

Chapter 3

Beneficial Microorganisms for the Management of Soil Phosphorus



Ioannis Ipsilantis, Mina Karamesouti, and Dionisios Gasparatos

Abstract The dependence of all life on phosphorus (P) availability has revealed serious P challenges such as the P deficiency in weathered and eroded soils, the high cost of phosphate fertilizers, the scarcity and unequal global distribution of rock phosphates, the regional over-accumulation of P and the agricultural non-point source P pollution. In this context, microorganisms capable of mobilizing P in the soil system may be applied as a low-cost technology to enhance plant growth and crop yields. Here we review the beneficial role of microorganisms, namely arbuscular mycorrhizal fungi and P-mobilizing bacteria, to mediate P availability and transform legacy P (insoluble, bound) into soluble forms.

We found that the arbuscular mycorrhizal symbiosis improves plant P nutrition, however, high soil P concentration is also known to suppress it. The effectiveness of the symbiosis depends on the richness of arbuscular mycorrhizal fungal species. Most studies show that arbuscular mycorrhizal fungal diversity and effectiveness are modified by soil management practices. Fertilization with slow-release inorganic fertilizers, organic fertilizers and mycorrhizal symbiosis gives satisfactory crop yields, but long-term studies are few. Bacteria are the predominant microorganisms that mobilize native and applied P in soils, as compared to fungi or actinomycetes. Strains from the genera *Pseudomonas*, *Bacillus* and *Rhizobium* have so far been recognized as the most powerful phosphate solubilizers. The principal mechanism for mineral phosphate solubilization is the production of organic acids, e.g. oxalic, citric, gluconic, tartaric, lactic, fumaric; and enzymes: phosphatases, phytases, phosphonates and C-P lyases.

I. Ipsilantis · D. Gasparatos (✉)
Soil Science Laboratory, School of Agriculture, Aristotle University of Thessaloniki,
Thessaloniki, Greece
e-mail: gasparatos@agro.auth.gr

M. Karamesouti
Department of Natural Resources Management & Agricultural Engineering,
Agricultural University of Athens, Athens, Greece

Keywords Soil phosphorus · Availability · Plant nutrition · Arbuscular mycorrhizal fungi · P – Mobilizing bacteria · Sustainable management

3.1 Introduction

3.1.1 Phosphorus Issues

Phosphorus (P) is a mineral nutrient with a key role in supporting global alimentation requirements. It is listed among the most essential elements for flora and fauna growth and evolution (Elser 2012). It is naturally occurring mainly from apatite and it is released through weathering processes (Lajtha and Schlesinger 1988). The released P ions can be either absorbed by CaCO_3 , Fe and Al oxides, or be incorporated into living organisms. Although P is usually abundant in soils, its availability to plants is limited, due to low solubility and soil fixation phenomena, resulting in plant growth restrictions (Gasparatos et al. 2006).

Although P fertilization is commonly used for achieving high agricultural productivity, in some areas, P fertilizers are used to prevent further land degradation and maintain even a basic level of productivity (Weikard and Seyhan 2009). The soil status, and mainly the type of parent material and the organic matter content, in combination with the climatic conditions, are important factors affecting the initial soil P concentration and availability. Indicatively, in areas with tropical climates, limited P concentration in soils suggests a significant issue for plant growth (Solomon and Lehmann 2000). In arid regions, the organic P compounds are typically in low percentages, due to the low soil organic matter (SOM) and water contents. Increases in temperature may also have a negative impact on the long-term soil P availability (Yu et al. 2016). Concerning the soil characteristics, soil aeration and saturated hydraulic conductivity appear as positively correlated to the available soil P, in contradiction to clay content and pH (Yu et al. 2016). In cases of compacted soils, limitations in plant root penetration reduce plants' capability to access the available soil P (Barzegar et al. 2016).

In an attempt to improve plant intake performance, P application from external sources was used as a common agricultural practice. Historically, soil fertilization with P was initially based on guano, human excreta and manure, while since the second half of the twentieth century, P fertilizers became the major source of this nutrient (Fig. 3.1).

In many developed countries, food production processes are highly dependent on phosphate fertilizers, with many reported cases of unsustainable over-fertilization (Yan et al. 2013). The irresponsible use of P, mainly due to its outwardly abundance and its low price, is lately attempted to be restricted (Sharpley et al. 2013). The cost of P-related environmental problems rehabilitation can no longer be considered insignificant. Governments are forced to increase investments, in an attempt to combat eutrophication caused by high quantities of phosphates which end up in aquatic

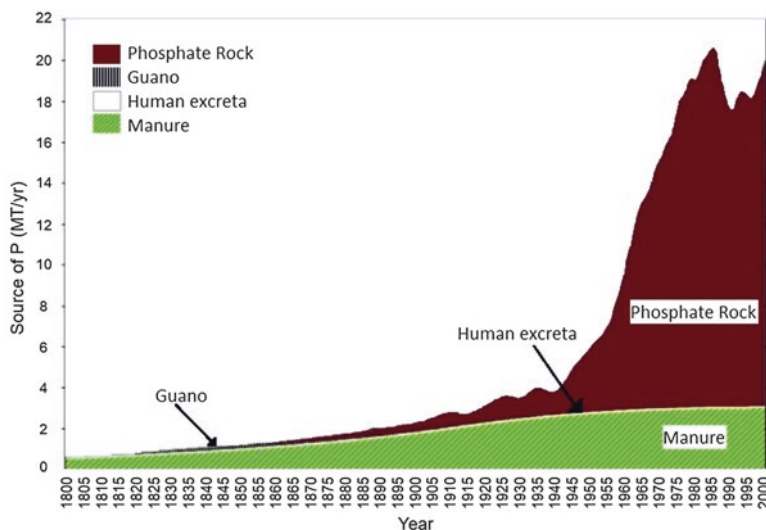


Fig. 3.1 Historical global sources of phosphorus (P) fertilizers (1800–2000). Increased food demand during nineteenth century, was met using manure as a P source. After mid-twentieth century, the Green Revolution was achieved through new agricultural practices including very high quantities of P fertilizers from mined phosphate rock. (Modified after Cordell et al. 2009)

systems (Dodds et al. 2008). However, the initial concerns for environmental problems, such as water pollution at the beginning and soil over-accumulation later, are lately evolved into Global awareness for potential socio-economic issues. Changes in alimentation preferences leading to increasing P demand, the significantly uneven spatial distribution of P on Earth and the uncertainty over the potential peak of global P production, suggest a new threat on food security (FAO 2015; ECSCU 2013; Cordell et al. 2012). Heckenmüller et al. (2014), discuss the unprecedented increase, in 2007–2008, of more than 900% of the prices in the global P trade. The export controls, such as those imposed by China in 2008, in order to protect its domestic supplies, can cause technical shortages and broader socio-economic turbulences. Under these circumstances countries with low or no P deposits are highly vulnerable to potential fluctuations in fertilizer and mineral P prices.

These concerns have opened an extensive debate about the quest of alternative sustainable use of P (Schröder et al. 2011; McLaughlin et al. 2011; Karamesouti and Gasparatos 2017). Some of these are summarized in P recycling procedures, such as P recovery from municipal and industrial wastewater, from other organic wastes, or from the soil itself, and in improved agricultural practices, targeting losses reduction from livestock rearing, crop cultivation or from any other losses in any level in the food chain (Rowe et al. 2016; Elser 2012).

Focusing on P recovery from soil, multiple approaches, providing economically feasible and environmentally friendly solutions, are already being developed (Table 3.1). The main common concept framing all these approaches is the reversibility of P fixation and the efficient use of its residual form.

Sattari et al. (2012) and Rowe et al. (2016) defined this residual P as the legacy P (P_{legacy}), described as

$$P_{\text{legacy}} = P_{\text{inputs}} - P_{\text{outputs}} - P_{\text{losses}}$$

Where

P_{legacy} = Legacy phosphorus

P_{inputs} = Phosphorus inputs to soils (fertilizers, manures)

P_{outputs} = Phosphorus removed by crop production

P_{losses} = Phosphorus losses (runoff and leaching)

and represents the P that has been accumulated in soils after continuous inputs of fertilizers and manures. In many cases, legacy P was reported as pollutant and major source of eutrophication of water bodies (Sharpley et al. 2013). However, efficient management of this potential pollutant could support adequate agricultural production without additional fertilization for many years (Rowe et al. 2016).

3.1.2 Beneficial Microorganisms and Soil Phosphorus

Among the strategies listed in Table 3.1, the use of microorganisms, such as fungi, bacteria and endophytes, in mobilizing legacy soil P is considered particularly environmental-friendly and of lower cost, compared to fertilization practices (Adhya et al. 2015; Sharma et al. 2013). Their populations are highly variable among different soil types, with the bacteria significantly predominating in proportion, compared to fungi, while the former might incorporate approximately 10–15% of the soil organic P (Richardson 2007; Khan et al. 2007). A plethora of microorganisms can be usually identified in close distance from plant rooting system, with which reciprocity relations are being established. The fundamental role of microorganisms is

Table 3.1 Strategies for improving the utilization of legacy soil P. Adapted from Rowe et al. 2016; Bindraban et al. 2015; Whithers et al. 2014; Shen et al. 2011

Soil – crop management	Plant breeding	Microorganisms
Depletion of readily available P at critical levels	Root genetic traits such as root elongation, branching and development of root hairs, and enhancement of early root growth	<i>Bacillus</i> , <i>Pseudomonas</i> and <i>Penicillium</i> genera
Maintain soil quality	Release of exudates, such as organic acids, carbon substrates and enzymes	Arbuscular mycorrhizal fungi
Modification of soil pH	Physiological alterations, i.e. low metabolic P demand and low photosynthetic needs	Bio-inoculant products
Tillage practices	Selecting crop varieties for high P – use efficiency	
Fertilizer inputs		
Crop rotation		

not restricted in making P accessible to plants, but they can also be used to improve plant growth and agricultural productivity with no further need for additions of chemicals (Sharma et al. 2013; Puente et al. 2009). Organic matter decomposition, soil detoxification and critical nutrients' assurance for the plants are some other main functions conducted by microorganisms' communities.

Since early twentieth century, the role of microorganisms in P mobilization processes was already discussed (Khan et al. 2007), while in 1948, Gerretsen had mentioned the contribution of bacteria in P plant nutrition under controlled conditions. In 1988, McLaughlin et al. studied the incorporation of native soil P, accumulated due to fertilization and plant residues, into the microbial biomass. However, the wide-scale applicability in uncontrolled environment is still a particularly challenging task. The microorganisms can be highly affected by inherent soil characteristics, such as soil temperature, pH, soil moisture content etc., and also by interactions between different species (Sharma et al. 2013; Richardson and Simpson 2011). In this regard, Richardson (2007), suggested two main strategies focusing on (a) *the management of existing microbial populations in order to optimize their capacity to mobilize phosphorus*, and (b) *the use of specific microbial inoculants that can increase phosphorus mobilization*.

Arbuscular mycorrhizal fungi and P – mobilizing bacteria are two broad categories of microorganisms mobilizing inorganic P and converting it into readily available to plant forms (Fig. 3.2). In this review, the mechanisms and the effectiveness of these microbes in P acquisition will be discussed.

The recognition of microbials' role to the improvement of soil P availability, highlights the need for detailed studies on the characteristics of the microbial communities, the interactions within the various soil environments, the impact of land management practices, as well as development of new technologies, in order to reach for promising solutions for efficient soil P management.

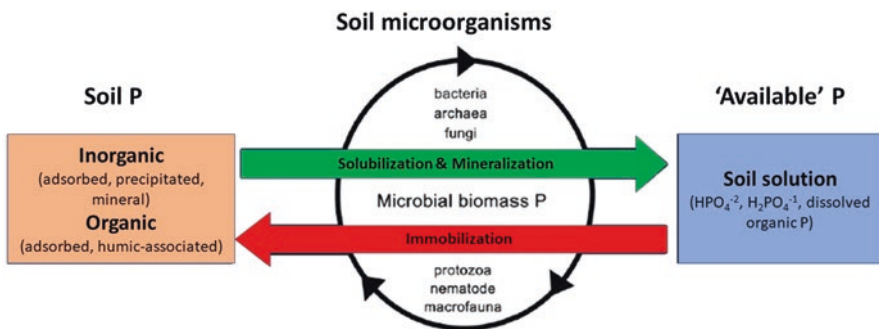


Fig. 3.2 The critical role of soil microorganisms in the cycling of phosphorus (P), which is the result of the biogeochemical processes of mobilization (solubilization/ mineralization) and immobilization (adsorption/precipitation). Modified after Richardson and Simpson 2011

3.2 Arbuscular Mycorrhizal Fungi

3.2.1 *The Symbiosis and P Uptake*

The arbuscular mycorrhizal fungi form symbiotic, mutually beneficial relations with plants in their roots. The plant provides photosynthetic carbon to the fungus and the fungus supplies nutrients with poor mobility in soil, particularly P (Smith and Read 2008). However, there is more to the symbiosis, as it is also known to suppresses losses to pathogens (Poza and Azcón-Aguilar 2007; Karagiannidis et al. 2002), provides drought (Augé 2001) and salt resistance (Evelin et al. 2009), may increase soil aggregation (Rillig and Mummey 2006) and increase resistance to potentially toxic elements (Burghel et al. 2015; Hildebrandt et al. 2007). There is a complex interaction between the partners and both the plant and the fungus, as well as the soil environment contribute to this complexity. As a result, although there are some well-known paradigms about the symbiosis, there are many cases that do not seem fit to the general dogma. For instance, a particular arbuscular mycorrhizal fungus-plant relationship was reported as parasitic (Modjo and Hendrix 1986).

It is well established that arbuscular mycorrhizal fungi improve plant P nutrition in soils with moderate or poor soluble P levels. At higher P levels the symbiosis is suppressed, manifested through lower root length colonization (Jensen and Jakobsen 1980). There is a threshold value of available P above which the carbon cost of the symbiosis is higher than the benefit of the arbuscular mycorrhizal pathway of P uptake and the plant response to arbuscular mycorrhizae is negative (Kahiluoto et al. 2000). This threshold may vary with the fungus, the plant and the environmental conditions, and may be determined by dose-response experiments showing how much P fertilizer can be saved by arbuscular mycorrhizal fungi, or how much P-fertilizer needs to be applied to achieve maximum yield with arbuscular mycorrhizal fungi (Ping et al. 2014; Medina et al. 1990; Elbon and Whalen 2015). At very low P levels addition of P increases the arbuscular mycorrhizal fungal colonization and the benefit of mycorrhiza to the plant, known as arbuscular mycorrhizae responsiveness (MR), calculated by: the ratio between the difference of arbuscular mycorrhizal fungal inoculated plant growth (DW_{AMF}) and non-inoculated plant growth ($DW_{control}$) over the non-inoculated plant growth, $MR = (DW_{AMF} - DW_{control}) / DW_{control} \times 100$. The symbiosis may decrease the critical soil P requirement below which plants cannot grow (Ryan et al. 2016; Janos 2007).

The mechanisms with which mycorrhizae improve plant P nutrition are related to an increase of the volume that is exploited by the mycorrhizosphere, compared to the soil volume of the rhizosphere (Marschner 1995; Li et al. 1991), or by synergism with P-solubilizing microorganism (Antunes et al. 2007). It seems that both the plant and fungus exploit the same sources of P (Blal et al. 1990). However, the fungus may have access to smaller soil pores, may produce more active phosphatases and have higher affinity for P (Bolan 1991). Accessing P from rock phosphate or other bedrock is more studied for ectomycorrhizae (van Schöll et al. 2008), while Koele et al. (2014), have shown that this may equally well happen by arbuscular

mycorrhizae. Increased nutrient uptake in arbuscular mycorrhizal plants has been shown from basaltic and rhyolitic parent rocks, with P uptake improvement from the latter (Burghelca et al. 2015). Use of rock phosphate in combination with arbuscular mycorrhizal fungi may be more beneficial in Oxisols where soluble chemical fertilizer P is rapidly converted to insoluble forms (Lin and Fox 1992) and mycorrhizal plants may have access to the NaOH-P pools (Cardoso et al. 2006).

3.2.2 Conventional-High Input Agriculture and Arbuscular Mycorrhizal Fungi

Mycorrhizae and conventional, well fertilized agriculture may seem incompatible. However, there are reports where mycorrhizae were effective in spite of high P soil concentrations. It is not high P in soil solution that reduces arbuscular mycorrhizal fungal presence, but high P in the root tissues, as it has been shown by Menge et al. (1978). On the other hand, plants with root systems like onion may depend on arbuscular mycorrhizae for P even at high soil nutrient levels (Galván et al. 2009). Miller et al. (1995) summarizing the Guelf field experiments suggested that arbuscular mycorrhizal fungi may be important for well fertilized crops. They explain that the inhibition of the symbiosis by high field P was not found to be that great, also observed by others (Hayman et al. 1976; Gryndler et al. 1989), that mycorrhizae may improve P nutrition at the early plant stages when P in plant tissues is not high, but critical for high yields, and that localized fertilizer application may reduce arbuscular mycorrhizal fungal colonization only at the part of the root system that is exposed to it, and not in the whole root system. In strawberries produced in high P compost substrate, a particular cultivar- arbuscular mycorrhizal fungal combination produced ~50% more daughter plants than the non-mycorrhizal control, although colonization never exceeded 12% but other inoculated cultivars had a reduced number of daughter plants (Stewart et al. 2005). Douds et al. (2016) found in soils with available P at 214–258 mg/kg, that on the average of 7 years and different pre-inoculated tomato cultivars, there was a 6% increase in yield, but for individual years, arbuscular mycorrhizal plants had lower to much higher yield than the uninoculated control.

In high P soils arbuscular mycorrhizal fungi may be effective when plants are under some stress (Douds et al. 2016). For example, well fertilized field maize under water stress (reduced irrigation) was well colonized and benefited by arbuscular mycorrhizal fungi compared to the fumigated control and the fully irrigated treatment (Sylvia et al. 1993). Mycorrhizal citrus plants grown in high P conditions recovered faster from moisture stress and had higher leaf P concentration than non-inoculated controls (Fidelibus et al. 2001). In sweat potato, low temperature suppressed the plant P uptake leaving the fungal pathway as the sole source of P showing increased yield with arbuscular mycorrhizal fungi in spite of the high P soil (242–599 mg available P /kg soil) (Douds et al. 2015). The same may be the case

for salinity/sodicity, a common problem of greenhouses, or other plant stresses that need to be examined. Furthermore, under low N, high P did not seem to inhibit arbuscular mycorrhizal fungi (Sylvia and Neal 1990) and at high P increasing intra-specific density increased the growth benefit to arbuscular mycorrhizal fungi (Hetrick et al. 1994), but this was not always the case (Schroeder and Janos 2005).

Under well fertilized conditions inoculation of plants with arbuscular mycorrhizal fungi may be effective if the indigenous population is ineffective (Medina et al. 1990). Combined application of NPK chemical fertilizers with arbuscular mycorrhizal fungal inoculum may improve plant P acquisition efficiency in P deficient soils than that with indigenous inoculum (Hu et al. 2010).

Soil management such as tillage and fertilization may impact arbuscular mycorrhizal fungal communities, changing species richness and evenness. In agricultural soils there is selection of arbuscular mycorrhizal fungal species with the genus *Glomus* being most prevalent, most likely based on its ability to sporulate relatively faster than the other genera and survive tillage disturbance and perhaps short plant cycles (Oehl et al. 2009; Voříšková et al. 2016). Furthermore, pesticides used in agriculture may affect the symbiosis (Trappe et al. 1984). There is evidence of reduced spore numbers, species diversity and selection for less effective arbuscular mycorrhizal fungi after long term fertilization using classic techniques based on spore morphologies and enumeration (Johnson 1993; Ortas and Coskan 2016; Oehl et al. 2004; Wang et al. 2011). These seem to be confirmed with molecular techniques (van Geel et al. 2016; Lin et al. 2012; Chen et al. 2014). On the contrary, species richness increased with fertilization in an alpine meadow (Liu et al. 2015) or was not different between organically and conventionally managed forage fields (Schneider et al. 2015). Cross inoculation experiments in soils with different histories of cumulative fertilization have shown that inorganic soluble P fertilization may decrease the infectivity and effectiveness of field arbuscular mycorrhizal fungal communities, with an indication of selection for arbuscular mycorrhizal fungi less sensitive to P (Kahiluoto et al. 2000). Changes in the arbuscular mycorrhizal fungal communities due to fertilization may take long time (Cheng et al. 2013), as the effects of intensive agricultural management may also last for more than 20–25 years (Voříšková et al. 2016; Schneider et al. 2015). Adoption of farm management practices that enhance the functioning of the arbuscular mycorrhizal fungal community indigenous to the soil and on farm inoculum production are the primary options available to row crop farmers for efficiently employing arbuscular mycorrhizal fungi (Douds et al. 2016).

Fertilization with slow release fertilizers, or less soluble forms of P such as organic amendments (manures, composts, biosolids, crop/legume residues) could supply sufficient P for plant growth and satisfactory yields and allow the benefits of mycorrhizae. Cavagnaro (2015) has recently reviewed the compatibility of composts with arbuscular mycorrhizal fungi. Composts seem to have a positive or neutral effect to arbuscular mycorrhizal fungal colonization and in most cases are compatible with arbuscular mycorrhizal fungal inoculum application. The impact of soil application of high rates of organic amendments may be negative and in any case unpredictable (Gosling et al. 2006) but this has not been studied extensively

(Cavagnaro 2015). A study from a long term (19 years) field inorganic fertilization experiment showed that application of organic amendments alone or in combination with inorganic fertilizers together with arbuscular mycorrhizal fungal inoculum had lower levels of arbuscular mycorrhizal colonization, but higher yield and total P acquisition than control and NK treatments and about the same levels as the NPK treatment (Hu et al. 2010). Jensen and Jakobsen (1980) found that farmyard manure and inorganic NPK fertilizer after 10 years of application both reduced colonization at the same low levels. Others have found after 74 years of experimentation that moderate quantities of farm yard manure may be less suppressive than equal amounts of NPK fertilizer (Joner 2000). Legume residues decreased colonization relative to the non-fertilized control, but some residues also decreased plant P uptake and results varied with residue quality (Hasbullah et al. 2011). High organic fertilizer rates may cause a temporary suppression of root colonization and an inhibition of plant growth when combined with arbuscular mycorrhizal fungal inoculum (Zhang et al. 2012). Use of slow instead of quick release fertilizers may increase arbuscular mycorrhizal fungal richness (van Geel et al. 2016), but organic, low P fertilizers seem to be more compatible with arbuscular mycorrhizal fungi than P rich, slow release inorganic fertilizers (Linderman and Davis 2004).

3.2.3 Legacy P and Arbuscular Mycorrhizal Fungi

Given the ability of arbuscular mycorrhizal fungi to mobilize soil P one would expect them to play a role in mobilizing legacy P, however, there is not a great volume of research targeting this. First we should identify the case scenario: A Legacy-P based agriculture in order to achieve satisfactory yields should cover at least part of the P needs by legacy P and for the rest it would either use chemical fertilizers, but in lower quantities than those used today, or no chemical fertilizers, but composts, manures or other organic P sources, or some combination of different forms of P. In any case, we would not expect a change of land management, as from agriculture to grassland.

The issue of legacy P may be examined in systems where soluble P fertilizer application has seized, such as in organic agriculture or in biodynamic systems. However, the potentially enhanced levels of arbuscular mycorrhizal fungi or other organisms may not compensate for decreased yields due to lack of fertilization (Ryan and Ash. 1999). The use of arbuscular mycorrhizal fungi in organic farming has been reviewed by Gosling et al. (2006). Research on previously well fertilized abandoned agricultural land is relevant, but not focused on the issue, since there is a change in land use after abandonment. Spohn et al. (2016), studied changes in soil P fractions and microbial community structure after abandonment of vineyards in Tokaj, Hungary using a chronosequence of fields covering 200 years of abandonment. The concentration of labile P decreased during the first 50 years after abandonment and then stabilized at a low level and vegetation changed to grassland, shrubby grassland, shrubland to forest, while arbuscular mycorrhizal fungi decreased

due to establishment of trees that form ectomycorrhizae. In a study of P fractions in arable or pasture soils not fertilized for at least 5 years, there was very low arbuscular mycorrhizal colonization in soils with the highest P, and this negatively affected the relationship between plant P and soil P (Fransson et al. 2003). In low P Danish soils, omitting P application for 10 years resulted in reduction of H₂SO₄ soluble P by 15–25% compared to the initial 8–12 ppm P levels and increased arbuscular mycorrhizal fungal infection that seemed to compensate for P nutrition (Jensen and Jakobsen 1980). In Bohemia, 25 years after abandonment of an intensively managed land, grassland plant species did not spread in and the arbuscular mycorrhizal fungal community was still different than that of the neighboring grasslands. In addition, the abandoned field arbuscular mycorrhizal fungi were fast colonizers, and had a lower number of propagules relative to that of grassland arbuscular mycorrhizal fungal communities, although operational taxonomic unit richness did not differ (Voříšková et al. 2016).

3.2.4 Plant Breeding for More Efficient Mycorrhizal Response

There is generally a large variation in the extent of plant root colonization among different plant species and within a plant species, among different landraces, lines, cultivars and accessions. This has led to exploring the possibility of breeding for better mycorrhizal response (van de Wiel et al. 2016). However, breeding plants for conventional, high input agriculture could have already made selections on the opposite direction, for plants dependent on fertilizers rather than on mycorrhizae. Such evidence was found for wheat (*Triticum aestivum*) (Hetrick et al. 1992; Zhu et al. 2001), with older landraces found to be more responsive to arbuscular mycorrhizal fungi than modern wheat cultivars. However, this was not the case for onion (Galván et al. 2009), durum wheat (Ellouze et al. 2016), sorghum (Leiser et al. 2016) and maize (Hao et al. 2008).

A strategy for breeding for more effective mycorrhizal symbiosis involves screening for plant genotypes that support the greatest extent of arbuscular mycorrhizal fungal root colonization. However, the level of colonization is not necessarily the best indicator of effectiveness of the symbiosis (Mensah et al. 2015) and very often it does not correlate with extractable soil P (Ryan et al. 2016), shoot dry weight (Baon et al. 1993), plant growth response (leaf tissue NPK) (Ellouze et al. 2016) and grain yield, while it may be highly variable and with low heritability (Leiser et al. 2016). Highly colonized plants may allocate a lot of photosynthetic carbon towards the fungus, and this cost may render the symbiosis ineffective, depending on soil nutrient levels and their availability via the plant uptake pathway. The N level in soil and the shoot N:P ratio should also be considered, since they may affect colonization (Liu et al. 2000). Selection of cultivars and arbuscular mycorrhizal fungi that form mycorrhizae rapidly, so that it would cover early plant P needs that are crucial for the final yield, has been proposed (Singh et al. 2012; Zhu et al. 2001), while high performance arbuscular mycorrhizal fungal isolates increase

plant N content (Mensah et al. 2015). Another strategy involves selection of plants that change root traits associated with P uptake upon formation of the symbiosis. There was not much difference in clover (Ryan et al. 2016) and maize lines with different root architecture did not seem to respond differently to arbuscular mycorrhizal fungal inoculation, but there were differences with arbuscular mycorrhizal fungal species used as inoculum (Hao et al. 2008). Selection for better rooting system did not lead to lower plant benefit by arbuscular mycorrhizal fungi in onion (Galván et al. 2009).

Breeding evaluations may involve indigenous arbuscular mycorrhizal fungal communities which may be practical for experimentation and realistic for broad scale application. However, results may vary with different arbuscular mycorrhizal fungi and indigenous arbuscular mycorrhizal fungal communities may not be very effective or at sufficient quantity, compared to applying arbuscular mycorrhizal fungal inocula (Ryan et al. 2016). A rich indigenous arbuscular mycorrhizal fungal community at the experimental area (Leiser et al. 2016) may not be as effective as the best possible cultivar-arbuscular mycorrhizal fungus combination. However, involvement of arbuscular mycorrhizal fungi may require a different kind of soil management that maintains arbuscular mycorrhizal fungal soil inoculum and supports more effective arbuscular mycorrhizal fungal communities. Adoption of farm management practices that enhance the functioning of the arbuscular mycorrhizal fungal community indigenous to the soil and on farm inoculum production are the primary options available to row crop farmers for efficiently employing arbuscular mycorrhizal fungi (Douds et al. 2016). Such practices may be the answer to the problem of lack of yield stability in breeding for more efficient symbiosis, since breeders prefer cultivars that may still be highly productive with or without arbuscular mycorrhizal fungi (Galván et al. 2009; Leiser et al. 2016; Singh et al. 2012).

3.3 Phosphorus Mobilizing Bacteria

3.3.1 Soil Bacteria Mediating Phosphorus Mobilization

Bacteria play a critical role in biogeochemical cycles and are the predominant microorganisms that mobilize native and applied P in soils, as compared to fungi or actinomycetes. Many bacteria genera such as *Alcaligenes*, *Arthrobacter*, *Azotobacter*, *Bradyrhizobium*, *Bacillus*, *Burkholderia*, *Chromobacterium*, *Enterobacter*, *Erwinia*, *Escherichia*, *Flavobacterium*, *Micrococcus*, *Pantoea*, *Pseudomonas*, *Salmonella*, *Serratia*, *Streptomyces*, and *Thiobacillus* have been isolated and studied for their ability to solubilize and mineralize inorganic and organic P respectively.

Among the soil bacterial communities the most important phosphate mobilizing strains belong to genera *Bacillus* and *Pseudomonas* due to their superior capacity and stability. *Bacillus megaterium*, *B. firmus*, *B. circulans*, *B. coagulans*, *B. licheniformis*, *B. subtilis*, *B. polymyxa*, *B. sircalmous*, and *Pseudomonas*

aeruginosa, *P. chlororaphis*, *P. fluorescens*, *P. liquifaciens*, *P. pickettii*, *P. putida*, *P. rathonis*, *P. savastanoi*, *P. striata*, and *P. stutzeri* could be referred to as the most important strains. In addition to *Bacillus* and *Pseudomonas* other P-solubilizing bacteria include *Nitrobacter*, *Nitrosomonas*, *Rhodococcus*, *Thiobacillus*, *Arthrobacter*, *Serratia*, *Synechococcus*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium*, *Delftia*, *Micrococcus*, *Xanthomonas*, *Enterobacter*, *Pantoea*, and *Klebsiella*. Many studies have been published on plant growth promotion by inoculating P-solubilizing bacteria. Pereira and Castro (2014) screened five bacterial strains for solubilization of phosphate in order to enhance *Zea mays* growth in an agricultural P-deficient soil. The best P-solubilizing strains were *Pseudomonas* sp. EAV and *Arthrobacter nicotinovorans* EAPAA, since both highly increased P availability in soils and promoted maize growth. Recently, Panta et al. (2016) studied the native population of phosphate solubilizing bacteria in the rhizospheres of maize, rice, ginger and large cardamom grown in different regions of Sikkim (India). Among the 26 isolates, *Bacillus*, *Pseudomonas*, *Micrococcus*, *Staphylococcus*, *Microbacterium* and *Delftia* were the main bacteria found, with a phosphate solubilization capacity that varied between 30.2 and 203.7 mg/L.

Numerous reports have shown that $\text{Ca}_3(\text{PO}_4)_2$ is most easily solubilized followed by FePO_4 , AlPO_4 and rock phosphate. According to Henri et al. (2008), *Pseudomonas fluorescens* can solubilize 100 mg P/L containing $\text{Ca}_3(\text{PO}_4)_2$ or 92 and 51 mg P/L containing AlPO_4 and FePO_4 , respectively. Strains of *Pseudomonas* and of *Acetobacter diazotrophicus* were found to release 160.5–162.5 and 142–431 mg P/L from tri-calcium phosphate, respectively. Sindhu et al. (2014) reported that *Pseudomonas striata* is more efficient to solubilizing TCP (tri calcium phosphate) than *Bacillus* spp. and *Aspergillus awamorii*. Recently, Ahmed et al. (2016) evaluated the effects of six P mobilizing bacterial strains (*Pantoea ananatis*, *Pantoea agglomerans*, *Pantoea* sp. *Burkholderia* sp.) and three P sources of tricalcium phosphate on yield and P uptake of wheat. They found that all the selected P-mobilizing bacteria increased the grain yield of wheat significantly as these bacteria mobilized insoluble mineral P. Sharon et al. (2016) reported the highest level of phosphate solubilization from the insoluble tri-calcium complex by *Pantoea* sp. Pot1, at a rate of 956 mg/L. Figure 3.3 shows a schematic summary of phosphate solubilization capacity of different bacteria genera.

3.3.2 Mechanisms of P Mobilization by Soil Bacteria

Bacteria are responsible for mobilizing the soil P through multiple mechanisms that are expressed with direct and indirect effects. In direct processes, the solubilization of inorganic and mineralization of organic P are the main mechanisms of P release. The solubilization of inorganic P related to the production and the action of low molecular weight organic acids such as acetic, lactic, oxalic, tartaric, malic, succinic, citric, formic, gluconic, ketogluconic, and glycolic acid (Table 3.2). These acids help in lowering the pH through excretion of H^+ and at the same time, hydroxyl/

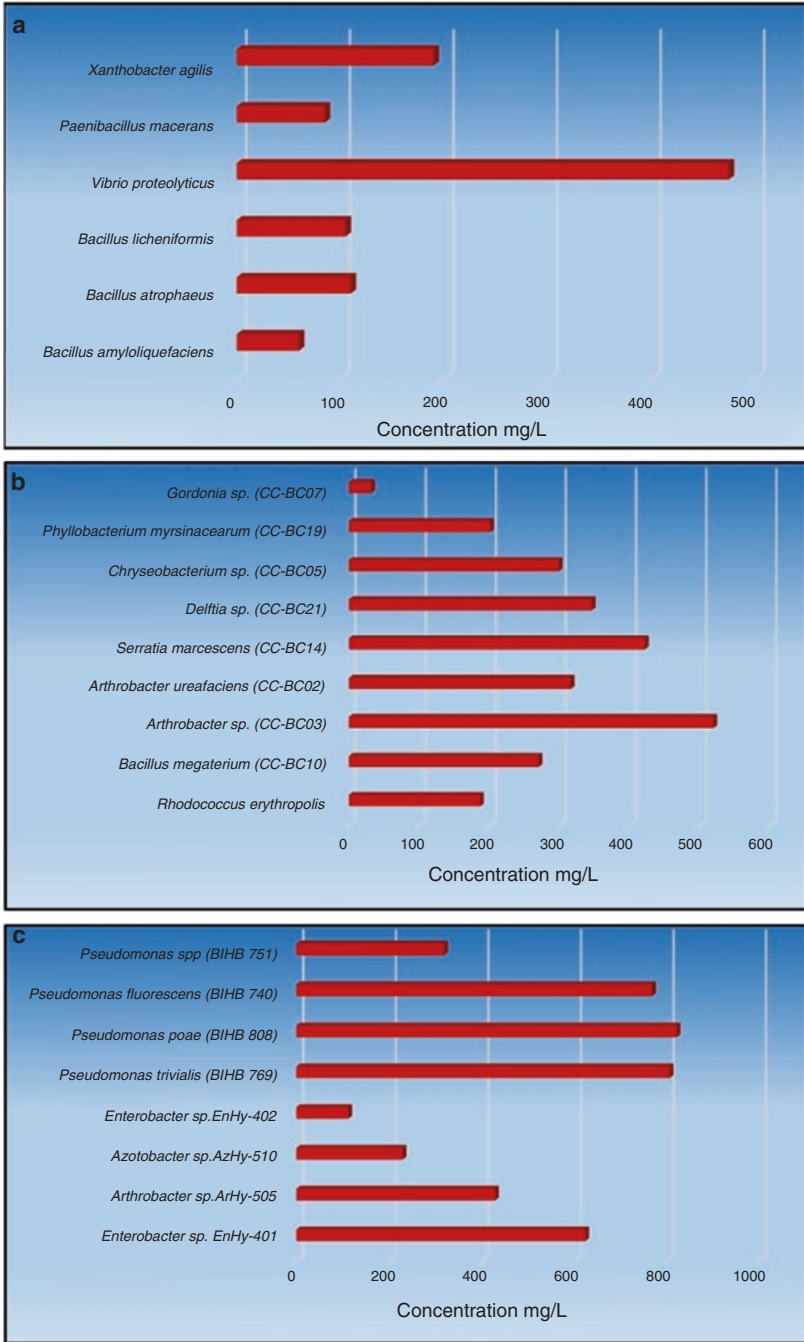


Fig. 3.3 Phosphorus solubilization capacity of bacterial cultures after (a) 24 h (b) 72 h and (c) 120 h of incubation. Data from Khan et al. 2013

Table 3.2 Production of organic acids by phosphate-solubilizing bacteria

Phosphate solubilizing bacteria	Organic acids	References
<i>Acetobacter</i> sp	Gluconic	Galar and Bolardi (1995)
<i>Arthrobacter</i> sp.	Oxalic, malonic	Banik and Dey (1982)
<i>Azotobacter</i> Hy-510	Oxalic, gluconic, tartaric, lactic, succinic, fumaric	Yi et al. (2008)
<i>Bacillus polymyxa</i> , <i>B. licheniformis</i> , <i>Bacillus</i> spp.	Oxalic, citric	Gupta et al. (1994)
<i>Bacillus amyloliquefaciens</i> , <i>B. licheniformis</i> , <i>B. atrophaeus</i>	Lactic, itaconic, isovaleric, isobutyric, acetic	Vazquez et al. (2000)
<i>Bacillus megaterium</i> (CC-BC10)	Citric, lactic, propionic	Chen et al. (2006)
<i>Enterobacter intermedius</i>	2-ketogluconic	Hwangbo et al. (2003)
<i>Enterobacter</i> sp.	Malic, gluconic	Shahid et al. (2012)
<i>Enterobacter aerogenes</i> , <i>E. taylora</i> , <i>E. asburiae</i>	Lactic, itaconic, isovaleric, isobutyric, acetic	Vazquez et al. (2000)
<i>Delftia</i> (CC-BC21)	Succinic	Chen et al. (2006)
<i>Micrococcus</i> spp	Oxalic	Banik and Dey (1982)
<i>Pantoea eucalypti</i>	Cluconic	Castagno et al. (2011)
<i>Pseudomonas cepacia</i>	Gluconic, 2-ketogluconic	Bar-Yosef et al. (1999)
<i>Pseudomonas poae</i>	Gluconic, 2-ketogluconic, succinic, citric, malic	Vyas and Gulati (2009)
<i>Pseudomonas fluorescens</i>	Gluconic acid, malic, succinic, lactic, fumaric, tartaric, and transaconitic	Henri et al. (2008)
<i>Rhizobium leguminosarum</i>	2-ketogluconic	Halder et al. (1991)
<i>Rhodococcus erythropolis</i> (CC-BC11)	Gluconic	Chen et al. (2006)
<i>Sinorhizobium meliloti</i>	Malic, succinic, fumaric acid	Bianco and Defez (2010)

carboxyl groups enhance chelation of the cations (Ca, Al and Fe) bound to phosphate, thereby converting it to soluble forms.

Moreover, as Zhang et al. (2014) reported, these anions are competing with P for adsorption sites of soil by the process referred to as ligand exchange.

While soil bacteria vary considerably in their ability to secrete organic acids, strains of *Pseudomonas*, *Bacillus* and *Rhizobium* have been identified as the most powerful phosphate solubilizers. The amount of mobilized phosphate depends on the strength and type rather than the total amount of acid produced, with gluconic acid being reported as the most frequent efficient agent of inorganic phosphate solubilization (Rodríguez and Fraga 1999; Rodríguez et al. 2006). Although, organic acids have been suggested as the principal mechanism of P solubilization, the mobilization of insoluble P by inorganic acids such as HCl, HNO₃ and H₂SO₄ has also been reported in some cases. Bacteria of the genera *Nitrosomonas* and *Thiobacillus* that oxidize nitrogen and sulfur substances respectively, can dissolve phosphate compounds by producing nitric and sulphuric acids. However, as Kim et al. (1997) reported, inorganic acids (HCl) are less effective to solubilize P from hydroxyapatite compared to organic acids (citric or oxalic) at the same pH.

Organic P constitutes between 30 and 65% of the total P in soil and is an important source of P for plants. Organic P in soil is largely in the form of phosphate monoesters (inositol phosphate) accounting for up to 50% of the total organic P. To make these organic P compounds available for plant nutrition they must undergo mineralization (hydrolysis). The microbial mineralization of organic P is strongly influenced by pedoenvironmental parameters and conditions favoring nitrogen mineralization also support the mineralization of organic P. In this process, P can be mobilized by means of three groups of enzymes a) phosphatases (e.g. acid and alkaline phosphatases) b) phytases, which cause P release from insoluble phytates and c) phosphonatases and C-P lyases that are released by soil microorganisms (Sindhu et al. 2014). Soil bacteria strains from the genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Enterobacter*, *Serratia*, *Citrobacter*, *Proteus* and *Klebsiela* produce a range of acid phosphatases that catalyzes the release of available P for plant nutrition from organic P (Hayat et al. 2010). Nevertheless, bacteria with phytase activity have been also isolated from rhizosphere belonging to genera *Tetrathioabacter* and *Bacillus* which promoted the growth of Indian mustard and significantly increased the P content (Kumar et al. 2013). About 30–50% of bacterial isolates from soil synthesize phytase which causes release of P from phytic acid and species of *Arthrobacter*, *Streptomyces* and *Pseudomonas* have been found capable to form this enzyme.

Jorquera et al. (2008) have isolated bacteria with both activities, P solubilization with production of organic acids and mineralization of organic P with production of phytase, from the rhizospheres of wheat, oat, perennial ryegrass, yellow lupin and white clover. According to Tao et al. (2008) the solubilization activity of soil bacteria strains as *Bacillus megaterium*, *Burkholderia caryophylli*, *Pseudomonas cichorii*, and *Pseudomonas syringae* ranges between 25.4–41.7 mg P/L while the mineralization of organic P of bacteria strains as *Bacillus cereus* and *Bacillus megaterium* ranges between 8.2–17.8 mg P/L.

Besides the direct mobilization of inorganic (solubilization) and organic (mineralization) P, there are several ways through which indirect mobilization of P can also occur, (Owen et al. 2015; Rashid et al. 2016) due to

- (i) The formation of carbonic acid through the release of CO₂ as result of microbial respiration.
- (ii) The nitrogen assimilation, where bacteria release H⁺ that cause decrease of soil pH and solubilization of P.
- (iii) The reduction of metals bound to phosphate as the result of the redox activity of microorganisms and/or exudates.
- (iv) The ability of P solubilizing bacteria to remove and assimilate P from the soil and thus stimulate the indirect dissolution of Ca-phosphates in order to re-establish the P-equilibrium (sink theory).

It is clear that P mobilizing bacteria have the capacity to convert insoluble forms of P (legacy P) into soluble and available P for plants through complex and dynamic mechanisms that must be well understood in order to predict how these bacteria may respond when applied to field conditions.

3.4 Conclusion

The strategy of employing microorganisms for mobilizing legacy soil P has a great volume of research behind it. Microorganisms with such a potential have been isolated and identified and the mechanisms with which they may mobilize legacy P have been studied. In addition, there is an even greater volume of research regarding microorganisms with other useful abilities (Plant Growth Promoting Microorganisms) that may lead to multifunctional inocula (Richardson et al. 2011). Nevertheless, the complexity of the subject is such that there is not much commercialization of biofertilizers yet (Vessey 2003), or for arbuscular mycorrhizal fungi the cost of production is still too high for broad scale agriculture, unless inoculum production technology is improved or there is on farm inoculum production (Douds et al. 2015, 2016). In addition, high variability with different host cultivars and field sites may lead to inconsistent results (Vessey 2003), or positive results may be attributed to random events (Karamanos et al. 2010). The further improvement of our knowledge on the interactions between plants, soil, inocula and indigenous microorganisms, the further exploration of the yet undiscovered wealth of the microbial world and introduction of the concept of soil management with the aim of enhancing effective microbial communities may eventually lead to success in employing microorganisms for mobilizing legacy soil P.

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