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REVIEW

Microbial interactions in the rhizosphere: beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process. A review

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Abstract Plant growth-promoting rhizobacteria (PGPR) are soil bacteria that are able to colonize rhizosphere and to enhance plant growth by means of a wide variety of mechanisms like organic matter mineralization, biological control against soil-borne pathogens, biological nitrogen fixation, and root growth promotion. A very interesting feature of PGPR is their ability of enhancing nutrient bioavailability. Several bacterial species have been characterized as P-solubilizing microorganisms while other species have been shown to increase the solubility of micronutrients, like those that produce siderophores for Fe chelation. The enhanced amount of soluble macro- and micronutrients in the close proximity of the soil-root interface has indeed a positive effect on plant nutrition. Furthermore, several pieces of evidence highlight that the inoculation of plants with PGPR can have considerable effects on plant at both physiological and molecular levels (e.g., induction of rhizosphere acidification, up- and downregulation of genes involved in ion uptake, and translocation), suggesting the possibility that soil biota could stimulate plants being more efficient in retrieving nutrients from soil and coping with abiotic stresses. However, the molecular mechanisms underlying these phenomena, the signals involved as well as the potential applications in a sustainable agriculture approach, and the biotechnological aspects for possible rhizosphere engineering are still matters of discussion.

Keywords Nutrient availability · Soil bacteria · Nitrogen · Phosphorus · Iron · PGPR

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Introduction

The maintenance of a high agricultural productivity, combined with an increasing global demand for food for a growing population and the depletion of natural resources, has become a major challenge in both developed and developing countries (Matson et al. 1997; Cassman 1999; Tilman et al. 2002). Up to now, traditional nutrient management for preserving high crop productivity has been mainly based on external fertilizer inputs (Zhang et al. 2010); however, in the last decades, crop yield has not increased proportionally with increasing fertilizer inputs, leading to low nutrient use efficiency and enhanced environmental risks (Zhang et al. 2010). Therefore, the overcoming of this challenge implies the improvement of crop nutrient use efficiency by exploiting the intrinsic biological potential of rhizosphere processes. One of the main driving forces of the rhizosphere processes is represented by rhizodepositions, which include low molecular weight (LMW: organic acids, amino acids, sugars, phenolic acids, flavonoids, etc.) and high molecular weight (HMW: carbohydrates, enzymes, etc.) organic compounds released by roots. The composition of root exudates is highly variable depending on plant species and/or environmental conditions (e.g., type of substrate, soil chemical characteristics, temperature, CO_2 concentration, light conditions) (Mimmo et al. 2011). LMW exudates could represent an easy accessible C source for

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microorganisms within the rhizosphere where the concentration of these compounds is usually higher than in the bulk soil (Hinsinger et al. 2009). As a consequence, microbes are unevenly distributed in soil, being the majority of them located within a radius of 50 μm from the root with a strong increase in their concentration within a radius of 10 μm (Pinton et al. 2001). This phenomenon is most likely ascribable to the higher growth of bacteria in the root proximity and chemoattractant function of LMW root exudates, that makes chemotaxis and motility fundamental features for root colonization (Yao and Allen 2006; Miller et al. 2007). This idea is corroborated by observations like the modulation of chemotaxis genes in *Pseudomonas aeruginosa* induced by the root exudates of sugar beet (Mark et al. 2005). Most rhizobacteria are commensals that establish neutral interactions, taking advantage of root exudates as nourishment without affecting plants. In negative interactions, pathogenic bacteria can produce metabolites with toxic effects on plants, thus having detrimental actions on the overall plant growth. Differently, there are bacteria that, when associated with roots, are able to induce positive effects on the plant growth and fitness; they are commonly termed plant growth-promoting rhizobacteria (PGPR). They can aggressively colonize the host and stimulate plant growth, either indirectly, i.e., acting as biocontrol agents, or directly, i.e., enhancing nutrient acquisition (Weller et al. 2002; Vessey 2003).

The colonization of the rhizosphere compartment is the result of a complex exchange of signals between the two partners and it determines the kind of relationship, which can be detrimental, neutral, or beneficial to plants (Lynch 1970; Glick 2012). Besides the already characterized molecules involved in the crosstalk between plant and rhizobacteria, vitamins represent an emerging class of organic compounds putatively involved in the plant/bacteria interaction and/or in the growth promotion mechanism (Palacios et al. 2014).

Even though the growth promotion and the biocontrol actions of PGPR on plants have been thoroughly studied, the roles played by these microorganisms on plant nutrient acquisition process and on the biochemical mechanisms underlying the nutritional processes taking place at the rhizoplane are still not fully explored. In the present review, we will focus on the interactions between plants and rhizobacteria that have an impact on plant mineral nutrition. Among the macro- and micronutrients, N, P, and Fe are the most critical being the most responsible of yield limitation of crops in the world (Schachtman et al. 1998; Zhang et al. 2010). Among macronutrients, also potassium might represent a limiting factor for plant fitness, especially in acidic soils and in the case of competition with other essential nutrients, as for instance Ca and Mg. Despite these aspects, recently, some authors (Zhang et al. 2010) highlighted that Fe represents one of the main constraints in plant growth and productivity of many agronomically important crops (e.g., peanut, soybean, peach, and apple trees, Marschner 2011) cultivated on alkaline/calcareous soils worldwide. Nutrient deficiencies might be overcome by rhizosphere management (e.g., root exudation, intercropping, and symbiosis with mycorrhizal fungi) as extensively documented by previous authors (Zhang et al. 2010); conversely, the likely role of non-symbiotic bacteria remains to be elucidated. In this context, soil microorganisms could represent a promising method to improve plant use efficiency of nutrients, already present in soil or supplied by fertilizers. In particular, we will discuss the pieces of evidence highlighting a possible role of bacteria in affecting nutrient availability in the rhizosphere and/or biochemical mechanisms underlying the nutritional process. The plant's abilities to shape the soil microbiome are also described along with promising approaches used in studies aiming at understanding these phenomena.

Microbial effects on plant nutrient acquisition

Rhizobacteria as PGPR can play an important role in promoting nutrient acquisition by plants, favoring factors inducing root biomass accumulation and/or hindering those that could have detrimental effects on root system development. This role of PGPR can be achieved via either an indirect (antagonism against pathogens) or direct (e.g., phytohormones production) mode of action (Glick 2012). Furthermore, microorganisms can also affect plant nutrient-acquisition processes by influencing nutrient availability in the rhizosphere and/or functionality of the biochemical mechanisms underlying the nutritional process.

Effects on nutrient availability in the rhizosphere

Plant growth and productivity depend considerably on the availability of nutrients at the soil-root interface, which in turn is influenced by a wide range of factors including the soil type and chemical-physical characteristics, plant species and genotype, soil macro- and microorganism communities, and environmental conditions. In this context, biological activities of both roots and microorganisms can play an important role (Marschner 2011). In addition to a brief introduction about the main mechanisms used by plants root for the acquisition of N, P, and Fe, in the following sections, the contribution of microbes to the dynamics of these three nutrients in the rhizosphere is described; moreover, a review of the effects of PGPRs on physiological and molecular mechanisms underlying the root acquisition of nutrients will be presented in the next sections.

Nitrogen

Plants are able to use different N sources, in both inorganic (i.e., nitrate [NO_3^-] and ammonium [NH_4^+]) and organic (e.g., urea, amino acids, and peptides) forms exploiting specific mechanisms (Nacry et al. 2013; Zanin et al. 2014). The root uptake of NO_3^- is a substrate-inducible, energy-requiring symport H^+/NO_3^- (Santi et al. 1995; Touraine and Glass 1997); the energy is supplied by a proton gradient maintained by the activity of plasma membrane H^+-ATPase (McClure et al. 1990a, b; Glass et al. 1992; Santi et al. 1995). At low NO_3^- concentration (below 1 mM), the anion is taken up by two saturable high-affinity transport systems (HATS, one constitutive and one substrate-inducible), while other two systems (cLATS and iLATS, the constitutive and inducible low-affinity transport systems, respectively) mediate a non-saturable transport at concentrations higher than 1 mM. Genes belonging to the *NRT1* and *NRT2* family (Plett et al. 2010; Nacry et al. 2013) have been identified to be involved in NO_3^- transport at the root plasma membrane. In the case of NH_4^+, the uptake of the cation, mediated by proteins belonging to the AMT/MEP/Rh family (von Wirén and Merrick 2004), is accompanied by an about equimolar H^+ release, most probably ascribable to the plasma membrane H^+-ATPase activity, leading to rhizosphere acidification (von Wirén et al. 2000). Urea can contribute to N uptake of plants via also the NH_4^+ pool produced after its hydrolysis in soil by microbial urease enzymes (Witte 2011). Nonetheless, plants are also able to take up directly urea through the root system (Kojima et al. 2007; Witte 2011) via a transport of urea exploiting both a high-affinity system (urea:H^+ symporter AtDUR3, Liu et al. 2003) and a passive transport system (by members of the major intrinsic proteins (MIP) family of aquaporins, Witte 2011).

In general, irrespectively to the forms, the extent of N acquisition by roots is strictly dependent on the availability of the source itself. In soil, about 90 % of total N is present in organic form (soil organic matter, SOM), and the biogeochemical cycle of the whole N pool (which includes also the N portion deriving from fertilization) is very important for the level of soil fertility (Jetten 2008). This cycle is mainly managed by microbial processes (SOM mineralization, atmospheric N_2 fixation, denitrification), and the role of microbial inoculants with an impact on N utilization by plants in both fertilized and non-fertilized soils has been widely described (Adesemoye et al. 2009). Considering the great extent of the organic N pool, it is evident that the mineralization, i.e., nitrification and ammonification, carried out by bacteria is crucial for plant mineral nutrition. In fact, microorganisms like mycorrhizal fungi and PGPRs mineralize OM by releasing hydrolytic enzymes and thus enhancing the nutrient availability in soil (Miransari 2011; Ollivier et al. 2011).

Biological N_2 fixation (BNF) is carried out by many prokaryotic microorganisms, known as diazotrophs, through normal metabolic activities. The nitrogen fixation primarily occurs in soil by either free-living or plant-associated diazotrophs (Galloway et al. 2008). Free-living diazotrophs are those bacteria that are not associated with plants, i.e., in the bulk soil (Reed et al. 2011), and include *Cyanobacteria*, *Proteobacteria*, *Archaea*, and *Firmicutes* (Kahindi et al. 1997; Widmer et al. 1999; Diallo et al. 2004; Duc et al. 2009). However, many diazotrophic cyanobacterial species can establish symbiotic relationships with eukaryotes, such as terrestrial plants, and contribute significantly to the N budget required for the growth of both organisms (Hobara et al. 2006). Nevertheless, the most efficient processes for BNF involve the formation of highly specialized organs, the so-called root nodules. The majority of BNF in terrestrial ecosystems is carried out by the well-known association between bacteria belonging to the family of *Rhizobiaceae* and leguminous plants. Jones et al. (2007). In addition, the diazothrophs belonging to the genus *Frankia* can also colonize a small group of woody, non-legume plants, known as actinorhizal plants, inducing the formation of nitrogen-fixing root nodules (Santi et al. 2013). Such capability of enhancing the N available fraction is supposed to be a key feature accountable for the plant growth-promoting activity of a part of the rhizosphere flora (Hurek et al. 2002; Iniguez et al. 2004).

The denitrification, or dissimilatory nitrate reduction, generates NO_2^- from NO_3^- anions, as an alternative electron acceptor in microbial cell respiration. Nitrite can be then converted to nitrogen oxides (NO_2 and NO) and eventually to NH_4^+, which can be taken up by plants. The presence of NO_x in the rhizosphere could play an important role having anyway at the end, even if indirectly, an impact on root-acquisition process. In fact, in the last decade, NO has received great attention considering that it was demonstrated to act as second messenger in indol-3-acetic acid (IAA) signaling pathway that drives plant developmental processes. It has been shown that NO plays a role in the induction pathway of both adventitious and lateral roots (Pagnussat et al. 2003; Correa-Aragunde et al. 2004). One of the characteristics of the PGPR *Azospirillum brasilense* is its ability to induce changes in plant root architecture, inducing the development of lateral and adventitious roots (Creus et al. 2005) and root hairs (Hadas and Okon 1987) in several plant species. Besides exuding IAA, *A. brasilense* was shown to be able of synthesizing NO by different aerobic pathways, giving evidence for an NO-dependent promoting activity on tomato root branching notwithstanding the capacity of this PGPR to synthesize IAA (Molina-Favero et al. 2008). Similarly, Pii and colleagues (2007) demonstrated that *Sinorhizobium meliloti* can produce NO through a NO synthase-like enzymatic activity and suggested that it could be implicated in the induction of root nodule organogenesis in *Medicago truncatula* roots.

Moreover, it is well known that NO induces the expression of genes involved in Fe acquisition (García et al. 2010), but to our knowledge, no study has demonstrated that microorganisms influence Fe acquisition via NO production.

Phosphorous

The form of P most readily accessed by plants is the monobasic $H_2PO_4^-$ (Pi) (Marschner 2011), which rarely exceeds 10 μM in soil solutions (Bieleski 1973). Root uptake of Pi is a process depending on metabolic energy, where the driving force is guaranteed by the activity of plasma membrane H^+-ATPase (Liang et al. 2014). A high-affinity system, working in the micromolar range of concentration, and a low-affinity system, responsible for the Pi uptake when the external concentration is in the millimolar range, appear to be involved (Ullrich-Eberius et al. 1984; Furihata et al. 1992). The phosphate/H^+ symporter belonging to *PHT1* gene family, which is highly expressed in roots, especially in the rhizodermis, root hairs, and in the outer cortical cells, is considered the main molecular entity responsible for Pi transport at the plasma membrane (Daram et al. 1998; Liu et al. 1998; Chiou et al. 2001; Mudge et al. 2002; Karthikeyan et al. 2002; Schünmann et al. 2004).

Soils may contain large amounts of P but is very scarcely available for plant use (Bhattacharyya and Jha 2012), since both inorganic and organic P forms are very insoluble compounds. The majority of the inorganic P present in soils is bound to Fe, Al, and/or Ca that reduce its solubility, leading to precipitation and adsorption processes (Igual et al. 2001; Gyaneshwar et al. 2002). Furthermore, the application of fertilizers might not solve plant nutritional issues, since P can easily bind cations and become insoluble once applied to the soil (Adesemoye and Kloepper 2009). From 20 to 80 % of P in soils is found in the organic form, of which phytic acid (inositol hexaphosphate) is usually a major component (Richardson 1994). Several bacteria belonging to the genera *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhizobium*, and *Serratia* (Sudhakar et al. 2000; Sturz and Nowak 2000; Mehnaz and Lazarovits 2006) have been characterized as P-solubilizing microorganisms. Nevertheless, recent findings highlighted the traditional method adopted for the screening of P-solubilizing bacteria, based on the use of tricalcium phosphate, has led to the isolation of microorganisms whose P-solubilizing ability could not be directly transferred to field, where the environmental conditions might be extremely different from those imposed for the selection. As a consequence, the number of bacteria that have been accounted for P-solubilization might be overestimated (Bashan et al. 2013a, b). However, microorganisms can have an impact on the availability of the nutrient in soil, and the major mechanism responsible for their ability is thought to be the exudation of organic acids (Bhattacharyya and Jha 2012), such as acetate, oxalate, succinate, citrate, and gluconate (Bulgarelli et al. 2013). Once released, organic acids can desorb Pi from soil adsorption sites by ligand exchange and thus solubilizing Pi from Ca/Fe/Al-Pi minerals (Tomasi et al. 2008). With respect to the organic P pool, plants can use this source only after its transformation in the Pi form. In this respect, it is well demonstrated that bacteria-derived phosphatases are able to mineralize P-containing organic molecules of soil (like phosphoesters, phosphodiesters [i.e., phospholipids and nucleic acids], and phosphotriesters) releasing consequently orthophosphate groups (Rodríguez et al. 2006). However, the mechanisms underlying the improved plant P nutrition by PGPRs are still largely unknown, considering that the increase in P content of plants might result from at least two concurrent processes, i.e., the increased nutrient bioavailability at the root/soil interface and the enhanced capacity of plants to take up Pi, or from a combination of these two mechanisms.

Iron

Plants are able to acquire Fe using mechanisms that are different between monocots and dicots (Kobayashi and Nishizawa 2012). In dicots, classified as *strategy I* plants (Marschner and Römheld 1994), the Fe acquisition is based on a mechanism at the plasma membrane level that involves the reduction of Fe^{III} to Fe^{II} and the uptake of Fe^{II} thanks to the transmembrane electrochemical gradient guaranteed by the activity of plasma membrane H^+-ATPase. In the case of Fe shortage, *strategy I* plants enhance the release of proton in the rhizosphere, causing the increase of Fe concentration in the close proximity of roots (Colombo et al. 2013). In addition, strategy I plants increase the Fe^{III} reduction activity, that is carried out by the ferric chelate reductase oxidase (FRO), and the transport of Fe^{II} across the membranes, that occurs through the iron-regulated transporter (IRT)-like protein (Connolly et al. 2003). Differently, grasses, also termed *strategy II* plants, base their capacity to take up Fe on the biosynthesis and exudation of phytosiderophores (PSs), which display a strong chelation affinity for Fe^{III} (Schaaf et al. 2004). PSs are released in the rhizosphere via the transporter of mugineic acid family phytosiderophores1 (TOM1) (Nozoye et al. 2011), while the complexes Fe^{III}-PS are then transported into root cells through specific transporters, the yellow stripe1 (YS1) and YS1-like (YSL) transporters (Curie et al. 2001; Inoue et al. 2009). Recent evidence suggested that the distinction between *strategy I* and *strategy II* plants might not be so sharp-cut (Ishimaru et al. 2006; Xiong et al. 2013).

In order to improve Fe availability in soil, plants and microbes have evolved similar strategies for the Fe mobilization from barely available sources relying on the exudation of a huge variety of organic compounds (e.g., organic acids, phenolic compounds, siderophores) that are able to complex Fe

(Mimmo et al. 2014). Once mobilized, these complexed Fe forms can represent an available source for Fe uptake by plants and microorganisms. However, at the rhizosphere level, where the nutritional needs of plants and microorganisms coexist and must be satisfied, a competition for the nutrient uptake between these organisms could easily occur (Colombo et al. 2013; Mimmo et al. 2014). In this context, microorganisms seem to be more competitive than plants. In fact, they are able not only to use the Fe complexes formed with their own exudates but also to degrade plant-derived exudates as C source (reducing their effectiveness in the nutrient mobilization process) and to immobilize nutrients in their biomass before the Fe complexes get in contact with the root surface. In root exudates of Fe-deficient grasses, for instance, non-proteinogenic amino acids named PSs are the main compounds; the exudation process takes place at the root tip and in the root zone immediately behind (i.e., root elongation zones) (Römheld 1991). Considering that the higher microbial growth rate (and hence the higher rate of C source consumption) is estimated to be in correspondence of the root distal elongation zone (Marschner et al. 2011), the very localized release of exudates (root tip) can prevent microbial degradation, enhancing their effectiveness in nutrient mobilization/solubilization. In this vision, the uneven distribution of the exudation process along the root axis might constitute a strategy to limit/counteract the competition for nutrients with soil bacteria.

Concerning the relation between soil pH and Fe availability in soil solution, microbes are able to give their contribution to soil acidification via their metabolism. In fact, as a consequence of their respiration, pCO_2 is increased, enhancing the concentration of carbonic acid in the surrounding soil (Hinsinger et al. 2003). The concomitant acidification activities of both plants and microorganisms can lead to an overall drop of 1–2 units in the pH of the rhizosphere as compared to bulk soil with a consequent increase of Fe mobilization from barely available forms (Pinton et al. 1997; Santi et al. 2005; Tomasi et al. 2009).

In addition, some compounds (mainly phenolics) are able to reduce Fe^{III} in the soil, thereby increasing its solubility. In the last years, many evidences about release of Fe-reducing compounds from roots have been published (Tomasi et al. 2008; Cesco et al. 2010, 2012). It can be reasonably hypothesized that this kind of compounds might also be released by some bacteria and thus might be important for Fe nutrition.

Another factor influencing Fe availability in soil is its redox status. In fact Fe^{II}, compared to Fe^{III}, is much more soluble (Marschner 2011). Many bacterial strains are able to use Fe^{III} as acceptor of electrons in anaerobic conditions. For instance, in anoxic paddy soils used for rice cultivation, the bacterial community is able to catalyze the reduction of Fe, nitrate, and sulfate, thus greatly influencing the availability of the nutrient in these flooded environments (Achtnich et al. 1995; Hori et al. 2009). On the contrary, in well-aerated soils, the importance of these anaerobic bacteria is limited, even if it is possible that within the heterogeneity of the soil, some anaerobic microenvironments exist and in densely compacted soil the oxygen might become scarce. In these environments, the availability of Fe^{II} might increase and be readily available for nearby roots.

Effects on the biochemical mechanisms underlying the nutritional process in plants

The PGPR-induced plant growth, clearly described by Vacheron et al. (2013), entails an increase in the amount of nutrients acquired by roots and accumulated in plant tissues, that can be achieved not exclusively via increased availability of nutrients but also via the functionality of plasma membrane entities involved in the nutrition process at the root level.

The transmembrane electrochemical gradient is the driving force governing the movement of the different ions across the membrane (White 2003); since this gradient is maintained by the plasma membrane H^+-ATPase, the activity of this enzyme is very important for the movement of solutes and, considering nutrient-acquisition process in plants, of nutrients. In this respect, it has been demonstrated that the inoculation of wheat seedlings with *A. brasilense* Cd increased proton efflux from roots (Bashan et al. 1989). The partial restoration of H^+ efflux in seedlings pretreated with orthovanadate (a plasma membrane H^+-ATPase inhibitor) and then inoculated with this strain clearly indicated that *A. brasilense* Cd might have an effect on plasma membrane H^+-ATPase activity, most likely through diffusible signal(s) released in the growth medium (Bashan et al. 1989; Bashan 1990). Also, in oil-seed-rape plants treated with a PGPR, an increased H^+ efflux from roots has been recorded (Bertrand et al. 2000). More recently, it has been shown that the treatment of maize seedlings with humic substances extracted from vermicompost and *Herbaspirillum seropedicae*, a diazotrophic endophytic bacterium that mostly colonize graminaceous plants, caused a stimulation of plasma membrane H^+-ATPase in maize roots (Canellas et al. 2013). Since Canellas et al. (2002) have demonstrated an IAA-like activity of humic substances and that *H. seropedicae* is able to produce IAA in vitro (Radwan et al. 2002), the bacterial stimulation of plasma membrane H^+-ATPase activity has been attributed to an IAA-derived effect (Canellas et al. 2013).

It has been demonstrated that the influx of H^+ is coupled with the transport of several nutrients (e.g., Pi and NO_3^-) (White 2003) and that the hyperpolarization of transmembrane electrochemical gradient favors nutrients movement across the membranes. For these reasons, the enhanced H^+ extrusion by PGPR inoculation might hold a crucial role in the nutritional process. However, indications about the mechanisms through which PGPRs are able to exert their stimulation of the plasma membrane H^+-ATPase activity (both at the

transcriptional and posttranscriptional level) are still lacking. With respect to the plant- and microbe-induced acidification of the rhizosphere soil, it is also important to highlight that, besides nutrients (e.g., Fe and P), the solubility of elements potentially toxic for plants (e.g., Al, Mn, Cd) could also be increased in the rhizosphere soil. For this reason, the possibility of using biological activities of both plants and microorganisms in relation to phytoremediation practices at the rhizosphere level has been extensively investigated (Rajkumar et al. 2012).

Nitrogen

Concerning the mechanisms underlying N acquisition by plants (reviewed by Nacry et al. 2013), Bertrand et al. (2000) observed an enhanced uptake of NO_3^- in roots of oilseed rape (*Brassica napus*) inoculated with the soil-isolate *Achromobacter* bacteria with a consequent higher content of this anion in the plant tissues. The authors hypothesized an action of *Achromobacter* bacteria on the cHATS transport system. Further pieces of research highlighted that the inoculation of *Arabidopsis thaliana* plants with *Phyllobacterium* STM196 prevented the inhibition of root growth in the presence of high concentration of NO_3^- (Mantelin et al. 2006). Interestingly, the inoculation caused also an overexpression of the *NRT2.5* and *NRT2.6* genes (Mantelin et al. 2006) that are required for the plant growth-promoting activity of *Phyllobacterium* (Kechid et al. 2013). In the light of the facts that both *NRT2.5* and *NRT2.6* are expressed in *A. thaliana* leaves and do not play an important role in NO_3^- transport, it was hypothesized that they might act as transceptors (Kechid et al. 2013). In such scenario, NRT2.5 and NRT2.6 might be involved in the perception of a systemic signal, from root-to-shoot and vice versa, elicited by rhizosphere bacteria (Kechid et al. 2013). Despite these observations, the possible involvement of rhizosphere microorganisms in altering the NO_3^- fluxes at the root plasma membrane are still contradictory (Bertrand et al. 2000; Mantelin et al. 2006). On the other hand, no indications regarding microbial effects on the mechanisms underlying the plant acquisition process of NH_4^+ and urea are available.

Phosphorus

Concerning the root mechanisms of Pi uptake (Liang et al. 2014), evidence showing that PGPR directly affect plant Pi acquisition are still missing. Nonetheless, the symbiotic interaction between roots and AMF favoring the P supply of plant (Smith et al. 2011) is a valid example of nutrient interplay between two different organisms. It is interesting to note that the establishment of the root/AMF symbiosis is a consequence of a complex exchange of signals between host plants and fungi, causing also cell reprogramming (Parniske 2008). In fact, plants colonized by AMF can exploit an additional pathway for P acquisition, occurring in different cell types, based on different molecular entities (i.e., transporters) and accessing P in different regions of soil. Pi uptake is achieved by the expression, in colonized cortical cells, of Pi transporters that can be either specifically induced by AMF symbiosis (Harrison et al. 2002; Paszkowski et al. 2002; Glassop et al. 2005; Nagy et al. 2005) or strongly induced during the symbiosis but having also a basal expression in non-mycorrhizal roots (Rausch et al. 2001; Chen et al. 2007). It is also worth noting that the activities of PGPR might also have a direct beneficial effect on AMF, as for instance enhanced germination of fungal spores and mycorrhization (Artursson et al. 2006; Pivato et al. 2009), and thus, they could indirectly affect the Pi availability for host plants associated with mychorrhizal fungi.

Iron

Even though Fe deficiency is one of the major causes of agricultural yield limitation, the literature does not report any experience of using PGPRs to induce a better utilization in crops of barely available Fe naturally present in soils. To our knowledge, evidence has been obtained with *A. thaliana* plants grown in vitro; the presence of *Bacillus subtilis* GB03 caused an increased accumulation of Fe in the plant tissues and an enhanced photosynthetic capacity (Zhang et al. 2009). It is interesting to highlight that in Fe-deficiency conditions, also rhizosphere microorganisms can synthesize and exude microbial siderophores (MSs) (Lemanceau et al. 2009) that show very high affinity for Fe^{III} (Guerinot 1994); the Fe^{III}-MSs complexes are acquired by bacterial cells through specific transporters (Neilands 1981). Interestingly, besides taking up the Fe complexed with their own MSs, bacteria can also absorb MSs produced and released by other bacterial species (Raaijmakers et al. 1995). Considering their very high stability, the Fe^{III}-MSs could hardly act as substrate for ligand exchange reactions with PSs in order to be acquired by grasses (Colombo et al. 2013; Mimmo et al. 2014). Nevertheless, recent evidence showed that purified *Pseudomonas fluorescens*-derived siderophore pyoverdine, as well as siderophores synthesized by the fungus *Trichoderma asperellum*, complexed with Fe^{III}, can directly act as Fe donor for plants, restoring the Fe-deficiency condition in hydroponic culture (de Santiago et al. 2009; Nagata et al. 2013). However, the mechanisms involved are still unknown and, since no evidence of the pyoverdine-Fe^{III} complex uptake were found, a two-step process was hypothesized: the pyoverdine-Fe^{III} complex reduction by SlFRO1 with the release of Fe^{II} that is transported into cells by SlIRT1 (Nagata et al. 2013). Anyhow, information concerning the possible applicability of PGPR to overcome the limited availability of Fe for crops in field conditions and/or to restore plants from Fe deficiency is not yet

available. In addition, these aspects are mainly related to the availability of the micronutrient in the soil; up to now, no evidence is available concerning the capability of microorganisms to influence the mechanisms responsible for Fe acquisition in *strategy I* and *strategy II* plants.

However, the molecular mechanisms involved in such "bacteria-stimulated" plant nutrition (i.e., nutrient uptake and translocation) are far from being elucidated in order to think to a rational application of PGPR alone or, in combination with fertilizers, to restore crops from nutritional disorders. It has been largely demonstrated that the capability of plants to recover from nitrate starvation (i.e., adaptation to adverse environmental conditions) is based on the increased expression (known as induction phenomenon) of a set of genes encoding proteins involved in the uptake and assimilation of the anion, with a subsequent feedback inhibition governed by the plant N nutritional status (Nacry et al. 2013). Similar responses to nutrient shortage have been also described for NH_4^+, P, and Fe (Kobayashi and Nishizawa 2012; Nacry et al. 2013; Liang et al. 2014). In this vision, it might be conceivable that PGPR could influence the molecular machineries that are physiologically involved in nutritional process, so as to stimulate uptake of nutrients from the rhizosphere. However, evidence showing that bacteria are able to increase the expression of the molecular entities involved in plant mineral nutrition is still lacking.

Despite being not strictly related to nutrient acquisition, there is further evidence concerning modifications of gene expression in the root tissue of abiotically stressed plants as a consequence of PGPR inoculation. In maize plants inoculated with *Bacillus megaterium*, the hydraulic conductance value was increased, regardless the plants were stressed or not (Marulanda et al. 2010). The enhanced water transport was in good agreement with both the higher expression of some aquaporin genes and the increased amount of aquaporin proteins. Similarly, the inoculation of *A. thaliana* plants with *B. subtilis* GB03 resulted in a tissue-specific modulation of high-affinity K^+ transporter (*HKT1*, a low-affinity Na^+ transporter, Rubio et al. 1995) expression, i.e., downregulation in roots and upregulation in shoots, determining the limitation of Na^+ intake into plants and the remobilization of Na^+ from shoot to root (Zhang et al. 2008). Considering that *B. subtilis* GB03 was demonstrated to emit volatile compounds able to induce a modulation of *A. thaliana* gene expression (Ryu et al. 2003, 2004), the author ascribed the tissue-specific regulation of *HKT1* to not yet identified volatile signal(s) released by the PGPR (Zhang et al. 2008).

Plants are able to shape the soil microbiome

Soil microbiota, being biofilm-forming bacteria, endophytes, or nitrogen-fixing bacteria, colonizes the root system and can influence plant fitness and plant functional traits. On the other hand, also plants have the ability to manipulate bacteria and modulate their activities in order to enhance those interactions that would help them overcoming stressed environments. Therefore, it is interesting to review how beneficial plant-associated microbes and plants respond to and influence each other by changing their transcriptomes and their phenotypic plasticities.

The ability of plants to select a species-specific microbiome was first postulated by cultivation-dependent approaches (Germida and Siciliano 2001) and afterwards further confirmed by molecular fingerprinting of the microbial communities inhabiting the rhizosphere of three different plant species (i.e., strawberry, oilseed rape, and potato) (Smalla et al. 2001). Plant genotype plays a crucial role in determining the core microbiome associated to the root system (Lundberg et al. 2012; Bulgarelli et al. 2013); this aspect is supported by the observation that genetically modified crops might affect, both positively and negatively, the biodiversity of soil-borne microorganisms as fungi, as well as their life cycle and their ecological roles that have a paramount importance in the functioning of agroecosystems (Hannula et al. 2014). However, notwithstanding plant genetic traits, there are several other factors, such as soil properties, plant nutritional status, and climatic conditions, influencing composition and activity of microbial community of rhizosphere soil (Berg 2009).

In the last 10 years, several experimental approaches have been applied to study the interaction between plants and microorganisms and some of them will be discussed in the following section. Furthermore, the analytical tools available and the relative target of investigation are summarized in Table 1.

Bacillus amyloliquefaciens FZB42 has been described as a PGPR that exerts great influence on plant growth, as it produces the plant hormone IAA and some secondary metabolites with antibacterial and antifungal activities. Microarray experiments have been performed to investigate the transcriptomic response of FZB42 to maize root exudates (Fan et al. 2012). The expression of 302 genes, representing 8.2 % of its whole transcriptome, was significantly modulated by the presence of plant exudates, being 260 of them upregulated (Fan et al. 2012). The induced genes with known function were mainly involved in nutrient utilization, chemotaxis and motility, and antibiotic production. Besides sigma factor and other transcriptional regulators, some small RNAs were also found to have a possible role in plant-microbe interaction (Fan et al. 2012).

In order to determine how a PGPR and its plant host biochemically and physiologically influence one another, proteome-level changes of both the PGPR *Pseudomonas putida* UW4 and its host *B. napus* were investigated by two-dimensional gel electrophoresis and mass spectrometry (Cheng et al. 2009). Many proteins resulted to be up- or down-regulated; mass spectrometry, sequence determination, and

Table 1 Methods to study the relationships between plants and rhizobacteria

Methodological approach	Analytical tools	Aim
Culture-dependent approach	Plate counting on selective media; confocal laser scanning microscopy; electron microscopy; biofilm assays; biosensors; imaging	Isolate novel beneficial microorganisms; clarify the molecular mechanisms of cell-to-cell interactions, colonization, phytostimulation
Metabolomics	HPLC-MS; GC-MS	Identification and characterization of novel bacterial secondary metabolites with plant growth potentials
Proteomics	Two-dimensional gel electrophoresis; MALDI-ToF/MS	Elucidation of the proteins prospective of plant-bacteria interactions; determine how a plant growth-promoting bacterium and its plant host biochemically and physiologically influence one another
Metagenomics/metatranscriptomics	RT-PCR; microarray; mutagenesis and library screening; DGGE; high-throughput sequencing and bioinformatics sequences processing	Provide a snapshot of transcriptional profiles that correspond to discrete populations within a microbial community and a certain environment at the time of sampling; offer novel insights into the functional potential of microbial communities; provide reference genes and genomes for metatranscriptomics; identify key plant and microbial genes that are responsible of plant-microorganisms interactions; estimate the active and potentially active microorganisms

comparison with related species allowed the assessment of proteins with altered expression levels. In particular, three unique *P. putida* UW4 proteins that mediate interactions between the bacterium and its plant host were identified. On the plant side, proteins with significantly altered expression levels in the presence of the bacterium were identified by mass spectrometry, too. With a similar approach, the interaction between *Gluconacetobacter diazotrophicus* and two varieties of sugarcane (i.e., SP70-1143 and Chunee) was studied (Lery et al. 2011). The most striking difference between the two sugarcane cultivars was their ability to benefit from biological nitrogen fixation, having SP70-1143 higher efficiency to profit from the symbiosis than Chunee. It was observed that, independently from the host genotype, root exudates elicited in *G. diazotrophicus* the upregulation of proteins involved in the colonization process. On the other hand, the presence of *G. diazotrophicus* caused reactions dependent on plant genotype. Sugarcane SP70-1143 expressed protein involved in cell adaptation and signaling aiming at favoring bacterial colonization, while Chunee variety elicited a strong defense reaction preventing *G. diazotrophicus* from colonizing roots (Lery et al. 2011).

Complementary DNA microarrays, representing approximately 14,300 genes, allowed the comparison of RNA transcript levels of *A. thaliana* infected by *Pseudomonas thievervalensis* and axenic control plants. The results, presented by Cartieaux et al. (2003), suggested that colonization affected the expression of both plant defense genes and photosynthesis-associated genes. In particular, inoculation led to the repression of chloroplast-associated genes, occurring for the first 2 weeks after colonization. A possible explanation is that the energy used for the synthesis of highly abundant messenger RNAs (mRNAs), such as those of photosynthesis-associated genes, is temporarily reallocated for the production of mRNA coding for proteins directly involved in the colonization.

Microbial populations inhabiting the bulk soil as well as those colonizing plant roots show a quorum sensing (QS) system based on N-acyl homoserine lactone (AHLs) production to monitor their own population abundance. Several bacterial species that interact with plants produce AHL autoinducer compounds in order to control a broad range of traits such as growth inhibition, nodulation, production of antibiotics, and others, still unknown (Brelles-Mariño and Bedmar 2001). Very interestingly, some bacterial auto-inducers seem to affect an extensive range of functional responses in plants as well as plants can manipulate bacterial QS by secreting compounds that mimic the bacterium own sensing signals (Teplitski et al. 2000; Pérez-Montaño et al. 2013). Quorum sensing mimics from host plants, as well as from other bacteria, may stimulate or disrupt bacterial sensing. Since plants and microorganisms coexist in the soil, it is not surprising that they sense each other.

Proteome analysis has been also used to show that a model eukaryotic host *M. truncatula* is able to detect up to nanomolar concentrations of bacterial AHL, by significantly accumulating more than 150 proteins, most of which have been identified by peptide mass fingerprinting. Of the known proteins,

approximately 25 % had a role in host defense responses; others are involved in primary metabolism, plant hormone responses, regulation of transcription, and protein processing. AHL structure, concentration, and time of exposure affected the accumulation of specific proteins and isoforms exhibiting also tissue-specific responses. Interestingly, AHLs increased the expression of IAA-induced and flavonoid-related genes; it is noteworthy that the induction of gene expression is not only restricted to cells at the local site of AHL contact (Mathesius et al. 2003). These results indicate that plants are able to detect at least two different AHLs (3-oxo-C_{12}-HL and 3-oxo-$C_{16:1}$-HL) even below the threshold concentrations used in vivo by bacteria, using this information for global and sophisticated responses.

Young seedlings of *M. truncatula* and seedling exudates were systematically extracted with organic solvents and the extracts were characterized by HLPC, demonstrating that this model legume plant produces at least 15 to 20 separable substances capable of specifically stimulating or inhibiting responses in reporter bacteria (Gao et al. 2003). Similarly, Teplitski et al. (2000) demonstrated that exudates from *Pisum sativum* seedlings contained several activities that mimicked AHL signals in reporter bacteria, stimulating AHL-regulated behaviors in some strains, while inhibiting such behaviors in others. Very recently, *Oryza sativa* and *Phaseolus vulgaris* have been found to produce, in roots and seeds, compounds that specifically interfere with the capacity of plant-associated bacteria to form biofilms, an essential trait for bacteria-eukaryotic host interaction (Pérez-Montaño et al. 2013).

These results support the idea that plants are not only affected by PGPRs but also have important tools to manipulate gene expression and behavior in the bacteria they encounter for their own benefits. However, the molecular mechanisms responsible for these interferences are currently unknown. Although the above data do not deal specifically with PGPRs affecting mineral nutrition of plants, it is very likely that future investigations will demonstrate that plant-microorganism sensing has a key role in this topic too and that the understanding of those relationships might lead to an improvement in crop production and agricultural management.

Conclusions

In the next decades, food supplies and agricultural productivity need to meet the requirements determined by the increasing human population. Plant growth and productivity depend on the availability of nutrients at the soil-root interface, and such availability is influenced by different factors, among which the biological activities of both roots and microorganisms in the rhizosphere. Up to now, crop nutrition has depended on the application of high amounts of fertilizers; however, in order to limit and/or prevent future environmental and economic issues, agricultural practices are moving towards more sustainable systems. In this context, the employment of PGPR as bioinoculants might represent a very promising approach, considering that they were capable of enhancing both plant development (increase in root and shoot biomass, more branched root system) and nutrient bioavailability.

Despite these encouraging evidence, there are still many aspects that have to be explored in order to gain a better understanding of all the interactions involved between plant and PGPRs, aiming at an increased nutrient use efficiency. The elucidation of the molecular mechanisms underlying the effects induced by bacteria on plants and vice versa as well as the derived physiological and ecological implications could allow the development of innovative fertilization practices in agriculture based on biotechnological approaches for rhizosphere engineering and management.

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