CHAPTER SEVEN

Advances in Elucidating Beneficial Interactions Between Plants, Soil, and Bacteria

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Abstract

Survival of every organism on earth depends on its interactions with other organisms. For example, animals form associations with the intestinal microflora, while plants develop symbiotic associations with neighboring plants, microflora, and microfauna. Most of the associations between plants and microorganisms are mediated by organic compounds released by the plant. The plant root system acts as a factory and exudes enormous amount of chemicals to effectively communicate with the surrounding soil organisms. Bacteria on roots and in the rhizosphere can also utilize these organic compounds as a source of nutrients and enhance their population size and metabolic activities. In return, plant-associated bacteria improve plant growth and development by

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different mechanisms including nitrogen fixation, provision of nutrients, and mediating resistance against pathogens. Although plant–bacterial partnerships have been found effective to enhance biomass production, their importance and relevance in agricultural systems are still underestimated. A better understanding of beneficial interactions between plant, soil, and bacteria could be exploited to improve growth and health of food and feed crops. Plant growth-promoting mechanisms of bacteria might enhance biomass production in a more sustainable manner, even on marginal land. Furthermore, plant growth-promoting and/or pollutant-degrading activities of bacteria could be exploited to improve the efficiency of phytoremediation of organic and inorganic pollutants from the soil and water or to protect the food chain by decreasing the concentrations of pollutants in food crops.

1. INTRODUCTION

As autotrophic organisms, plants play a major role in sustaining all other life forms. The plant root system is a chemical factory that mediates several interactions of the plant with soil microorganisms. Roots release organic compounds, which act as signaling agents to attract beneficial microbes and to combat pathogenic ones. Generally, these interactions are mutualistic with beneficial microbes, such as rhizobia, mycorrhizae, endophytes, and plant growth-promoting rhizobacteria (PGPR). However, these plant–microbe interactions are not only driven by organic compounds released by the roots but are highly integrated with and influenced by biotic and abiotic factors (Lichtenthaler, 1998; Phillips et al., 2004). Root-released organic compounds also enhance the abundance and diversity of beneficial microorganisms in the rhizosphere and plant environment. In return, plant-associated microbes may enhance plant growth and health by several activities such as nitrogen fixation, synthesis of plant hormones and vitamins, the improvement of nutrient uptake, and induction of stress resistance. They also outcompete invading pathogens by different mechanisms such as niche occupation by competition for space, nutrients, and physical niches of the rhizosphere/rhizoplane and endophytic tissues. Some of the beneficial rhizo- and endophytic bacteria can secrete not only antibiotics but also lytic enzymes enabling the inhibition of various pathogens (Pleban et al., 1997). Plant–microbe interactions are affected by many different regulatory signals, of which only few have been explored, recalling a quote by Leonardo da Vinci saying that "We know better the mechanisms of celestial bodies than the functioning of the soil below our feet" (Badri et al., 2009).

Most of the plant-associated bacteria are also soil inhabitants (Rasche et al., 2006a,b). They may move from the bulk soil to the rhizosphere of the living plant and aggressively colonize the rhizosphere and roots of plants. Some of them can penetrate plant roots, and some strains may move to shoots, leaves, flowers, and even seeds (Compant et al., 2010a; Reinhold-Hurek and Hurek, 2011). However, different plant species host different microbial communities (Berg and Smalla, 2009), which is mostly due to the different composition of root exudates excreted by different plants. Root exudates play an important role in signaling and developing microbial communities in different compartments of plants.

Plant growth-promoting mechanisms differ between bacterial strains and to a great extent depend on the type of organic compounds released by these strains. For example, plant growth-promoting hormones and other secondary metabolites released by the bacteria can alter plant growth and development. Recently, it has been reported that associations between plant and associated bacteria have reached such levels that the host plant cannot develop properly without their associated bacteria (Carlier and Eberl, 2012). In addition to sustainable growth of food and feed crops, bacteria may enhance plant growth and the remediation of organic and inorganic pollutants from the soil and water. The enhanced microbial population in the rhizosphere can mineralize organic contaminants in the soil. In case of inorganic pollutants, microorganisms enhance the uptake of heavy metals and other inorganic pollutants from the soil. In this regard, interactions among plant, soil, and bacteria have received great attention because of the biotechnological potential of microorganisms for improving growth of food and feed crops and the remediation of pollutants from the contaminated environment.

Although many studies showed that plant-associated microbes have beneficial effects on their host, their importance during plant growth and development is still underestimated. A better knowledge of the interactions between plant, soil, and bacteria could be made applicable for higher yields of food and feed crops, and to improve phytoremediation of contaminated soil and water. In this review, we describe beneficial interactions between plant, soil, and bacteria and how these can be exploited in agriculture as biofertilizers, growth stimulants, or biopesticides replacing chemical pesticides or fertilizers supporting a sustainable use of natural resources. Furthermore, plant-associated bacteria that possess pollutant-degrading and/or plant growth-promoting activities can assist in remediating marginal lands polluted by organic pollutants and/or toxic metals, in addition to improving biomass production.

2. MICROBIAL HABITATS IN RELATION TO PLANT–SOIL–MICROBE INTERACTIONS

Plants consist of a rich habitat for microbial life. They do not only act as source of energy, but provide bacteria with specific niches, where they can thrive and multiply. The association of bacteria with plants reaches from a loose connection of leaf epiphytic and root-associated bacteria to bacteria living in intercellular spaces as pathogens or as commensal or beneficial endophytes to highly adapted organisms capable of inhabiting the intracellular spaces, again as pathogens, commensialists, or endosymbionts (Reinhold-Hurek and Hurek, 2011; Ryan et al., 2008). In the commensal situation, the environment in or at the plant provides a niche for bacterial life benefitting the bacteria, but the interaction has no known effect on the plant host (Newton et al., 2010), though this situation might simply reflect our limited knowledge on the function of plant-associated bacteria in nature. Pathogens and commensal endophytic bacteria share very similar habitats in the plants, which makes them good potential candidates for biocontrol, as they can compete with pathogens for niches in or next to the plant and are in close physical connection with plant pathogens (Ryan et al., 2008).

The root surfaces and their surroundings, the rhizosphere, are inhabited with up to a concentration of 10^{10} bacteria per gram, due to the existence of nutrient-rich root exudates and corresponding niches (Lynch, 1990). This concentration is clearly higher than in nonrooted bulk soil. Bacteria on roots and in the rhizosphere can benefit from these root exudates, and both beneficial bacteria and plant pathogens can densely inhabit root surfaces, thereby forming organized biofilms with complex organization and high persistence capability (Ramey et al., 2004). A subset of the rhizosphere microflora may also enter the plant as endophytes, which, by definition, do not harm the host plant, but form commensal or mutualistic communities with plants (Rosenblueth and Martinez-Romero, 2006). Bacteria can enter plant tissues at root hairs, elongation zones, root tips, and at emergence sites of secondary roots and then colonize areas of lysed plant cells and intracellular spaces, and less frequently, also xylem cells and vascular tissues (Compant et al., 2010a; Reinhold-Hurek and Hurek, 2011). The invasion of plant cell tissue may require the production of lytic enzymes facilitating the colonization process. Alternatively but less frequently documented points of entry of endophytes include above-ground natural openings such as stomata, wounds created

by herbivore feeding, and occasionally documented transfer to the next generation in seeds. Niche occupation within the plant can be very similar to plant pathogens and indeed certain strains of bacteria can form devastating pathogens, while very closely related species or even strains inhabiting a similar plant niche are harmless or even protective. This is, for example, the case for the causal agent of Pierce disease of grapevine, *Xylella fastidiosa*, where specific strains cause a devastating disease, while others can be harmless or even act as beneficial biocontrol agents (Hopkins, 2005).

The plant colonization processes of endophytes have been visualized by autofluorescent proteins convincingly demonstrating the colonization of wide range of vascular plants by endophytic bacteria (Rosenblueth and Martinez-Romero, 2006; Ryan et al., 2008). Endophyte concentration in plants is considerably lower than in the surrounding rhizosphere, and concentrations generally decrease in upper parts up to the reproductive organs. Nevertheless, certain endophytes are capable of colonizing even the reproductive tissue and even seeds, as demonstrated for *Burkholderia phytofirmans* PsJN and other endophytes in grapevine (Compant et al., 2008a, 2011). Colonization pattern of beneficial bacteria might also depend on the host plant (Sessitsch et al., 2005). While root hairs are generally favored by *Bacillus amyloliquefaciens* FZB42 in both maize and *Arabidopsis*, this bacterium colonizes tips of primary roots in *Arabidopsis*, but not in maize (Fan et al., 2012). The colonization of the leguminous tree *Robinia pseudoacacia* by the endophytic *Bacillus subtilis* strain GXJM08 starting at root hairs is even accompanied with morphological changes of the root hairs (Huang et al., 2011).

In legumes, a highly specialized endosymbiotic relationship with rhizobia (mostly *Proteobacteria*, *Rhizobiales*) has evolved. This relationship results in the formation of special organs, root nodules, on the roots of the host plants. There, nitrogen fixation occurs supporting the host plants with nitrogen, while the rhizobia are accommodated intracellularly in nodule cells and are supplied with carbon sources by the plant. This close relationship has been investigated intensively, also at the molecular level, and has been recently reviewed by Murray (2011). In addition, recently, various *Burkholderia* strains have been shown to form nodules on legumes like rhizobia (reviewed in Compant et al., 2008b). Other nodule-forming, nitrogen-fixing bacteria belong to the genus *Frankia* (*Actinobacteria*), where nodule formation occurs in roots of different plant species in the orders Cucurbitales, Fabales, and Rosales. The nodule structure of this actinorhizal symbiosis is different from rhizobia–legume nodules and has been reviewed very recently by Pawlowski and Demchenko (2012).

In addition, specific bacteria of the genus *Burkholderia* such as *B. kirkii* have specialized in their adaption to the endophytic life within plants so far that they inhabit specific leaf nodules and are transmitted vertically. The dependency has reached such levels that the host plant (*Psychotria* spp., *Rubiaceae*) cannot develop properly without these symbiotic bacteria. Interestingly, as the genome sequence suggests, these nodule bacteria do not seem to benefit the host plant in nitrogen fixation, but may function as producers of secondary metabolites, thereby protecting the host plant against herbivores or pathogens (Carlier and Eberl, 2012).

3. ECOLOGY OF PLANT-ASSOCIATED BACTERIAL COMMUNITIES

3.1. Diversity of plant-associated bacterial communities

Due to the availability of root exudates and decayed plant cells providing important nutrients, the rhizosphere is known as a hot spot of microbial activity (Lynch, 1990). This microenvironment supports also high bacterial abundance of approximately 10^{10} bacterial cells per gram rhizosphere soil, which is generally one or two magnitudes higher than bacterial abundance in bulk soil. Rhizosphere microorganisms have a major force on plant performance, that is, plant growth and health, as they can be pathogenic, beneficial, or neutral (Lynch, 1990).

Numerous studies have revealed the presence of a tremendous diversity in the rhizosphere comprising thousands of bacterial species. By cultivation, copiotrophs (i.e., *r* strategists) as well as oligotrophs (i.e., *K* strategists) have been found in the rhizosphere, but they have been reported to occupy different niches (Semenov et al., 1999). Niches providing high nutrient availability including zones of root exudation such as root hairs will be colonized rather by *r* strategists, whereas nutrient-poor or -depleted niches will tend to be colonized by *K* strategists (Semenov et al., 1999). For many years, cultivation-based methods were used to assess the diversity and richness of bacteria colonizing the rhizosphere revealing the presence of many different Gram-negative and Gram-positive bacteria. Famous representatives include *Pseudomonas*, *Burkholderia*, *Azospirillum*, and many more *Proteobacteria*, *Firmicutes* comprising mostly *Bacillus* and *Paenibacillus* as well as *Actinobacteria* such as *Streptomyces*. Many of these isolates have been further tested for plant growth-promoting and other activities and their functional capacities are discussed below.

Since the application of cultivation-independent analysis approaches, we have obtained a far better understanding on the diversity and ecology of microbial communities in general. Due to the fact that still many bacteria are unknown or have not been isolated yet, we do not know yet how to cultivate the huge diversity of prokaryotes. Furthermore, bacteria can enter a viable-but-nonculturable state depending on environmental conditions (Vriezen et al., 2012). The use of specific cultivation conditions introduces also a bias as a subset of the bacterial richness is able to grow under specific conditions or on a particular growth medium, whereas other bacterial fractions need different cultivation conditions. However, instead of cultivating and isolating bacteria, whole community DNA can be isolated and subjected to a diversity analysis. This is achieved by the use of phylogenetic markers such as the 16S rRNA gene, which are amplified by PCR and further analyzed by community fingerprinting methods including denaturating gradient gel electrophoresis or terminal restriction fragment length polymorphism analysis, pyrosequencing, ion torrent technology, sequence analysis as well as by other tools including microarray analysis or hybridization. Sequence analysis in particular has revealed a huge bacterial diversity in the rhizosphere as well as in many other environments, and many new taxa have been identified. In the rhizosphere, *Proteobacteria* have been generally identified as the dominant bacterial phylum (Buée et al., 2009), which is generally in agreement with cultivation-based analysis. Several prominent plant growth-promoting genera belong to this phylum such as nitrogen-fixing and symbiotic *Beta-* and *Alphaproteobacteria* including many different genera (e.g., *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Burkholderia*, *Cupravidius*) and species. Additional well-known representatives include *Azospirillum*, which has found agricultural application as phytostimulators, biofertilizers (Hungria et al., 2010), or *Pseudomonas* comprising strains with plant growth promotion or biocontrol activities (van Loon et al., 1998) but also some other genera as outlined later in this chapter. Nevertheless, even the phylum *Proteobacteria*, which is considered to be culturable, comprises many novel taxa and intraspecific diversity assessment may lead to different findings when analyzed by cultivation-dependent or -independent analysis. Molecular methods revealed that taxa, which have been rarely cultivated so far and for which very limited information is available, seem to play an important role in the plant environment as well. Sophisticated approaches such as pyrosequencing or microarray analysis of 16S rRNA genes revealed the presence of *Acidobacteria*, TM7, *Verrucomicrobia*, and *Chloroflexi* in the rhizosphere or inside roots

(Manter et al., 2010; Sessitsch et al., 2012; Weinert et al., 2010). In addition, by applying other cultivation-independent approaches targeting the 16S rRNA gene have identified these taxa as well, although their occurrence seems to be variable and certain subgroups seem to be particularly encountered in the rhizosphere (da Rocha et al., 2009). In particular, *Acidobacteria*, which are usually very abundant in soils, but hardly culturable, have been found in the rhizosphere in highly varying numbers (Buée et al., 2009). Information regarding functional characteristics or the interaction with plants is very limited; however, it has been recently reported that *Acidobacteria* respond to root exudates (Vandenkoornhuyse et al., 2007). da Rocha et al. (2009) suggested novel cultivation approaches targeting rarely cultivated taxa such as *Acidobacteria* or *Verrucomicrobia*, which would enable further functional analyses and better understanding on their functional role in the plant environment. Other taxa including *Actinobacteria*, *Firmicutes*, or *Bacteroidetes* are commonly found in the rhizosphere, but in variable abundance. Still a quite high percentage of bacterial 16S rRNA genes encountered in the rhizosphere belong to yet-unclassified taxa (Buée et al., 2009). Inceoglu et al. (2011) found by pyrosequencing of 16S rRNA genes in the rhizosphere of field-grown potato plants yet-unclassified bacteria as a dominant group together with *Actinobacteria* and *Alphaproteobacteria*. Furthermore, this study showed that the community was composed of few highly dominant species together with numerous rare species.

Apart from the interactions of plants with soil bacteria, plants may host also bacterial communities inside the plant. A well-known endosymbiotic, beneficial interaction is between legumes and rhizobia, in which the microsymbionts live in specific plant structures, so-called nodules, and are thereby entrapped and surrounded by a host membrane. Unlike endosymbionts, endophytic bacteria generally do not colonize intracellular spaces but colonize vascular tissues and intercellular spaces. Endophytes have been defined as microorganisms, which live inside plants but do not do any harm to their hosts (Wilson et al., 1995). Different definitions can be found, however, in the literature (see, for instance, the ones of Stone et al., 2000; Kobasyashi and Plumbo, 2000). Although already in 1887, Galippe postulated that bacteria can colonize plants internally; for a long time, it was believed that only phytopathogens can enter the plant and colonize internally (Compant et al., 2012). This work was followed by studies of Jorissen, Marcado, and some other criticized and forgotten scientists. However, nowadays it is clear that endophytic bacteria mostly derive from the rhizosphere environment (Compant et al., 2005; Hardoim et al., 2008; Sessitsch et al., 2002a).

Although other sources can also be the carposphere, anthosphere, laimosphere, spermosphere, as well as the caulosphere, numerous studies have shown that endophytic communities are diverse and almost all of them are facultative (Hardoim et al., 2008). It is not completely understood how endophytes overcome plant defense reactions, but they generally colonize the rhizosphere and rhizoplane before entering plant tissues (Compant et al., 2010a). Passive penetration may occur at the root tip level and at cracks such as those occurring at root emergence sites, but generally many endophytes are equipped with cell wall-degrading enzymes, which are probably needed for efficient plant colonization and spread within plant tissues (Compant et al., 2010a; Lodewyckx et al., 2002).

As most endophytes derive from the rhizosphere, root endophytic communities are most diverse. Cultivation-based as well as -independent approaches indicate that as in the rhizosphere, *Proteobacteria* seems to be the most important phylum among bacterial endophytes, comprising a range of different *Alpha*-, *Beta*-, and *Gammaproteobacteria* (Berg et al., 2005; Sessitsch et al., 2012). However, different intraspecific diversity of rhizosphere and endophytic bacterial communities have been reported, indicating that different strains belonging to the same genus or species are adapted to live in the rhizosphere or endosphere (Idris et al., 2004). Furthermore, even within the *Proteobacteria*, different taxa are found in both environments. *Enterobacteriaceae*, for example, comprising *Pantoea* and *Enterobacter* have been found as frequent endophytic plant colonizers (Holden et al., 2009; Montañez et al., 2009; Yousaf et al., 2011), but are far less frequently found in the rhizosphere. Even human pathogenic members of the *Enterobacteriaceae* including *Salmonella* and *Escherichia coli* have been repeatedly reported as endophytes (Holden et al., 2009). In addition to *Proteobacteria*, Gram-positive taxa occur as endophytes and seem to be very important in some plant environments (Francis et al., 2009). Both *Firmicutes* (e.g., *Bacillus*) and *Actinobacteria* (e.g., *Streptomyces*) are well known for their ability to produce antibiotics and other secondary metabolites, and they became particularly interesting for biotechnological applications and bioprospection (Qin et al., 2011).

3.2. Interplay between soil, plant, and environment in shaping plant-associated microbial communities

Microbial communities, including rhizosphere and endophytic assemblages, are highly complex and their structure as well as their functioning strongly depends on environmental parameters. They rapidly sense nutrient conditions as well as certain stress factors influencing the survival and competitiveness of

individual community members leading to community shifts under altered conditions. Such altered communities may also mediate different functional activities. Alternatively, different environmental conditions may directly affect microbial communities (e.g., by altering gene regulation), which will not only influence functioning, but may on the longer term also result in community shifts. The most important drivers regarding the structure of plant-associated microbial communities are the soil, the plant, and other environmental parameters. Soils themselves host distinct microorganisms serving as reservoir for rhizosphere as well as the endosphere bacteria (Rasche et al., 2006a,b). Soil type, structure, pH, water content as well as other factors shape soil microbial communities. Therefore, the same plant growing in different soils or soil types will be colonized by different strains; however, at the genus or species level, similar species might colonize, depending on the kind of microorganisms prevalent in a particular soil.

3.2.1 The plant host structures plant-associated microbial communities

The plant host is a very important driver of plant-associated microbial communities, in both the rhizo- and endosphere (reviewed by Berg and Smalla, 2009). The root type might affect microbial communities (Garbeva et al., 2004) as roots alter soil structure, water flow, or oxygen availability and therefore are also likely to influence soil microbiology. Furthermore, it is well known that different plant species host different microbial communities (Berg and Smalla, 2009), which is very likely due to different root exudation patterns attracting different types of bacteria. Plant host specificity is not fully understood, but root exudate composition and abundance differ from plant to plant and therefore seem to provide a specific nutrient composition attracting specific microorganisms. Low molecular weight carbon compounds including sugars, organic acids, and amino acids are prominent root exudates and are readily assimilated by soil microorganisms. They have been proposed to be an important driver of microbial community structuring in the rhizosphere (Bais et al., 2006; Baudoin et al., 2003; Weissknopf et al., 2008). The influence of root exudate fractions or compounds on microbial community structures has been assessed (Henry et al., 2008; Paterson et al., 2007; Shi et al., 2011), confirming that root exudates play a primary role for regulating the formation of rhizosphere microbial communities. Root exudates might not only serve as nutrient but may also contain certain signal molecules supporting the interaction with the plant. The cross talk between legumes and rhizobial symbionts (reviewed by Cooper, 2007) is well known and is initiated by flavonoids released by roots and required for the initiation

of the nodulation process by inducing rhizobial *nod* genes. A range of different flavonoid molecules are known, and the type of molecule seems to determine the specificity of the interaction. Flavonoids or mixtures of flavonoids released by roots exhibit their gene-inducing activity at micromolar or even nanomolar concentrations. Flavonoids can serve as inducers of certain rhizobial types but act as anti-inducers of others (Cooper, 2007). Consequently, by means of such signal molecules, plants can select very specifically their microsymbionts. Furthermore, plants may produce secondary metabolites such as antimicrobial compounds affecting below-ground diversity.

Different root exudate patterns determine the structure of microbial communities in the rhizosphere either generally by providing a certain environment and source of nutrients or specifically by antagonizing or interacting with specific microorganisms. As an example for the effect of the plant species on plant-associated microbial communities, Yousaf et al. (2010a) found different, host-specific hydrocarbon-degrading bacterial communities in the rhizosphere as well as the endosphere of Italian ryegrass and birdsfoot trefoil grown in the same soil. Similarly, Li et al. (2011) reported that the plant species is the main driver of microbial composition in the rhizosphere of five pioneer plants grown at a mine-tailing site. Also, agricultural plants including oilseed rape and strawberry were reported to host distinct, specific rhizosphere bacterial communities and the plant species in particular shaped *Actinobacteria* communities (Costa et al., 2006). Furthermore, seven different medicinal plants grown in Panxi, China, hosted unique actinobacterial communities (Zhao et al., 2012a).

It can be assumed that different cultivars belonging to the same genotype produce similar root exudates and therefore are likely to host similar microbial communities. Accordingly, Weinert et al. (2010) found that the diversity and structures of tuber-associated bacterial communities of different potato cultivars were nearly identical, and a cultivar effect was only found on *Pseudomonas* spp., but not on other analyzed taxa. Furthermore, an in-depth analysis by phylochip analysis of 16S rRNA genes revealed that 9% of all operational taxonomic units were cultivar specific (Weinert et al., 2011). This might be due to slight differences in plant physiology potentially resulting in slightly differing root exudation and some variations in associated microbial communities. However, such variations seem to also depend on other parameters such as the soil type or climatic factors as cultivar-specific effects are not consistently found. Experiments performed at different field sites with distinct potato cultivars revealed that cultivars generally host many common taxa and that at different sites varying

effects of the cultivar were found (Weinert et al., 2010, 2011). Rasche et al. (2006a,b) planted different potato cultivars in different soils and found strong plant genotype effects in one soil, whereas in the other soil, the different cultivars hosted very similar rhizosphere and endophytic communities. Various studies addressed potential effects of genetically modified plants on soil- and plant-associated microbial communities; however, generally only few differences were found between transgenic lines and their nearly isogenic parental lines (Gschwendtner et al., 2009; Gyamfi et al., 2002; Prischl et al., 2012; Weinert et al., 2009). Mostly, these differences were comparable to the differences found between different cultivars. Recently, Gschwendtner et al. (2009) found that rhizosphere microbial communities of two potato cultivars differed in metabolizing root-derived carbon. This was determined by incubation of plants with $^{13}CO_2$ and subsequent analysis of ^{13}C incorporated in phospholipid fatty acids (PLFAs) of bacterial communities. One cultivar incorporated higher levels of ^{13}C in PLFAs and might indicate more rapid turnover of root exudates and/or an enhanced ^{13}C:^{12}C of root exudates (Gschwendtner et al., 2009). Similarly, hybrid rice showed greater CO_2 flux and total microbial biomass, bacterial and fungal abundance, and enzymatic activities than other rice cultivars (Hussain et al., 2011). Rasche et al. (2009) used ^{13}C-labeling techniques and analyzed endophytic bacteria in two potato varieties, which were to a certain time point able to metabolize plant photosynthates. The two varieties showed different active endophytic communities, maybe due to a different timing of the photosynthesis pathway resulting different set of metabolites available for endophytes. This confirms that cultivars may show differences in rhizodeposition or plant physiology resulting in changes of microbial diversity and/or activity; however, such differences are usually small in comparison to those differences found between different plant species.

The vegetation stage has been found to greatly determine the structure of plant-associated microbial communities. Monteiro et al. (2011) studied rhizosphere and root endosphere bacterial community structures of vetiver plants at five plant growth stages. Predominant bacterial communities, both in the rhizosphere and inside roots, varied greatly with plant age. This is likely due to different root exudation patterns or metabolite profiles at different vegetation stages. Recently, Andreote et al. (2010) compared the effects of plant cultivar, developmental stage, and bacterial inoculation on the structure of potato-associated rhizosphere and endophytic bacterial communities. The developmental stage followed by the plant genotype was the main driver of community structures. However, also inoculation with plant growth-promoting

bacterial (PGPB) strains such as a *Paenibacillus* and a *Methylobacterium* influenced microbial community structures (Andreote et al., 2010). Comparative analysis of rhizosphere bacterial communities of field-grown potato plants by pyrosequencing of 16S rRNA genes again revealed different community structures at different plant growth stages (Inceoglu et al., 2011). Furthermore, a cultivar effect was only found at the young plant stage, whereas no significant differences between rhizosphere bacterial communities of different potato cultivars were found at the flowering or senescence stage.

3.2.2 Effects of environmental parameters on plant-associated microbial communities

Finally, other biotic and abiotic factors affect microbial community structure in the rhizosphere or inside plants. Biotic factors include, for instance, the presence of plant pathogens and/or the subsequent effect of a diseased plant on the plant-associated microflora. Pathogens generally induce a cascade of reactions in plants leading to the synthesis of stress metabolites including H_2O_2, phytoalexins, or stress signals such as jasmonic acid, ethylene, or salicylic acid (SA) (Lichtenthaler, 1998). Furthermore, pathogen-infected plants have shown different root exudates composition containing different amounts of sugars or organic acids (Kamilova et al., 2006; Neumann and Römheld, 2007; Phillips et al., 2004). Consequently, a pathogen-infected or diseased plant may attract and interact with different types of microorganisms due to the production of different metabolites. This was confirmed by various studies showing that diseased plants show different rhizosphere or endophytic communities. Yang et al. (2001) compared rhizosphere bacterial communities of healthy avocado trees and trees that were infected with the root-rot pathogen *Phythophthora cinnamoni*. Although plants were free of disease symptoms, they hosted different rhizosphere communities. However, trees treated with a disease-suppressive *Pseudomonas fluorescens* strain hosted comparable rhizosphere communities as healthy, noninfected plants. Similar findings were obtained with potato plants infected with *Erwinia carotovora* ssp. *atrospetica* revealing significantly different rhizosphere and endophytic communities in healthy and infected plants (Rasche et al., 2006a,b; Reiter et al., 2003). Recently, Trivedi et al. (2012) studied how *Candidatus* Liberibacter asiaticus, causing Huanglongbing disease in citrus, affects the diversity and functioning of the rhizosphere microflora. This pathogen is an obligate endophyte and caused significant changes in the rhizosphere microflora, although there is no direct interaction between the pathogen and rhizosphere bacteria. As the pathogen causes a blockage of photoassimilate transport to the roots,

the authors postulate that qualitative and quantitative changes in partitioning of photoassimilates were responsible for the observed changes. In that study, healthy plants showed a higher abundance of *Proteobacteria*, whereas *Acidobacteria*, *Actinobacteria*, and *Firmicutes* were more represented in pathogen-infected plants. Furthermore, many genes involved in key ecosystem functions such as nitrogen cycling, phosphorus utilization, or carbon fixation were more abundant in healthy than in infected plants, indicating also that important ecological processes may be impacted by alterations in the rhizosphere microflora (Trivedi et al., 2012).

Similar to biotic stress factors, abiotic stress factors such as chilling, drought, and the presence of toxic substances such as heavy metals may influence the structure of the plant-associated microflora. Various stress factors may directly influence microorganisms altering, for example, their activity and as a consequence also community structure. Furthermore, the plant will be affected by stress and respond with the production of stress metabolites and altered physiological behavior, which may result in different activity and/or diversity of associated microorganisms. Potato plants suffering from light deficiency hosted less diverse endophyte bacterial communities than healthy and robust plants (Sessitsch et al., 2002a). Similarly, chilling had a major force on the structure of endophyte communities (Rasche et al., 2006c).

Other parameters such as agricultural management or climatic conditions may affect the diversity as well as the activity of plant-associated microorganisms. Agricultural management practices such as crop rotation or the type of fertilizer applied have been reported to be important drivers of soil microbial diversity and functioning (Orr et al., 2011; Wakelin et al., 2007; Wu et al., 2008). As such also plant-associated microbes will be affected indirectly. However, they might also be directly affected, for example, due to different nutrient availabilities. It has also been reported that the agricultural management may influence plant gene expression (van Dijk et al., 2012) potentially resulting in slightly altered root exudation or metabolite profiles associated with altered microbial community structures. Various climatic factors such as temperature and precipitation are likely to affect plants and their associated microflora in many ways. Even climate change parameters such as elevated atmospheric CO_2 have been reported to affect plant microbiology (Compant et al., 2010b; Drigo et al., 2009; Nguyen et al., 2011). Drigo et al. (2010) found that arbuscular mycorrhizal fungi act as a major conduit in the transfer of carbon derived from elevated CO_2 between plants and rhizosphere bacteria again illustrating the complex interactions between plants, associated microorganisms, and the environment.

4. BENEFICIAL PLANT–MICROBE INTERACTIONS

4.1. Plant growth promotion and nutrition

In the late 1970s, Kloepper and Schroth introduced the term "PGPR" to describe bacteria that colonize plant roots after seed inoculation and that stimulate plant growth (Kloepper and Schroth, 1978). Many plant-associated bacteria—rhizosphere bacteria but also endophytes—can stimulate plant growth and nutrition (for a review, see Lugtenberg and Kamilova, 2009; Fig. 7.1). The best studied plant growth-promoting genera are *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Pantoea*, and *Pseudomonas*. Today, we observe an increasing scientific interest in bacteria with the ability to stimulate plant growth and nutrition, which is reflected in a rapidly growing number of publications on this topic. In Table 7.1, we summarized recent reports in which the molecular mechanisms underlying the plant-stimulating activity of bacteria have been identified.

So far, proposed mechanisms by which bacteria stimulate plant growth and nutrition include plant hormone production, decreasing ethylene levels, biological nitrogen fixation, and increasing the availability of nutrients such as iron or phosphate. Besides those frequently reported activities, other modes of bacterial growth promotion are discussed such as the production of volatiles, the synthesis of vitamins, and microbial photosynthetic activity or promotion of photosynthetic efficiency in plants. The plant growth-promoting activity of most PGPR or PGPB is based on the combination of two or more mechanisms. Moreover, synergistic effects of coinoculated PGPB were also reported (Chatterjee et al., 2011). Tilak et al. (2006), for example, tested dual inoculations of various PGPBs such as *Pseudomonas putida*, *P. fluorescens*, or *Bacillus cereus* strains with *Rhizobium* sp. (AR-2-2 k) and *Rhizobium* on pigeonpea and observed increased plant growth, nodulation, and improved nitrogenase activity. *Azospirillum* spp. enhanced nodulation and plant growth of common bean (*Phaseolus vulgaris* L.) when coinoculated with *Rhizobium* in a plant genotype-dependent manner (Remans et al., 2008).

4.1.1 Biological nitrogen fixation

Plant-associated microorganisms may play an important role for plant nutrition. One of the most prominent mechanisms is biological nitrogen fixation, which was discovered by Beijerinck (1901) and is a process in which

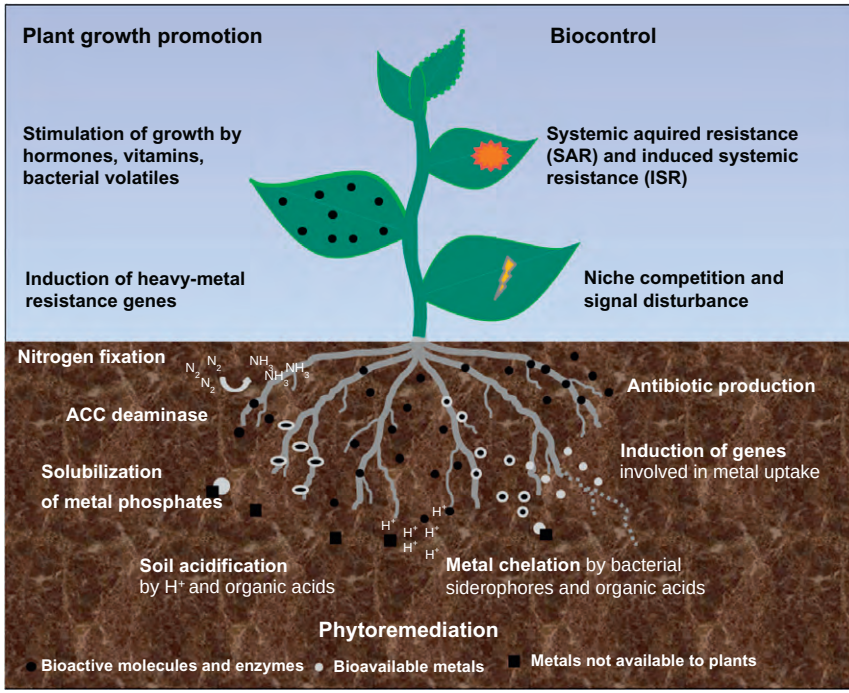

Figure 7.1 Potential beneficial effects of plant-associated bacteria on plant growth and health.

atmospheric nitrogen (N_2) is reduced to ammonia (NH_3) by the enzymatic activity of nitrogenases. Plants can assimilate NH_3 to produce nitrogenous biomolecules. In the context of plant–soil–microbe interactions, we distinguish between three main groups of nitrogen-fixing bacteria: (i) free-living, diazotrophic soil bacteria, such as *Azotobacter*; (ii) diazotrophic bacteria establishing associations with plants endophytically or epiphytically, such as *Azospirillum*; and (iii) bacteria forming tight symbiosis with plants by elicitating the formation and colonization of specialized organs, the root nodules, such as rhizobia.

Symbiotic nitrogen fixation has doubtless great impact on plant nutrition and is an integral component of sustainable agriculture (Sessitsch et al., 2002b). It has been estimated that symbiotic nitrogen fixation makes up at least 70 million metric tons of nitrogen per year worldwide (Brockwell and Bottomley, 1995). Despite the optimistic expectations on the impact of associative diazotrophic nitrogen fixation, most inoculation experiments did not show substantial contribution to plant growth (Dobbelaere et al., 2003).

Table 7.1 Observed effects of plant-beneficial bacteria in regard to plant growth promotion

Proposed mechanism PGPR/endophyte	Plant	Experimental conditions	Plant response to PGPR/endophyte inoculation	References
Phytohormone production—indole-3-acetic acid (IAA)				
Paenibacillus polymyxa RC05, *Bacillus* spp. RC23	Strawberry	Field trial	Increased yield, average fruit weight, and quality fruit ratio up to 21%, 19%, and 32%, respectively	Erturk et al. (2012)
Azospirillum brasilense strain SM	Sorghum	Axenic	Increased shoot length (29%) and dry biomass (83%) compared to control	Kochar and Srivastava (2012)
Pseudomonas aeruginosa Am3	Wheat	Axenic/pot trials	Increase in spike length (33%), number of tillers (71%), and weight of seeds (39%)	Hussain and Hasnain (2011)
Providencia sp. WRB4, *Alcaligenes* sp. WRB10	Wheat	Pot trial	Increased plant biomass (18%) and grain yield (94%)	Manjunath et al. (2011)
Enterobacter cloacae GS1	Rice	Axenic/pot trials	Significant increase in fresh plant weight, root length, shoot length, and N-content	Shankar et al. (2011)
Bacillus licheniformis MML2501	Groundnut	Axenic/pot trials	Increase in seed germination (90%), shoot length (44%), root length (55%), plant biomass, (67%) and grain yield (155%)	Prashanth and Mathivanan (2010)
Bacillus sp. NpR-1, MiR-4, *Pseudomonas* sp. AvH-4, *Staphylococcus* CdR-1, *Escherichia* sp. SnR-1	Wheat	Axenic/pot trial	Increase in shoot length, no. of tillers/plant, and spike length up to 29%, 97%, and 25%, respectively	Ali et al. (2009)
Azospirillum brasilense SM	Sorghum	Axenic	Improved shoot length and seedling dry weight up to 28% and 62%, respectively	Malhotra and Srivastava (2009)

Continued

Table 7.1 Observed effects of plant-beneficial bacteria in regard to plant growth promotion—cont'd

Proposed mechanism PGPR/endophyte	Plant	Experimental conditions	Plant response to PGPR/endophyte inoculation	References
Bacillus sp. SVPR30	Rice	Greenhouse	39% increase in plant dry biomass	Beneduzi et al. (2008)
Azospirillum brasilense Sp245 and an IAA-deficient mutant	Wheat	Greenhouse	Seeds inoculated with wild-type strain gave 12% and 25% higher plant biomass and ears number compared with the IAA-deficient mutant and uninoculated seeds	Spaepen et al. (2008)
P. putida subgroup B strain 1	Tomato	Greenhouse	15% increase in tomato fruit	Gravel et al. (2007)
Burkholderia sp. 1, *Pseudomonas* sp. 10	Kidney bean	Sterile water	Increased stem height up to 7.8-fold (*Pseudomonas*) and threefold higher root number (*Burkholderia*)	Tsavkelova et al. (2007)
Rhizobacterial strains Ha 21, Ha 22, Ha 23, Ha30	Wheat	Pot/field trials	Stimulatory effects on grain yields in pot (up to 14.7% increase) and field experiments (up to 27.5% increase)	Khalid et al. (2004)
Pseudomonas putida GR12-2 and an IAA-deficient mutant	Canola, mungbean	Growth pouch/ sterile vermiculite	Seeds inoculated with wild-type gave 35–50% longer roots compared to the IAA-deficient mutant and the roots from uninoculated seeds	Patten and Glick (2002)
Phytohormone production—indole-butyric acid (IBA)				
Azospirillum brasilense UAP 154	Maize	Axenic	Increased 74% higher root dry weight	Martinez-Morales et al. (2003)

Phytohormone production—gibberellins				
Burkholderia sp. KCTC 11096BP	Cucumber	Pot trial	Increased shoot length, shoot and root biomass, and chlorophyll contents up to 40%, 38%, 32%, and 10%, respectively	Kang et al. (2010)
Bacillus cereus MJ-1	Red pepper	Pot trial	Increased plant height, root length, and biomass up to 14%, 50%, and 30%, respectively	Joo et al. (2004)
Bacillus licheniformis CECT 5106 and *B. pumilus* CECT 5105	*Pinus pinea* L.	Pot trial	Increased root length (92%) and dry biomass (83%)	Probanza et al. (2002)
Phytohormone production—cytokinins				
Bacillus subtilis, strain IB-22	Wheat	Axenic	Increased seedling biomass, up to 16%	Arkhipova et al. (2006)
Pseudomonas BA-8, *Bacillus* OSU-142	Sweet cherry	Field trials	Increased fruit yield, up to 16%	Esitken et al. (2006)
ACC deaminase activity				
Serratia proteamaculans J119	*Cicer arietinum* L.	Axenic/pot/field trials	Increase in root weight, shoot weight, number of pods, and grain yield up to 51%, 52%, 92%, and 60%, respectively	Shahzad et al. (2010)
Pseudomonas entomophila strain PS-PJH	*Raphanus sativus*, *Lactuca sativa*	Axenic	Increased seedling vigor in *R. sativus* (43%) and *L. sativa* (34%) plants	Kamala-Kannan et al. (2010)

Continued

Table 7.1 Observed effects of plant-beneficial bacteria in regard to plant growth promotion—cont'd

Proposed mechanism PGPR/endophyte	Plant	Experimental conditions	Plant response to PGPR/endophyte inoculation	References
Pseudomonas putida UW4	*Arabidopsis thaliana*	Axenic	Increased root hair length (2.35-fold)	Contesto et al. (2008)
Rhizobium sp. strain TAL1145, transconjugants of TAL1145	*Leucaena leucocephala*	Leonard jar	Multiple copies of the native- and BL3-*acdS* genes in TAL1145 resulted in significant increases in numbers and dry weight of nodules compared to native strain TAL1145	Tittabutr et al. (2008)
Methylobacterium fujisawaense strains CBMB 20, CBMB 10	Canola	Gnotobiotic	Increased root length up to 78%	Madhaiyan et al. (2008)
Burkholderia caryophylli ACC7, *Pseudomonas fluorescens* ACC50	Wheat	Pot/field trials	Increase in root weight and grain yield up to 83% and 43% (*B. caryophylli*), *Pseudomonas* sp. performed better under field conditions	Shaharoona et al. (2007)
Pseudomonas putida biotype A, *P. fluorescens*, *P. fluorescens* biotype G	Maize	Pot trial	Improved plant biomass and cob weight up to 12% and 20%, respectively	Shaharoona et al. (2006)
Pseudomonas spp. strains PGPR1, PGPR2, PGPR4, PGPR7	*Arachis hypogaea* L.	Axenic/pot/field trials	Significantly enhanced pod yield (23–26%, 24–28%, and 18–24%, respectively), haulm yield, and nodule dry weight under field conditions	Dey et al. (2004)
Nutrient solubilization/uptake—P-solubilization				
Pontibacter niistensis NII-0905	Cowpea	Axenic	1.3-fold increase in seedling biomass	Dastager et al. (2011)

Pseudomonas fluorescens strain DR54 and *Enterobacter radicincitans* strain DSM 16656	Maize/ oilseed rape	Pot/field trials	*P. fluorescens* is more effective in P mobilization than *E. radicincitans*	Krey et al. (2011)
Micrococcus sp. NII-0909	Cowpea	Pot trial	Higher root (100%) and shoot (39%) lengths and biomass (54%)	Dastager et al. (2010)
Pantoea sp. DHRSS, *Citrobacter* sp. PP1	Pigeon pea	Axenic/pot trials	Inoculation with *Pantoea* strain PP1 and *Citrobacter* strain DHRSS improved significantly shoot biomass and P-content compared to control	Patel et al. (2010)
Streptomyces filipinensis no. 15	Tomato	Gnotobiotic conditions	Increased root–shoot length (1.1- and 1.03-fold) and root–shoot weight (2.6- and 2.7-fold)	El-Tarabily (2008)
Nutrient solubilization/uptake—N_2-fixation/uptake				
Klebsiella sp. LGI4RJ	Canola	Greenhouse	Significant increase in shoot N-content	Farina et al. (2012)
Bacillus subtilis OSU-142, *Azospirillum brasilense* Sp245	Grapevine	Pot trial	Significantly improved the chlorophyll concentrations of the leaves (*A. brasilense*) and stimulated vegetative development and mineral acquisition of the plants (*B. subtilis*)	Sabir et al. (2012)
Bacillus amyloliquefaciens IN937a and *Bacillus pumilus* T4	Tomato	Greenhouse	Increased nitrogen uptake	Adesemoye et al. (2010)
Azospirillum brasilense strain Sp7, *Bacillus sphaericus* strain UPMB10	Banana	Hydroponics	Increased the bunch yield up to 51%	Mia et al. (2010)

Continued

Table 7.1 Observed effects of plant-beneficial bacteria in regard to plant growth promotion—cont'd

Proposed mechanism PGPR/endophyte	Plant	Experimental conditions	Plant response to PGPR/endophyte inoculation	References
Azospirillum amazonense	Rice	Greenhouse	Increased dry matter and N accumulation up to 18% and 27%, respectively	Rodrigues et al. (2008)
Pseudomonas sp. strain K1	Rice	Pot trial	Increased dry weight and yield up to 60% and 93%, respectively	Mirza et al. (2006)
Nutrient solubilization/uptake—siderophore production				
Ochrobactrum haematophilum H10	Cucumber	Pot trial	Leaf and root length were increased by 27% and 58%, respectively	Zhao et al. (2012b)
Streptomyces strains AzR-051	Tomato	Axenic	Increased root and shoot length up to 31% and 30%, respectively	Verma et al. (2011)
Bacillus subtilis CAS15	Pepper	Pot trial	36.92% and 49.68%, increase in fruit weight (37%) and yield (50%)	Yu et al. (2011)
Pseudomonas fluorescens R81	*Vigna mungo*/ *Triticum aestivum*	Pot/field trials	Improved grain yield up to 46%	Saharan et al. (2010)
Pseudomonas sp. strain GRP3	Mung bean	Pot trial	Increased shoot mass, root mass and total chlorophyll content up to 101%, 39%, and 40%, respectively	Sharma et al. (2003)

Moreover, nitrogen fixation by associative diazotrophs has been rarely proven, but these bacteria exhibit several other plant growth-promoting activities, such as the synthesis of plant hormones and vitamins, the improvement of nutrient uptake, induction of stress resistance, or stimulating nodulation of legumes by rhizobia (Dobbelaere et al., 2003).

4.1.2 Production of plant hormones, vitamins, and bacterial volatiles

Many plant-associated bacteria synthesize plant growth regulators such as hormones and volatiles. Phytohormones produced by bacteria are mainly cytokinins, auxins, and gibberellins. Interestingly, there seems to be plant organ-specific differences in the type of phytohormone produced by plant-associated bacteria. Whereas auxins were identified in isolates of any type of plant organ, gibberellins were typically found in root-associated bacteria and cytokinines in leaf-colonizing bacteria (Pirttilä, 2011).

Auxins are indole derivatives that play a central role in plant growth and are essential for plant body development. Genes involved in the production of indole-3-acetic acid (IAA), the major naturally occurring auxin, are frequently found in plant-associated bacteria, and it is believed that approximately 80% of rhizobacteria produce IAA (Khalid et al., 2004). There is evidence that IAA synthesis in bacteria might be stimulated by plant signals. The expression of IAA synthesis genes in *Azospirillum brasilense* is upregulated by IAA (van de Broek et al., 1999). The role of bacterial IAA synthesis in plant growth promotion is well documented (Lambrecht et al., 2000; Spaepen et al., 2007; Steenhoudt and Vanderleyden, 2000) and has been proven in the interaction between canola and *P. putida* GR12-2 (Patten and Glick, 2002). Canola roots inoculated with a mutant deficient in synthesis of IAA showed significantly reduced growth in comparison to roots colonized by the wild type (Patten and Glick, 2002). Besides the direct effects on plant growth and development, IAA indirectly affects plant nutrition by stimulating nitrogen fixation activity and P-solubilization (Bianco and Defez, 2010; Imperlini et al., 2009). A variant of *Sinorhizobium meliloti* 1021, strain RD64, with enhanced IAA synthesis ability showed improved nitrogen fixation ability as compared to the wild-type strain (Imperlini et al., 2009). Strain RD64 also showed enhanced P-solubilization activity reflected by the upregulation of genes coding for the high-affinity P transport system, the induction of acid phosphatase activity, and the increased secretion into the growth medium of malic, succinic, and fumaric acids (Bianco and Defez, 2010). On the other

hand, gene expression microarray analysis with *in vitro* plantlets of potato inoculated with the IAA-producing endophyte *B. phytofirmans* PsJN revealed no changes for genes responsive to auxin (Trognitz et al., 2008).

Although not as intensively studied as auxins, cytokinins and gibberellins have also been reported to stimulate plant growth (Cassán et al., 2009; van Loon, 2007). Cytokinins comprise a group of compounds with either an adenine or a urea backbone and regulate cytokinesis in plants (Skoog and Armstrong, 1970). In particular, they are involved in the induction of seed germination, the break of dormancy of buds, and apical dominance. Additionally, they induce chlorophyll synthesis and chloroplast proteins in the early leaf development (Skoog and Armstrong, 1970). Gibberellins stimulate plant growth in stems and leaves and modulate in certain species flowering time and the development of flowers, fruits, and seeds (Sun and Gubler, 2004). The importance of gibberellins can be seen with the gal-3-deficient *Arabidopsis* mutant, which is a nongerminating, extreme dwarf, late flowering, and male-sterile.

The role of cytokinin signaling in plant growth promotion by *Bacillus megaterium* has been studied with *Arabidopsis thaliana* mutants in which cytokinin receptors were disrupted (Ortíz-Castro et al., 2008). *B. megaterium* showed reduced plant growth promotion in mutants lacking one or two receptors, whereas a cytokinine receptor triple knockout of *Arabidopsis* did not respond at all to inoculation with *B. megaterium*.

Some PGPB are able to produce vitamins, especially B-group vitamins (Ivanova et al., 2006; Marek-Kozaczuk and Skorupska, 2001). Mutants of *P. fluorescens* strain 267 impaired in the synthesis of thiamine and niacin lost the ability to promote growth of red clover roots. The niacin auxotroph fully failed in colonizing red clover (Marek-Kozaczuk and Skorupska, 2001). Vitamins may also exhibit synergistic effects on other plant growth-promoting mechanisms. B-group vitamins produced by *Pseudomonas* sp. strain 267 stimulated symbiotic nitrogen fixation activity of *Rhizobium leguminosarum* bv. *trifolii* in clover (Derylo and Skorupska, 1993).

The emission of volatiles is a recently discovered novel mechanism by which bacteria promote plant growth (Ping and Boland, 2004; Ryu et al., 2003a). Ryu et al. (2003a) demonstrated that 2*R*,3*R*-butanediol and acetoin produced by *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a significantly enhance growth in *Arabidopsis*. Tests with mutants of *A. thaliana* indicated that 2*R*,3*R*-butanediol and acetoin act via the modulation of cytokinin and ethylene signaling (Ryu et al., 2003a).

4.1.3 1-Aminocyclopropane-1-carboxylate deaminase

Ethylene affects growth and development in plants. It regulates cell size and cell division, and in terms of development, ethylene is involved in ripening, senescence, and abscission (Schaller, 2012). 1-Aminocyclopropane-1-carboxylate (ACC) is an immediate precursor in the synthesis of ethylene in plants and is degraded by ACC deaminase enzymes to 2-oxobutyrate and ammonia. This enzyme activity is frequently found in soil microorganisms (Glick et al., 2007). ACC deaminase may play a role in balancing the plant ethylene levels (Glick et al., 2007). Glick et al. (2007) suggested the following mechanism: ACC deaminase-producing rhizosphere bacteria degrade ACC directly when it is excreted by plant roots. As a consequence, the amount of ethylene is decreased and the plant protected from growth-retarding effects of high ethylene levels produced by plants in response to biotic and abiotic stress (Glick, 2005). This idea is supported by the finding that canola (*Brassica napus*) roots colonized by the ACC deaminase-producing *P. putida* UW4 upregulate genes involved in cell division and proliferation but downregulate stress-related genes (Hontzeas et al., 2004). More recently, it has been shown that during inoculation of *B. napus* with *P. putida* UW4 defective in ACC deaminase activity, plant genes for auxin responsive factors were upregulated and stress-responsive genes were downregulated (Stearns et al., 2012) as compared to the wild-type strain. However, the role of ACC deaminase enzyme activity in plant growth promotion has been clearly demonstrated in the symbiosis of *B. phytofirmans* PsJN and canola. Sun et al. (2009) constructed a knockout mutant of *B. phytofirmans* PsJN lacking ACC deaminase activity. The mutant was no longer able to promote the elongation of the roots of canola seedlings (Sun et al., 2009).

4.1.4 Iron uptake and phosphate solubilization

Many Gram-negative bacteria synthesize and excrete siderophores, molecules with high affinity to iron. The main groups of siderophores are the hydroxamates and catecholates (Miethke and Marahiel, 2007). The siderophores excreted into the extracellular environment bind iron. The resulting ferric–siderophore complexes are recognized then transported into the cell via specific receptor proteins (TonB-dependent receptors). The effect of microbial siderophores in promoting plant growth might be indirect. Kloepper et al. (1980) proposed that siderophores produced and released by PGPR deprive the native microflora of iron which led to the suppression of potential pathogenic bacteria. Furthermore, siderophores contribute to the rhizosphere competence of bacteria that synthesize plant hormones or exhibit ACC deaminase activity (Crowley, 2006). On the other hand, plants were found to

be able to take up microbial ferric–siderophores complexes (Crowley et al., 1988). However, the proof that the symbiosis between plants and siderophore-producing bacteria results in better iron supply of plants is still missing (Crowley, 2007). Phosphate is probably the most limiting factor in plant growth, and although P is abundant in soils, the bioavailable soluble form of phosphate is limited. Because of the negative charge of the phosphate ion, they quickly form insoluble mineral complexes which are not available for plants. In addition, high amount of phosphate is fixed in organic matter. Many PGPR have the potential to release fixed P, whereby different mechanisms are involved in inorganic or organic phosphate solubilization (reviewed by Rodriguez et al., 2006). In principle, inorganic phosphate-solubilizing bacteria produce and excrete small organic acids such as gluconic, citric, lactic, propionic, and/or succinic (Chen et al., 2006; Vyas and Gulati, 2009). The hydroxyl and carboxyl groups bind the cations in mineral phosphate complexes releasing soluble phosphate (Kpomblekou and Tabatabai, 1994). The release of phosphate from organic matter is maintained by the activity of three types of enzymes: nonspecific phosphatases, phytases, and phosphonatases or C–P lyases. The ecologically most relevant enzymes are the acid phosphatases and phytases because of the predominance of their substrates in soil. Phosphatases catalyze the dephosphorylation of phosphoesters or phosphoanhydride bonds in general, whereas phytases act specifically on phytic acid. Phosphonatase and C–P lyases catalyze the cleavage of C–P bonds in organophosphonates (Rodriguez et al., 2006).

The most efficient phosphate-solubilizing bacteria known so far include strains of the genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Micrococcus*, *Flavobacterium*, *Burkholderia*, *Achromobacter*, *Erwinia*, and *Agrobacterium* (Vyas and Gulati, 2009). Recently, Trivedi and Sa (2008) reported the correlation of inorganic phosphate solubilization efficiency and plant growth promotion intensity in *Pseudomonas corrugata* (NRRL B-30409). Two mutants of the strain with enhanced ability to solubilize rock phosphate exhibited also enhanced plant growth-promoting activity (Trivedi and Sa, 2008).

4.1.5 Photosynthesis and polyamines

Plant inoculation with many PGPR and endophytes results in increased chlorophyll content and photosynthesis activity. *Bacillus pumilus* and *Acinetobacter johnsonii*, respectively, significantly increased the maximum photochemical yield and total chlorophyll content in leaves of sugar beet (Shi et al., 2010). Bacterization of *Vitis vinifera* L. cv. Chardonnay (grapevine) by *Burkholderia phytofirmans* PsJN resulted in a 1.3 times higher

CO_2-fixation rate and a 2.2 times higher O_2 evolution as compared to non-inoculated control plants (Ait Barka et al., 2006). More recently, Fernandez et al. (2012) monitored various photosynthesis parameters such as net photosynthesis, intercellular CO_2 concentration, stomatal conductances, activity of photosystem II, and total chlorophyll concentration in cold-stressed grapevine plantlets inoculated with *B. phytofirmans* PsJN as compared to nonbacterized controls. The authors clearly showed that the increase in plant photosynthetic activity was not due to a modulation of stomata conductance in grapevine colonized by strain PsJN. Thus, the mechanism underlying the stimulation of plant photosynthesis by *B. phytofirmans* PsJN remains elusive. Recently, the genome of *B. phytofirmans* PsJN was fully sequenced (Weilharter et al., 2011). Based on the occurrence of pfam domains and sequences affiliated to certain COG categories, we identified eight genes for carbonic anhydrase (CA) in the genome of *B. phytofirmans* PsJN (unpublished data). The CAs represent a family of enzymes that catalyze the reversible conversion of carbon dioxide and water to bicarbonate and protons (Badger and Price, 1994). In plants, CAs help raising the concentration of CO_2 in order to increase the carboxylation rate of the enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (Badger and Price, 1994). However, the activity and functionality of the putative CA genes in strain PsJN have not been analyzed and we may only speculate whether strain PsJN directly modulates CO_2 levels in the host plant.

Microbial photosynthetic activity or at least the presence of relevant genes has been shown for various plant-associated *Proteobacteria* such as *Bradyrhizobium* spp. (Giraud et al., 2007; Hungria et al., 1993), *S. meliloti* (Pickering and Oresnik, 2008), or *Azospirillum amazonense* (Sant'Anna et al., 2011). All photosynthetic strains encode one or more bacteriophytochromes (Jaubert et al., 2008; Kaneko et al., 2010; Sant'Anna et al., 2011) and gene cluster implicated in carbon fixation via the Calvin–Benson–Basham cycle including ribulose-1,5-bisphosphate carboxylase genes. All of these strains are nitrogen-fixing bacteria, and it is supposed that the central role of photosynthetic activity is during the initial steps of the symbiosis between bacteria and plants by ensuring survival of the bacteria and later on in the plant by generating the energy needed for nitrogen fixation (Giraud et al., 2007).

4.2. Biocontrol properties against plant pathogens

Many plant-associated bacteria have the ability to protect plants from pests. Some examples of rhizosphere and/or endophytic bacteria with biocontrol

properties against different pathogens are given in Table 7.2. Biocontrol of pathogen infections can be achieved directly or indirectly. The principal mechanisms involved in biocontrol by endophytic and soil bacteria are illustrated in Fig. 7.1 and have been summarized in a number of reviews (Berg, 2009; Francis et al., 2009; Schrey and Tarkka, 2008; Tarkka et al., 2009; Zamioudis and Pieterse, 2012). Bacteria may act directly

- by niche occupation, which means by colonizing the rhizosphere or phyllosphere and thereby occupying the physical niche for plant pathogens, by limiting nutrients required for pathogen growth, and by competing for limiting elementary nutrients such as iron;
- by producing signal components interfering with pathogen reproduction, toxin production, or virulence;
- by antibiosis, by producing toxins and antibiotics, by producing lytic enzymes, and by acting as parasites or predators of pathogens.

Indirect mechanisms of biocontrol include activation or alteration of plant defense or recruiting additional players in the plant–pathogen–beneficial bacteria interactions and might be achieved

- by inducing plant resistance,
- by stimulating plant hormones resulting in outgrowth or altered host acceptance,
- by attracting or stimulating additional organisms capable of inhibiting pest or pathogens.

Important factors for the execution of these mechanisms are molecular patterns associated with biocontrol strains (Pal and McSpadden Gardener, 2006). These can be all kind of secondary metabolites, for example, lipopeptides, phenazines, polyketides and pyrrolnitrin, surface and structural components of bacteria such as flagellins and lipopolysaccharides, metabolic (side) products such as ammonia or cyanide as well as proteins, and enzymes. Each biocontrol strain and even each involved chemical signal do not exclusively activate a single of the above described mechanisms but are regularly responsible for various direct and indirect biocontrol mechanisms. For example, *B. amyloliquefaciens* FZB42 produces different polyketides and the lipopeptides bacillomycin D, fengycin A, and surfactin (Chen et al., 2007), of which surfactin alone has been discussed to a play vital role in swarming, root niche colonization and occupation, in direct antibiosis toward bacteria and fungi, and in the activation of plant resistance (Ongena and Jacques, 2008). Even more ambivalent interactions have been described for the biocontrol activity of *Streptomyces* sp. GB 4-2 against *Heterobasidion* root and butt rot in Norway spruce seedlings (Lehr et al., 2008). While the bacterium even promotes

Table 7.2 Examples of rhizosphere and/or endophytic bacteria with biocontrol properties against different pathogens in various host plants

Biocontrol bacteria	Target pathogen/ diseases	Plants	References
Pseudomonas aeruginosa 7NSK2	*Botrytis cinerea*	*Phaseolus vulgaris*	de Meyer and Hofte (1997)
Pseudomonas fluorescens WCS374	*Fusarium* wilt	*Raphanus sativus*	Leeman et al. (1995)
S. marcescens 90-166, *Bacillus pumilus* SE34, *P. fluorescens* 89B61, *Bacillus pasteurii* C9, *Paenibacillus polymyxa* E681, *Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937a, *Enterobacter cloacae* JM-22, and *Bacillus pumilus* T4	*P. syringae* pv. tomato DC3000 and *P. syringae* pv. Maculicola ES4326	*Nicotiana tabacum*, *Capsicum annuum*, *Cucumis sativus*, *Solanum lycopersicum*, *Arabidopsis thaliana*	Wei et al. (1991, 1996), Raupach et al. (1996), Yan et al. (2002), Zhang et al. (2002), Ryu et al. (2003b)
Pseudomonas fluorescens WCS374	*Colletotrichum falcatum*/red rot disease	*Saccharum officinarum*	Viswanathan and Samiyappan (1999)
Pseudomonas putida 89B-27 and *Serratia marcescens* 90-166	*Fusarium oxysporum* f. sp. *cucumerinum*	*Cucumis sativus*	Liu et al. (1995)
Bacillus pumilus SE 34 p	*F. oxysporum* f. sp. *radicis-lycopersici*	*Solanum lycopersicum*	Benhamou et al. (1998)
P. fluorescens 63-28	*Pythium ultimum*	*Pisum sativum*.	Benhamou et al. (1996)
P. fluorescens 63-28	*F. oxysporum* f. sp. *radicis-lycopersici*	*Solanum lycopersicum*	M'Piga et al. (1997)
Bacillus cereus	*F. solani*, *Sclerotium rolfsii*	*Gossypium hirsutum*, *Phaseolus vulgaris*	Pleban et al. (1995)
P. fluorescens EP1	*Colletotrichum falcatum*	*Saccharum officinarum*	Viswanathan and Samiyappan (1999)

Continued

Table 7.2 Examples of rhizosphere and/or endophytic bacteria with biocontrol properties against different pathogens in various host plants—cont'd

Biocontrol bacteria	Target pathogen/ diseases	Plants	References
Serratia marcescens 90-166, *Bacillus pumilus*, and *Pseudomonas fluorescens* 89B-61	*P. tabacina*	*Nicotiana tabacum*	Zhang et al. (2002)
Pseudomonas aeruginosa 7NSK2 p	*Botrytis cinerea*	*Solanum lycopersicum*	Audenaert et al. (2002)

growth of the pathogen, it also induces local and systemic defenses in Norway spruce thereby increasing resistance to the rot pathogens.

4.2.2 Outcompetition of pathogens

Looking more closely at these involved mechanisms, niche occupation as competition for space, nutrients, and physical niches of the rhizosphere/rhizoplane and endophytic tissues (Fig. 7.1) can be exerted by different beneficial Gram-positive and Gram-negative bacteria. The root surface and surrounding rhizosphere are full of root exudates containing up to 40% of the photosynthates and are rich sources of nutrients including organic acids, sugars, vitamins, and amino acids. Thus, along root surfaces are suitable nutrient-rich niches that can attract a great diversity of microorganisms and also phytopathogens (Compant et al., 2005; Lynch, 1990). Competition for these nutrients and niches is a fundamental mechanism by which beneficial bacteria derived from the rhizosphere protect plants by depriving phytopathogens of essential nutrients. Chemotaxis toward nutrients exuded in the rhizosphere of the host plants could explain how niche occupation at the rhizosphere level is achieved (Compant et al., 2005). This implies that beneficial bacteria should have strong chemotactic abilities to reach exudate components before pathogens to be able to protect the plants (Compant et al., 2005).

A particularly limited nutrient is iron. Important factors in the competition for this nutrient are siderophores produced by certain bacteria as described firstly by Kloepper et al. (1980). Siderophores sequester iron (III) and are used largely by their producers and by certain plants (Datnoff et al., 2007). This limits the availability to other microbes and pathogens and suppresses their growth (Kloepper et al., 1980). Various bacteria are able

to produce siderophores, as, for example, members of *Actinobacteria*, *Gammaproteobacteria*, and *Alphaproteobacteria* (Bendale et al., 2010; Datnoff et al., 2007; Paulsen et al., 2005; Sayyed et al., 2005; Yamanaka et al., 2005). Beneficial bacteria from these phyla such as *Pseudomonas* spp., *Streptomyces* spp., and rhizobia secrete chemically different siderophores with high iron affinity, which can reduce the availability of iron for plant pathogens. The list of bacterial groups is not exhaustive, and many other beneficial rhizosphere and endophytic bacteria can secrete siderophores as well.

Dense biofilms can then be formed on nutrient-rich root surfaces by various beneficial bacteria such as *Pseudomonas* spp. or *A. brasilense*, which occupy root elongation zones and root hairs (Ramey et al., 2004). Such biofilms may be a physical barrier to root pathogens, but also endophytes can physically occupy specific niches. The causal agent of Pierce disease of grapevine, *X. fastidiosa*, is inhabitant of the xylem vessels (Hopkins, 2005). Certain strains of *X. fastidiosa* such as EB92-1 are nonvirulent and have been suggested as biocontrol agent of Pierce disease. A possible mechanism is the occupation of the xylem niches and competition, but other mechanisms such as induction of resistance have also been discussed for this strain (Hopkins, 2005).

4.2.3 Disturbance of pathogen signaling

Both Gram-positive and Gram-negative bacteria have been described to use cell-to-cell communication in a density-dependent manner to regulate, for example, biofilm formation, exopolysaccharide, and virulence factor production (Fuqua and Greenberg, 2002). These factors play important roles in the establishment of successful infections of phytopathogenic bacteria, and consequently, disturbance or interruption of this quorum signaling has the potential to inhibit plant diseases. One of the most prominent examples of quorum signaling is achieved by homoserine lactones of a number of Gram-negative bacteria including the phytopathogens such as *Agrobacterium* spp., *Dickeya* spp., and *Pectobacterium* spp. Degradation of homoserine lactones can be achieved by lactonases of *Bacillus* spp. or acylase of *Variovorax paradoxus* (Fuqua and Greenberg, 2002) and have been described for a number of other bacterial groups and strains, partly with other mechanisms such as oxidoreductases (Czajkowski and Jafra, 2009). Indeed, a homoserine-lactonase from a *B. amyloliquefaciens* strain (Yin et al., 2010) has been shown to inhibit carrot infection by *Pectobacterium carotovorum* ssp. *carotovorum* in laboratory tests and has the potential to act as biocontrol agent against *P. carotovorum*. However, this strategy might be problematic for field applications as it can also interfere with beneficial bacteria signaling, for example,

from rhizobia (Czajkowski and Jafra, 2009). Future applications of signal interference might be expanded to disturb signaling in fungi and *Oomycota*, as they also use chemical signaling, for example, in the communication of zoospores during plant infections (Cottier and Mühlschlegel, 2012; Kong et al., 2010).

4.2.4 Direct antagonism against phytopathogens

Beneficial microbes have also been described to produce a broad collection of secondary metabolites inhibiting the growth or acting as toxins against phytopathogens (Fig. 7.1). Similar or even identical metabolites might even be produced by different bacterial groups. For example, pyrrolnitrin is known from *Burkholderia* and *Pseudomonas* species (Raaijmakers et al., 2002). This antibiotic has shown activity against *Rhizoctonia solani*, *Botrytis cinerea*, *Verticillium dahliae*, and *Sclerotinia sclerotiorum* (Ligon et al., 2000). A wide variety of compounds with antibiotic activity have been identified in biocontrol strains including specifically produced lipopeptides and polyketides, but also more unregulated waste products of metabolism such as hydrogen cyanide (Pal and McSpadden Gardener, 2006). Described metabolites with antibiotic activity from biocontrol strains include compounds such as amphisin, cyclic lipopeptides, 2,4-diacetylphloroglucinol, hydrogen cyanide, oomycin A, phenazine, pyoluteorin, pyrrolnitrin, tensin, and tropolone produced by pseudomonads (Défago, 1993; de Souza et al., 2003; Nielsen and Sørensen, 2003; Raaijmakers et al., 2002) and lipopeptides, kanosamine, oligomycin A, xanthobactin, and zwittermicin A produced by *Bacillus*, *Streptomyces*, and *Stenotrophomonas* spp. (Hashidoko et al., 1999; Kim et al., 1999; Milner et al., 1996; Nakayama et al., 1999; Ongena and Jacques, 2008). Agrocin 84 can be also secreted by *Agrobacterium radiobacter* strains (Kerr, 1980), 2,3-de-epoxy-2,3-didehydro-rhizoxin by *Pseudomonas borealis* MA342 (Hokeberg et al., 1998). Also Enterobacteriaceae such as *Pantoea agglomerans* EH318 are known to produce metabolites with antibiotic activity such as pantocin A and B (Wright et al., 2001), but secondary metabolites secreted by beneficial bacteria are continuously explored and a large variety of metabolites having antibacterial as well as oomycetal and fungal activities very likely remain to be discovered, especially from the large reservoir of metabolite-rich actinobacteria (Qin et al., 2011). These are in fact an important source of antibiotics that are linked to the inhibition of phytopathogens. It has been shown that *Streptomyces* sp. S-70 and *Streptomyces* sp. TP-A0569 suppress infection of *Alternaria brassicicola* on Chinese cabbage seedlings (Igarashi et al., 2002) inhibiting the formation of infection hypha that is necessary for *A. brassicicola*

to accomplish its infection. Sasaki et al. (2001a) also identified new bioactive compounds TPU-0031-A and B produced by actinomycete *Streptomyces* sp. TP-A0556 against *Aspergillus fumigatus* TFO 886. They also found cedarmycins A from *Streptomyces* sp. TP A0456 and found it to be active against *Candida glabrata* IFO 0622, as well as *Cryptococcus neofonnans* ATCC90, *in vitro* (Sasaki et al., 2001b). Other compounds such as alnumycin were also reported in *Streptomyces* sp. DSM 11575 isolated from root nodules of *Alnus glutinosa* (Bieber et al., 1998) as well as actinomycin X2 and fungichromin from the endophytic actinomycete *Streptomyces galbus* strain R-5 showing antibacterial and antifungal activities *in vitro* against *Pestalotiopsis sydowiana*, a major pathogen of rhododendron (Shimizu et al., 2004). Additionally, *Streptomyces* sp. NRRL30562 produces antibiotics designated as munumbicins A-D40 possessing a wide-spectrum activity against phytopathogenic fungi like *R. solani* (Castillo et al., 2002). *Streptomyces* sp. NRRL30566, which was isolated from a fern-leaved grevillea (*Grevillea pteridifolia*), produced also novel wide-spectrum antibiotics named kakadumycins found to be effective against *Bacillus anthracis in vitro* (Castillo et al., 2003). The actinomycetes and the compounds mentioned above are a few examples of biocontrol actinomycetes and agroactive compounds isolated from actinomycetes.

It has been demonstrated also that beneficial bacteria from the rhizosphere and endophytes can secrete not only antibiotics but also lytic enzymes enabling to reduce the growth of various phytopathogens (Fig. 7.1). Enzymes like chitinases, cellulases, and 1,3-β-glucanases could be, for instance, secreted by beneficial bacteria. For example, biocontrol of *Phytophthora cinnamomi* was obtained by using a cellulose-producing isolate ATCC 39149 of *Micromonospora carbonacea*. Control of *Phytophthora fragariae* causing raspberry root rot was suppressed by 1,3-β-glucanases-producing actinomycete isolate (EF-72, EF-22, and EF-97; Valois et al., 1996). Chitinolytic enzymes produced by *B. cereus* strain 65 also appear to be responsible for biocontrol of *R. solani* (Pleban et al., 1997). Similarly, biocontrol of *Pythium ultimum* in the rhizosphere of sugar beet by *Stenotrophomonas maltophila* W5 is likely due to the production of extracellular proteases (Dunne et al., 1997). *Lysobacter enzymogenes* strains produce a number of extracellular enzymes including chitinases, glucanases, and proteases making them active against various fungi and oomycetes (Kobayashi et al., 2005). Strain *L. enzymogenes* C3 (formerly classified as *S. maltophila* C3) has been suggested as biocontrol agent against different fungi and *Pythium* spp. (Kobayashi et al., 2005), and its large reservoir of lytic enzymes makes *L. enzymogenes* act as a predatory strain causing lysis in plant pathogens.

While fungal hyperparasitic strains have been reported (e.g. *Ampelomyces quisqualis* attacking powdery mildews (Pal and McSpadden Gardener, 2006)), bacterial strains parasiting on phytopathogens have not been described yet. However, endophytic bacteria of soil fungi exist (Frey-Klett et al., 2007), leaving open the possibility that a similar bacterial biocontrol strain might be discovered in future. In this context, it is interesting to note that the type III secretion system of the biocontrol strain *P. fluorescens* KD is required for activity against the oomycete pathogen *P. ultimum* indicating that the systems target the oomycete, which is often indicative for parasitism on hosts (Rezzonico et al., 2005).

4.2.5 Indirect mechanisms of biocontrol: Induction of systemic resistance responses in plants

Beneficial bacteria from the soil environment and/or entering plant internal tissues may not only directly target the survival, reproduction, and virulence of phytopathogens but also protect indirectly, for example, throughout defense induction in plants to increase resistance to phytopathogenic infections. This induced resistance corresponds to a state of the plant, where previous contact with an induction agent, an allelochemical, a virus or an organism makes the plant not only locally but often systemically more resistant to later infections (Fig. 7.1; van Loon et al., 1998; Bakker et al., 2007). Systemic acquired resistance (SAR) is thereby referred to as resistance phenomenon occurring after infecting with necrotizing pathogen, while induced systemic resistance (ISR) occurs after plant contact with a number of beneficial bacteria and is especially well characterized for *P. fluorescens* (Bakker et al., 2007; Zamioudis and Pieterse, 2012). Both systemic resistances are effective against a broad spectrum of pathogens and even insect herbivores. Hereby, SAR is dependent on SA, while ISR phenomena require functional jasmonate and/or ethylene signaling (Bakker et al., 2007; Pieterse et al., 1998; Zamioudis and Pieterse, 2012). Interestingly, the independency on SA seems to be even the case for some beneficial bacterial strains belonging to *Pseudomonas* spp. and *Serratia marcescens*, which have the ability to produce SA themselves (Bakker et al., 2007). The effectiveness of SAR and ISR is, at least in *Arabidopsis*, dependent if SA or jasmonate/ethylene signaling is required for plant defense. However, recent research has been shown that modulating plant defense is not only dependent on these defense signaling hormones, but a complicated signaling network and almost all described plant hormones such as abscisic acid, auxin,

brassinosteroids, cytokinins, and gibberellins have been implicated to play a role in defense modulation and systemic resistance (Pieterse et al., 2009).

Beneficial microbes and specific substances (e.g., β-aminobutyric acid) do not result in a strong transcriptome change of treated plants as observed after pathogen challenge but are priming the plant defenses to result in a quick response when a pathogen infects systemic parts of the plants (Conrath et al., 2002; Jakab et al., 2001, 2005; Ton et al., 2005). For instance, challenge inoculation of plants with the leaf pathogen *Pseudomonas syringae* pv. tomato showed a faster and stronger defense induction when plants are ISR-positive, which means they have been treated with *P. fluorescens* strain WCS417r (Verhagen et al., 2004). In recent years, a considerable number of reviews on the mechanisms and applications of priming, plant immunity, and induced resistance have been published (see, e.g., Conrath, 2011; Gust et al., 2010; van Loon and Bakker, 2005; Zamioudis and Pieterse, 2012), and it seems that epigenetic mechanisms involved in the priming state (Conrath, 2011) could be even transferred vertically to next generations (Slaughter et al., 2012). For the actual execution of priming effects in plants, both a wide range of secreted or even volatile components and parts of structures on the surfaces of the microbes can be responsible of. These microbial-associated molecular patterns induce a systemic resistance toward different kinds of phytopathogens and include not only allelochemicals such as siderophores and antibiotics but also flagella, lipopolysaccharides, as well as many others (Bakker et al., 2007).

Apart from the effects of biocontrol bacterial strains on defense signaling, bacteria can also influence hormones involved in plant growth, which might result in faster growth and thereby escaping pathogen pressure both locally or timely. Importantly, all the mechanisms cannot be seen isolated, but of course, a strong interplay between plant hormonal pathways exist and effects on plant growth can have effects on plant defense and vice versa. The complexity of defense signaling networks and the role of classical growth hormones have been reviewed recently (Pieterse et al., 2009). Additional aspects of indirect biocontrol mechanisms include the wide range of potential tri- and multitrophic interactions. Such phenomena have been described for a number of parasitic wasps and mites, which are attracted by plant volatiles (e.g., by maize) released after pest feeding (Heil, 2008). Similarly, it has been recently suggested that infection of green pepper with whitefly might result in attracting plant-associated rhizobacteria, which in turn can elicit enhanced resistance to further pathogen attacks (Yi et al., 2011), and *Arabidopsis* roots have been shown to secrete L-malic acid after *P. syringae*

pv. tomato DC3000 attack, which attracts beneficial *B. subtilis* FB17 to colonize plant roots and to further protect plants against subsequent infections (Rudrappa et al., 2008). It remains to be seen how common such a recruitment of additional players is in beneficial plant–microbe interactions and if application of biocontrol strains also can attract additional beneficial bacteria.

4.3. Phytoremediation

Human activities such as mining, industry, traffic, agriculture, and military enhance the release of organic and inorganic pollutants in the environment. Consequently, soil, water, and air have been contaminated with different types of pollutants (Capuana, 2011; Mansour and Gad, 2010). Phytoremediation is an emerging green technology that uses living organisms mainly plants and their associated microbes to remediate toxic organics, metals, and radionuclides from soil, sediment, surface-, and groundwater (Bolan et al., 2011; Ma et al., 2011). It is an ecofriendly and cost-effective technology that is currently receiving considerable global attention (Glick, 2010).

Plants can remediate contaminated soil by different processes such as degradation, adsorption, absorption, accumulation, and volatilization of pollutants (Newman and Reynolds, 2005). Plants can have more than 100 million miles of roots per acre, which enhance the bioavailability of contaminants (Boyajian and Carreira, 1997). Plant root system improves soil structure which facilitates fast movement of water and gases through the soil. It also provides a biologically active soil region (i.e., rhizosphere), where enhanced microbial diversity, population, and metabolic activities improve plant growth, pollutant uptake, and degradation (Gerhardt et al., 2009; Newman and Reynolds, 2004; Wenzel, 2009). Inorganic contaminants cannot be degraded, but they can be remediated by plants via absorption followed by sequestration. For ideal phytoremediation, plants should have tolerance to high concentrations of pollutants, rapid growth rate, and produce high biomass and profuse root system (Garbisu et al., 2002).

A number of technologies can be included in the term of phytoremediation. For example, the process involves the degradation of organic pollutants by plant enzymes is known as phytodegradation (Wild et al., 2005). The transportation of contaminants into plant tissue and then their volatilization is called phytovolatilization (Terry et al., 1995). Another process in which plant absorbs the contaminants from the soil and water and deposits them in above-ground biomass is known as phytoextraction (Blaylock and Huang, 2000). In respect to phytoremediation of toxic

organic pollutants, which are slowly moved from soil to plant, rhizodegradation (i.e., degradation of organic pollutants by microbes in the rhizosphere) is the main mechanism of detoxification (McCutcheon and Schnoor, 2003). Plants can also stabilize contaminants in the soil, and this phytoremediation type is known as phytostabilization. Although different phytoremediation techniques were developed for the remediation of organic and inorganic pollutants (Pilon-Smits, 2005), rhizodegradation for organics and phytoextraction for inorganics were extensively studied and applied for the remediation of contaminated soil (Afzal et al., 2012; Bolan et al., 2011; Glick, 2010; Weyens et al., 2009a).

During rhizodegradation, interactions among root, root exudates, rhizosphere soil, and microbes play an important role in the degradation of organic pollutants. The rich microflora in the rhizosphere can mineralize organic contaminants using their own metabolic pathways before they can negatively impact the plant (Kuiper et al., 2004).

The effectiveness of phytoextraction of inorganics as an environmental-cleanup technology relies on many factors including the type of the plant, concentration of the contaminant, metal availability for plant uptake, and the plant's ability to absorb and accumulate metals in above-ground biomass (Aggarwal and Goyal, 2007; Ernst, 1996). Some plant species can tolerate and accumulate high amount of metals and were defined as hyperaccumulators (Baker and Brooks, 1989; Freitas et al., 2004). Effective remediation of metal-contaminated soil requires hyperaccumulators with characteristics of rapid growth and a high amount of biomass (Nie et al., 2002). However, the presence of high concentration of heavy metals slows the growth of the hyperaccumulators and inhibits biomass production (Mohanty et al., 1989; Sheoran et al., 1990). Similarly, one of the major limitations of rhizodegradation is that many plant species are sensitive to higher concentration of organic contaminants in soil (Chaudhry et al., 2005; Huang et al., 2005) and cannot effectively support the growth of soil microorganisms and contaminant degradation. To overcome this problem, interactions among pollutants, microbes, and plants have received great consideration because of the possible role of microbes on pollutant degradation and/or plant growth promotion in contaminated soil (Glick, 2010; Rajkumar et al., 2009; Weyens et al., 2009a).

4.3.1 Plant uptake of contaminants

During phytoremediation, different plant processes and mechanisms are involved in the tolerance, accumulation, complexation, volatilization, and degradation of contaminants (Cherian and Oliveira, 2005; Jabeen et al., 2009;

Pilon-Smits, 2005). The contaminants uptake in plants mainly occurs through the root system. Plant roots show variation in the uptake of organic and inorganic contaminants from soil. Organic contaminants are usually man-made or released in the environment due to human activities and xenobiotic to the plant. As a result, the plant membrane does not possess transporter proteins for these organic contaminants. Therefore, organic contaminants are taken up by the plants through simple diffusion and depend on the hydrophobicity of the contaminant (Alkio et al., 2005; Kuhn et al., 2004). Hence, the transportation of organic compounds into plants is a physical rather than biological process (Davis et al., 2003). As inorganics (nutrients) are required by the plants for their own growth and metabolic activities, inorganics move into plants by biological processes via membrane transporter proteins (Campbell et al., 2003; Geisler et al., 2005; Jabeen et al., 2009).

Generally, the detoxification of organic pollutants in plants involves transformation, conjugation, and sequestration (McCutcheon and Schnoor, 2003; Reichenauer and Germida, 2008). In transformation, the xenobiotics are made more polar and thus more water soluble by oxidation, reduction, or hydrolysis (Komives and Gullner, 2005). In conjugation, xenobiotics are made less toxic for the plant by making a complex with compounds such as sugars and peptides. Finally, modified xenobiotics are sequestered in the vacuole or covalently bonded to the molecules of the cell wall (Burken, 2003; Rea, 2007). In contrast to uptake and sequestration in plant tissues, many organic pollutants are completely mineralized in the rhizosphere of plants. Plant exudates induce microbial genes involved in the degradation of organic compound or act as a cometabolite to facilitate microbial pollutant degradation (Fletcher and Hegde, 1995; Leigh et al., 2002; Olson et al., 2003). Recently, we have observed that inoculated bacteria were metabolically active in the degradation of organic pollutants in the rhizosphere of different plants (Afzal et al., 2011; Andria et al., 2009; Yousaf et al., 2010b).

As inorganic pollutants are either nutrients themselves (e.g., nitrate, phosphate, copper, manganese, zinc) or chemically similar to nutrients (e.g., arsenate, selenate), therefore, plants naturally have transporter proteins for these pollutants (Abedin et al., 2002; Shibagaki et al., 2002). Inorganics also require transporter proteins for their movement from root endodermis to root xylem (Krämer et al., 1996; von Wirén et al., 1999). However, organics pass the membrane between root symplast and xylem apoplast by diffusion (Taiz and Zeiger, 2002). The movement of inorganic contaminants from leaf xylem to leaf cells involves another membrane transport step. Specific membrane transporter proteins uptake the inorganics and transfer

them into leaf cells, whereas organics reach the leaf symplast from the shoot xylem by simple diffusion. Once a pollutant reaches the leaf symplast, it may be localized in specific tissues or cellular sites. Generally, poisonous organic and inorganic contaminants are sequestered in sites where they can do the least disturbance to important cellular functions. In the cell, contaminants are generally localized in the vacuole or cell wall (Burken, 2003; Cobbett and Goldsbrough, 2002). At the tissue level, pollutants may be localized in the epidermis and trichomes (Hale et al., 2001; Küpper et al., 2004).

4.3.2 Microbial processes in phytoremediation

For a long period, PGPB have been largely applied in agriculture for facilitating plants to uptake nutrients from the environment or preventing plant disease. However, the combined use of plant- and pollutant-degrading bacteria, and/or PGPB is relatively a new concept in the field of bioremediation of contaminated soil and water (Glick, 2010; Weyens, et al., 2009a; Zhuang et al., 2007). Although some studies reported that fungi can enhance pollutant remediation potential of plants (Soleimani et al., 2010a,b), plant-associated bacteria (rhizo- and endophytic) are the most important group capable of improving phytoremediation potential of plants (Korade and Fulekar, 2009; Wang et al., 2011; Weyens, et al., 2009a,b; for an overview, see Table 7.3 and Fig. 7.1). These bacteria are ubiquitous in plant's environment and play an important role in plant growth and the phytoremediation of contaminants from soil and water.

Generally, plant-associated bacteria involved in phytoremediation possess pollutant-degrading and/or plant growth-promoting activities (Johnson et al., 2005; Koo and Cho, 2009; Zhuang et al., 2007). Although several different bacterial strains were reported, *Pseudomonas*, *Pantoea*, and *Methylobacterium* sp. strains were most frequently isolated from the rhizosphere and endosphere of different plants and reinoculated to host plant to enhance the remediation of organic and inorganic soil contaminants. A naphthalene-degrading strain, *P. putida* PCL1444, enhanced the phytoremediation of naphthalene from soil (Kuiper et al., 2002). In studies performed in our lab, *Pseudomonas* and *Pantoea* sp. strains, showing hydrocarbon-degrading (Tesar et al., 2002; Yousaf et al., 2010a), and *Pseudomonas* and *Methylobacterium* sp., strains showing heavy metal-resistant and plant growth-promoting activities (Idris et al., 2004, 2006; Kuffner et al., 2008), were isolated from the rhizosphere of different plants. Hydrocarbon-degrading strains could utilize all tested alkanes and contained *alkB* and CYP153 alkane hydroxylase gene. Heavy metal-resistant strains

Table 7.3 Successful application of rhizo- (RH) and endophytic (EN) bacteria to plants for the remediation of organic and inorganic contaminants from soil

Contaminant	Plant	Bacteria	RH/EN	References
Petroleum oil	*Cyperus rotundus*	*Mycoplana*, *Pandoraea*, *Pseudomonas*, *Rhizobium*, *Rhodococcus*	RH	Jurelevicius et al. (2010)
Diesel	*Lolium multiflorum*	*Pantoea* sp. BTRH79, *Pseudomonas* sp. ITRH76, *Rhodococcus* sp. ITRH43	RH	Yousaf et al. (2010b), Afzal et al. (2011, 2012)
Naphthalene	*Lolium multiflorum*	*Pseudomonas putida* PCL1444	RH	Kuiper et al. (2001, 2004)
Chlorpyrifos	*Lolium multiflorum*	*Pseudomonas nitroreducens* PS-2	RH	Korade and Fulekar (2009)
Phenanthrene	*Hordeum sativum* L.	*Pseudomonas* sp. strains	RH	Anokhina et al. (2004)
Cadmium, zinc	*Salix caprea*	10 different rhizosphere bacteria	RH	Kuffner et al. (2008, 2010)
Chromium	*Brassica juncea*	*Pseudomonas* sp. PsA, *Bacillus* sp. Ba32	RH	Rajkumar et al. (2006)
Cadmium	*Vigna mungo*	*Pseudomonas aeruginosa* MKRh3	RH	Ganesan (2008)
Diesel	*Lolium multiflorum*	*Pantoea* sp. ITSI10, *Pseudomonas* sp. strains, *Rhodococcus* sp. ITRI43, *Enterobacter ludwigii* strains	EN	Yousaf et al. (2010b, 2011), Afzal et al. (2011, 2012)
2,4-Dichlorophenoxy acetic acid	*Pisum sativum*	*Pseudomonas putida* strain POPHV6	EN	Germaine et al. (2006)
Naphthalene	*Pisum sativum*	*Pseudomonas putida* VM1441 (pNAH7)	EN	Germaine et al. (2009)
Ni	*Thlaspi goesingense*	*Methylobacterium* sp. strain V3, *Sphingomonas* sp. strain pfB27, *Curtobacterium* sp. strain VKM, *Curtobacterium* sp. strain VKM	EN	Idris et al. (2004, 2006)

Table 7.3 Successful application of rhizo- (RH) and endophytic (EN) bacteria to plants for the remediation of organic and inorganic contaminants from soil—cont'd

Contaminant	Plant	Bacteria	RH/EN	References
Ni	*Alyssum bertolonii*	*Microbacterium* O1, *Pseudomonas* B7, *Curtobacterium* C2, *Staphylococcus* A3, *Bacillus* B3, *Arthrobacter* F3B	EN	Barzanti et al. (2007)
Pb	*Brassica napus*	*Pseudomonas fluorescens* G10, *Microbacterium* sp. G16	EN	Sheng et al. (2008)
Zn and Cd	*Thlaspi caerulescens*	*Sphingomonas* sp., *Methylobacterium* sp.	EN	Lodewyckx et al. (2002)
Cd	*Lycopersicon esculentum*	*Methylobacterium oryzae* strain CBMB20 and *Burkholderia* sp.	EN	Madhaiyan et al. (2007)
Ni, Cu, Zn	*Ricinus communis*	*Pseudomonas* sp. M6, *Pseudomonas jessenii* M15	EN	Rajkumar and Freitas (2008)
Ni, Cr	*Brassica juncea*	*Enterobacter aerogenes*, *Rahnella aquatilis*	EN	Kumar et al. (2009)
Zn	*Orychophragmus violaceus*	*Flavobacterium* sp.	EN	He et al. (2010)

showed Zn, Cd, and Pb resistance and the ability to produce IAA, ACC deaminase, and siderophores. Recently, we observed that the inoculation of Italian ryegrass with rhizosphere bacteria, *Pseudomonas* sp. ITRH76 and BTRH79, showing hydrocarbon degradation and ACC deaminase activities, enhanced plant biomass production and hydrocarbon remediation from soil (Afzal et al., 2011, 2012; Yousaf et al., 2010b). van Aken et al. (2004a) isolated a hydrocarbon-degrading *Methylobacterium* strain from the rhizosphere of poplar trees. This strain improved plant growth and remediation of different hydrocarbons (van Aken et al., 2004b). Similarly, hydrocarbon-degrading *Pseudomonas* sp. strains were isolated from the rhizosphere of *Cyperus rotundus* L. (Jurelevicius et al., 2010).

Several PGPR have also been found to enhance phytoremediation of heavy metals from contaminated environment (Dimpka et al., 2008a,b;

Kuffner et al., 2008, 2010). These bacteria improve phytoremediation potential of plants by different mechanisms and, most certainly, depend on the production of plant growth-promoting hormones such as auxins, cytokinins, gibberellins, and ethylene (Forchetti et al., 2007; Perrig et al., 2007). These hormones can affect plant growth and development and consequently phytoremediation of inorganic pollutants (Aslantaş et al., 2007; Dimpka et al., 2009; Ryu et al., 2005).

Although endophytic bacteria exist in plant variably and transiently (van Overbeek and van Elsas, 2008), several recent studies have shown that they can enhance pollutant remediation potential of plants (Luo et al., 2011; Rajkumar et al., 2009; Weyens et al., 2009b; Yousaf et al., 2011). The potential of endophytes to show resistance to heavy metals and degrade organic pollutants probably originates from their exposure to various compounds in the plant/soil niche. Siciliano et al. (2001) observed that plants vegetated in xenobiotic-contaminated soil naturally recruited endophytes with the necessary pollutant-degrading genes. A methylotrophic endophytic bacterium that was isolated from poplar trees showed degradation capabilities of many organic pollutants, suggesting that the endophytic bacteria can be applied for the remediation of soil contaminated with organic pollutants (Van Aken et al., 2004a,b). Barac et al. (2004) reported that an endophytic bacterium, *P. putida*, enhanced yellow lupine plant tolerance to toluene and reduced the volatilization of toluene from the plant into the atmosphere. In another study, a *Pseudomonas* endophyte, capable to degrade herbicide, inoculated to pea plants reduced the accumulation of the herbicide into plant tissues (Germaine et al., 2006). Recently, Dashti et al. (2009) isolated *Pseudomonas* sp. diazotrophic endophytic bacterial strains showing more efficient hydrocarbon degradation. They suggested that these bacteria can be applied to enhance phytoremediation of hydrocarbon-contaminated soil without applying any nitrogen fertilizers, which makes the phytoremediation process more economical and environment friendly.

Endophytic bacteria isolated from different plants vegetated in contaminated soils exhibited different bacterial populations (Lodewyckx et al., 2002). In recent studies performed in our lab (Yousaf et al., 2010a,b), cultivation-dependent and -independent analysis showed that birdsfoot trefoil and Italian ryegrass vegetated in diesel-contaminated soil hosted distinct alkane-degrading bacterial populations. Specific genes encoding beneficial bacterial traits, such as the *ncc* responsible for Ni resistant and *alkB* and CYP153 genes responsible for alkane degradation, were determined to assess metal resistant and alkane degradation potential of endophytic

bacteria (Idris et al., 2004; Yousaf et al., 2010a). Furthermore, in a very recent metagenomic study of our lab revealed that a high population of endophytic bacteria, isolated from rice roots grown in an uncontaminated site, showing potential to degrade alkanes as well as aromatic hydrocarbons (Sessitsch et al., 2012). In another very recent study, heavy metal-resistant endophytic *Methylobacterium* strains were isolated from mangrove growing in a hydrocarbon-contaminated and uncontaminated soil (Dourado et al., 2012). Similarly, heavy metal-resistant endophytic bacteria were isolated from Cd-hyperaccumulator *Solanum nigrum* L. (Luo et al., 2011). These above-mentioned studies suggested that endophytic bacteria are the most promising resource and may be excellent candidates of bioinoculants for improving the phytoremediation efficiency. Upon exposure to inorganic contaminants such as heavy metals, plant-associated microbes can modify plant cell metabolism, so that plants are able to tolerate high metal concentrations (Welbaum et al., 2004).

5. APPLICATION POTENTIAL IN AGRICULTURE AND CONCLUDING REMARKS

As outlined above, numerous reports exist on the huge diversity of plant-associated bacteria and their various activities, which contribute to plant growth and health. Conventional agricultural practices have so far paid only little attention to beneficial plant–microbe interactions. Plant breeding generally focuses on the improvement of higher yields or development of stress- or disease-resistant plant lines but does not consider aspects supporting beneficial microorganisms. It is well known that different plant genotypes interact differently with microorganisms (Remans et al., 2007); however, this aspect has not yet resulted in breeding programs making use of a plant's capacity to interact more efficiently with microorganisms. One of the bottlenecks is the limited availability of high-throughput screening programs to select for efficient plant–microbe interactions. Remans et al. (2007) explored responsiveness to auxin for mapping of quantitative trait loci (QTL) in common bean, which could be also used as a screening method of QTLs being responsive to certain plant-beneficial bacteria. This might be particularly applicable for bacteria, which produce auxins and thereby cause plant growth-promoting effects. A better understanding of the mechanisms involved in and signals responsible for the interactions between plants and microorganisms might lead to the development of screening tools, which can be implemented in plant-breeding

programs resulting in plant lines making better use of naturally occurring plant growth-promoting microorganisms.

Alternatively, soil microbial communities may be managed to better support plant growth. Such a management might involve the application of certain agricultural practices to stimulate the soil microflora. Crop rotation, particularly with legumes, or the use of organic fertilizers is known to increase microbial diversity. Smart agricultural systems may, for example, make use of specific crop rotations stimulating specific types of bacteria frequently involved in plant growth promotion. As an example, for a long time, farmers mixed soil after legume cropping with soil in which nonlegumes were grown and thereby increased yields (Bashan, 1998). However, the most straightforward way to make use of microbial activities is the application of the microorganisms or their products directly in agriculture. Actually, inoculation of leguminous plants with rhizobia forming nodules and providing a great contribution to the nitrogen demand of the plant is a common practice. Already at the end of the nineteenth century, farmers "inoculated" legume seeds with soil containing rhizobia (Smith, 1992). Later on, the practice of legume inoculation developed to a common practice, and partly, for example, in Brazil, legumes such as soybean are not fertilized with nitrogen and only inoculated with selected rhizobial strains (Bashan, 1998).

Other plant-beneficial bacteria have been applied only rarely, although large-scale production in Russia in the 1930s and 1940s was reported (Bashan, 1998). However, inconsistent results were reported (see Bashan, 1998), and probably also due to the increasing availability of inorganic fertilizers, microbial inoculation was no longer used. Due to the limited availability of natural resources such as phosphorus and the increasing awareness to environmental problems, the application of microbial inoculants as biofertilizers, biostimulants, or biopesticides has attracted attention. Particularly, bacteria belonging to *Azotobacter* and *Azospirillum* have been applied to enhance nonlegume growth, and mainly *Bacillus* and *Pseudomonas* have been applied for biocontrol of plant diseases (Bashan, 1998; Bravo et al., 2011). Although advancements have been made to better understand the mechanisms underlying beneficial plant–microbe interactions and plant experiments performed under controlled conditions, for example, in the greenhouse, have shown great and highly promising effects, effects of field application remain inconsistent. This inconsistency may depend on various issues. One reason might be inappropriate strain selection. Beneficial bacteria are frequently selected based on their beneficial activities such as production of antimicrobial substances or hormones in the laboratory; however, it

is generally not known or investigated whether these effects are also expressed in the field. Secondary metabolite production or other processes are well known to be induced only under specific conditions or might be quorum sensing-dependent. This aspect needs to be considered when applying strains, which show activities, which are tightly controlled by environmental parameters. Furthermore, some PGPB have a broad host range colonizing different plant species; however, others target more specifically certain plant genotypes or may even interact well with some plant cultivars but not with others. Successful competition in the soil/plant environment is an additional aspect, which has to be considered. Soils are colonized by thousands of bacterial species, and therefore, any introduced microorganism has to be adapted to its new environment and compete with the resident microflora. Successful plant colonization is a prerequisite for conferring any plant-beneficial effects, but this aspect is generally not considered in microbial screening programs. Resistance to harsh environmental conditions such as drought, high temperature, salinity, or acidity may influence the competitive ability of an inoculant strain in such an environment.

Different inoculation methods have been developed. For a long time, peat-based inoculants, particularly for *Rhizobium*, have been applied; however, the quality has not been satisfactory also contributing to inconsistent effects in the field. Other approaches are liquid inoculation or seed coating. Generally, a formulation is required or recommended to help the microorganisms to perform better at the site of application (Xavier et al., 2004). Usually, a carrier material (such as peat) together with additives, which improve the stability of the formulation, protects the microorganisms from environmental influence during storage and transport. In addition, certain formulation components may support the coating of seed with microbial cells. Although several products exist on the market, improvement is still needed to warrant high microbial numbers and activity in the field (John et al., 2011). A promising approach, which has been addressed in the recent years, is bioencapsulation or microencapsulation of microbial cells leading to increased shelf-life and microbial activity (John et al., 2011).

Making better use of beneficial plant–microbe interactions has great potential to contribute to more sustainable agricultural practices and is in line with current policy priorities with regard to the protection of natural resources and food safety and security. However, we, on the one hand, need to better understand the mechanisms of interaction and communication or signaling between plants and microbes but also have to improve application and field technology. Finally, a more systemic approach investigating the

system involving soil, plant, microbes, and environment will be better able to solve problems related to application in agriculture rather than looking at individual components only.

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