al. 2011; [4]Berg et al. 2002; [5]Berg et al. 2005; [6]Berg et al. 2006; [7]Cattelan et al. 1999; [8] Cavalca et al. 2010; [9]de Souza et al. 2003; [10]Dell'Amico et al. 2005; [11]Donate-Correa et al. 2004; [12]Egamberdleva et al. 2008; [13]Garbeva et al. 2008; [14]Idris et al. 2004; [15]Idris et al. 2009; [16]Khamna et al. 2009; [17]Malik et al. 1997; [18]Oliveira et al. 2009; [19]Oyaizy-Masuchi and Komagata 1988; [20]van Overbeek and van Elsas 2008; [21]Yang et al. 2008; [22]Ashoub and Amara 2010; [23]Kluepfel et al. 1993; Kloepper et al. 1992; [25]Krechel et al. 2002; [26]Racke and Sikora 1992; [27]Insunza et al. 2002; [28]El-Tarabily et al. 2000

Lolium perenne (Mariley and Aragno 1999), but, for *Trifolium repens* grown in the same soil, Acidobacteria relative abundance in all rhizosphere compartments was lower than in the bulk soil. For the class Holophagae, within Acidobacteria, a complex response to root proximity was described (da Rocha et al. 2010). The abundance of Holophagae increased between the bulk soil and outer rhizosphere of leek (*Allium porrum*), but at the inner rhizosphere abundance had dropped below the bulk soil levels. With a rare exception (Zhang et al. 2011b), a high level of Acidobacterial dominance appears to be more common among trees in native habitats and wild plant species relative to agricultural crops.

The advantage of culture-independent strategies is highly evident in fine resolution description of microbial communities. Cultivation-independent methods facilitate the discovery and investigation of novel important lineages (at the genera and species level), even within the most common root-associated ones (Kowalchuk et al. 2010). We focus on the genus *Massilia* (Oxalobacteraceae, β-proteobacteria) as an example. Members of *Massilia* were first isolated from clinical samples and were defined as a novel genus less than 15 years ago (La Scola et al. 1998; Lindquist et al. 2003). In recent years, *Massilia* were described in environmental samples of many sources (including air, dust, and soil samples) over a wide geographic distribution, using culture-independent techniques (Nagy et al. 2005; Pakarinen et al. 2008; Blatny et al. 2011). Such techniques have also placed *Massilia* among dominant and important root-colonizing bacteria of many plant species (Dohrmann and Tebbe 2005; Abou-Shanab et al. 2007; Green et al. 2007; Weinert et al. 2010; Brooks et al. 2011; Weisskopf et al. 2011), indicating high underestimation of this group's prevalence using cultivation strategies (Weisskopf et al. 2011). Particularly high dominance of *Massilia* was found in the spermosphere and roots of young seedlings of cucumber (Green et al. 2007; Ofek et al. 2009; Ofek et al. 2011). Similarly, root age-related decline in *Massilia* dominance was reported in cluster roots of white lupin (Weisskopf et al. 2011). Like numerous other "novel" root-associated bacterial lineages, the ecological significance and role of this group in the rhizosphere niche remains to be elucidated.

Role of Archaea

Since their discovery in the late 1970s (Woese and Fox 1977), Archaea were traditionally associated with extreme

Table 4.3

Examples of composition of rhizosphere and rhizoplane bacterial communities in different plant species

Plant species	Method[u]	Sample	Proteobacteria				Firm	Actin	Bact	Acid	Planc	Verru	Cyan	Chlo	Uncl
			α	β	γ	δ									
Cucumis sativus[a]	IS (1,790)	RP	2–11	0.5–26	19–63		9–20	4–10	7–18						3–9
Medicago sativa [b]	IS (452)	RS/RP	1–30	9–17	16–74			15–32	0.4–5						
Chenopodium album[b]	IS (407)	RS/RP	15–17	61–62	5–18			5–9	2–8						
Brassica napus[c]	IS(111)	RP	15	28	37		5	14	0.9						
	CL (103)	RP	52	9	6		3	0.97	30						
Solanum tuberosum[d]	IS(283)	RS/RP	4–6	10–25	28–45		4–20	10–12	5–14						1–8
Pinus contorta[e]	CL (709)	RS	24	19	9	3		3	3	19		3			15
Thlaspi caerulescens[f]	CL (142)	RS	20	12	2	0.7	0.0	33	0.7	15	9	7			
Lasiurus sindicus[g]	CL (58)	RS/RP	5	5–7	0–2	0–2	16–33	45–49	0–3	0–2					10–12
Hordeum vulgare[h]	CL (466)	RP	11–13	35–41	11–12	7–10	1–3	3–5	11–15	0–3	0–1	3–6		1–7	
Citrus sinensis[i]	CL (528)	RP	31–72	0–19	3–17	0–2	3–11	0–10	0–9	0–2					8–13
Zea mays[j]	CL (274)	RS	48				1.8	10.3	9.9	5		7	0.4	2	13
Gossypium hirsutum[k]	CL (600)	RS	0–38	0–30	0–30	0–19	0–4	0–3.7	0–10	7–45	0–15	0–7	0–4		0–10
Oryza sativa[l]	CL (731)	RP	4–12	11–24	12–16	0–0.6	0.3–4	3–28	9–12	6–8	0–0.3	1–2	0.3	2–5	7–13
Picea mariana[m]	CL (300)	RS	0–3	0–18	7–21	0–5	0–9	9–22		10–36		0–6			0–8
Solanum tuberosum[n]	TeP	RE	20	13	21	0.5	0.9	5	30	2	0.1	0.2	0.47	0.2	5
Capsicum annuum[o]	TeP (20,142)	RS	47–72				5–6	7–10	12–30						
Cucumis sativus[p]	TeP (55,105)	RP	0.1–21	8–72	13–86		0.2–23		0.03–3		0–0.7	0–0.1			
Quercus sp.[q]	TeP (133,231)	RS	38–41				0.3–0.8	11–12	2	20–27	0.5–2	1–2			18–20

Table 4.3 (continued)

Plant species	Method[u]	Sample	Proteobacteria				Firm	Actin	Bact	Acid	Planc	Verru	Cyan	Chlo	Uncl
			α	β	γ	δ									
Beta vulgaris[r]	PhyloChip	RS	39				20	9	4	2	2	2	1	1	16
Lolium arundinaceum[s]	FISH	RS	3–8	3–8	3–8			10–40	4–32		32–79				
Cirsium arvense[t]	FISH	RS/RP	13–14	24	33–56		0.1–1	0.1–0.9	0.3–0.6						

Abbreviations: *Firm* Firmicutes, *Act* Actinobacteria, *Bact* Bacteroidetes, *Planc* Planctomyces, *Verru* Verrucomicrobia, *Cyan* Cyanobacteria, *Chlo* Chloroflexi, *Uncl* Unclassified, *IS* Isolates obtained by cultivation, *CL* Clone libraries, *TeP* Tag-encoded pyrosequencing of 16S rRNA gene fragments, PhyloChip, *FISH* Fluorescence in situ hybridization, *RS* rhizosphere soil, *RP* rhizoplane, *RE* root endophytes

[a]Mahaffee and Kloepper 1997
[b]Schwieger and Tebbe 2000
[c]Kaiser et al. 2001
[d]Heuer et al. 2002
[e]Chow et al. 2002
[f]Gremion et al. 2003
[g]Chowdhury et al. 2009
[h]Buddrus-Schiemann et al. 2010
[i]Trivedi et al. 2010
[j]Chauhan et al. 2011
[k]Zhang et al. 2011a
[l]Ikeda et al. 2011
[m]Filion et al. 2004
[n]Manter et al. 2010
[o]Kolton et al. 2011
[p]Ofek et al. 2011
[q]Uroz et al. 2010
[r]Mendes et al. 2011
[s]Jenkins et al. 2006
[t]Cavalca et al. 2010
[u]The numbers in parentheses indicate the total (cumulative) size of the samples analyzed

environments and therefore rarely studied in soils, and even less in association with plant roots. Rhizosphere colonizing Archaea first received attention due to observation of methane production by rice roots placed under anoxic conditions (Frenzel and Bosse 1996). Soon after, it was reported that Archaea may appear in substantial relative abundance in the rhizoplane of mature rice plants, as indicated by the Archaeal signature compounds—diether lipids (Richardt et al. 1997). It was then confirmed by analysis of Archaea-specific clone libraries that the rhizoplane of rice was inhabited by Archaea including both Crenarchaeota and Euryarchaeota (Grosskopf et al. 1998). The composition of Archaea associated with rice and other waterlogged plant roots and rhizosphere is dominated by Euryarchaeota (Conrad et al. 2008; Cadillo-Quiroz et al. 2010; Kao-Kniffin et al. 2010), including important families of known methanogens such as Methanosarcinaceae, Methanosaetaceae, Methanomicrobiaceae, and Methanobacteriaceae. Novel Euryarchaeal lineages discovered in the rice rhizosphere (Grosskopf et al. 1998; Ramakrishnan et al. 2001), mainly rice cluster I, were later classified as methanogens with wide global distribution (Conrad et al. 2006) and may substantially contribute to methane emission from rice fields into the atmosphere.

In moderate dry oxic soils, rhizosphere-associated Crenarchaeota were first reported for young and senescent roots of tomato grown in field soil (Simon et al. 2000). Crenarchaeota were consistently detected in various plant species grown in a native temperate environment (Sliwinski and Goodman 2004). In contrast, in rhizosphere samples of plants grown in high altitude, detection of Archaea was rare and inconsistent (Ferrero et al. 2010). Furthermore, no Archaea were detected in the rhizosphere of different proteaceae species (Stanford et al. 2005). In contrast to plants with waterlogged root systems, Crenarchaea dominate the Archaeal community associated with rhizosphere, roots, and mycorrhiza of plants growing in such soils (Nelson et al. 2010; Bomberg et al. 2011).

Another archaeal group of functional importance is ammonia oxidizing Archaea (AOA). AOA were found in the rhizosphere and on roots of several plant species, including *Zea mays*, *Vicia faba*, *Brassica oleracea*, and the macrophyte *Littorella uniflora* (Herrmann et al. 2008; Fan et al. 2011; Kleineidam et al. 2011; Nelson et al. 2010). Similarly to soils (Leninger et al. 2006), AOA appear to predominate the ammonia-oxidizing consortium in the rhizosphere (Kleineidam et al. 2011; Nelson et al. 2010). However, the diversity of rhizosphere colonizing AOA may be lower than that of ammonia oxidizing bacteria (Fan et al. 2011). *Table 4.4* describes the composition of Archaea associated with different plant species.

Effect of Mycorrhizal Association

Arbuscular mycorrhizal and ectomycorrhizal fungi (AMF and EMF, respectively) create a new structure and function for the rhizosphere, also termed "mycorrhizosphere." The unique relationships in the mycorrhizosphere, compared to the non-mycorrhizal rhizosphere, change the allocation of plant resources between the rhizosphere bacteria and the symbiotic partner. On the other hand, the contribution of the mycorrhizal fungi affects the plant's physiology and root environment with respect to mineral nutrition and water availability (Bending et al. 2006).

The effect of AMF on rhizosphere bacterial communities has been investigated mostly by inoculation studies. Such experiments have revealed consistent differences between bacterial consortia associated with mycorrhitic and non-mycorrhitic roots and the activity of selected microbial enzymes (Vázquez et al. 2000; Marschner et al. 2001a; Söderberg et al. 2002; Wamberg et al. 2003; Marschner and Timonen 2005; Roesti et al. 2006; Vestergard et al. 2008; Solís-Domínguez et al. 2011). Offre et al. (2007) compared and distinguished bacterial communities colonizing mycorrhiza of *Medicago truncatula* and roots of a mutant plant that does not form mycorrhiza. EMF effects have been studied by inoculation and by analysis of mycorrhizal and non-mycorrhizal roots sampled in the field (Olsson and Wallander 1998; Timonen et al. 1998; Probanza et al. 2001; Faye et al. 2009). These reports present mycorrhiza-related shifts in the bacterial community assemblages.

Infection with mycorrhizal fungi results in systemic changes in the plant. Therefore, changes in the rhizosphere bacterial community structure and/or function could be an indirect response to the mycorrhiza. Such an indirect effect was demonstrated by Marschner and Baumann (2003) in maize using a split-root system. The bacterial communities in the non-mycorrhitic half of the root system were different from respective controls where neither half of the root system was inoculated. Unfortunately, however, this exciting topic has not yet been further explored.

Changes observed in the mycorrhizosphere bacterial community can be attributed to local and direct effects of the fungi or indirect effects mediated by systemic changes in the infected plant. A direct effect might simply be attachment of soil bacteria to the hyphae of the mycorrhizal fungus. For example, Scheublin et al. (2010) showed rapid colonization of bacteria from the family of Oxalobacteraceae and *Pseudomonas*. Based on the high frequency of Oxalobacteraceae, those authors suggested the existence of a specific interaction (Scheublin et al. 2010). Offre et al. (2007) also identified bacterial groups belonging to the Oxalobacteraceae preferentially associated with mycorrhizal roots of *Medicago truncatula*. FISH analysis of the ectomycorrhizosphere of beech (*Fagus sylvatica*) growing in a natural forest revealed bacteria of the α-, β, and γ subclasses of the Proteobacteria attached in high numbers to the mantle surfaces (Mogge et al. 2000). One mechanism suggested for the direct effect is the influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community composition. Toljander et al. (2007) used a split Petri dish system to produce mycelial exudates. Following amendment of soil with these exudates, a significant shift in soil bacterial community composition occurred, marked by significant enrichment of specific Enterobacteriaceae members. Frey-Klett et al. (2005) argued that ectomycorrhizal symbiosis also has an indirect positive effect on the plant via its selective pressure on bacterial communities.

Table 4.4

Composition of Archaea associated with plant roots (R), rhizosphere soil (RS) and mycorrhiza (Myc)

Taxonomy	Rice [a]	Acid bog plants[b]	Wetland[c]	Scot pine[d]	Silver brich[d]	Norway sprouce[d]	Maize[e]	Soybean[f]	Macrophyte [g]	Tomato[h]	Various grasses[i]	Barley[j]
Euryarchaeota							RS	RS				
Methanosarcinaceae	R, RS	R	RS	R, Myc	R, Myc	Myc						
Methanomicrobiaceae	R, RS	R	RS									
Methanobacteriaceae	R, RS	R	RS									
Methanosaetaceae	R, RS	R	RS									
Rice cluster I	R, RS	R	RS									
Rice cluster II	R											
Rice cluster III	R, RS	R										
Rice cluster V	R											
LDS cluster	R											
Halobacteriales				Myc	R							
Crenarchaeota												
Rice cluster IV	R, RS											
1.1a							R, RS	RS	RS			
1.1b				Myc			RS	RS	R	RS	RS	RS
1.1 C		R		R, Myc	R, Myc	R	RS	RS			RS	
1.2	R											
1.3b		R										

[a] *Oryza sativa* L. (Grosskopf et al. 1998; Lehmann-Richter et al. 1999; Scheid et al. 2003; Lu et al. 2005; Krüger et al. 2005; Lu and Conrad 2005; Conrad et al. 2008; Wu et al. 2009b)
[b] *Dulichium arundinaceum, Sarracenia purpurea* (Cadillo-Quiroz et al. 2010)
[c] Forbs and graminoids (Kao-Kniffin et al. 2010)
[d] *Pinus sylvestris, Betula pendula, Picea abies* (Bomberg and Timonen 2007; Bomberg et al. 2010; Bomberg et al. 2011)
[e] *Zea mays* (Chelius and triplett 2001; Nelson et al. 2010)
[f] *Glycine max* (Nelson et al. 2010)
[g] *Littorella uniflora* (Herrmann et al. 2008)
[h] *Lycopersicum esculentum* L. (Simon et al. 2000)
[i] Pasture grasses (Nicol et al. 2003)
[j] *Hordeum vulgare* L. (Poplawski et al. 2007)

They showed that ectomycorrhizal symbiosis determines the structure of *Pseudomonas fluorescens* populations in the soil and selects for potentially beneficial bacteria. Soil bacteria can promote mycorrhizal formation by means of a variety of mechanisms (Poole et al. 2001; Rigamonte et al. 2010), and such communities have been termed "mycorrhization helper bacteria" (MHB). Among the identified lineages of MHB are bacteria belonging to diverse groups and genera, such as Gram-negative Proteobacteria (*Agrobacterium, Azospirillum, Azotobacter, Burkholderia, Bradyrhizobium, Enterobacter, Pseudomonas*, *Klebsiella*, and *Rhizobium*), Gram-positive Firmicutes (*Bacillus, Brevibacillus*, and *Paenibacillus*), and Gram-positive actinomycetes (*Rhodococcus, Streptomyces*, and *Arthrobacter*) (Bending et al. 2002; Artursson et al. 2006; Frey-Klett et al. 2007).

Bacterial Communities Associated with Roots of Pathogen-Infected Plants

Pathogen infection and disease propagation affect the host plant's physiology in many ways which, in turn, can locally (at the site of infection) or systemically affect plant-bacteria interactions. This issue is relatively unexplored. However, several studies have compared the composition and structure of microbial communities associated with healthy and diseased plants.

Yang et al. (2001) compared rhizosphere bacterial communities associated with healthy and *Phytophthora*-infected avocado roots using 16S rRNA gene fingerprinting. In that study, bacterial communities from healthy roots were represented by a few predominant species, and were approximately 80% similar in structure among replicates. In contrast, roots that were infected with *Phytophthora*, but which did not yet show visible symptoms of disease, were colonized by much more variable bacterial communities with significantly different structures from those of healthy roots. The effect of oomycete pathogens, including *Phytophthora cryptogea*, *Pythium aphanidermatum*, and *Pythium* group F, was also examined in a soilless growth system with tomatoes (Cavalo-Bado et al. 2006). There, an increase in bacterial abundance was found associated with oomycete-infected roots, but the community composition was unaltered. In another study, infection of tomato plants with *Phytophthora nicotianae* did not significantly affect the bacterial community structure (Lioussanne et al. 2010). Comparison to infection with the AM fungi *Glomus intraradices* or *Glomus mosseae* suggested that rhizospheric bacteria are less sensitive to pathogen invasion than to mycorrhizal colonization. Tomato rhizosphere bacterial communities were also examined in response to infection with *Fusarium oxysporum* f. sp. *radicis lycopersici* and its biocontrol antagonistic *Fusarium* strain (*F. solani* strain FsK) (Karpouzas et al. 2011). These introductions also resulted in only marginal response of the bacterial community.

In a *Pythium aphanidermatum*-cucumber experimental pathosystem, multiple aspects of the spermosphere bacterial communities significantly differed between inoculated and control germinating seeds (Ofek et al. 2011). Microscopic examination of germinating seeds revealed bacterial crowding at sites of seed infection by *Pythium* hyphae and heavily colonizing the hyphae themselves (Fig. 4.1). Furthermore, the spermosphere of infected seeds had significantly lower diversity and was dominated (66% of the total bacteria) by members of the genus *Massilia* (Oxalobacteraceae).

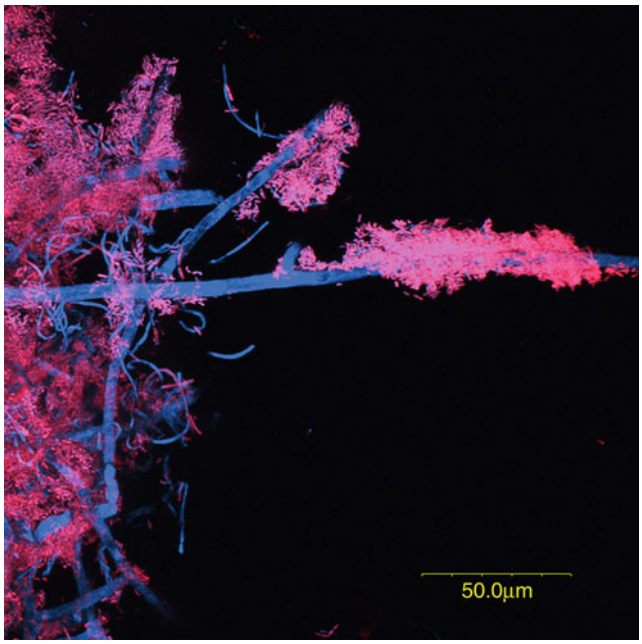

Fig. 4.1
***Pythium aphanidermatum* hyphae (*white arrows*) infecting the seed coat of cucumber seed following 24 h of germination in *P. aphanidermatum*-inoculated perlite. Seed samples were stained with DAPI (*blue*) and hybridized with fluorescently labeled probe EUB338, targeting the domain Bacteria (*red*) (Image was taken by confocal laser-scanning microscopy)**

Two interesting studies examined the rhizosphere of healthy plants and plants with natural incidence of disease. Filion et al. (2004) selected healthy and diseased root rot-symptomatic samples of roots from black spruce (*Picea mariana*) seedlings growing in a nursery. The rhizosphere-associated bacterial and fungal communities of healthy and diseased *P. mariana* seedlings differed: the main differences described at the community level were a higher proportion of Acidobacteria, Gammaproteobacteria, and Homobasidiomycetes clones associated with healthy seedlings, while the diseased-seedling rhizosphere showed a higher proportion of Actinobacteria, Sordariomycetes, and environmental clones. The authors debated on whether the communities associated with healthy roots might be responsible for disease suppression or whether their presence is simply a direct consequence of the absence of the pathogen. In a recent study, the rhizosphere of scab-diseased apple trees was compared to that of disease-free ones (Shanmugam et al. 2011). There, while the rhizosphere bacterial community composition and structure were similar, the activities of chitinase and β-1,3 glucanase were higher in rhizosphere samples from disease-free plants.

Contradictory observations could be the result of variation between the studied systems or of higher complexity of the rhizosphere of diseased plants and its multiple effects. Microbial communities in the rhizosphere of healthy and diseased plants may promote suppression via antagonism, induce resistance, or modify patterns of root-exudate release. Thus, the effects on the community could be either direct or indirect. Nevertheless, additional studies may shed more light on the interactions occurring in the rhizosphere of infected plants and may assist in developing ecologically based control methods. It is assumed that specific populations provide protection and that these will eventually be developed for biological control.

Effects of Agrosystem Management on Rhizosphere Bacterial Communities

Agricultural practices designed to improve plant performance and yield may result in nontargeted rhizosphere modulation. For example, the composition of rhizosphere bacterial communities of cucumber and sudan grass seedlings shifted following nitrogen or phosphorus fertilization of nitrogen- and phosphorus-deficient soils (Marschner et al. 2004). In iron-limited soil, foliar application of iron shifted the composition of the root-associated bacterial community (Yang and Crowley 2000). Changes in rhizosphere bacterial community composition and activity have been observed to result from crop rotation practices and land-use history (van Elsas et al. 2002; Alvey et al. 2003; Salles et al. 2004; Garbeva et al. 2008). Shifts in bacterial community composition in response to herbicides (Sessitsch et al. 2004) or pesticides (Lin et al. 2007) and a strong effect of tillage practice (Griffiths et al. 2007) have also been reported.

Other soil treatments aim to modify or manipulate specific or general rhizosphere components. These include organic soil amendments, introduction of plant-beneficial organisms via inoculation (i.e., *Rhizobium*, mycorrhiza, associative plant-growth-promoting rhizobacteria), application of chemical or biocontrol agents, and genetically engineered plants.

Effect of Organic Soil Amendment

Long-term experiments (16–50 years) have confirmed that different fertilization regimes, both organic and inorganic, affect soil bacterial communities to varying degrees, in terms of biomass, activity, and composition (Enwell et al. 2005; Ros et al. 2006; Widmar et al. 2006; Chu et al. 2007; Esperschütz et al. 2007; Toljander et al. 2008). Generally, organic amendments (manures, green and dry plant residues, sewage sludge, and compost) have more pronounced effects on the soil microbial communities than mineral fertilization. Organic soil amendments and compost improve soil structure, elevate soil content of organic matter, and supply macro- and micronutrients. Moreover, compost application to soil results in the introduction of a rich and diverse microbial community. Thus, the effects on the rhizosphere community can be either direct or indirect, by changing the abiotic root environment. Several studies have provided evidence for the persistence of amendment-derived microbes in association with the rhizosphere. Germinating seeds were colonized by amendment-derived microbes and this community changed during the transition from spermosphere to rhizosphere (Green et al. 2006; Ofek et al. 2011). The rhizosphere bacterial community is distinct in compost-amended soil compared to non-amended soil (Benitez et al. 2007; Tiquia et al. 2002). Root-associated communities of cucumber seedlings grown in perlite medium were more diverse but less abundant in the presence of disease-suppressive compost than in the non-amended controls (Ofek et al. 2009). Rhizosphere colonization by *Streptomyces* was affected by compost amendment (Inbar et al. 2005). This impact was strongly affected by proximity to the root and compost concentration. While the compost's effect on the community was mitigated with increasing proximity to the root, high levels of compost amendment resulted in the detection of compost-derived species, even on the root surface. On the other hand, in both rhizosphere and non-rhizosphere soils, the community composition of *Streptomyces* was strongly affected by even modest compost amendment (Inbar et al. 2005).

Jack et al. (2011) tested the effect of organic amendments on growth, field performance, and rhizosphere bacterial communities of tomato plants. They showed that different amendments significantly affect rhizosphere bacterial communities. These differences persisted for at least 1 month after seedlings were transplanted to the field, then diminished over the course of the field season (Jack et al. 2011). In cucumbers, compost had qualitative and quantitative effects on bacterial communities colonizing roots of young cucumber plants. These effects were dynamic in nature and strongly related to plant age (Ofek et al. 2009, 2011). Soil amendment with chitin resulted in shifts in both soil and rhizosphere bacterial community size and composition (Hallmann et al. 1999). On the other hand, Scott and Knudsen (1999) found that residues of rape as green manure had no effect on heterotrophic bacteria colonizing the rhizosphere of pea.

Inoculation with Plant-Growth-Promoting Rhizobacteria (PGPR) and Biocontrol Agents

Introduction of microorganisms by inoculation represents a technically simple approach to directly modifying the rhizosphere. Indeed, this approach has high appeal as it proposes a targeted solution for the purposes of sustainable agriculture and is considered inexpensive and environmentally benign. The objectives of inoculation are diverse and include enhancement of symbiotic and associative nitrogen fixation, plant-growth promotion, improvement of plant nutrition, control of plant-pathogenic microorganisms, and degradation of contaminating xenobiotic compounds (Vessey 2003; Lugtenberg and Kamilova 2009). PGPR and biocontrol species of bacteria are primarily rhizosphere, rhizoplane, and endophytic microorganisms; however, their natural quorum is relatively low and insufficient to

induce the desired positive effect. Enrichment through inoculation can potentially increase their abundance so that their phytoeffective potential can be expressed. Several recent reviews have described the high and still growing number of formulated and tested inoculants, and their plant-growth-promoting and biocontrol mechanisms and activities (Rodríguez-Díaz et al. 2008; Lugtenberg and Kamilova 2009; Compant et al. 2010a; Dutta and Podile 2010; Hayat et al. 2010). Here, we focus on the successful establishment of inoculated bacteria and their effect on the indigenous resident community.

Integration and nontarget effects on bacterial communities were studied for different plant-growth-promoting and biocontrol agents. Apparently, a prominent effect of crop plant inoculation with PGPR or biocontrol bacterial agents on resident bacterial communities is rare, transient, and spatially limited. This was the case with associative nitrogen-fixing *Azospirillum* (Bashan et al. 1995; Herschkovitz et al. 2005a, b; Lerner et al. 2006; Felici et al. 2008; Pedraza et al. 2009), antibiotic-producing *Pseudomonas* (rev. in Castro-Sowinski et al. 2007), siderophore-producing *Pseudomonas* (Buddrus-Schiemann et al. 2010), phytohormone-producing *Pseudomonas*, *Serratia*, and *Pantoea* (Lottmann et al. 2000; Mishra et al. 2011), among others.

One clear exception to the rule is the response of resident rhizospheric microbial communities to inoculation with host-compatible symbiotic nitrogen-fixing rhizobia. The establishment of *Sinorhizobium meliloti* in the rhizoplane of its host plant, *Medicago sativa*, and in the rhizoplane of a non-host plant, *Chenopodium album*, was examined in a field experiment (Schwieger and Tebbe 2000). Following inoculation of the soil by spraying and 12 weeks of growth, the abundance of *S. meliloti* had increased in the rhizoplane of both plants. However, the numbers of *S. meliloti* were two orders of magnitude higher for the host compared to the non-host plant. Marked changes in the composition of total and cultivable bacterial communities were found in the host plant, while communities of non-host plants were unaffected. A specific effect of *S. meliloti* on the indigenous rhizospheric bacterial community in the host but not non-host plants was also demonstrated by Miethling et al. (2000) in a mesocosm experiment. Similarly, significant shifts in bacterial community composition due to host-compatible rhizobial inoculation have been reported for common bean (Robleto et al. 1998), faba bean (Zhang et al. 2010), and soybean (Zhang et al. 2011a).

Another emerging exception is the effect of PGPR inoculation in forest trees. Inoculation with two phytohormone-producing *Bacillus* PGPRs resulted in shifts in total and cultivable bacterial communities associated with roots of *Pinus pinea* seedlings (Probanza et al. 2001, 2002). This effect lasted months after a single inoculation. Lucas-García et al. (2004) inoculated pine and holm oak with PGPR strains belonging to *Enterobacter*, *Pseudomonas*, *Cryseobacterium*, and *Phosphoric bacillus*. There, perturbation of the tree seedlings' rhizospheric bacterial communities was robust, but varied in degree for the different specific bacteria-plant pair examined. In another survey of ten isolates selected for their plant-growth-promoting potential, inoculation of one strain (*Arthrobacter* sp.) resulted in a strong alteration of *P. pinea* seedlings' rhizospheric bacterial community, along with a strong positive effect on the seedlings' growth (Barriuso et al. 2008). Inoculation of European alder with auxin-producing *Bacillus pumilus* showed contrasting results for two different soils (Ramos et al. 2003): in the native soil from which the isolate was retrieved, the inoculation effect appeared early and was transient; in the second soil, the effect of inoculation on the resident bacterial community was most pronounced at late stages of the experiment (6 and 8 weeks).

Some inoculants, such as biocontrol agents, are selected for their ability to compete with other microorganisms. Nevertheless, it seems that their ability to change the bacterial balance in the rhizosphere is limited in most cases and transient in others.

Plant Genetic Manipulation Targeting Rhizosphere Associations

Relying on the concept that root deposits are the major selective factor in root-microbe associations, Ryan et al. (2009) reviewed the possibilities for rhizosphere engineering. One suggested route for manipulation was interference with central metabolic pathways. For example, a fourfold greater efflux of citrate from tobacco seedlings was achieved by transformation with a citrate synthase gene from *Pseudomonas aeruginosa* (de la Fuente et al. 1997). The effect of extensive citrate release on rhizosphere bacteria can be demonstrated by the case of white lupin (*Lupinus albus*) cluster roots. This specialized type of root is produced in response to low phosphorus availability. When the cluster root matures, large amounts of citrate are released for the purpose of phosphorus chelation. This event coincides with a significant decrease in the number of root-associated and rhizospheric bacteria and a dramatic shift in their composition (Weisskopf et al. 2005). Another possibility for the manipulation of root exudate composition or amount is through modification of transporter proteins. Recently, this was demonstrated in *Arabidopsis thaliana* (Bardi et al. 2009). A single mutation in an ABC transporter (abcg30) resulted in more phenolics and fewer sugars in the exudates, compared to the wild type. This shift in exudate profile resulted in a substantial shift in the root-associated bacterial community, including an increase in the relative abundance of operational taxonomic units (OTUs) related to known PGPR species. These examples may be limited, but clearly demonstrate the potential for designed rhizospheres. However, the magnitude and consequences of such modifications in root depositions will require a thorough determination of possible undesirable effects.

Plant Genetic Manipulation: Rhizosphere Bacteria as Nontarget Organisms

Genetic engineering has been applied to crop plants to address different agricultural traits, for example, resistance to chemical herbicides, insect pest resistance, stress tolerance, and food quality.

Herbicide-resistant transgenic crop lines are the most widespread transgenic crops in commercial use. Among these, glyphosate- or glufosinate-resistant lines have been most studied with respect to possible nontarget rhizosphere effects (Kremer and Means 2009). Studies of oilseed rape (*Brassica napus*) cultivars yielded variable results. Siciliano and Germida (1999) isolated heterotrophic rhizospheric bacteria and endorhiza of cv. Excel and its glyphosate-resistant derivative "Quest" and found that in the genetically modified line, bacteria of the genera *Bacillus, Micrococcus*, *Variovorax*, and *Arthrobacter* were negatively affected whereas *Flavobacterium* and *Pseudomonas* were enriched. Confirming this result, both fatty acid methyl ester and carbon-substrate utilization profiles of the total endorhizal communities were found to vary between these lines (Dunfield and Germida 2001). Conversely, comparative analysis using PCR-DGGE revealed only a minor and growth-stage-dependent effect of glufosinate-tolerance introduction on the total rhizosphere bacterial community and on the composition of *Pseudomonas* populations (Gyamfi et al. 2002). Similarly, Sessitsch et al. (2004) found that the effect of the transgenic modification on rhizosphere bacterial communities' DGGE profiles and selective activities was more apparent at early stages of oilseed rape growth. The total (Schmalengerger and Tebbe 2002) and denitrifying (Philippot et al. 2006; Hart et al. 2009) bacterial communities in the rhizosphere of maize were similar for conventional and glyfosate-resistant lines, whereas a study of sugar beet (*Beta vulgaris*) varieties revealed differences in the compositions of rhizosphere bacterial communities of conventional versus herbicide-resistant plants, as determined by genetic fingerprinting of 16S rRNA genes (Schmalenberger and Tebbe 2003). In contrast, a reduction in cultivable fluorescent *Pseudomonas* was found in a comparison of conventional and glyphosate-resistant soybean (Kremer and Means 2009).

Another example of a widely commercialized transgenic trait is insect resistance, conferred by genetic modification for expression of the crystal (Cry) protein from the bacterium *Bacillus thuringiensis* (Bt crops). The protein may be released from the roots into the rhizosphere through natural wounding of roots and from sloughed-off and senescent cells, resulting in nontarget effects. Brusetti et al.'s (2004) study indicated a significant effect on cultivable and total bacterial communities in Bt compared to nontransgenic maize. In addition, the numbers of some cultivable bacterial groups (nitrogen-fixing, phosphorus-solubilizing, potassium-solubilizing) were lower in Bt lines of cotton compared to the parental line during the early and mid-stages of growth (Rui et al. 2005). In contrast, reports from experiments with maize (Baumgrate and Tebbe 2005), rice (Liu et al. 2008; Wu et al. 2009a), and *Brassica rapa* (Jung et al. 2008) concluded that the nontarget effect of Bt transformation is marginal.

T4 lysozyme expression in transgenic crops is a strategy developed to overcome plant diseases for which the pathogenic agent is a bacterium (e.g., *Erwinia carotovora*). Indeed, in cell-free extracts of tubers from transgenic potatoes, the lytic activity against bacterial cultures was higher than that present in the nontransgenic lines (De Vries et al. 1999). Those bacteria included Gram-positive and Gram-negative plant-pathogenic species, but also plant-growth-promoting species, such as *Rhizobium leguminosarum*. In addition, Ahrenholtz et al. (2000) demonstrated increased killing of inoculated *Bacillus subtilis* at the root-hair zone of potato roots. It is therefore surprising that a set of subsequent experiments concluded that the effect of T4 lysozyme expression in potatoes on rhizosphere or root endophytic bacterial communities is minor compared to the effects of other factors, such as the soil or site, or plant growth stage (Lottmann et al. 1999, 2000; Heuer et al. 2002; Rasche et al. 2006 FEMS; van Overbeek and van Elsas 2008). This lack of effect was explained by accelerated degradation of the T4 lysozyme by proteases in the soil, and by inaccessibility of the residing bacterial population. Similar results were obtained with transgenic plants modified to produce other enzymes, including lytic peptides (Sessitsch et al. 2003; Rasche et al. 2006FEMS) and lectins (Griffiths et al. 2000), and with zeaxanthin- (Weinert et al. 2009) and amylopectin-accumulating (Gschwendtner et al. 2010a, b; Gschwendtner et al. 2011) transgenic plants.

Overall, the different genetic modifications of plants rarely result in an overhaul of the rhizosphere bacterial community. It is therefore likely that the fraction of affected populations is small, and high-resolution methods are required for their detection and identification. Nevertheless, such effects should be considered on a case-by-case basis.

Consequences of Climate Change

One of the most important challenges faced by the scientific community today is predicting the outcome of global climate change on ecosystem functioning. With respect to soil microbial communities, this challenge is deemed difficult to impossible, due to its complexity and the virtually infinite ways in which different climate drivers (CO_2 and O_3 concentrations, temperature, precipitation, UV-B radiation) and their interactions might affect soil microorganisms and their activities (Bardgett et al. 2008). As the "hotspot" of microbial activity in soil, the effects of changes in climate drivers may be most pronounced in the rhizosphere. Moreover, rhizosphere processes may be central to plant productivity responses to elevated atmospheric CO_2 and, consequently, important controllers of the ecosystem response (Phillips 2007). Among rhizospheric processes, those related to the status of mineral nutrients should be specifically considered, since their availability may determine the plant's response to climate changes (Lewis et al. 2010; Tobita et al. 2011).

The most explored changing climate driver in rhizosphere research is elevated atmospheric CO_2 (eCO_2) (Drigo et al. 2008). Generally, atmospheric enrichment in CO_2 increases productivity of both C3 and C4 plants through stimulation of photosynthesis and improved water-use efficiency (Wand et al. 1999; Morgan et al. 2004; Lopes and Foyer 2012). However, the effect of eCO_2 varies with plant species and in response to variations in abiotic conditions, including nutrient availability, temperature, soil moisture, and salinity, among others (Lopes and

Foyer 2012). With respect to below-ground plant responses, increased root biomass (Ferris and Taylor 1993; Rogers et al. 1994; Phillips et al. 2009), changes in root morphology (Pregitzer et al. 2000; Larigauderie et al. 1994), and increased mycorrhization (rev. by Drigo et al. 2008 and by Compant et al. 2010b) have all been reported. However, most important might be changes in the amount and composition of root depositions. Increases in rhizodeposition have been reported in several studies (de Graaff et al. 2009; Phillips et al. 2009, 2011), but the opposite situation has also been indicated (Augustine et al. 2011). All of the above are considered key factors affecting the root-associated prokaryotes. Therefore, shifts in rhizospheric microbial communities' biomass, composition, and activity are anticipated (Díaz et al. 1993; Paterson et al. 1997). However, in comparison to the fairly conclusive results regarding fungi, and in particular mycorrhiza (Compant et al. 2010b), the responses of rhizospheric prokaryotes to eCO_2 have been much more difficult to generalize.

A number of methods have been used to estimate the effect of eCO_2 on the size of rhizosphere microbial communities, including chloroform fumigation, determination of phospholipid fatty acids (PLFA), direct viable counts, cultivation on defined media, and quantitative real-time PCR, with mixed results (Zak et al. 2000; Drigo et al. 2008). Rattray et al. (1995), Paterson et al. (1996) and Griffiths et al. (1998) reported a significant reduction in the proportion of root-derived carbon assimilated by rhizospheric bacteria under eCO_2. This was hypothesized to be related to reduction in the availability of nutrients, including nitrogen, due to higher consumption by the plant. Levels of nutrient limitation could explain the variability in bacterial biomass response to eCO_2, as do other variables such as water limitation (Augustine et al. 2011). Indeed, microbial biomass was found to increase under eCO_2 following addition of mineral nutrients (Klironomos et al. 1996) or organic matter (Dorodnikov et al. 2009). However, in other experiments, viable rhizosphere bacterial count (Rillig et al. 1997) or number of cultivable heterotrophic bacteria (Grayston et al. 1998a) remained steady under eCO_2, regardless of fertilization.

Community-level examination of composition and structure, using PLFA profiles and PCR-DGGE, has also produced mixed results. Responses to eCO_2 manifested by shifts in composition have been reported for different plant-soil systems (Ringelberg et al. 1997; Jossi et al. 2006; Drigo et al. 2007; Kao-Kniffin and Balser 2007; Kohler et al. 2010), but reports of stability are equally common (Montealegre et al. 2002; Rønn et al. 2002; Wasaki et al. 2005; Haase et al. 2008; Paterson et al. 2008). No response in archaeal community composition was found in maize, but in soybean the relative abundance of Crenarchaeota was reduced (Nelson et al. 2010). Using PLFA-based stable isotope probing, a specific response of a group of Gram-positive bacteria was detected within the metabolically active subset of a mixed-grasses rhizosphere community (Denef et al. 2007). In addition, Jossi et al. (2006) showed better manifestation of the effect of eCO_2 in active rhizosphere populations compared to the total community, based on a comparison of RNA- and DNA-based community profiles. This suggests that the responsive population may not necessarily be numerically dominant.

The effect of eCO_2 may be more pronounced when specific microbial groups are targeted. For instance, significant effects of elevated eCO_2 on *Pseudomonas* and *Rhizobium* populations were reported (Marilley et al. 1999; Drigo et al. 2009; Schortemeyer et al. 1996; Montealegre et al. 2000). This response varied in trend among different plant hosts and among different soils. In the rhizosphere of *Larrea tridentate*, the response to changes in CO_2 level was restricted to Firmicutes (Nguyen et al. 2011). In the rhizosphere of a wetland plant, *Typha angustifolia*, relative abundance of acetate-consuming methanogenic Archaea increased in response to eCO_2 (Kao-Kniffin et al. 2011). Succession of root-inhabiting methanogenic Archaea in rice was slowed down under eCO_2 (Hashimoto-Yasuda et al. 2005). In contrast, where examined, the composition of nitrifying or denitrifying rhizosphere bacteria remained stable under eCO_2 (Deiglmayr et al. 2004; Bowatte et al. 2007; Nelson et al. 2010; Pereira et al. 2011).

The effects of additional climatic drivers on soil and rhizosphere microbial communities and their interactions have been much less studied. For the Antarctic plant *Deschampsia antarctica*, changes in UV-B irradiation level affected community-level physiological profiles (CLPP) but not the number of cultivable bacteria (Avery et al. 2003). Increased UV-B irradiation over *Eriophorum russeolum plants* resulted in shifts in PLFA profiles and CLPP, with no effect on total microbial biomass (Rinan et al. 2008). Ozone-stressed grasses showed remarkable similarity in the composition of their associated rhizosphere bacterial communities compared to respective controls (Dohrmann and Tebbe 2005). In contrast, following long-term exposure to ozone stress, composition of rhizosphere bacterial communities of *Fagus sylvatica* trees was significantly altered (Schloter et al. 2005; Esperschütz et al. 2009).

The data accumulated so far describe only the response of the community to relatively short-term changes. However, predictive hypotheses regarding adaptation of the rhizosphere prokaryotes and plants to climatic and atmospheric changes are, at this stage, somewhat premature. This results, in part, from the relative lack of long-term experimental data. In addition, all experiments, regardless of their excellent design, suffer from the bias of rather rapid changes in conditions. In reality, however, one would expect the shifts to be orders of magnitude slower, possibly allowing evolution and coevolution of the plants and associated microorganisms.

Genetic Traits Related to Rhizosphere Competence

Rhizosphere competence is a term that describes the specific ability of a microorganism to successfully colonize and survive in the rhizosphere. Several studies in recent years have demonstrated a number of bacterial functions, such as motility, attachment, growth, type III secretion, transport, stress resistance, and production of secondary metabolites, linked to rhizosphere

competence (for review see Kiely et al. 2006 and Barret et al. 2011). For example, Matilla et al. (2007) conducted a microarray-based experiment in which they studied *Pseudomonas putida* KT2440 (a known root-colonizing bacterium) genes, expressed during the interaction of the cells with corn (*Zea mays*) roots. They compared these to genes expressed under three other conditions: planktonic cells growing exponentially in rich medium, planktonic cells in stationary phase, and sessile populations established in sand microcosms. The expression level of a large number of genes was upregulated in the rhizosphere, many of which were highly induced relative to the other three control conditions (90 genes were upregulated at least twofold in the rhizosphere versus all three controls and of those, over 50 genes were induced more than sixfold!). One of the most impressive findings of their study was that amid the extensive rhizosphere-induced enhancement of gene expression, not one significantly downregulated gene could be found. This phenomenon might have been related to the mixed physiological status of individual cells within the rhizosphere population. The rhizosphere-activated genes included genes involved in amino acid uptake and metabolism of aromatic compounds, reflecting the availability of particular nutrients in this plant's root exudates. In addition, efflux pumps and enzymes for glutathione metabolism were upregulated, suggesting that adaptation to adverse conditions and stress (oxidative) response plays an important role in rhizosphere competence in this system. The finding of a GGDEF/EAL domain response regulator among the induced genes suggests a role for the secondary messenger c-diGMP in root colonization and survival of *P. putida* in this rhizosphere system (Matilla et al. 2007).

When *P. fluorescens* WCS365 was applied to tomato monoaxenic root system, several genes were identified as involved in competitive root colonization (Lugtenberg et al. 2001; Lugtenberg and Kamilova 2009). Among the genes and traits identified were those related to motility and chemotaxis toward, and utilization of, root exudates. Amino acids and dicarboxylic acids, but not sugars, were important root attractants in this *P. fluorescens* WCS365 and tomato system, while in *Arabidopsis*, malate was a major attractant of *Bacillus subtilis* FB17 (Rudrappa et al. 2008). Other competitive root-colonization-related genes and traits were involved in adhesion, synthesis of amino acids, uracil, and vitamin B1, lipopolysaccharide structure, the ColR/ColS sensory system, the putrescine-uptake system, site-specific recombinases, NADH:ubiquinone oxidoreductase, protein secretion, and the type III secretion system (Lugtenberg et al. 2001; Lugtenberg and Kamilova 2009).

When *Rhizobium leguminosarum* was grown in the rhizospheres of pea (its legume nodulation host), alfalfa (non-host legume), and sugar beet (non-legume), several host-specific traits were identified (Ramachandran et al. 2011). Many plasmid (pRL8)-encoded genes were specifically induced in the pea nodulation host. As expected, *nod* genes were induced only in the rhizospheres of the two legumes. In the pea rhizosphere, a specific transporter, possibly for monosaccharides, was also found to be important. In addition, increased expression of genes encoding enzymes of the glyoxylate cycle was found in the pea rhizosphere. The study also identified bacterial responses common to rhizospheres of all three host plants, such as organic acid, C1-C2 and aromatic amino acid metabolism, hypoosmotic regulation, detoxification and multidrug resistance (MDR) family efflux pump, genes involved in the response to stress (general and oxidative), and many genes encoding proteins of unknown function.

So far, studies with single strains, PGPR, or *Rhizobium* have provided valuable information on gene expression of these organisms and on symbiotic microbe-legume interactions (Becker et al. 2004; Ruffel et al. 2008). However, despite advances in metagenomic and metatranscriptomic techniques, due to the extreme complexity of the system, the functions of the complex natural rhizosphere community have not yet been described. As nicely put by Schenk et al. (2012) in a recent review, "It is likely that an unbiased multi-species approach such as metatranscriptomics will lead to the discovery of potentially interesting (yet unknown) plant-microbe relationships."

Conclusions

The importance of rhizosphere communities to plant health and development is clear.

This chapter attempted to illustrate and analyze the microbial ecology in the rhizosphere, as revealed by enormous body of literature, resulting from over a century of research. Nevertheless, our ability to draft a comprehensive and ubiquitous ecological theory on the behavior of microorganisms in the rhizosphere becomes impossible, due to the ambiguous and partial picture still arising from the current knowledge. This is in contrast to the currently established theories in macroecology, and results from the enormous complexity of the system, affected by multiple parameters such as plant species and its physiological state and age, soil characteristics and environmental conditions, as well as the microbial diversity. We are therefore limited in our current ability to draw general hypotheses regarding the rhizosphere prokaryotes and this area is therefore restricted to case-by-case studies.

Several future possibilities may be envisioned: One is that additional research and technological advances in in situ studies of microbial structure and function will lead to general understanding of the rhizosphere ecology. Alternatively, indeed due to the diversity and complex nature of the system, and of different rhizospheres, they are directed to individual unique paths. In either case, it is imperative to move forward rhizosphere research, taking advantage of the advanced molecular and imaging tools developed in recent years.

Many questions still remain open: What makes an organism rhizosphere competent? What makes one population dominant? Is there a cross-talk between the plant and the bacteria in nonspecific interactions? Is it possible to detect coevolution between plants and their rhizosphere community? If so, could different mechanisms occur in different plant species? How to make inoculation with beneficial microorganism a success?

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