
Soil Microbiome and Their Effects on Nutrient Management for Plants

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Abstract

The soil microbiome is a diverse system composed of microorganisms with different functions. Microorganisms known as plant growth-promoting microorganisms (PGPMs) can help plants with nutrient uptake and consequently with crop yields. From this class of microorganisms, we can isolate nitrogen-fixing bacteria (NFB), phosphorus-solubilizing microorganisms (PSMs), and the microbes that are able to produce phytohormones. The use of these microorganisms in improving nutrient uptake by plants has been acceptable because of reduced costs and the safety of application for humans and the environment. It is for this reason that inoculant products have been developed. During the process of inoculant development, it is possible to use molecular biology techniques, such as 16S rRNA gene sequencing. This technique helps with the identification of potential microorganisms adapted for different conditions and crops. Moreover, these microorganisms can be used in degradable areas or as pathogen controls. It is also important to consider the siderophore, which is a biological molecule produced by various bacteria, and which has an immense application in agriculture. Another important symbiosis that occurs is realized by mycorrhizas, which are essential for transferring nutrients and water from the soil to plants.

6.1 Introduction

The association between plants, soil, and soil microbes is like a system, which influences plant health and productivity. To illustrate this, recent advances in “omics” research can provide a common understanding and management of these interactions (Chaparro et al. 2012).

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The phytomicrobiome is characterized by microbial communities related to plants (Smith and Zhou 2014; Smith et al. 2015). This phytomicrobiome can be divided into the rhizomicrobiome, which is located in and around the roots or the rhizosphere (Lundberg et al. 2012), the phyllosphere, which refers to the microbiome present in aerial parts of the plant (Rastogi et al. 2012; Kembel et al. 2014), and the endosphere, which is inside the plant (Berg et al. 2014). The structure of these microbial communities can vary according to the interactions between plant – microorganism and/or microorganism-microorganism. These connections are mediated by compounds that are released by plants or microorganisms as exudates (East 2013). Understanding the form and function of these compounds is essential for the possibility of using these microbes to develop new technologies for crop growth promotion, industrial process optimization (e.g., fermentation), and biocontrol mechanism development (East 2013).

Of all the microbial communities, the rhizomicrobiome shows most relevance for field crops. This group of microorganisms is very diverse and dynamic in response to environmental conditions and the interactions between plants and microbes, which in some cases are specific. Plant growth-promoting microorganisms (PGPMs) are one group from the rhizomicrobiome which live in soil or close to plant roots (Gray and Smith 2005; Mabood et al. 2014). These groups of bacteria are distinguished by some inherent characters: (i) able to be established at the root surface; (ii) remain and compete with other microbes; (iii) promote plant growth (Kloepper 1994).

PGPMs have acquired relevance in agriculture because they are considered an alternative to the traditional management of crops (Bhattacharyya and Jha 2012), and an environmentally friendly practice. A huge miscellanea of microbes have been used as PGPMs (Ahemad and Kibret 2014); one of the most used is Rhizobia, due to the high yield increases that result when inoculated in plants (Rathore 2014). Moreover, PGPMs are classified according to their functionality (Gray and Smith 2005; Mabood et al. 2014). As biofertilizers, they can intensify the acquisition of nutrients by plants, through nitrogen fixation (Vessey 2003; Bhattacharyya and Jha 2012) and phosphate solubilization (Inui-Kishi et al. 2012; Trabelsi and Mhamdi 2013). Other uses of PGPMs are as phytostimulators (inducing plant growth through phytohormes), rhizomediators (used for restoration of degraded environments) (Antoun and Prévost 2005), and for the production of metal chelators and siderophores (Vessey 2003; Bhattacharyya and Jha 2012).

Other mechanisms of PGPMs include the production of 1-aminocyclopropane-1-carboxyla deaminase (maintaining ethylene levels in plant tissues under stress situations) (Penrose and Glick 2003), the induction of innate resistance or suppression of disease by antibiotics produced by fungi or bacteria (Antoun and Prévost 2005; Bhattacharyya and Jha 2012), the production of cell wall lytic enzymes (Haas and Defago 2005; Rathore 2014), and quorum sensing and interference on biofilm formation (Bhattacharyya and Jha 2012).

PGPMs can be divided into two groups according to the proximity of bacteria to the root (Gray and Smith 2005). One group is called ePGPM (extracellular) and is present in the rhizosphere or on the rhizoplane. *Agrobacterium*, *Arthobacter*, *Azospirillum*, *Pseudomonas*, and *Serratia* are just some examples of ePGPMs

(Bhattacharyya and Jha 2012). Another group is iPGRM (intracellular), which are present inside roots cells and are represented by *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium* (Gray and Smith 2005).

In summary, microorganisms can act in coordination with the soil microbiome for the purpose of benefiting plant health and development. Much evidence shows that plants are able to determine microbial communities through root exudates. These exudates maintain a molecular conversation according to the plants' phenological stage, interaction with others species, and management techniques (Chaparro et al. 2012). This chapter discusses the detail and actual knowledge about the importance of the soil microbiome on nutrient acquisition together with other applications of these microorganisms.

6.2 Soil Microbiome Diversity and Function

The rhizosphere of plants is a huge source of soil microbes (Köberl et al. 2013), which are captivated by root secretions and/or rhizodeposits (Compant et al. 2010). Plant species can co-ordinate the rhizosphere microbiome, which is dependent on the soil microbial community (Smalla et al. 2001). Furthermore, microbial communities are contingent on soil type, pedoclimatic conditions, plant health, phenological stage, and edaphoclimatic factors (Singh and Mukerji 2006).

The higher activity observed by microbes in the rhizosphere brings several biological and ecological benefits to the environment and improves plant yield. The rhizosphere contains a large number of microorganisms with the ability to fix nitrogen, solubilize phosphorus (P), enhance plant pathogen resistance (Arjun and Harikrishnan 2011), and help recover degraded environments (Antoun and Prévost 2005). These microorganisms assume an important aspect from an agronomic point of view, as we can outline below.

Knowledge of the diversity of the rhizosphere is very limited. It has been estimated that less than 1% of the soil microbiome has been isolated in pure culture. In order to understand the soil microbiome, metagenomics can help in analyzing complex genomes of microbial communities through culture-independent molecular approaches (Peix et al. 2007). Moreover, with molecular approaches it is possible to verify the existence and determine the quantity of microorganisms (Oliveira et al. 2009). For bacterial diversity analysis, the molecular marker 16S rRNA gene is utilized (Richardson et al. 2011). Arjun and Harikrishnan (2011) investigated the microbial diversity present in the rice rhizosphere from a paddy field ecosystem in Kerala, India. They used culture-independent molecular techniques, 16S rRNA clone library generation obtained by RFLP, sequencing, and phylogenetic analysis. Through sequence analysis of 16S rRNA genes, they observed major diversity in the bacterial community, with the majority of microbes being related to Proteobacteria. Just a small portion of the 16S rRNA sequences were highly similar to rRNA from the Acidobacteria, Firmicutes, and Bacterioides groups. Knowledge of the less known microbial community is very useful for the comprehension of their individual roles as related to plant health, yield, and metabolic capabilities. Moreover, metagenomics

promises to bring many more questions regarding the uncultivable fraction of the rhizosphere community.

Köberl et al. (2013) present a study performed with the purpose of analyzing the microbiome of medicinal plants (*Matricaria chamomilla* L., *Calendula officinalis* L., and *Solanum distichum* Schumach. and Thonn.) planted in an organic desert farm in Egypt. These plants have a distinguished microbiome due to their particular and structurally divergent active secondary metabolites. These secondary metabolites present the major reason for their high specificity for related microorganisms (Qi et al. 2012). Soil microbiomes of desert environments are more abundant in Gram-positive bacteria related to pathogen suppression. These authors observed an evident selection of specific microbes by plants, as well as highly specific diazotrophic communities that demonstrated the importance of plant species on microbial diversity. Moreover, they found *Bacillus* spec. div. strains were able to promote plant growth and improve flavonoid production. These results emphasize the numerous connections between the plant microbiome and the plant metabolome.

Several surveys have demonstrated that the soil microbiome diversity has been reduced due to the intensification of land use in the agriculture (Maeder et al. 2002; de Vries et al. 2013), This demonstrates some of the negative effects of agriculture on the environment and the unsustainability of agricultural production (Sala et al. 2000). The decline in soil biodiversity is sometimes discussed in terms of functional redundancy. Functional redundancy suggests that different species can have the same function in an ecosystem, and therefore declines in species diversity do not necessarily affect ecosystem functioning. Research by Philippot et al. (2013) counters this viewpoint, suggesting that microbial diversity loss can affect ecosystem processes.

Mendes et al. (2015) hypothesize that the microbial community diversity and functional diversity are much lower in undisturbed than disturbed soils, with consequences for functional redundancy in the soil microbiome. To explain this hypothesis in detail, they used soil DNA shotgun metagenomics to assess the soil microbiome in a chronological sequence of land use with native forest, followed by deforestation and cultivation of soybean and pasture in different seasons. The results obtained by these authors demonstrated that an agriculture and pasture soil shows the most diversity and higher functional redundancy. Conversely, the equilibrium in forest ecosystems was maintained with a lower diversity and higher abundance of microorganisms. These results indicate that land use is an important factor in the composition of the soil microbiome. Knowledge of the diversity of the soil microbial community could help in the identification of microbial candidates to act as PGPMs and for development of inoculant products.

6.3 Biological Nitrogen Fixation

Nitrogen (N) is one of the most important elements for plant development because it is an essential part of nucleic acids, enzymes, and proteins. Seventy-eight percent of N is in gaseous form. Despite this, N is unavailable to plants and is thus considered one of the most growth-limiting nutrients (Dalton and Krammer 2006). To become

available to plants, atmospheric nitrogen (N_2) needs to be modified or fixed to ammonia (NH_3) by nitrogen-fixing microorganisms (Kim and Rees 1994). Biological nitrogen fixation (BNF) contributes to two-thirds of the nitrogen fixed worldwide. Mild temperature is generally one of the conditions that promotes BNF by diazotrophic microorganisms, which are dispersed in nature (Raymond et al. 2004).

Microorganisms with BNF activity are separated into groups as being (a) symbiotic N_2 -fixing bacteria, including the rhizobiaceae family (Ahemad and Khan, 2012b); (b) non-leguminous trees (e.g. *Frankia*); and (c) non-symbiotic (free living and endophytes) nitrogen-fixing forms like cyanobacteria *Anabaena*, *Nostoc*, *Azospirillum*, *Azoarcus*, and others (Battacharya and Jha 2012). Non-symbiotic microorganisms provide a small amount of the fixed nitrogen that is required by plants (Glick 2012) due to the limitation of carbon and the inhibition of nitrogenase by oxygen, which is the enzyme responsible by nitrogen fixation (Oldroyd and Downie 2004).

For the purpose of acquiring nutrients, plants have formed symbiotic interactions with microorganisms such as legumes and rhizobia. In this symbiosis, the bacteria penetrate the plant root and remain restricted in intracellular space, such as nodules, where N_2 is transformed into ammonia, which is then absorbed by plants (Oldroyd and Downie 2008).

6.3.1 Molecular Signaling in Nitrogen-Fixing Bacteria

The molecular communication between plant and bacteria occurs due to the detection of flavonoids and related molecules that are secreted from legume roots by rhizobia (Perret et al. 2000). Flavonoids are transcriptional regulators recognized by NodD proteins that bind to a signaling molecule and have the possibility to activate gene expression (Long 1996).

The formation of nodules in legume roots is activated by nodulation (Nod) components (NC), which are signaling molecules that induce developmental changes in plants. Nod components have in their structure a chitin backbone with an N-linked fatty acid moiety connected with a non-reducing terminal sugar. Some modifications can occur in NC structure among species of rhizobia. These modifications can define the specificity between the rhizobia and the host plant (Oldroyd and Downie 2008).

Bacterial invasion normally happens by root hair cells or disruption of root cells. The entry via root hair cells begins by bacterial attachment to root hairs (Oldroyd and Downie 2004). Concurrently, cortical cells activate cell partitioning to establish the nodule meristem. The epidermal response to the entry of roots is correlated with the recognition of nodulation components that govern calcium spiking-subordinate signaling pathway, and with root hair distortion through a signaling pathway autonomous to calcium spiking. Cortical cell division is correlated with an increase in the concentration of cytokinin and auxin. Transcription factors (TFs) from nodulating signaling pathway, NSP1 and NSP2, are essential for nodulation and are obligatory in the epidermis with induction of initial nodulation genes (INODs), cortical cell division, and nodule inception (NIN). These TFs are responsible for activating NC gene expression. In disruption invasion, violation occurs through the epidermis and the microbes receive

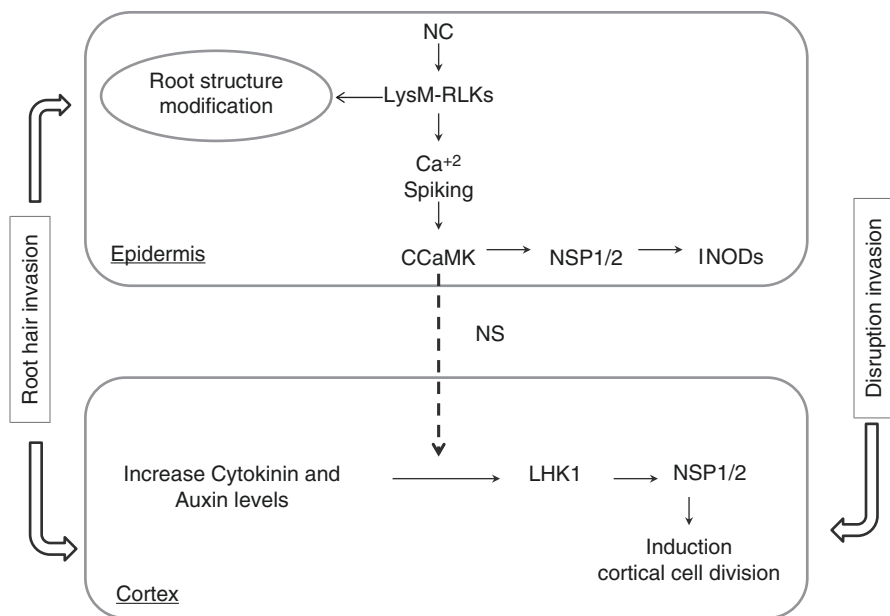


Fig. 6.1 Changes in the roots during the nodulation process. *NC* nodulation components, *INODs* initial nodulation genes, *NS* nodule start, *LysM-RLK* lysin motif receptor kinase, *LHK1* Lothusthistidine kinase (Adapted from Oldroyd and Downie 2008)

access to cortical cells. The relation with Nod components is considered important in some species, which endure disruption entry, but NC-independent of disruption invasion also exists and may be associated with rhizobial modifications of cytokinins (Fig. 6.1) (Oldroyd and Downie 2008; Oldroyd et al. 2011).

After the nodule formation occurs, the bacteria enlarge and differentiate into nitrogen-fixing forms, and are denominated as bacteroids. These bacteroids are surrounded by plant membrane, known as a symbiosome that is a kind of organelle, which has the function of reducing nitrogen (Oldroyd and Downie 2004).

The enzyme responsible for nitrogen fixation in diazotrophs is generally molybdenum nitrogenase. As an alternative to molybdenum nitrogenase, some diazotrophic microorganisms have vanadium and/or iron nitrogenases. The structure of the molibdenum nitrogenase enzyme is composed of *nifDK* and *nifH* genes (Rubbio and Ludden 2008).

6.3.2 Optimization of Elements of Biological Nitrogen-Fixing System

One of the main topics discussed in the Edinburg Declaration on Reactive Nitrogen (2011) was related to improving nitrogen availability to plants (Gutierrez 2012). Here we can consider biological nitrogen fixation (BNF) (Galloway et al. 2004).

Due to the importance of BNF in decreasing the necessity for chemical nitrogen fertilizers, it will be interesting to understand how to improve the biological process. For this, we can verify what happens during the optimal use of a nitrogen-fixing system, search for new plant-microorganism fixing associations, and transfer the ability of BNF to non-fixing microbes (Olivares et al. 2013).

There are many ways to improve the BNF through legumes, like legume adoption by farmers during combined cultivation and rotations between crops (Sessitsch et al. 2002). With the purpose of maximizing BNF by legumes, nodulation with the appropriate rhizobia should be evaluated. However, there are soils with low numbers of compatible rhizobia, thus it is necessary to carry out inoculation and to select an inoculant strain. For the selection of this strain it is necessary to verify the bacterial compatibility and nitrogen-fixing efficiency with the plant. Moreover, environmental conditions need to be analyzed because they may limit BNF activity and periodical inoculation must also be adopted (Hungria et al. 2005).

The election of inoculants is usually based on existing microbe diversity. Therefore, there are some genetic modifications that can be done with the purpose of enhancing the BNF of a given strain, by reiteration or overexpression of genes related to nitrogenase enzyme activity. Peralta et al. (2004) investigated improving the symbiotic efficiency in *Rhizobium etli* – *Phaseolus vulagris*. With the purpose of improving nitrogenase production, these authors built a chimeric *nifHDK* operon regulated by a strong *nifHc* promoter and verified it in symbiosis with *P. vulgaris*. Bacterial strains with overexpression of nitrogenase had increased nitrogenase activity, plant weight (improved around 32%), concentration of nitrogen in plants and seed, and seed yield. Moreover, the overexpression of the chimeric *nifHDK* operon contributed to increased symbiosis. In another study, Wang et al. (2013) recognized a cluster consisting of nine *nif* genes in the genome of *Paenibacillus* sp. WLY78. With the purpose of analyzing the genetic requirements for fixing nitrogen, they inserted a *Paenibacillus nif* gene cluster in *Escherichia coli*. A minimum *nif* gene cluster allows the production of active nitrogenase in *E. coli*. However, on deletion analysis it was verified that in addition to the core *nif* genes, *hesA* (one of the genes of *nif* clusters) participates in an important aspect on nitrogen fixation and is sensitive to molybdenum. Wang et al. (2013) wanted to demonstrate the possibility of transferring the BNF activity with a short set of *nif* gene cluster. Breeding for enhanced nitrogen fixation is not an easy task, but you can analyze characteristics such as plant and seed yield, and others, to quantify the efficiency of BNF (Olivares et al. 2013).

6.4 Phosphorus in Soil

Phosphorus and nitrogen are important to keeping a healthy nutritional life for plants, but, unlike nitrogen, phosphorus is not present in large amounts that can become available to plants.

Many peculiarities are associated with phosphorus nutrition and this element shows an important role in metabolic processes (Khan et al. 2010). Microbial associations are associated with P-fixation as with N-fixation in legumes. Phenological

development, crop yield, and resistance to plant diseases are also described in relation to P nutrition (Hao et al. 2002).

A considerable amount of inorganic P is quickly retained in insoluble mineral complexes after frequent application of phosphate fertilizers (Rodriguez and Fraga 1999; Igual et al. 2001). The retention of P is around 75% of the total amount applied. Organic forms (20–80% of P in soils) are the other important storage of immobilized P (Richardson et al. 1994). Phosphorus is present in soil on average at around 0.05% (w/w); however, only 0.1% of it is usable by plants (Zhu et al. 2011). Physicochemical (adsorption – desorption) and biological (immobilization-mineralization) means are responsible for soil P dynamics and consequently for P fixation. Most P that is administrated as fertilizer becomes static through a condensation reaction with Al^{3+} , Fe^{+3} , and Ca^{+2} (Hao et al. 2002).

The application of chemical fertilizers represents an extra cost to agricultural production and moreover causes negative impacts on different environments (Tilman et al. 2001). Reduction of fertility by lost microbial diversity, which consequently reduces the crop yields, is also observed (Gyaneshwar et al. 2002). Beyond that, P has limited sources in rock phosphate and there are estimations that the reserve of P will be exhausted in the current century (Cordell et al. 2009). The high cost of P chemical fertilizers and problems with P availability make it necessary to search for an environmental alternative and a production strategy for improving crop yields without environmental problems. One option available to achieve this purpose is the use of microbe inoculated fertilizer with P-solubilizing properties in agriculture (Sharma et al. 2013).

6.4.1 Phosphorus-Solubilizing Microorganisms

In 1903 the natural occurrence of phosphorus-solubilizing microbes (PSMs) was observed. These have the ability to use diverse means to solubilize and mineralize P, with the purpose of converting inorganic and organic soil P into available forms for plants (Khan et al. 2007).

Bacteria represent the majority of the microbial community with 1–50%, with fungi constituting only 0.1–0.5% of the total respective population. Several species of bacteria and fungi have been tested in relation to their potential as a PSM. Generally, these microbes are found in the phytomicrobiome and soil areas with P deposits. The isolation can be done by serial dilution methods or through enhancement culture techniques (Zaidi et al. 2009). Another area that a PSM could be isolated in is in stressful environments, such as the moderately halophilic bacterium, *Kushneria* sp., found by Zhu et al. (2011), in the solid residue of Daqiao saltern on the east coast of China, YCWA18.

Many factors could affect the potential of these PSMs, such as the amount of iron ore, temperature, carbon, and nitrogen origin. One of the biggest problems that generates controversy is the source of insoluble P used to isolate PSMs: tricalcium phosphate (TCP). The TCP is able to select a huge number of isolates. However, when these isolates are evaluated in relation to the available P provided to plants,

many of them fail as PSMs because there are often other sources of P that are less soluble than TCP such as iron/aluminum/calcium phosphate (Bashan et al. 2013).

Soil is complex and shows a lot variation depending on pH and chemical properties; in this way no P source can be used as a universal selection factor. Thus, the best way to assess how these microbes are evaluated is in which type of soil (alkaline, acid, or rich in organic matter) the PSMs will be applied. Bashan et al. (2013) suggested the use of specific compounds such as calcium phosphate (alkaline soils), iron/aluminum phosphate (acidic soils), and phytases (organic soils). The PSMs that show greater solubilization *in vitro* are selected for field trials before the production of biofertilizer (Sharma et al. 2013).

Excessive numbers of microorganisms show PSM capacity, and include bacteria, fungi, and actinomycetes. Among the bacterial communities, *Pseudomonas* and *Bacillus* have been described as PSMs. Some of the bacteria with PSM skills are *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium*, *Delftia* sp. (Wani et al. 2005), *Enterobacter* sp., *Pantoea*, *Klebsiella* (Chung et al. 2005), *Vibrio proteolyticus*, *Xanthobacter agilis* (Vazquez et al. 2000) (Sharma et al. 2013), and *Burkholderia* (Inui-Kishi et al. 2012).

There are some nitrogen-fixing microorganisms such as rhizobia that have also shown PSM activity (Ahemad and Kibret 2014; Zaidi et al. 2009). Among fungi *Penicillium* and *Aspergillus* represent the most effective solubilizers (Reyes et al. 2002).

6.4.2 Mechanisms of P-Solubilization by Soil Microbial Communities

Microorganisms are able to increase the ability of plants to obtain P from soil through different mechanisms, such as increased root extension by mycorrhizal associations, or by hormonal stimulation of root hair development and root growth (Hayat et al. 2010; Richardson and Simpson 2011). Another method is through metabolic mechanisms that are efficient in providing unavailable P present in soil as organic and inorganic forms (Fig. 6.2). Moreover, the existence of labile C in these microorganisms appears as a reservoir of P, through immobilization. Thus, the

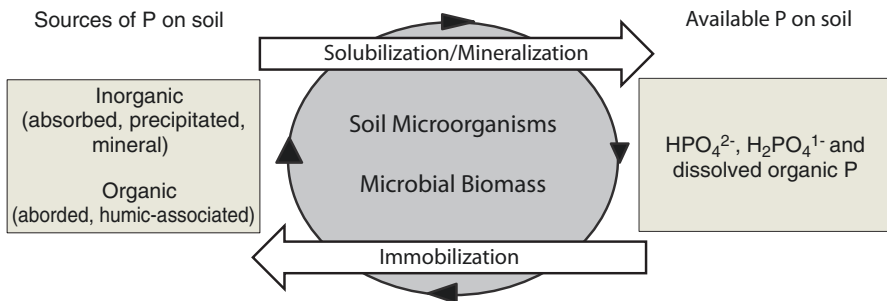


Fig. 6.2 Diagram of phosphorus cycle (Adapted from Richardson and Simpson 2011)

dispensation of P retained by microbes occurs when the cell dies (Richardson and Simpson 2011).

6.4.3 Inorganic P-Solubilization

The majority of available inorganic phosphate is H_2PO_4^- , which normally occurs at a lower pH. Nevertheless, with the increase in pH, other phosphate forms such as HPO_4^{2-} and HPO_4^{3-} become more predominant.

The availability of inorganic P through PSMs occurs mainly by organic acid production (Zaidi et al. 2009). Other ways include: lowering pH by H^+ extrusion (Parks et al. 1990), improved capitation of cations ligated with P, or establishment of a soluble compound with metal ions (calcium, aluminum, and iron) that releases P (Maliha and Samina 2004) and the release of protons accompanying respiration or NH_4^+ assimilation when the solubilization occurs without acid production (Illmer and Schimer 1995). The effect on pH is due the liberation of organic acid, originated from microbial metabolism, mostly by oxidative respiration or fermentation processes (Trolove et al. 2003). The predominant acids that are related to PSM activity are gluconic, oxalic, citric, succinic (Khan et al. 2007), lactic, tartaric (Venkateswarlu et al. 1984; Khan et al. 2007), and aspartic (Venkateswarlu et al. 1984) acids. There are also inorganic acids (sulphur and nitric acid) (Siqueira and Franco 1988). One example of higher potential in solubilizing P is caused by gluconic and 2-keto gluconic acids synthesized by direct oxidation in *Erwinia herbicola* and *Pseudomonas cepacea* (Goldstein et al. 1993; Goldstein 1994; Goldstein 1995). The capacity of PSMs to utilize inorganic phosphate is regulated by specific genes. Understanding these genes is very important because it is possible to use them in biotechnology applications. Genes correlated with PSMs are glucose dehydrogenase (GDH), gluconate dehydrogenase (GADH), and pirrolo-quinoline–quinone (PQQ), which are already identified and cloned in different bacteria (Sashidhar and Podile 2010). However, the recombinant bacteria that express these genes need to be studied in more depth and approved by regulatory laws, because the use of these PSMs can enhance the eutrophication of rivers (Siqueira et al. 2004). Fraga et al. (2001) observed accumulation of extracellular phosphatase when the *napA* phosphatase gene from *Morganella morganii* was cloned in *Burkholderia cepacia* IS-16 (strain used for inoculant). There may be more advantages in developing genetically modified microorganisms (PSMs) over transgenic plants for improved plant development. It is possible to combine more than one plant growth–promoting characteristic in a unique organism, and develop an inoculant that can be used for different cultivated plants (Ahemad and Kibret 2014; Rodriguez et al. 2006). Molecular genetics yield information that elucidates the mechanisms associated with PSMs. Comparative genomic and transcriptomic sequencing of the microbiome, and differential gene expression analyses have found potential targets such as enzymes, metabolites, and transport proteins that are related to the PSM process that leads to the enhancement of P availability and use by plants (Krishnaraj and Dahale 2014).

6.4.4 Organic P-Solubilization

While inorganic P becomes unavailable by precipitation and chemical adsorption, the organic P is retained in the organic matter of soil (Sharma et al. 2013).

Organic P represents 30–80% of the total soil (Menezes-Blackburn et al. 2013). It is found as inositol phosphate (30–50% of total amount of organic P), nucleic acids, and nucleotides (3–5%), phospholipids, and others (low quantities) (Siqueira et al. 2004). The use of organic P by plants and microbes requires hydrolysis of organic P from soil (Richardson and Simpson 2011; Sharma et al. 2013). Hydrolysis is known as the mineralization of organic P in soil and occurs mainly by the action of phosphatase enzymes (Fig. 6.3).

In general, fungi have more hydrolytic activity on phytate than bacteria; however, bacteria and plants can produce phytate. The nucleases are mainly produced by rhizospheric microorganisms and phospholipases by actinomycetes (Siqueira et al. 2004).

Phytate is the main stock form (60–80%) of organic P in several soils and plant tissues (1–5% of weight) (Singh and Satyanarayana 2011). In plants, phytases cause the liberation of P from phytate degradation. However, the capacity of plants to obtain P immediately from phytate is very limited. *Arabidopsis* plants supplemented with phytate were considerably benefited with P when they were engineered with the phytase gene (*phyA*) originated from *Aspergillus niger* (Richardson et al. 2005).

Phosphatases are a class of abundant enzymes that are used by PSMs and are widely present in studies. These enzymes can be set into acid and alkaline phosphatase, according to soil characteristic (acid or alkaline) (Jorquera et al. 2008). In plants the production of acid enzymes is more predominant than alkaline phosphatase, suggesting that this is a specific characteristic of PSMs (Criquet et al. 2004).

Microorganisms are the main source of phosphorus mineralization enzymes (Richardson 1994). The activity and synthesis process of these enzymes depends on environmental conditions that are suppressed with high contents of phosphorus or stimulated in limited conditions. In conditions with low availability of P, bacteria have the ability to acquire P in their biomass, which at the final cycle will be mineralized and become available to plants and other organisms (Gyaneshwar et al. 2002).

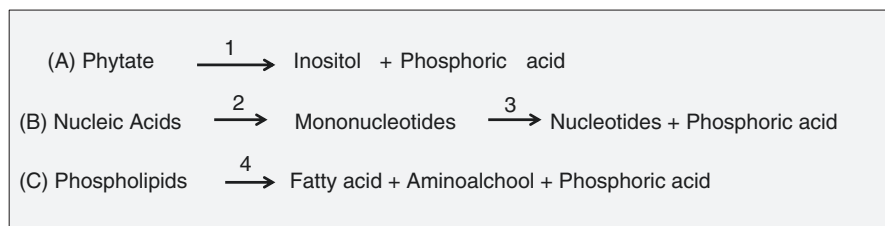


Fig. 6.3 Mineralization reaction of organic phosphorus by (1) phytases, (2) nucleases, (3) nucleotidases, (4) phospholipases (Adapted from Siqueira et al. 2004)

6.5 Phytohormone Production

A phytohormone is defined as an organic signal molecule synthesized in plant organs or tissues that can be translocated to other regions and presents a specific response. However, phytohormones can also be active in tissues where they are created (Baca and Elmerich 2007). Their production has been studied as one of the main instruments by which PGPMs may increase plant growth (Iqbal and Hasnain 2013).

Auxins, cytokinins, gibberellins, ethylene, and abscisic acid are classes of widely recognized phytohormones (Zahir et al. 2004).

In nature, two modes of phytohormones are accessible to plants. They are endogenous production by the plant tissues, and phytohormones that are made available by associated microbes (Patten and Glick 1996).

Fungi inoculants are advantageous compared with bacterial ones because of their efficiency at spreading over the rhizosphere. *Trichoderma* species represents a class of fungi found in the rhizosphere. *Trichoderma* strains can colonize plant roots and improve plant progress in growth and development. These effects are influenced by microbial production of indole-3-acetic acid (IAA) and indolic compounds (Ortíz-Castro et al. 2009).

During plant growth and development, signaling molecules intermediate the contact with microorganisms, performing a relevant communication. Microbes have the means to recognize a plant host and start colonizing the rhizosphere by production of plant growth-regulating substances like phytohormones. Furthermore, these microbial-produced compounds are perceived by plants, which respond and further influence the type of microorganisms found. This represents a molecular conversation that determines the relationship between plants and microbes from pathogenesis to symbiosis (Bais et al. 2004).

Many bacteria and fungi can produce auxins using different pathways, which increases the potential to form associations with plants. Moreover, epiphytic and rhizospheric microfloras of plants are of utmost relevance in the conversion of tryptophan (which is present in plant exudates) into IAA (Tsavkelova et al. 2006).

The main known phytohormone is IAA. At least 80% of the rhizospheric bacteria synthesize IAA (Patten and Glick 1996). In addition to IAA, other indolic compounds that are physiologically active for plants are also produced by rhizospheric microbes (Lebuhn et al. 1997; El-Khawas and Adachi 1999).

On the other hand, IAA and cytokinins derived from bacteria are also related to the virulence of several interactions between microorganisms like genus *Agrobacterium*, *Pseudomonas*, and pathogenic *Erwinia* (Lichter et al. 1995; Morris 1986; Spaepen et al. 2007).

Cytokinins are other relevant phytohormones. The physiological effect of cytokinin is the enhancement of cell division (Frankenberger and Arshad 1995). Although it is difficult to identify these molecules, they can be detected using bioassays (Nieto and Frankenberger 1990).

Microorganisms have the ability to synthesize kinetin, zeatin, isopentenyladenine, and other cytokinin derivatives. Rhizobacteria of the genera *Azotobacter*, *Azospirillum*, *Arthrobacter*, *Bacillus*, *Rhizobium*, *Pseudomonas*, and also streptomycetes are capable of synthesizing cytokinins (Tsavkelova et al. 2006).

PGPMs also produce gibberellins (GAs). There are over 89 known GAs (Dobbelaere et al. 2003), which are numbered GA1 through GA89 in approximate order of their discovery (Frankenberger and Arshad 1995; Arshad and Frankenberger 1998). The most accepted gibberellin is GA3, while the most active is GA1. The main physiological role of gibberellins is stem elongation and increased internode length (Davies 1995).

The fourth phytohormone to be discovered is abscisic acid (ABA). This was detected by radioimmunoassay or thin-layer chromatography in supernatant cultures of plant-associative bacteria *Azospirillum* and *Rhizobium* sp. (Dangar and Basu 1987; Dobbelaere et al. 2003). ABA responses are related to stomatal closure and root proliferation. Therefore, its presence in the rhizosphere is of paramount relevance for plant growth in water-deficient environments (Frankenberger and Arshad 1995).

Ethylene is another important phytohormone. Its role is related to root elongation inhibition, auxin transport, senescence, and abscission promotion of various organs, and fruit ripening (Bleecker and Kende 2000; Glick et al. 2007). Reducing levels of ethylene in plants may be one of the growth-promoting activities of PGPMs. These reductions are due to the activity of enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces ACC, the precursor of ethylene (Yang and Hoffman 1984).

Cadaverine, a poliamine that enhances root growth and helps to reduce osmotic stress, was reported in rice inoculated with *Azospirillum brasilense* Az39 (Cassán et al. 2009).

6.5.1 Applications

Associative rhizobacteria may provide favorable progress in plant development due to production of phytohormones, nitrogen fixation, biosynthesis of antimicrobial substances, and enhanced water or mineral nutrition uptake (Saharan and Nehra 2011).

There are many reports presenting the beneficial impact of bacteria inoculation on orchids. An early paper was published by Knudson (1922), who inoculated the seeds of *Epidendrum* and *Laeliocattleya* with a diazotrophic strain, *Rhizobium leguminosarum*, to stimulate germination. Wilkinson et al. (1989, 1994) described the propagation of *Pterostylis vittata* seeds co-inoculated with a mycorrhizal fungus and strains of orchid-associated bacteria belonging to *Pseudomonas putida*, *Bacillus sphaericus*, *B. cereus*, and *Arthrobacter* sp.

The *in vitro* germination of mature seeds of the species *Dendrobium moschatum* was enhanced by inoculation of bacterial cultures (Tsavkelova et al. 2007). Seed germination was enhanced by *Mycobacterium* sp. and *Sphingomonas* sp. in *in vitro* inoculations.

Strains of *Bacillus* sp. and *Enterobacter* sp. isolated as endophytic bacteria were used to stimulate *Cattleya walkeriana* seedlings. This was done by increasing such characteristics as fresh weight, dry weight, and plant survival during *ex vitro* acclimatization, which is considered the bottleneck stage for orchid seedling

propagation (Galdiano Júnior et al. 2011). One of these isolates, *Enterobacter asburiae*, produces an acid ectophosphatase, which can be a mechanism for the solubilization of mineral phosphates (Sato et al. 2016), configuring a PGPM with two growth-promoting activities (IAA production and solubilization of mineral phosphate).

Growth promotion was also observed when seedlings of *Cattleya loddigesii* generated *in vitro* were inoculated with a bacterial suspension of *Paenibacillus lentimorbus* and *P. macerans* strains (Faria et al. 2013). *Sphingomonas paucimobilis* ZJSH1 significantly promoted the growth of *D. officinale* seedlings, enhancing fresh weight and stem length (Yang et al. 2014).

6.6 The Importance of Siderophores

The siderophore is a biological molecule produced by various bacteria and has wide applications in various fields, such as improving soil fertility in agriculture. Bacterial strains that do not use any other means of biocontrol can act as biocontrol agents by using the siderophores that they produce. Therefore, siderophores from PGPMs prevent phytopathogens from acquiring iron and can be a limiting factor for their proliferation (Kloepper et al. 1980).

Available results indicate PGPM siderophores have a much better affinity for iron than to pathogens (Schippers et al. 1987). As a result, lack of iron in the rhizosphere incapacitates proliferation of fungal pathogens. By reason of biocontrol, PGPMs out-compete fungal pathogens for accessible iron.

However, plant growth is not altered by the iron reduction in the rhizosphere caused by the siderophores, because most plants use less iron than microorganisms (O'Sullivan and O'Gara 1992). Also, some plants can bind and consequently make up the biocontrol PGPM iron-siderophore complex (Bar-Ness et al. 1991; Wang et al. 1993).

6.7 Mycorrhizae

Mycorrhizal symbioses are widespread and common in terrestrial ecosystems around the globe, occurring in nearly all soils (Smith and Read 2008). The symbiotic fungi are often crucial for absorbing water and nutrients from the soil and transferring them to plants (Orwin et al. 2011).

Mycorrhizae are grouped into two types: ectomycorrhizae and endomycorrhizae. Endomycorrhizae are defined by dense mycelial sheaths near the roots with intercellular hyphal invasions of the root cortex. They are limited to forest trees in temperate regions. All other plants represent endomycorrhizae, characterized by fungi forming external hyphal networks in the soil and penetrating the cortical cells of roots (Bolan 1991).

Mycorrhizal fungi are known to secrete phytohormones such as GA₃, IAA, ABA, zeatin, and zeatin riboside (Wu et al. 2002; Liu et al. 2010). The mycorrhizal

fungus *Trichoderma* sp., isolated from *Pleione bulbocodioides*, increased seed germination up to 84.6%, while the control presented lower germination (77.6%) on OMA medium (Yang et al. 2008).

Pathogenic and growth-promoting fungal species are IAA yielders (Tsavkelova et al. 2006). Four different *Fusarium* species isolated as endophytic fungi from *Dendrobium moschatum* also produced IAA (Tsavkelova et al. 2003, 2012), while mycorrhizal fungus in association with *Dendrobium densiflorum* produced vitamins and GA (Wu et al. 2002).

6.8 Alternative Use of Plant Growth-Promoting Microorganisms

Several bacterial genera are necessary elements in maintaining the balance of soils. They are implicated in distinct biotic activities of soil ecosystems, making them a functional for nutrient turnover and enhancing maintenance for agricultural production (Ahemad et al. 2009; Chandler et al. 2008). The association of plants with bacteria can be considered good, pernicious, or neutral depending on the motif of their action on plant growth (Dobbelaere et al. 2003).

The use of PGPMS has become a habitual practice in various regions of the world. PGPMS are native to the soil and plant rhizosphere, and play an important function in biological control of plant pathogens, suppressing a broad spectrum of bacteria, fungi, and nematodes. PGPMS can also give protection against viral diseases (Sivasakthivelan et al. 2013).

Bacteria in the genera *Agrobacterium*, *Bacillus*, *Burkholderia*, *Pseudomonas*, and *Streptomyces* are frequently studied biocontrol agents. They eliminate plant disease through at least one mechanism: induction of systemic resistance and production of siderophores or antibiotics (Tenuta 2003). Among others, actinobacteria commonly inhabit the rhizosphere making it possible to characterize them as PGPMS (Franco-Correa and Chavarro-Anzola 2016).

These microorganisms are found very close to the roots epidermis, which secretes signal molecules for defense versus invasion of distinct microorganisms in the root area. At this stage, the distinction takes place between symbiotic, associative, pathogenic, or neutralistic association of the microorganisms with the plant (Hayat et al. 2010).

PGPM strains occur in many taxonomic groups and are present in the rhizosphere of plants in any given soil (Kyselková et al. 2009; Almario et al. 2013). This suggests that PGPMS colonize and coexist in the same rhizosphere soil as non-PGPM groups of the bacterial community. Studies have shown the existence of a particular gene (Table 6.1) and of relevant properties of PGPMS, which provide positive effects on plant growth, health, and their ability to inhibit phytopathogens (Bertrand et al. 2001; Barriuso et al. 2005; Upadhyay et al. 2009).

The biological control lineage *Pseudomonas fluorescens* Psd was analyzed for IAA organic synthesis and the logical preparation on it as a PGPM. While the indole pyruvic acid (IPyA) route usually connected with PGPMS was absent, the indole

Table 6.1 Gene functions of plant growth-promoting microorganisms studied in plants

Function	Gene	Phylum	References
Phosphate solubilization	<i>pqqB</i> <i>pqqC</i> <i>pqqD</i> <i>pqqE</i> <i>pqqF</i> <i>pqqG</i>	Proteobacteria	Bruto et al. (2014)
2,4-Diacetylphloroglucinol synthesis	<i>phlA</i> <i>phlB</i> <i>phlC</i> <i>phlD</i>		
Hydrogen cyanide synthesis	<i>hcnA</i> <i>hcnB</i> <i>hcnC</i>		
Acetoin/2,3-butanediol synthesis	<i>budA</i> <i>budB</i> <i>budC</i>		
Nitric oxide synthesis	<i>nirK</i>		
Auxin synthesis	<i>ipdC</i> <i>ppdC</i>		
ACC deamination	<i>acdS</i>		
Nitrogen fixation	<i>nifD</i> <i>nifH</i> <i>nifK</i>		
Biosynthesis of tryptophan	<i>Trp</i>		Zahir et al. (2010)
Nitrogenase	<i>nifH</i>	Actinobacteria	Valdés et al. (2005) Gauthier et al. (1981)
Nitrogenase	<i>nifDK</i>		Fedorov et al. (2008)

acetamide (IAM) pathway is commonly noticed in plant pathogens and was expressed in the Psd strain. Overexpression of IAM pathway genes *iaaM-iaaH*, from *P. syringae* subsp. *savastanoi* radically increased IAA levels and demonstrated a prejudicial effect on sorghum root development (Saranraj et al. 2013; Sivasakthivelan and Saranraj 2013).

PGPMs are efficient in secreting molecules as antibiotics into the rhizosphere to control pathogenic microbes, producing iron-chelating molecules (Raaijmakers et al. 2002). They also induce phytoalexin production in association with plants, and have broad acceptance as providing an agricultural advantage (Lifshitz et al. 1986; Halverson and Handelsman 1991). Phytoalexins are antimicrobial compounds with low molecular weights that are both synthesized by and accumulated in plants after exposure to microorganisms (Dakora 1985; Dakora et al. 1993; Van Peer et al. 1990, 1991).

In the rhizosphere of various leguminous and non-leguminous crops, species of *Pseudomonas* and *Bacillus* have been identified (Table 6.2) that help in plant colonization and suppression of phytopathogens (Parmar and Dufresne 2011).

Table 6.2 Plant growth-promoting microorganisms (PGPMs)

PGPM	PGPM and agricultural crop	Plant growth promoting traits	References
<i>Bacillus cereus</i> UW 85	Grain legumes	Lowers the toxicity of chromium to seedlings by reducing Cr (VI) to Cr (III)	Vessey and Buss (2002)
<i>P. fluorescens</i> CHA0	<i>Arabidopsis</i> sp.	Increased plant growth	Iavicoli et al. (2003)
<i>Bacillus</i> spp.	Banana	Promoted significantly the root and shoot growth	Jaizme-Vega et al. (2004)
<i>P. putida</i> KD	Tomato and cucumber	Promoted the plant growth, reduced Pb and Cd uptake	Rezzonoco et al. (2005)
<i>P. fluorescens</i> PCL1606	Avocado	Increased plant growth	Cazorla et al. (2006)
<i>Bacillus</i>	Raspberry	Promoted significantly the root and shoot growth	Orhan et al. (2006)
<i>B. pumilus</i>	Wheat variety Orkhon	Increased plant growth	Hafeez et al. (2006)
<i>B. mucilaginosus</i>	Cucumber	Increased plant growth	Han et al. (2006)
<i>B. mucilaginosus</i>	Pepper	Increased plant growth	Supanjani et al. (2006)
<i>P. Marginali</i>	Indian mustard and rape	Increased plant growth	Belimov et al. (2007)
<i>P. oryzihabitans</i>			
<i>P. putida</i>			
<i>Alcaligenes xylooxidans</i>			
<i>P. brassicacaerum</i>			
<i>Agrobacterium amazonense</i>			
<i>Pseudomonas</i> BA-8	Strawberry	Increased plant growth	Pirlak and Kose (2009)
<i>Bacillus</i> OSU-142			
<i>Bacillus</i> M-3			
<i>Comamonas acidovorans</i>	Kiwi	Increased plant growth	Erturk et al. (2010)

PGPMs produce beneficial effects on plant health by accelerating nutrient availability, assimilation, and growth by suppressing diseases caused by phytopathogens (Franco-Correa and Chavarro-Anzola 2016). In the quest to improve soil fertility and crop yield while reducing the negative impact of chemical fertilizers on the environment, there is a need to exploit PGPMs for beneficial agriculture. Moreover, PGPMs can also prevent the deleterious effects of stresses from the environment (Paul and Nair 2008). They are also able to increase the capacity of plants to sequester heavy metals and can help plants withstand abiotic stresses (Jing et al. 2007; Saharan and Nehra 2011; Tak et al. 2013).

Bio-inoculants with diverse symbiotic (*Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*) and non-symbiotic (*Azomonas*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Klebsiella*, *Pseudomonas*) microbes are used to promote plant growth and development under various stresses like heavy metals (Ma et al. 2009a, b; Wani and Khan

2010), herbicides (Ahemad and Khan 2010), insecticides (Ahemad and Khan 2009), fungicides (Ahemad and Khan 2012a), and salinization (Mayak et al. 2004). Diverse varieties of rhizobacteria help to improve plant nutrition thus increasing plant health or stress tolerance (Vacheron et al. 2013).

Ferreira et al. (2010) showed similarities between cepacian exopolysaccharide (EPS) produced by members of the *Burkholderia cepacia* complex (BCC complex) and the EPS synthesized by *B. graminis*, *B. phytofirmans*, *B. phymatum*, and *B. xenovorans* (Estrada-De Los Santos et al. 2001). According to Ferreira et al. (2010), EPS may have a role in the tolerance of *Burkholderia* species to ion stress and desiccation.

Bloemberg and Lugtenberg (2001) showed the expression of some genes involved in the defensive response as well as genes expressed under conditions of drought, salt, and stress. The experiments with isolates of *B. graminis*, a species that has been isolated from the rhizosphere of pasture, corn, and wheat, resulted in an improvement in shoot height and neck diameter, as well as inducing a protective response to salt and drought stress in tomato plants (Barriuso et al. 2005, 2008).

PGPMs are able to produce gibberellic acid or ABA, or to control the level of these hormones in plants (Richardson et al. 2009; Dodd et al. 2010). The ABA is well known for its involvement in drought stress. Bauer et al. (2013) showed that during water stress, increases in ABA levels cause closing of stomata, thereby limiting water loss.

Habib et al. (2016), studying the ACC deaminase-containing PGPM isolate *Enterobacter* sp. UPMR18, concluded that it could be an effective bio-resource for enhancing salt tolerance and growth of okra plants under salinity stress. Microorganisms synthesizing the ACC deaminase enzyme can cleave ACC to α -ketobutyrate and ammonia, thus decreasing ethylene stress in plants (Rashid et al. 2012).

Ethylene is a simple gaseous hormone critical for many plant developmental stages (Abeles et al. 1992). The ethylene-mediated stress response can be activated by many environmental factors such as heavy metal contamination, high salinity, flooding, drought, and phytopathogens. Ethylene can also inhibit stimulation of cell proliferation and elongation by repressing auxin response factor synthesis (Dugardeyn and Van Der Straeten 2008). PGPMs, besides promoting plant growth by employing certain mechanisms and protecting the plant from salinity, can also increase plant tolerance against stress conditions (Shrivastava and Kumar 2015).

Conclusion

Understanding the mechanisms used by PGPMs enables the elucidation of their impact on nutrient cycling and on the protection of crops against disease. Moreover, functioning analysis, diversity, and gene expression patterns of PGPM populations in soil will be a precondition to developing a management action plan for sustainable agriculture. Future research and understanding of the mechanisms of PGPMs will pave the way to finding more competent rhizobacterial strains. These yet-to-be-found strains may work under diverse agro-ecological conditions to protect the environment, and produce enough food for an increasing world population.

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