Plant Soil (2016) 400:193–207
DOI 10.1007/s11104-015-2727-7

REGULAR ARTICLE

Ecological role of bacterial inoculants and their potential impact on soil microbial diversity

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Received: 16 March 2015 / Accepted: 29 October 2015 / Published online: 6 November 2015

Abstract
Background Microbial inoculants are an alternative method of increasing crop productivity that can reduce the use of chemical fertilizers, which is one of the more controversial agricultural practices that affect the environment. Beneficial bacteria, collectively known as plant growth-promoting bacteria (PGPB), enhance plant growth and protect plants from disease and abiotic stresses through a wide variety of mechanisms. Bacterial inoculation efficiency is associated with the beneficial features of the inoculated bacterium, as well as with the complex network of interactions occurring in the soil.
Scope Beneficial bacteria have previously been examined for interactions with different plant hosts, soil types, and agricultural practices, but there is limited information concerning the potential effects of the release of microorganisms on soil functionality. Despite the plant growth promotion characteristics, the survival, abundance, and persistence of inoculant in soil or plant roots are characteristics that could potentially lead to its invasiveness. Inoculants can also interfere with soil health and microbial and faunal community composition.
Conclusion This review presents an overview of plant-PGPB interactions and their impacts on microbial communities, hypothesizing about the potential of these interactions to promote positive disturbances in soil, mainly in poor environments. The inoculation of free-living bacteria seems to cause a short-term impact to agricultural soils, while rhizobia-based inoculants or bacterial inoculations performed under stress conditions are long-term processes. However, there is great variability amongst results concerning the effects of bacterial inoculation into different plant and soil conditions.

Keywords PGPB · Free-living bacteria · Rhizobia · Disturbance · Impact · Microbial diversity

Responsible Editor: Yoav Bashan.

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Introduction

In agroecosystems the biodiversity performs a variety of ecological services beyond the production of food, including nutrient recycling, disease control (suppression of undesirable organisms), detoxification of noxious chemicals, control of local microclimate, and regulation of local hydrological processes (Altieri 1999). The diversity of species and functional groups is also strongly associated with soil health and ecosystem multifunctionality (Wagg et al. 2014), and the ability of soil to respond to disturbances is influenced by the resistance and resilience of the soil microbial community (Griffiths and Philippot 2013). The interactions among microorganisms mediate nutrient and energy transfer to higher trophic levels (microbial loop) (Saleem and Moe 2014), making essential nutrients present in the biomass of one generation available to the next, and maintain the nutritional conditions required by other inhabitants of the biosphere (Madsen 2005).

Plants mediate multiple interactions between below and aboveground heterotrophic communities that have no direct physical contact (van Dam and Heil 2011). Microbes associated with plant roots play a substantial importance on the soil biodiversity, because they can be pathogenic to plants, as well as they can also influence the plant vigor by the deposition of nutrients, antibiotics and plant hormones around the roots (de Vrieze 2015). The plant-associated microbial community is shaped in response to nutritional status and developmental stages of different plant genotypes, as well by the presence and type of pathogens, predators, and beneficial organisms (Kreuzer et al. 2006; Pineda et al. 2010; Chaparro et al. 2013; Nakagawa et al. 2014). The soil health and fertility support soil food webs in which the bacteria-based energy channel, microfauna (nematodes and protozoa), and earthworms play an important role in nutrient cycling, whereas infertile soils tend to support food webs dominated by fungi and arthropods (notably mites, springtails, and millipedes) (reviewed by Wardle et al. 2004).

The plants release between 40 and 60 % of photosynthetically fixed carbon (C) to roots and associated microorganisms via sloughed-off root cells, tissues, mucilage and a variety of exuded organic compounds (reviewed by Keiluweit et al. 2015). The plant-associated microbial community, also referred to as the second plant genome or microbiome, is crucial to plant health and development (Mendes et al. 2011; Berendsen et al. 2012; Panke-Buisse et al. 2014). Several bacteria and fungi actively cooperate (syn. associative symbiosis) with the plants (Moënne-Loccoz et al. 2015). Beneficial microorganisms can be found inside the roots or be present on the rhizoplane (surface of roots) or in the rhizosphere (soil adhered and influenced by the roots). Concerning bacteria, this ability is mainly found in plant growth-promoting bacteria (PGPB).

Both plants and PGPB participate in numerous molecular signaling events that establish specific symbiotic, endophytic or associative relationships (see Fig. 1). Such relationships vary according to plant genotypes and bacterial strains and with respect to the degree of proximity between the roots and surrounding soil (Fig. 1a), as well as with the abilities of bacteria to improve plant growth through mechanisms in favor to nutrient deposition, production of plant-hormones, stress alleviation, and defense against pathogens (Fig. 1b). PGPB inoculation is an important strategy for the sustainability of agriculture, as the successfully utilization of this practice enables to reduce or even eliminate the use of pesticides and/or fertilizers without yield-culture losses. Also, microbial inoculants may offer a cheaper alternative than fertilizer usage for smallholder farmers. In this way, many bacteria classified as PGPB have been extensively isolated from host plants to test their abilities related to the plant growth (biofertilizers or biostimulants) and defense against pathogens (biocontrol agents or biopesticides) aiming prospection of microbial inoculants (Caballero-Mellado et al. 2007; Ambrosini et al. 2012; Souza et al. 2013; Calvo et al. 2014). Microbial inoculants mainly include free-living bacteria, but also are made from fungi and arbuscular mycorrhizal fungi (AMF) (Calvo et al. 2014).

Plant biostimulants are diverse substances and microorganisms used to enhance plant growth, as well as microbial inoculants, humic acids, fulvic acids, protein hydrolysates and amino acids, and seaweed extracts (Calvo et al. 2014). A “microbial inoculant” (referred as inoculants in this review) can be defined as the final product of one formulation containing a carrier and a bacterial agent or a consortium of microorganisms. “Carrier” refers to the abiotic substrate (solid, liquid, or gel) that is used in the “formulation”. The “formulation” refers to the laboratory or industrial process of unifying the carrier with the bacterial strain in liquid, organic, inorganic, polymeric, or encapsulated formulations (Bashan et al. 2014). Technical aspects are also essential for the success of the inoculant, as the soil or seed application and its shelf life that must last more than one season (Bashan et al. 2014). The bacterial inoculation technologies are important for the higher efficacy of this practice. To fulfill its purpose bacteria need survive in the soil and this can be eased through of carrier type and formulation of a “well protected” inoculant (Bashan et al. 2014; Jayaraman et al. 2014).

The survival in soil and the colonization of rhizosphere, rhizoplane or plant roots by bacteria are processes involved in an intricate ecological context (Revellin et al. 2001; Ciccillo et al. 2002; Ramachandran et al. 2011; Chamam et al. 2013; Chowdhury et al. 2013). Plant-inoculant interactions are specific to plant and bacteria genotypes, varying with the geochemical characteristics of different types of soil and localities, and with the biological interactions among the soil biota,

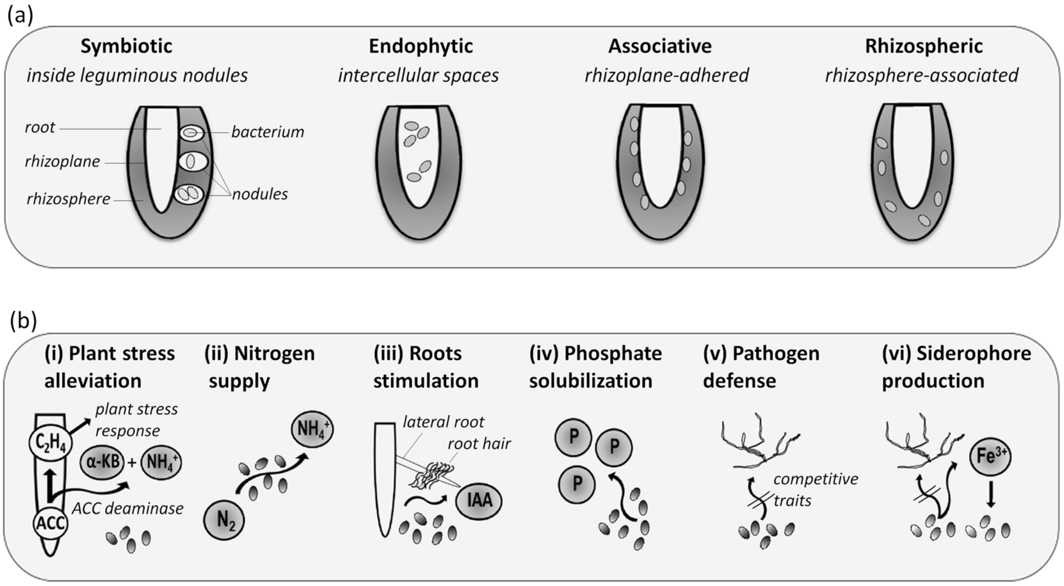

Fig. 1 **a** The different types of association between plant roots and beneficial soil bacteria; **b** Following the colonization or association with plant roots and/or the rhizosphere, bacteria can promote plant growth through (*i*) the alleviation of plant stress through the reduction of ethylene levels; (*ii*) the increase of nitrogenous resources through N_2 fixation; (*iii*) the stimulation of root development by phyto-hormone production; (*iv*) P solubilization around roots; (*v*) the defense against pathogens via the presence of competitive traits such as antibiotic and siderophores production; (*vi*) Fe solubilization around roots via siderophores production. C_2H_4 (ethylene), ACC (ethylene precursor in plants), α-KB (α-ketobutyrate), NH_4^+ (ammonia), IAA (indole-3-acetic acid)

especially those surrounding roots. The plant roots orchestrate many of biological interactions in the soil because the rhizosphere is a rich environment for microbial and faunal communities (Badri and Vivanco 2009; Wagg et al. 2014). Bacteria need to be able to compete and colonize plant roots efficiently. In gram-negative bacteria these activities are rather associated to the production and perception of acylated homoserine lactones (AHLs), which are synthesized by LuxI homologs and participate of intraspecific communication among individuals (Weiland-Bräuer et al. 2015).

Successful roots colonizers respond and interact with different host plants. However, these relationships are also considerably dependent of the biotic and abiotic soil proprieties (Lange et al. 2014). Microorganisms associated with plants are mainly bacteria, fungi, and protozoa to a lesser extent (Moënne-Loccoz et al. 2015). Protozoa are the main microbial predators, which regulate bacterial populations in various ecosystems (Moënne-Loccoz et al. 2015). Protozoa and nematodes are a crucial link between microflora and larger fauna, regulating the populations of bacteria and fungi and playing a major role in the mineralization of nutrients (Fortuna 2012). In this review we will present and discuss the most common disturbances in agricultural soils and the potential of plant-inoculant interactions to impact rhizosphere microbial communities.

Disturbances on soil microbial communities

Many anthropogenic practices have resulted in intensive soil degradation and, in the case of agricultural soils, in the progressive loss of their fertility (Miransari 2011). The management techniques cause constant disturbances that directly or indirectly affect microbial communities in agricultural ecosystems (Bissett et al. 2011; Derpsch et al. 2014; Ollivier et al. 2011; Paula et al. 2014). Among the most widely used management techniques in the agriculture is the use of pesticides and fertilizers, affecting the function of microbial communities by reaching natural and managed ecosystems with high concentrations of environmental pollutants (Edwards 2002; Ollivier et al. 2011). The microbial products of metabolic oxidation or reduction of C and nitrogen (N) compounds in soils include greenhouse gases, as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) (Fortuna 2012).

Fungicides and fumigants are generally potent nitrification inhibitors, and tend to have a greater initial and longer lasting effect on nitrification than either herbicides or insecticides (Wainwright 1999). The N fertilization stimulates specific functional microbial groups, such as ammonia-oxidizing microorganisms and denitrifying bacteria (Enwall et al. 2005; Hallin et al. 2009). The use of nitrogenous industrials fertilizers is among the principal anthropogenic disturbance on the multiple biogeochemical cycles, contributing to nitrate (NO_3^-) leaching, ammonia (NH_3) volatilization, and N_2O emissions (Robertson and Vitousek 2009; Shcherbak et al. 2014). Moreover, in the relationships among phosphorus (P) concentrations and mycorrhiza, an increase of soil P content generally decreases the populations of this fungus (Smith et al. 2011), although the response to the P content can also be variable according to plant species (Gosling et al. 2013).

Some authors emphasize as fundamental characteristics of a disturbance its discrete nature in time and space (Pickett and White 1985), its direct or indirect nature of single or multiple factors acting locally or regionally (Wan et al. 2014), and its temporary and localized effect (Dornelas 2010). However, the disturbances can also be classified according to their duration as either pulses (discrete and short-term events) or presses (continuous and long-term events) (Shade et al. 2012). Dornelas (2010) focuses on disturbances not as causes, but as ecological effects of an event with important aspects on biodiversity. Thus, the disturbance can have a positive connotation if it is seen as something that can also contribute to the release of funds in the ecosystem due to changes in survival or reproductive rates, and/or the increase in the number of individuals that the community can accommodate (Holt 2008; Dornelas 2010).

According to Wan et al. (2014), external or internal disturbances may result in both positive and negative effects (referred to as “two-sided effects”) on the structure and functions of any complex ecosystems, because disturbances enter the ecosystem as information, material or energy flow, which subsequently produces profitable or unprofitable effects. In this way, a number of factors must be taken into account when characterizing a disturbance, including the spatial and temporal scale of the disturbance, the number of occurrences per unit time, the magnitude of the disturbance, the proportion of the ecosystem affected, and the regularity of the disturbance (Shade et al. 2012). Independently of ecological effects or causes, a disturbance arise in response to external factors that trigger changes in the structural and functional components of different aspects of the system, including at the levels of the individual, population, community, ecosystem, and landscape (Pickett et al. 1989; Berga et al. 2012).

The functional resiliency of soil is related to the effect of disturbance on the physicochemical structure of the microbial community in terms of composition and physiology (Griffiths et al. 2008; Berga et al. 2012). Resistance (i.e., the ability to return to a state of equilibrium following disturbance or to resist a change) and resilience (i.e., the rate of return to a state of equilibrium following disturbance) are related to the stability of the microbial community, a functional property based on changes to community dynamics that arise in response to disturbance (Robinson et al. 2010; see Fig. 2). Land use alters the resistance and resilience of soil food webs to drought, for example, and the extensively managed grassland promotes more resistant and adaptable fungal-based soil food webs (de Vries et al. 2012).

Litchman (2010) defined invasive microbes as microorganisms (viruses, archaea, bacteria, protists, and fungi) that proliferate in a new range and impact local communities or ecosystems. An alien species is defined by Saccà (2015) as the one that colonize an area beyond its natural range, where it reproduces and establishes a population. It can also be called non-indigenous or non-native species. According to Vilà et al. (2009), the DAISIE project (Delivering Alien Invasive Species Inventories for Europe) (www.europe-aliens.org) follows the classification of species based on the invasion status proposed by Occhipinti-Ambrogi and Galil (2004) and Pyšek et al. (2004), which is: alien species are those introduced by humans that colonize outside their natural range and dispersal potential, whereas invasive species are those alien species that spread over a large area and attain high local abundances.

As well placed by Litchman (2010), the notion of invasive microbial species is complicated due to the difficulties associated with establishing the ‘non-nativeness’ of microbes and with applying the very concept of ‘species’ in many microbial taxa (Staley 2006). Here, we agree with Litchman (2010) concerning the definition of invasive microbes, since microbes are very susceptible at the surrounding environment and their responses are extremely variable according different strains of a same species. Microbe may belong to different functional groups that contribute to changes in the ecosystem where they were introduced. Regardless of species identification, the genomic and phenotypic plasticity is common

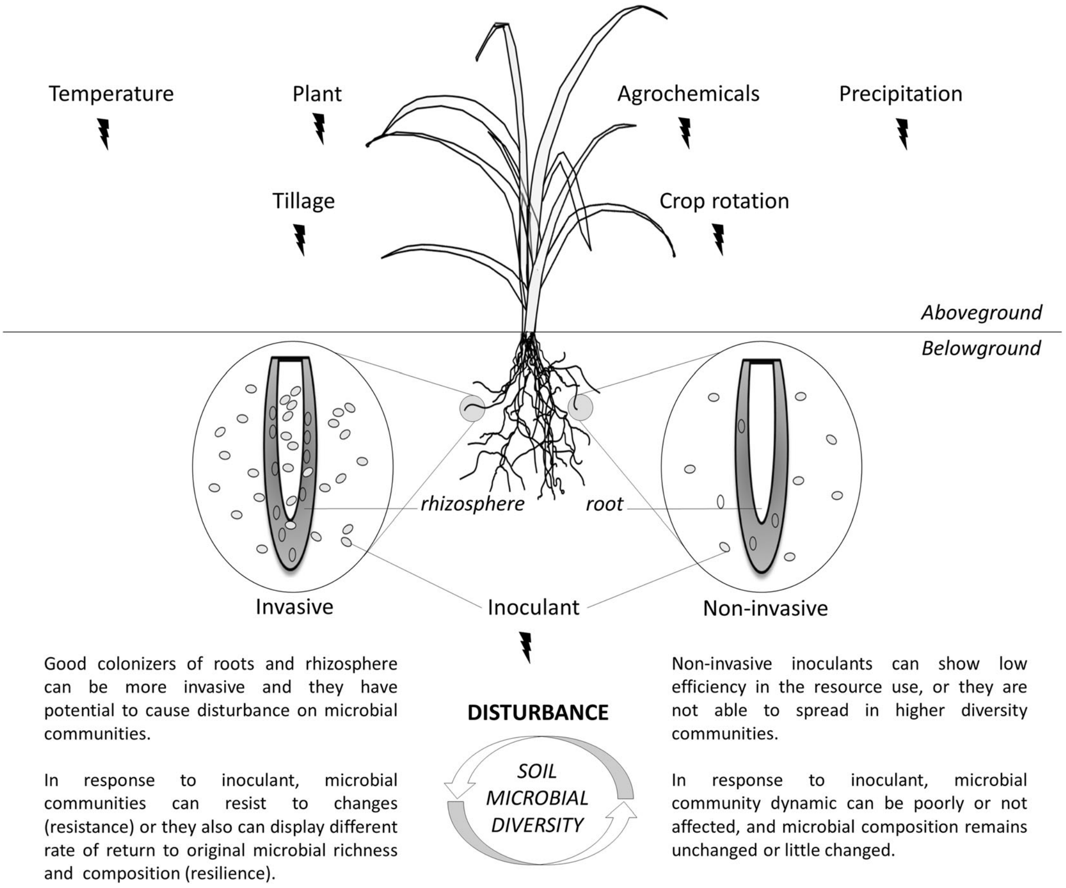

Fig. 2 In agricultural fields, several factors (as depicted by rays) affect soil health and, consequently, microbial community and ecosystem function. In a broad context, the success of microbial inoculation is highly dependent upon specific interactions between plants and bacteria and is mediated through exudates and bacterial competitive traits, such as high growth rates and the efficiency of resource use. Inoculants are invasive microbes and have the potential to significantly alter community composition through the efficient colonization of roots (*left circle*), particularly in contrast to microbes that are inefficient at root colonization (*right circle*)

among bacteria and many of them have genic products based on a content received of other individual(s) by genetic transference, which confuses the definition about bacterial species and their respective functional groups (Sullivan and Ronson 1998; Tuller et al. 2011).

The more diverse biological communities are often they are less prone to (micro) organisms' invaders than simpler ones (Litchman 2010). Invasive microbes tend to have superior competitive abilities that facilitate their spread in lower diversity communities (van Elsas et al. 2012). An invasive microbe has general similarities with natives species, since both have needs to adaptation to the same environment, but also it shows an enhanced performance when uses more efficiently the resources or possesses traits that enable the access to resources unavailable to other species (Litchman 2010; van Elsas et al. 2012). Experiments using different genotypes of *Pseudomonas fluorescens*, which differ in their ability to use resources, have showed that functional dissimilarity have greater significance than taxonomic richness to the success of invader (Eisenhauer et al. 2013). The initial community evenness favors functionality under selective stress (Wittebolle et al. 2009), and multiple predators result in higher bacterial species evenness across bacterial richness (Saleem et al. 2012).

The biodiversity of the resident community reduces invader success at high niche dimensionality via complementary niche preemption; on the contrary, at low niche dimensionality, where complementary interactions are restricted, invader success is driven by identity effects, that is, by pairwise interactions between invaders and resident taxa (Eisenhauer et al. 2013). According to Clark (2013), many experimental studies agree that diversity can contribute to invasion resistance by two main mechanisms: identity effects and species complementarity: (i) identity effects are the chance of inclusion of species that are particularly proficient at resisting invaders, such as strong competitors or those with unique invader repelling traits; (ii) species complementarity refers to differences in resource use amongst species, such that the most diverse communities leave fewer resources available to potential invaders.

Plant-soil feedback (PSF) is a term used to describe an interactive loop involving plants and the biological, chemical, and physical properties of the soil (Ehrenfeld et al. 2005). Lou et al. (2014) propose that microorganisms are most likely to play a role in PSF loop when they possess an affinity for a particular plant and the capacity to strongly affect the growth of plants. However, the functional redundancy of bacteria can relieve the effects of changes to diversity, as the microorganisms that are unaffected by the presence of invasive microbes may perform similar functions in soil. For example, microbes that work to decompose various elements of the soil are likely not greatly impacted by the presence of introduced bacteria, as their functional specificity is limited and redundant (van der Putten et al. 2007).

Inoculants and their potential disturbances on soil communities

Inoculants are selected according to the beneficial characteristics that they can impact on plant growth and fitness, although the potential effects on the microbial community are not frequently assessed. To efficiently achieve the beneficial features of this practice, a high concentration of inoculant must be introduced into the environment (Lupwayi et al. 2000), that can induce changes to the local biological structure (Litchman 2010). As it is expected that plants and inoculants actively cooperate in the root zone, these interactions may establish relationships to allow a better adaptation to the environment and thereby alter in some way the surroundings (Fig. 2). In this sense, if bacterial diversity is predominantly modulated by the alterations of plant exudates in the rhizosphere (Baudoin et al. 2009; Berendsen et al. 2012), the ability to cooperatively and specifically interact with plant roots expectedly gives to the inoculant an enhanced performance in soils. However, this is not a simple trajectory.

The establishment of beneficial associations requires mutual recognition and substantial coordination of plant and microbial responses (Zamioudis and Pieterse 2012), and these reciprocal interactions correspond to a feedback loop (Lemanceau et al. 2015). In fact, bacteria are able to modulate their genetic expression according to compounds secreted by plant roots. Chaparro et al. (2013) observed a strongly correlation between microbial functional genes involved in the metabolism of carbohydrates, amino acids and secondary metabolites with the corresponding compounds released by *Arabidopsis* roots at particular stages of plant development. Likewise, plants seems selectively attract beneficial bacteria through the secretion of specific signaling molecules, such as malic-acid secreted by *A. thaliana* after foliar infection with *P. syringae* pv *tomato* (Rudrappa et al. 2008). This compound was a signal to recruit *Bacillus subtilis* FB17, which is responsive to it (Rudrappa et al. 2008). Elevated levels of malic-acid promoted binding and biofilm formation of FB17 on *Arabidopsis* roots only in the presence of pathogens, since plant roots do not secrete malic-acid during their regular growth (Rudrappa et al. 2008; Beauregard et al. 2013).

Biotic and abiotic elicitors stimulate defense mechanisms in plant cells and greatly increase the diversity and amount of exudates (Cai et al. 2012). A major part of plant response to bacterial interaction is the recognition of microbial-associated molecular patterns (MAMP) such as chitin, peptidoglycan, lipopolysaccharides or flagellum structures, and the initiation of efficient plant defense reactions (Hartmann et al. 2014). The perception of secondary metabolites (Garcia-Gutiérrez et al. 2013) and volatile compounds (Yi et al. 2010), for example, can also be related to bacteria-induced plant responses towards improved resistance to pathogens. Beneficial bacteria evolved to reduce stimulation of the host's immune system, as rhizobia and the suppression of salicylic acid–dependent defense responses by utilizing the Nod signaling pathway, and phase variation by PGPR (Zamioudis and Pieterse 2012). Through phase variation the bacteria can modify surface molecules by site-specific recombination and epigenetic regulations mediated by DNA methylation, for example, and thus generate bacterial subpopulations within a clonal population in order to increase their overall fitness in the environment (van der Woude 2011).

The N-acyl-homoserine lactones (AHLs) play a role in the biocontrol activity of bacteria through the induction of systemic resistance (ISR) in plants (De Vleesschauwer and Höfte 2009). ISR is the result of multiple response cascades employed by the plant host and it is highly modulated by plant-hormones, such as salicylic acid, which can be increased in leaves when AHL-producing bacteria colonized the rhizosphere (Schuhegger et al. 2006). Schuhegger et al. (2006) observed that the absence of these molecules makes an AHL-negative mutant bacterium less effective in reducing both plant symptoms and pathogen growth as compared to the wild type. At changing the plant responses to the environment, ISR plays an important role in mediating belowground and aboveground interactions and does not only affect pathogens, as may inhibit the growth of beneficial organisms (van Dam and Heil 2011).

The "quorum sensing" (QS), or the more broadly defined concept of "efficiency sensing" (Hense et al. 2007), is mediated by AHLs among Gram-negative bacteria, while cyclic peptides as QS-signals were only found in Gram-positive bacteria (Hartmann et al. 2014). Plants perceive, react, and transport AHLs, or plants can even produce AHL-mimic substances or to develop other activities influencing QS of plant associated bacteria (Gao et al. 2003; Bauer and Mathesius 2004; Hartmann et al. 2014). Auto-inducers of the AHL type vary in structure and plant reactions. Schenk et al. (2012) observed a negative correlation between the length of AHLs' lipid chains and the growth promotion in *A. thaliana*, and the authors speculate about a positive correlation between the reinforcement of defense mechanisms and the length of the lipid moieties. Several studies have evaluated the direct AHL impact on different plants, as reviewed by Hartmann et al. (2014).

Among bacterial traits involved in the ability of colonize the rhizosphere (i.e., rhizosphere competence), QS highly influences the performance and interactions within the microbial communities. Many toxins and antibiotics are also regulated by QS and stress responses, which enable bacteria to infer the presence of ecological competition (Hibbing et al. 2010; Cornforth and Foster 2013). The biological interactions around roots meet important part on the efficiency of an inoculant, such as microbial competition and predation by faunal communities, which are crucial relationships to bacterial life in the environments. Bacterial predation by protists depends on a number of interacting factors, such as bacterial phenotypic plasticity (Hahn et al. 1999; Queck et al. 2006), cell size (Šimek and Chrzanowski 1992), biofilm formation (Huws et al. 2005; Weitere et al. 2005), and microevolution (Friman et al. 2014).

Protozoan predators play a crucial role in structuring complex communities, since bacterial grazers improve plant growth via nitrogen mineralization by microbial loop (e.g., Bonkowski 2004). Schmitz et al. (2010) suggest that protists predators can impact bacterial abundance and activity by recycling of nutrients that are used by the prey (consumptive effects) or improving habitat conditions for better prey foraging (non-consumptive effects). Soil microbes are important regulators of plant productivity, especially in nutrient poor ecosystems where plant symbionts are responsible for the acquisition of limiting nutrients (van der Heijden et al. 2008; Fließbach et al. 2009). A same bacterium may be able to survive and colonize poor soil while stimulating microbial diversity (Bashan et al. 2010), or it may have little chance at survival and colonization but not majorly affect the microorganism communities already present in rich soils (Lerner et al. 2006; Felici et al. 2008). This phenomenon seems to occur because plants are able to select the root's microbiota according to their needs, favoring the interaction with growth hormone producers under rich nutrient conditions, while they favor nutrient solubilizers under poor nutrient conditions (Costa et al. 2014).

Moreover, the effects of microbial inoculation can be direct or indirect, not only through the presence of an inoculant around the root but also through the promotion of plant growth. If an inoculant is able to improve the distribution of roots into soil there will be more root colonization sites for microbiota because higher soil volume was explored by plant roots (Baudoin et al. 2009; Trabelsi et al. 2011). To promote plant-growth, inoculants must either establish themselves in the soil or become associated with the host plant; however, the permanence of these inoculants in the soil has potential to cause disturbances on the native microbial populations (Fig. 2). As suggested by Bashan et al. (2010), the microbial stimulation causes effects on plant growth and these effects remain in soil, even that the relative dominance of the inoculated population decreased over time. If the effects of microbial inoculation are positive to other microbes and subsequent trophic levels beyond plants, the picture of this highly productive system may help us to better understand the agricultural soil dynamics.

PGPB inoculation and its impact on the taxonomic diversity and functionality of soil microorganisms

Strains of the genus *Azospirillum*, which are free-living, N_2-fixing, Gram-negative Alpha-proteobacteria, are commonly found in the soil and are commercially used as inoculants to agricultural plants; examples include maize (Revellin et al. 2001; Reis et al. 2011), rice, and wheat (Naiman et al. 2009; Hungria et al. 2010). *A. brasilense* is known to promote plant growth and colonize the rhizosphere. While the survivability of *A. brasilense* is independent of soil aridity, it is directly and rapidly affected by soil disturbances caused by water percolation or plant removal (Bashan et al. 1995). For example, to achieve growth promotion of maize cultured in Brazilian Cerrado by *A. brasilense* a higher dose of bacterial inoculation in clay soils was needed, as opposed to sand soils, where there were no differences between the applications of diluted or concentrated doses of bacterial inoculant (Ferreira et al. 2013). Additionally, the production of PHA (polybetahydroxyalkanoates) has been associated with the increased survivability of *A. brasilense* following exposure to various stressors and is thus critically important to improving the shelf life, efficiency, and reliability of commercial inoculants (Kadouri et al. 2005; Fibach-Paldi et al. 2012).

Some researchers have concluded that rhizosphere-related microbial communities are highly buffered against the introduction of foreign bacteria (Björklöf et al. 2003). Minor changes to the diversity of the indigenous bacterial community that is present within rhizospheric soil were observed following bacterial inoculation with *Azospirillum* spp. into soil containing different plant cultures, such as maize (Herschkovitz et al. 2005a, b; Lerner et al. 2006; Baudoin et al. 2009), rice (de Salamone et al. 2010), tomato (Felici et al. 2008), and wheat (Naiman et al. 2009). Non-prominent effects on the structure of the rhizosphere's microbial population have also been observed in the context of free-living bacteria belonging to genera *Bacillus*, *Brevibacillus*, and *Pseudomonas* (Björklöf et al. 2003; Felici et al. 2008; Fließbach et al. 2009; Piromyou et al. 2011, 2013; Chowdhury et al. 2013).

However, the bacterial inoculation of *A. brasilense* Sp6 to support quailbush (*Atriplex lentiformis*) growth in acidic metalliferous mine tailings resulted in changes to the DGGE profile of the rhizospheric community at 15, 30, and 60 days following bacterial inoculation, and the community structure changed even more significantly as plants established themselves and grew (Bashan et al. 2010). The inoculum increased plant biomass production and was able to colonize the root surface and persist there throughout the 60-day experiment (Bashan et al. 2010). Moreover, the stimulation of adventitious root growth, which allow an increased in nutrient uptake and alleviation of the effects of salt stress on different plant species, has been associated with different *Azospirillum* strains that are able to establish and maintain colonies under salt stress conditions (Barassi et al. 2007; Bacilio et al. 2004; Nabti et al. 2010; Fasciglione et al. 2012; Zarea et al. 2012).

When N_2-fixation is a trait important to the establishment of positive interactions between plants and symbiotic bacteria, as is the case among leguminous and rhizobia, the interference of the inoculant on microbial diversity is of greater impact than that produced by free-living bacteria (Zhang et al. 2010; Trabelsi et al. 2011; Bakhoum et al. 2012). Due to the degree of symbiotic specialization and the variability of plant and microbial symbiotic responses (van der Putten et al. 2007), the diversity of host communities is likely a key determinant of the invasion success of symbiotic microbes (Litchman 2010). Bulk soil analyses performed during the flowering and grain harvesting of the common bean following bacterial inoculation with *S. meliloti* 4H41 and *Rhizobium gallicum* 8a3 demonstrated increased richness of the total bacterial community, particularly the Rhizobiaceae family. Additionally, populations of Alpha- and Gamma-proteobacteria, together with Firmicutes and Actinobacteria, were enhanced by bacterial inoculation (Trabelsi et al. 2011). On the other hand, rhizospheric soil analyses of faba beans (*Vicia faba* L.) inoculated with *R. leguminosarum* bv. *viciae* CCBAU01253 showed a decrease in bacterial diversity that was negatively correlated with microbial biomass (Zhang et al. 2010).

Interactions between species play a critical role in biological invasiveness; for example, mutualism between exotic plants and microbes can facilitate the spread of each as they co-invade novel locales (Porter et al. 2011). Some researchers have indicated that exotic rhizobial symbionts might have been co-introduced with host leguminous into new areas (Stępkowski et al. 2005; Porter et al. 2011; Crisóstomo et al. 2013; Ndlovu et al. 2013; Horn et al. 2014) and that some rhizobial plasmids can impair symbiotic N_2-fixation, enhancing host invasion (Crook et al. 2012). A genetically modified strain of *Sinorhizobium meliloti* Rm42 was inoculated to promote the growth of alfalfa seeds and persisted in the soil for at least 6 years despite the absence of a host plant (Morrissey et al. 2002). Additionally, the horizontal transfer and microevolution of a genetic modified plasmid (pPR602 harboring the *thyA* gene) were observed between *S. meliloti* strains (Morrissey et al. 2002). Sullivan and Ronson (1998) also reported that the 500 kb chromosomal symbiotic element of *Mesorhizobium loti* strain ICMP3153 is transmissible in laboratory matings to at least three genomic species of nonsymbiotic mesorhizobia. The authors postulated that this region may represent a class of genetic element that contributes to microbial evolution by acquisition and, as it converts the recipient strain into a symbiotic one, it was denominated a symbiosis island.

Co-inoculation is an important example of the importance of ecological interactions to maintain sustainability, because organisms can cooperate among themselves and contribute to better plant performance and soil health. Co-inoculation with arbuscular mycorrhizal fungi and rhizobia enhances productivity of several agronomic plants as lentil (Xavier and Germida 2002), pea (Xavier and Germida 2003), and soybean (Wang et al. 2011). The mineralization of microbial biomass and dead organic matter by protists also enhances the nitrogen supply to the plants via arbuscular mycorrhizal fungi (Koller et al. 2013). Changes on community composition and spatial distribution of bacteria in the rhizosphere of rice were also attributed to the presence of a bacterial grazer (*Acanthamoeba castellanii*) and to the increase of bacterial activity (Kreuzer et al. 2006). The authors concluded that the interactions over three trophic levels (i.e., between plants, bacteria and protozoa) modified significantly root architecture and nutrient uptake by plants.

Furthermore, the analyses of key bacterial genes, such as those related to the N-cycle, can also facilitate understanding regarding how specific microbial functional groups are impacted, such as denitrifies, nitrifies, and N_2-fixing groups. For example, following the bacterial inoculation of faba beans in soil possessing resident rhizobia, N_2-fixation was only improved at the highest rate of inoculation (Denton et al. 2013). Sun et al. (2009) evaluated Alfalfa-Siberian wild rye intercropping, the predominant cropping system used to produce forage in China, and the effects that rhizobial inoculation produced on the intercropping with respect to T-RFLP patterns in the 16S rRNA and the ammonia monooxygenase subunit A (*amoA*) genes. Both treatments showed a tendency to increase the diversity of *amoA*; however, following the intercropping-rhizobial inoculation treatment, the relative abundance of *Nitrosomonas* increased while the relative abundance of *Nitrosospira* decreased. In an experiment that examined the bacterial inoculation effects in alfalfa using two different indigenous strains of *S. meliloti* (OS6 and S26), the effectiveness of inoculation with OS6 was found to be associated with the abundance of *nifH* genes (related to N_2-fixation) in the late flowering phase. A higher number of *nirS* (related to nitrite reduction) copies were also observed in the late flowering phase following treatment with the OS6 strain (Babić et al. 2008).

It was stated by Zak et al. (1994) that "we understand little about the degree to which genetic diversity is translated into taxonomic diversity, and even less about the manner in which genetic and taxonomic diversity affects functional diversity or ecosystem properties". Interestingly, even after 20 years of research, the nature by which taxonomic diversity affects functional-group diversity in soil systems is still not well understood, although it is accepted that higher-diversity ecosystems are frequently associated with soil fertility (Litchman 2010; Ding et al. 2013). On a global scale, the effects of continuous agricultural practices, such as fertilization and soil management, influence important biogeochemical cycles, such as C and N (Robertson and Vitousek 2009). Bacterial inoculation also has the potential to cause disturbances to the functional activity of soil microbial communities, and greater understanding into the effects produced by inoculation is still required. In this way, the constant improvement of next-generation DNA and RNA sequencing technologies represents a significant step forward to obtaining detailed analysis of the expression profiles of more complex communities (Warneckea and Hess 2009; Li et al. 2012). Specific genes that regulate biogeochemical cycles or important enzymatic events can also alter soil community features and represent another target that could be analyzed using quantitative Real-Time PCR (qRT-PCR) (Mao et al. 2011), and microarray (Bai et al. 2013) and metagenomics techniques (Fierer et al. 2012).

Conclusions

The effect of PGPB inoculation on the efficiency of plant growth and the impact on microbial communities is related to the inoculant establishment in the rhizosphere and its survival in soil. The long-term abundance of inoculants may improve its invasive ability. *Azospirillum* spp. seems to be a "good inoculant" but a "bad invader" of agricultural soils, as this species promotes plant growth without persisting in the environment and produces little to no effects on soil resistance and resilience. On the other hand, rhizobia have been shown to more greatly affect the microbial community and can be co-introduced with plant-mutualists into novel environments. However, the real impact of bacterial inoculation on agricultural systems remains unknown and varies considerably according to geographical location and the species of plants and microorganisms used. Moreover, it is possible that the agricultural regime of successive bacterial inoculation may result in changes related to the periodicity of the inoculation event.

This approach becomes difficult to quantify in light of the breadth of variables that can influence soil responsiveness to invasive species. Researchers have largely assessed the diversity of species by employing molecular fingerprinting techniques. However, the taxonomic diversity associated with variations in functional activity could provide relevant information concerning the relationship between the impact of inoculants on resident microbial communities and the turnover of nutrients and soil functioning. The availability of molecular methods that can evaluate changes in microbial communities in response to environmental changes has led to notable insights linking diversity and functional dynamics in several ecosystems (Bao et al. 2013; Erlacher et al. 2014; Schreiter et al. 2014).

According to Fierer et al. (2012), although our understanding of the phylogenetic and taxonomic biogeography of soil microbial communities continues to expand, there has been limited progress in understanding how the functional capabilities of soil microbial communities change across biomes. In this way, the use of mRNA analyses seems like a promising method to obtain specific or whole metabolic activity profiles. As there have been few studies employing expression analyses of the microbial community, the use of newer technologies and long-term experiments should provide more robust results concerning how the degree of soil functioning is affected by bacterial inoculation. Long-term experiments to evaluate the functional diversity of communities in successive crop planting may provide more information into the impact of bacterial inoculation on microbial species and soil functionality.

There is still insufficient knowledge allowing us to determine the effect of the introduction of bacterial species in the environment and the resulting impact of this practice on the soil microbiota. We hypothesize that the resulting interactions of PGPB inoculation can be positive not only to plant growth, but also to soil fertility via short- or long-term processes. This response can be reinforced through successive PGPB inoculations. We might think more about the inoculants as biotechnological tools to recuperate degraded agricultural soils, or only to keep them fertile, or yet to estimate a design of microbial communities for biotechnological applications (Pagaling et al. 2014). Once knowing more about the resulting ecological alterations of PGPB inoculation with microorganisms on the soil, new strategies could help us to maximize this practice, such as the increase of positive effects in local soils, especially in poor environments.

Acknowledgments We thank to "Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul" and "Conselho Nacional de Desenvolvimento Científico e Tecnológico - Instituto Nacional de Ciência e Tecnologia de Fixação Biológica do Nitrogênio", Brazil.

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