Phosphate Biofertilizers as Renewable and Safe Nutrient Suppliers for Cropping Systems: A Review

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Abstract

Sustainable agriculture highly depends on soil microorganisms to supply essential nutrients for plants and circulate the nutrient cycles in cropping systems. These microorganisms which are commercially formulated and briefly named "biofertilizers" can significantly reduce fossil fuel consumption, environmental degradation, and production cost related to agriculture. Phosphate biofertilizer is one of the most important groups of these beneficial microorganisms which plays a notable role in nutrient preparation for crops. Although these biofertilizers are usually known as phosphate suppliers for cropping systems, they can also provide other macro- and micronutrients to crops. Fungi and bacteria form two major groups of phosphate biofertilizers which can live freely or as symbiont organisms in agricultural soils. Mycorrhiza is a symbiont fungus which increases plant uptake of phosphate, nitrogen, and micronutrients and improves soil structure via formation of an extensive and dense mycelial network connected to plant roots. In contrast, phosphate solubilizing microorganisms are usually free living and able to solubilize insoluble phosphate compounds in soil mainly via releasing a wide range of organic acids and chelating metabolites. However, the effectiveness of these microorganisms is significantly influenced by edaphic factors and field management practices. For example, tillage as a usual practice in most of the cropping systems has negative effects on the absence and activity of mycorrhizal fungi. Application of chemical fertilizers which is another routine operation in modern agriculture also notably reduces the survival and effectiveness of phosphate biofertilizers. This review article presents the results on the main phosphate biofertilizers which can potentially be applied in sustainable agriculture, their action mechanisms, and important factors influencing their effectiveness.

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5.1 Introduction

Nowadays, agriculture relies on chemical fertilizers in order to satisfy the demand of crops with a high yield potential and produce economically viable yields. The synthesis of these fertilizers requires high amounts of fossil fuels as an energy source. Fossil fuels are nonrenewable resources, and their oxidized products such as CO_2 pose hazards to the environment and to human health. Moreover, fossil fuel reserves are finite and therefore unsustainable in long-term scale.

Phosphorus (P) is the second important element after nitrogen which is necessary to survival and growth of plants (Ogbo 2010). However, in the soil solution, it usually exists in very low quantities (a micromolar level) as compared with most of the other vital nutrient elements which are present in millimolar levels (Ozanne 1980). To ameliorate P deficiency, high amounts of chemical P fertilizers are used which can lead to the environmental degradation, pollution of natural resources, water eutrophication, and increased crop production cost. Moreover, a notable section of the P added into the soil as chemical fertilizers is rapidly converted to unavailable compounds such as calcium phosphate or other fixed forms. As reported by Gyaneshwar et al. (2002), about 75–90% of the chemical P fertilizers applied in agricultural soils become unavailable quickly due to P combination with other elements such as Fe, Al, Ca, and Mg depending on the soil pH level. Generally, in the alkaline soils, P is fixed by Ca or Mg, whereas in the acidic ones, it forms insoluble compounds via reaction with Fe or Al. Therefore, there are large reserves of P in most agricultural soils resulted from the massive use of the synthetic P fertilizers (Rodriguez and Fraga 1999); as in a global scale, these reserves can sustain crop yields in their maximum levels for about one century (Goldstein et al. 1993). On the other hand, major P chemical fertilizers are originated from rock phosphates as their mother materials which are known to be finite resources, and their reserves may be depleted during the next 100 years (Herring and Fantel 1993). Phosphate biofertilizers can play an important role in agroecosystems as renewable and ecofriendly nutrient suppliers for plants and are proposed as possible alternatives for conventional chemical P fertilizers. According to Raghuwanshi (2012), the use of these biofertilizers can be included as an efficient approach in Integrated Nutrient Management (INM) and Integrated Plant Nutrition System (IPNS). They can biologically transform soil P from unavailable to available forms.

These biofertilizers contain different types of microorganisms which increase the accessibility of plants to soil P reserves which are unavailable in normal conditions. This can be attributed to their ability to dissolve insoluble P compounds and extension of plant root system via establishment of a symbiotic relationship with the roots of different plant species. These microorganisms belong to different taxonomic groups especially fungi and bacteria.

5.2 Mycorrhiza

An important symbiotic relationship between soil fungi and vascular plant roots is called mycorrhizae which through it nutrients and energy are exchanged between two symbionts (Brundrett 2002). Roots of about 95% of plant species can be

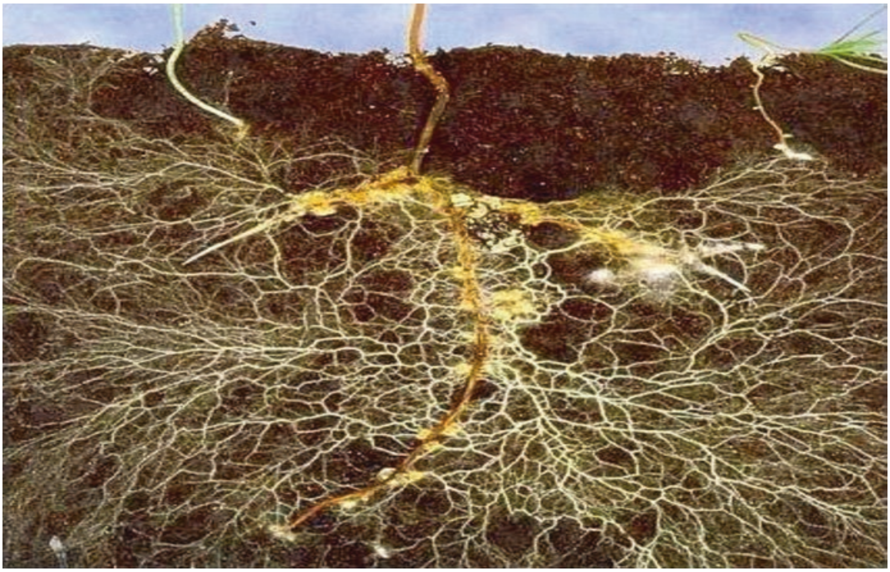

Fig. 5.1 AM fungi form an extensive and dense mycelia network in soil by which cover the depletion zone around plant roots (Source: http://www.sarcozona.org/tag/mycorrhizae)

colonized by soil fungi and establish mutualistic relationships named arbuscular mycorrhizae (AM) (Smith and Read 2008). Terrestrial plants and AM fungi (AMF) have been evolved side by side during their evolutionary history. A symbiotic relationship between AM fungi and land plants has been distinguished in the fossils belonging to Ordovician era, approximately 460 million years before this (Redecker et al. 2000).

Plant roots are colonized by AM, and the fungi transmit nutrient elements such as P into the host plant in exchange for the photoassimilate produced by plant. Arbuscules are highly branched intracellular fungal structures which are formed in the cortex of host plant roots, and at the same time fungi constitute their mycelial network in the soil (Fig. 5.1). P uptake by plants can be enhanced due to symbiotic relationship with AM (Bolan 1991). Moreover, these beneficial microorganisms can increase nitrogen (Barea et al. 1991) and micronutrient (Burkert and Robson 1994) availability to host plants and aggregate soil particles leading to an improved soil structure (Tisdall 1994). However, supply host plant with P which is an extremely nonmobile macronutrient in most soils can be defined as the main benefit caused by AMF (Bucher 2007).

5.2.1 Some Benefits of Mycorrhiza

As mentioned previously, increased phosphorus availability to plants is known as the main advantage resulted from the symbiosis with AMF. Because of low solubility and mobility, P is proposed as one of the most limiting essential soil elements needed for plant survival and growth. It is estimated that crop inoculation with AMF can reduce the use of P chemical fertilizers by 80% in field conditions (Jakobsen 1995). In a study, plants inoculated with AM showed a sixfold increase in Pi and fourfold increase in the other nutrients as compared with uninoculated fertilized plants. Other workers showed that inoculation with AM fungi increased plant ability to utilize soluble P from rock phosphate (Antunes and Cardoso 1991; Guissou et al. 2001).

Moreover, mycorrhizal roots can acquire nitrogen organic compounds, such as amino acids and small peptides, and transport them to host plants (Bajwa and Read 1985; Bajwa et al. 1985). Ericoid, a group of mycorrhizal fungi, can degrade organic nitrogen and transmit it to mycorrhizal plants in the experiments conducted in controlled environments (Abuzinadah and Read 1986; Read 1991; Read et al. 1989). Michelsen et al. (1996) also suggested that ericoid mycorrhizae enabled the host plants to access soil organic N sources under natural conditions.

AM fungi can also effectively protect soil against erosion. This can be achieved by their extraradical hyphae which are able to connect soil particles (Miller and Jastrow 1992) leading to an improved soil aggregate stability and consequently a lower soil erodibility. AMF can also produce a sticky glycoprotein named glomalin which cements soil particles (Wright and Upadhyaya 1998; Wright et al. 1999; Rillig et al. 2002) and improves the stability of soil aggregates via binding soil particles (Peters 2002).

5.2.2 Mechanisms by Which Mycorrhiza Interacts with Plants and Improves P and N Availability for Them

Before the physical contact between plants and AMF (i.e., at the pre-symbiotic stage), it is known that some molecular signals are exchanged between them. Some studies have been shown that on the one hand AMF modulate root gene expression (Kosuta et al. 2003; Weidmann et al. 2004), intracellular signaling (Navazio et al. 2007; Kosuta et al. 2008), development (Oláh et al. 2005), and metabolism (Gutjahr et al. 2009) via diffusion of some produced compounds. On the other hand, plants release some special biochemicals via their roots which stimulate fungi to establish a symbiotic relationship (Gianinazzi-Pearson et al. 1989; Siqueira et al. 1991; Tsai and Phillips 1991; Giovannetti et al. 1996; Buee et al. 2000). Strigolactones (SLs) have been distinguished as the main secondary metabolites which are produced by host plants and are able to stimulate the symbiont fungi (Akiyama et al. 2005; Besserer et al. 2006). Some important morphological and developmental events in AM fungi including spore germination, hyphal branching, and increasing fungal respiration and mitochondrial activity are usually induced by SLs (Besserer et al. 2006, 2008).

The soil volume exploited by plants can be extended by several times when plant roots are in association with AMF mycelial network (Fig. 5.2). Therefore, P uptake can be achieved more efficiently by a mycorrhizal than a non-mycorrhizal plant root system (Smith and Read 2008). In other words, mycorrhizal plants can access

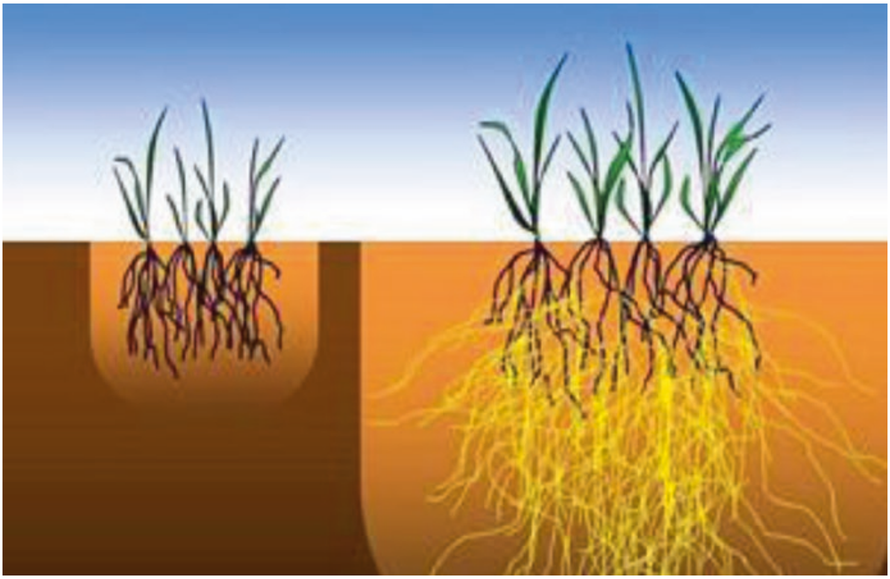

Fig. 5.2 The soil volume which can be explored by a plant can be increased by several times of magnitude via the network of fungal mycelium connected to AM roots (Source: http://www.dirt-goddessseeds.com/category_s/1901.htm)

nutrients such as phosphorus which exist outside the rhizosphere zone where they are not accessible for non-mycorrhizal plants. This is achieved through the fungal mycelial network connected to plant root system (Friese and Allen 1991). For example, one centimeter of colonized roots might produce 50–150 cm of extraradical hyphae (Harley 1989). Moreover, in comparison with plant roots, fungal hyphae are much thinner (Bago et al. 1998), which can enable them to penetrate in the soil microscopic pores which are unavailable to plant roots.

Another mechanism by which AMF increase P availability to plants is related to their ability to produce different organic acids (Lapeyrie 1988) which can transform soil mineral phosphates from insoluble to soluble forms. This inevitably leads to the higher plant access to acid-labile insoluble P compounds such as calcium phosphate. In addition, phosphatase produced by AMF can enable them to release P from organic phosphate forms (Koide and Shreinner 1992).

Although the plant growth-promoting effect of AMF is mainly attributed to their ability to dissolve insoluble P compounds and increase phosphate uptake by plants, there are some evidences on the effectiveness of these fungi to increase nitrogen accessibility to plants (Ames et al. 1984; Azcón-Aquilar et al. 1993). Matsumura et al. (2013) reported that under different amino acid treatments, the nitrogen content of mycorrhizal plants was notably higher than that for non-mycorrhizal plants. In another study, Hobbie and Hobbie (2006) observed that in arctic tundra, 61–86% of the nitrogen acquired by plants was resulted from an ectomycorrhizal symbiotic relationship. Govindarajulu et al. (2005) also found that AM fungi are able to obtain soil inorganic nitrogen by their extraradical mycelium which then is converted to arginine and translocated to the intra-radical fungal mycelium located in the roots of host plant.

Some studies have demonstrated that the nitrogen present in the soil organic compounds can be accessible to AMF (Hodge et al. 2001; Whiteside et al. 2009; Hodge and Fitter 2010). Hodge and Fitter (2010) showed that decomposing soil organic materials are responsible for 31% of the nitrogen acquired by AMF hyphae system. This can be explained by the AMF ability to produce a diverse range of hydrolytic enzymes including cellulase, pectinase, and xyloglucanase in their external mycelial network (Garcia-Romera et al. 1991; Garcia-Garrido et al. 1992). It clearly is known that these enzymes are responsible to decompose the soil organic matters.

Chitinases are another group of metabolites produced by AMF species which are proposed as one of the factors involved in plant root protection against soil pathogens (Azcón-Aguilar and Barea 1997; Gianinazzi-Pearson 1996). Whiteside et al. (2012) showed that recalcitrant (i.e., a molecule with relatively large and complex structure) organic N compound such as chitosan can be absorbed by AMF in situ.

5.3 Phosphate Solubilizing Microorganisms (PSMs)

P is proposed as one of the most important elements participant in growth, development, and biological processes of different organisms. It is also known as an essential limiting factor for plants due to its insufficient solubility and mobility in soils (Vessey 2003) especially in extraordinary pH conditions. However, insoluble P compounds such as calcium phosphate and apatite can be solubilized by phosphate solubilizing microorganisms (PSMs) mainly bacteria and fungi which are in association with plant roots. *Bacillus* and *Pseudomonas* are known as the most important genera of mineral phosphate solubilizing bacteria (PSB) (Illmer and Schinner 1992), while main genera of fungi involved in P solubilization process are *Aspergillus* and *Penicillium* (Motsara et al. 1995). In soil, bacterial and fungal PSMs form 1–50 and 0.1–0.5% of the total soil phosphate solubilizing microorganisms, respectively. It means that the number of PSB is higher by 2–150 times than that for fungal solubilizing agents (Kucey 1983). Generally, production of organic acids and chelating factors by PSMs can explain their ability to solubilize insoluble phosphate compounds (Deinum et al. 1996; Dong and Pierdominici 1995).

However, there are some evidences which indicate inorganic acids can also be produced by PSMs. For example, the bacteria belonging to the genus *Acidithiobacillus* produce sulfuric acid via reaction with elemental sulfur (Garcia Junior 1992). This biologically produced acid plays an effective role in natural P solubilizing process via reducing soil pH which consequently leads to the improved plant growth (Stamford et al. 2002). However, it has been shown in both liquid and solid media that fungi have a higher ability to produce organic acids and therefore are more efficient to solubilize insoluble P compounds when compared with PSB (Venkateswarlu et al. 1984).

In a soil with P limited resources, PSMs can notably increase plant accessibility to this important element. According to Mohammadi et al. (2015), in a weedy condition along with a reduced sowing uniformity (i.e., when high intra- and interspecific competitions were intensified), phosphate biofertilizers containing fungi and bacteria could significantly improve soybean yield indicating the essential role of these microorganisms to support plants in a P limited condition.

5.4 Mechanisms by Which PSMs Improve P Availability for Plants

The improvement of P availability by PSMs can be achieved through different mechanisms (Fig. 5.3). However, it seems that the production of different organic acids by PSMs is the main reason explaining their solubilizing activity (Alam et al. 2002). Diverse organic acids such as gluconic, ketogluconic, oxalic, citric, succinic, fumaric, tartaric, α-ketobutyric, lactic, itaconic, isovaleric, isobutyric, acetic, malic, glyoxylic, and malonic can be produced by PSMs. The results of some studies show that the most efficient organic acid involved in P solubilization process is gluconic acid which is produced by Gram-negative bacteria (Goldstein et al. 1993; Kim et al. 1998). Khan et al. (2009) also suggested that gluconic and ketogluconic are the main low molecular weight organic acids produced by PSMs which are able to solubilize insoluble phosphate compounds in soil. The glucose oxidative metabolism by glucose dehydrogenase in the presence of a cofactor named pyrroloquinoline quinone (PQQ) is the mechanism by which gluconic acid is produced by PSMs (Fig. 5.4).

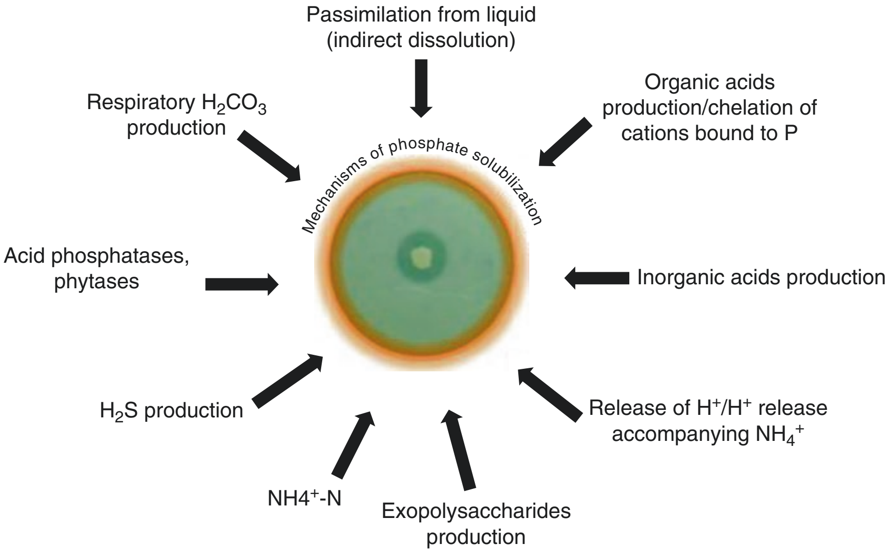

Fig. 5.3 Different mechanisms by which PSMs improve P availability for plants (Adapted from Zaidi et al. 2009)

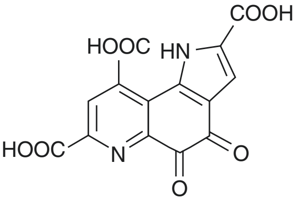

Fig. 5.4 Molecular structure of pyrroloquinoline quinone (PQQ) which acts as a cofactor in gluconic acid production process (Adapted from Matsumura et al. 2014)

In general, the reduced soil pH caused by organic acids produced by PSMs can explain their ability to dissolve insoluble P compounds (Nahas 1996). However, it appears that increasing P solubilization rate cannot be achieved by acidifying reaction alone (Subha Rao 1982). According to Kucey (1988), another major factor influencing solubilization process is the capacity of organic acids to chelate insoluble P compounds; as in a study when 0.05 M EDTA was added to the medium, solubilization rate was the same as inoculation with *Penicillium bilaii*.

PSMs can also produce inorganic acids, synthesize exopolysaccharides, and release H^+ as other important mechanisms contributing to inorganic P solubilization process (Gamalero and Glick 2011). Moreover, phosphatase produced by PSMs can play a key role in solubilization of organic P compounds (Park et al. 2011).

5.5 Factors Influencing the Efficiency of P-Related Microorganisms

The effectiveness of PSMs as biofertilizers can be influenced by diverse factors. Ho and Ko (1985) showed that after artificial introduction of PSMs into the soil, the size or density of their populations was decreased quickly. The success level of PSMs after introducing them into the soils highly depends upon their ability to compete with other soil microorganisms and the presence of a notable PSM saprophytic capacity. According to Kucey et al. (1989), the effectiveness of the inoculated PSMs to improve plant growth and yield can be varied in relation to several factors including:

1. If inoculated PSM can survive and colonize in the plant rhizosphere.
2. Its competitive ability with native microorganisms.
3. Essence and characteristics of the inoculated soils and plant varieties.
4. Inadequate rhizospheric nutritional level which can lead to the sufficient organic acid production by PSMs to dissolve insoluble P compounds.
5. PSM infirmity to dissolve soil P.

It is concluded that extensive studies should be carried out to distinguish the PSM strains with high durability and competitive ability under the environments with high complexity such as a plant rhizosphere in order to access to highly efficient P biofertilizers.

5.5.1 Soil Factors

Edaphic factors including soil composition (Bashan et al. 1995), physiological condition, temperature, pH, water content (Van Elsas et al. 1991), and the existence of recombinant plasmids (Van Veen et al. 1997) can significantly affect the survival of the inoculated PSMs. While competition, predation, and the growth of plant roots which supplies the substrates needed to PSMs form the main biotic factors influencing PSM survival as inoculants. Since the survival of AMF as obligatory endosymbionts only depends on the carbohydrates produced by the root cells of host plants, all edaphic agents determining the metabolism and growth of host will certainly affect AMF efficiency.

The soils with high buffering capacity can notably reduce PSM efficiency to solubilize insoluble P compounds, especially when PSM strains are not able to release acceptable levels of organic acids. Khan et al. (2007) also found that the presence of diverse environmental conditions is an important reason which can explain the variation in PSM efficiency. The low effectiveness of PSMs can be related to an unsuitable soil environment as may be observed in high alkaline soils. As in the soils with high alkalinity level that are commonly found in arid and semiarid climatic conditions (e.g., many areas of Iran) and usually have high temperatures and salinity levels, PSMs may colonize plant roots poorly resulting in a low P solubilizing activity. Therefore, it seems that searching for PSM strains with high efficiency in unfavorable environmental conditions is necessary.

5.5.2 Agronomic Practices

Sole cropping, conventional tillage, and fertilizer application are some of the common techniques to produce yield in most modern agricultural systems which can negatively affect AMF abundant and diversity in soils (Helgason et al. 1998; Oehl et al. 2005).

5.5.2.1 Tillage Practices

Tillage operations have been shown to reduce the number of AMF spores present in the soil (Kabir et al. 1998) and AM fungi colonization in some agricultural crops (Jasper et al. 1989; Miller et al. 1995; McGonigle and Miller 1996). Annual soil disturbances produced by conventional tillage systems showed reducing effects on AMF colonization when compared with reduced tillage practices (Miller and Jastrow 1992; Miller et al. 1995; Al-Karaki 1998; Miller 2000).

In general, conservation tillage practices have positive effects on AM fungi parameters and other soil factors. Positive consequences caused by no tillage consisted of higher soil carbon, nitrogen, sulfur, and phosphorus quantities and a greater AM fungal propagules remaining in the soil as compared with conventional tillage, as well as a simultaneously increased phosphorus accessibility for subsequent crops.

In a study, the amount of total glomalin produced by AMF enhanced in the soils under reduced tillage and no tillage than conventional tillage and soil carbon content was known as an important factor determining this enhancement (Borie et al. 2006).

5.5.2.2 Fertilization

AMF diversity and abundance have increasingly been declined in response to mineral nutrient application in agroecosystems (Lin et al. 2012; Liu et al. 2012). Among the mineral nutrients, Pi and nitrate have solely shown adverse effects on AMF, while these beneficial fungi were not negatively affected even by high levels of other essential elements including potassium, calcium, magnesium, sulfate, and iron.

Although the adverse effect of Pi on AMF has been recognized for a long time (Abbott et al. 1984; Thomson et al. 1986; Amijee et al. 1989; Breuillin et al. 2010; Balzergue et al. 2011), the increased AMF-plant symbiotic relationship caused by N deficiency can significantly overcome the reducing influence resulted from high P levels on AMF. This indicates that symbiosis can be enhanced by plants as long as there are limiting levels of one of these two important elements in rhizosphere.

Phosphorus

Crop production through the extensive use of chemical P fertilizers can notably decline AMF existence and abundance in soils (Johnson 1993). In a P-enriched environment, plant roots are not usually colonized severely by AMF (Amijee et al. 1989) as it has been indicated that when adequate accessible P is present in the soil, the growth of certain plant species may be reduced due to AMF colonization (Son and Smith 1995).

Pi can systemically suppress AM development which is in relation to the nutritional condition of host plant shoot. Inasmuch as a notable section of the photosynthate produced by host plant is usually used by AMF (Smith et al. 2009; Douds et al. 2000), the inhibiting effect of the elevated Pi levels on AMF development may be attributed to an energy-saving negative feedback mechanism in the environments in which the P needed for plant can adequately be provided in the absence of a symbiotic relationship with fungi. In other words, at a high level of phosphorus, plant preferentially adopts a nonexpensive and direct approach to acquire P (Nagy et al. 2008), and therefore, the plant root colonization by AMF can significantly be declined.

Moreover, long-term previous P applications can also affect AM fungi colonization of subsequent crops (Kahiluoto et al. 2000; Dekkers and van der Werff 2001). Dekkers and van der Werff (2001) reported that after 10 years without P fertilization, AM fungi colonization of winter wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) was greater when previous long-term annual P fertilization ranged from 0 to 17.5 kg ha^{-1} compared to when the rate of P application was 52.5 kg ha^{-1}.

The main metabolites including amino acids and carbohydrates which are secreted by host plant roots and are usable for AMF can be reduced in a P-enriched soil (Graham et al. 1981; Thomson et al. 1986). The genes involved in carotenoid biosynthesis and those responsible for symbiotic relationship, e.g., PT4, were suppressed in the presence of Pi (Breuillin et al. 2010). In contrast, the roots exposed to a P-deficient condition can exude some essential flavonoid signals which induce the growth and activity of AMF at the pre-symbiotic phase (Nair et al. 1991).

Based on some conducted studies, low quantities of strigolactones (key factor to trigger plant-AMF symbiosis) can usually be produced and exuded by different plant species when the soil phosphorus is high (Yoneyama et al. 2007a, b; López-Ráez et al. 2008), and strigolactones may not be present in the plant root exudates exposed to high P levels, and consequently these plants don't show stimulating effects on AMF.

Therefore, it can be assumed that the suppressive effect of P-enriched soils on AMF symbiosis is related to the decreased plant ability to produce sufficient levels of strigolactones in these conditions (Bouwmeester et al. 2007; Yoneyama et al. 2007b). Balzergue et al. (2011) reported that the exudates extracted from the plant roots developed in a P-enriched soil were not able to induce branching of fungal hyphae.

Other researchers also demonstrated that there is a negative correlation between the levels of strigolactones produced by host plant and soil available phosphorus (Yoneyama et al. 2007a, b; López-Ráez et al. 2008) and these metabolites could not be detected in the root exudates obtained from the plants developed in P-enriched environments. However, the number of the roots colonized by AMF and plant ability to produce strigolactones is mainly determined by shoot Pi content compared to the externally soil available phosphorus or the Pi levels which locally exist in plant roots (Balzergue et al. 2011).

Nitrogen

Previous studies in controlled environments and the field have found that low N levels (20 mM N) increased mycorrhizal infection (Goulart et al. 1995, 1996; Stribley and Read 1976). Whiteside et al. (2012) suggested that increasing nitrogen accessibility can decrease plant tendency to establish a symbiotic relationship with AMF, because the cost-effectiveness of fungal association is significantly reduced under this condition. Consequently, in the soils with high N levels, a decreased AMF frequency can be expected as is usually happened in different ecosystems (Treseder 2004). Cappellazzo et al. (2008) also reported that the ability of AM fungus *G. mosseae* to transport amino acids was notably declined in the presence of high inorganic nitrogen levels. The suppressing effects of N-enriched environments on AM colonization and activity have been demonstrated in several works. For example, Whiteside et al. (2012) observed a lower AMF ability to organically derived nitrogen uptake when accessible nitrogen was increased. In their study, the use of nitrogen fertilizer notably reduced the rate of specific uptake (i.e., per unit biovolume) of labile organic N by AMF.

However, if soil available N is so low that it reduces plant growth, establishment of the mycorrhizal association may be affected. In a study, the limited N supply to the host plants could have resulted in a reduced C supply to support mycorrhizal association, thus leading to a reduced mycorrhizal infection level (Yang et al. 2002).

Other studies showed that serious nitrogen deficiency in plants may contribute to low root carbohydrate content which lowers infection levels in vesicular-arbuscular mycorrhizal associations (Hepper 1983; Same et al. 1983). It can be concluded that the presence of a critical N level to achieve an efficient plant-AM association in soil is necessary.

5.5.2.3 Rotation

Since the development of AM fungi is biotrophic (Morton 1990), the absence of mycorrhizae hosts could cause a decrease in soil residual AM propagules and their vitality for crops seeded afterward in a rotation.

Including non-mycorrhizal crops in rotation might affect the concentration and vitality of indigenous AM species in soil, thereby affecting the growth of AM-dependent crops following in the rotation (Dalpè and Monreal 2004). Gavito and Miller (1998) reported that intra-radical AM colonization of corn (*Zea mays* L.) was delayed in field plots when canola rather than corn was the previous crop.

In general, the crops belonging to *Chenopodiaceae*, *Brassicaceae*, and *Caryophyllaceae* (Barker et al. 1998) families don't form symbiotic associations with AM fungi, and thus including them in rotations can significantly reduce the absence and activity of AM fungi in agroecosystem soils. Moreover, since AM fungi are obligate symbionts and their survival is fully dependent to live hosts, including black fallow in a rotation has negative effects on these beneficial microorganisms.

Conclusion

In general, phosphate biofertilizers can be proposed as suitable alternatives to synthetic chemical fertilizers which are extensively applied in modern agricultural ecosystems. Maintaining and invigorating these beneficial microorganisms via adoption of appropriate agronomic practices and introducing them into the agricultural soils intentionally can notably reduce fossil fuel consumption and environmental hazards caused by chemical inputs used in cropping systems while reclaiming the soil ecosystem. These microorganisms which mainly belong to fungi and bacteria groups can increase crop accessibility to nutrient reserves in soil via different mechanisms such as formation of a dense and extensive mycelial network connected to crop roots and production of a wide range of organic acids and chelating metabolites. However, some conventional operations which are extensively used in crop production systems today have shown negative effects on these beneficial microorganisms which consequently have been led to the increased dependency of these systems to external inputs.

It is concluded that in order to attain the self-sufficient and sustainable agricultural systems, the essential role of phosphate-related microorganisms as efficient nutrient suppliers for crops should seriously be considered. Moreover, the reasonable crop production practices including the use of conservation tillage (no or reduced tillage), organic manures instead of synthetic chemical fertilizers, and suitable and black fallow-free crop rotations as well as the artificial introduction of these microorganisms as biofertilizers into the agricultural soils should be included in cropping system management programs.

References

Abbott LK, Robson AD, De Boer G (1984) The effect of phosphorus on the formation of hyphae in soil by the vesicular arbuscular mycorrhizal fungus, *Glomus fasciculatum*. New Phytol 97:437–446

Abuzinadah RA, Read DJ (1986) The role of proteins in the nitrogen nutrition of ectomycorrhizal fungi. New Phytol 103:481–493

Akiyama K, Matsuzaki K, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435:824–827

Alam S, Khalil S, Najma A, Rashid M (2002) In vitro solubilization of inorganic phosphate by phosphate solubilizing microorganisms (PSM) from maize rhizosphere. Int J Agric Biol 4:454–458

Al-Karaki GN (1998) Benefit, cost and water-use efficiency of arbuscular mycorrhizal durum wheat grown under drought stress. Mycorrhiza 8:41–45

Ames RN, St. Porter LK, John TV, Reid CPP (1984) Nitrogen sources and 'A' values for vesicular- arbuscular and non-mycorrhizal sorghum grown at three rates of 15^N-ammonium sulphate. New Phytol 97:269–276

Amijee F, Tinker PB, Stribley DP (1989) Effects of phosphorus on the morphology of VA mycorrhizal root-system of leek (*Allium porrum* L). Plant Soil 119:334–336

Antunes V, Cardoso EJBE (1991) Growth and nutrient status of citrus plants as influenced by mycorrhiza and phosphorus application. Plant Soil 131:11–19

Azcón-Aguilar C, Barea JM (1997) Arbuscular mycorrhizas and biological control of soil-borne plant pathogens – an overview of the mechanisms involved. Mycorrhiza 6:457–464

Azcón-Aquilar C, Alba C, Montilla M, Barea JM (1993) Isotopic (15^N) Evidence of the use of less available N forms by VA mycorrhizas. Symbiosis 15:39–48

Bago B, Azcon-Aguilar C, Goulet A, Piche Y (1998) Branched absorbing structures (BAS): a feature of the extraradical mycelium of symbiotic arbuscular mycorrhizal fungi. New Phytol 139:375–388

Bajwa R, Read DJ (1985) The biology of mycorrhiza in the ericaceae. IX. Peptides as nitrogen sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. New Phytol 101:459–467

Bajwa R, Abuarghub S, Read DJ (1985) The biology of mycorrhiza in the ericaceae X. The utilization of proteins and the production of proteolytic enzymes by the mycorrhizal endophyte and by mycorrhizal plants. New Phytol 101:469–486

Balzergue C, Puech-Pagès V, Bécard G, Rochange SF (2011) The regulation of arbuscular mycorrhizal symbiosis by phosphate in pea involves early and systemic signalling events. J Exp Bot 62:1049–1060

Barea JM, El-Atrach F, Azcon R (1991) The role of VA mycorrhizas in improving plant N acquisition from soil as assessed with 15^N. The use of stable isotopes in plant nutrition. In: Fitton C (ed) Soil fertility and environmental studies. Joint AIEA, FAO, Division, Vienna, pp 677–808

Barker SJ, Tagu D, Dalpè G (1998) Regulation of root and fungal morphogenesis in mycorrhizal symbiosis. Plant Physiol 116:1201–1207

Bashan Y, Puente ME, Rodriquea MN, Toledo G, Holguin G, Ferrera-Cerrato R, Pedrin S (1995) Survival of *Azorhizobium brasilense* in the bulk soil and rhizosphere of 23 soil types. Appl Environ Microbiol 61:1938–1945

Besserer A, Puech-Pages V, Kiefer P, Gomez-Roldan V, Jauneau A, Roy S, Portais JC, Roux C, Bécard G, Séjalon-Delmas N (2006) Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. PLoS Biol 4:e226

Besserer A, Bécard G, Jauneau A, Roux C, Séjalon-Delmas N (2008) GR24, a synthetic analog of strigolactones, stimulates the mitosis and growth of the arbuscular mycorrhizal fungus *Gigaspora rosea* by boosting its energy metabolism. Plant Physiol 148:402–413

Bolan NS (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plant. Plant Soil 134:189–207

Borie F, Rubio R, Rouanet JL, Morales A, Borie G, Rojas C (2006) Effects of tillage systems on soil characteristics, glomalin and mycorrhizal propagules in a Chilean Ultisol. Soil Tillage Res 88:253–261

Bouwmeester HJ, Roux C, Lopez-Raez JA, Bécard G (2007) Rhizosphere communication of plants, parasitic plants and AM fungi. Trends Plant Sci 12:224–230

Breuillin F, Schramm J, Hajirezaei M, Ahkami A, Favre P et al (2010) Phosphate systemically inhibits development of arbuscular mycorrhiza in *Petunia hybrida* and represses genes involved in mycorrhizal functioning. Plant J 64:1002–1017

Brundrett MC (2002) Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304

Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhizal interfaces. New Phytol 173:11–26

Buee M, Rossignol M, Jauneau A, Ranjeva R, Bécard G (2000) The pre-symbiotic growth of arbuscular mycorrhizal fungi is induced by a branching factor partially purified from root exudates. Mol Plant Microbe Interact 13:693–698

Burkert B, Robson A (1994) Zn uptake in subterranean clover (*Trifolium subterraneum* L.) by three vesicular-arbuscular mycorrhizal fungi in a root free sandy soil. Soil Biol Biochem 26:1117–1124

Cappellazzo G, Lanfranco L, Fitz M, Wipf D, Bonfante P (2008) Characterization of an amino acid permease from the endomycorrhizal fungus *Glomus mosseae*. Plant Physiol 147:429–437

Dalpè Y, Monreal M (2004) Arbuscular mycorrhizae inoculum to support sustainable cropping systems. Crop Manag 3. doi:10.1094/CM-2004-0301-09-RV

Deinum B, Sulastri RD, Zeinab MHJ, Maassen A (1996) Effects of light intensity on growth, anatomy and forage quality of two tropical grasses (*Brachiaria brizantha* and P*anicum maximum* var. trichoglume). Neth J Agric Sci 44:111–124

Dekkers TBM, van der Werff PA (2001) Mutualistic functioning of indigenous arbuscular mycorrhizae in spring barley and winter wheat after cessation of long-term phosphate fertilization. Mycorrhiza 10:195–201

Dong M, Pierdominici MG (1995) Morphology and growth of stolons and rhizomes in three clonal grasses, as affected by different light supply. Vegetatio 116:25–32

Douds DD, Pfeffer PE, Shachar-Hill Y (2000) Carbon partitioning, cost, and metabolism of arbuscular mycorrhizas. In: Kapulnik Y, Douds DD (eds) Arbuscular mycorrhizas: physiology and function. Kluwer Academic Publishers, Dordrecht

Friese CF, Allen MF (1991) The spread of VA mycorrhizal fungal hyphae in the soil–inoculum types and external hyphal architecture. Mycologia 83:409–418

Gamalero E, Glick BR (2011) Mechanisms used by plant growth-promoting bacteria. In: Maheshwari DK (ed) Bacteria in agrobiology: plant nutrient management. Springer, Berlin, pp 17–46

Garcia Junior O (1992) O enxofre e suas transformações microbianas. In: Cardoso E, Saito MT, Neves MCP (eds) Microbiologia do solo Campinas: SBCS, pp 243–255

Garcia-Garrido JM, Garcia-Romera I, Ocampo JA (1992) Cellulase production by the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe. New Phytol 121:221–226

Garcia-Romera I, Garcia-Garrido JM, Ocampo JA (1991) Pectolytic enzymes in the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae*. FEMS Microbiol Lett 78:343–346

Gavito ME, Miller MH (1998) Changes in mycorrhiza development in maize induced by crop management practices. Plant Soil 198:185–192

Gianinazzi-Pearson V (1996) Plant cell responses to arbuscular mycorrhizal fungi: getting to the roots of the symbiosis. Plant Cell 8:1871–1883

Gianinazzi-Pearson V, Branzanti B, Gianinazzi S (1989) In vitro enhancement of spore germination and early hyphal growth of a vesicular-arbuscular mycorrhizal fungus by root exudates and plant flavonoids. Symbiosis 7:243–255

Giovannetti M, Sbrana C, Citernesi AS, Avio L (1996) Analysis of factors involved in fungal recognition responses to host-derived signals by arbuscular mycorrhizal fungi. New Phytol 133:65–71

Goldstein AH, Rogers RD, Mead G (1993) Mining by microbe. Bio Technol 11:1250–1254

Goulart BL, Demchak K, Yang WQ (1995) Organic matter and nitrogen level effects on mycorrhizal infection in 'Bluecrop' highbush blueberry plants. J Small Fruit Viticult 3:151–164

Goulart BL, Demchak K, Yang WQ (1996) Effect of cultural practices on field grown 'Bluecrop' highbush blueberries, with emphasis on mycorrhizal infection levels. Acta Hortic 46:271–278

Govindarajulu M, Pfeffer PE, Jin H, Abubaker J, Doud DD, Allen JW, Bücking H, Lammers PJ, Shachar-Hill Y (2005) Nitrogen transfer in the arbuscular mycorrhizal Symbiosis. Nature 435:819–823

Graham JH, Leonard RT, Menge JA (1981) Membrane-mediated decrease in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. Plant Physiol 68:548–552

Guissou T, Bâ AM, Guinko S, Plenchette C, Duponnois R (2001) Mobilisation des phosphates naturels de kodijari par des jujubiers (*Ziziphus mauritiana* Lam.) mycorhizes dans un sol acidifié avec de la tourbe. Fruits 56:261–269

Gutjahr C, Novero M, Guether M, Montanari O, Udvardi M, Bonfante P (2009) Presymbiotic factors released by the arbuscular mycorrhizal fungus Gigaspora margarita induce starch accumulation in Lotus japonicus roots. New Phytol 183:53–61

Gyaneshwar P, Naresh Kumar G, Parekh LJ, Poole PS (2002) Role of soil microorganisms in improving P nutrition of plants. Plant Soil 245:83–93

Harley JL (1989) The significance of mycorrhiza. Mycol Res 92:129–139

Helgason T, Daniell TJ, Husband R, Fitter AH, Young JPW (1998) Ploughing up the wood-wide web. Nature 394:431

Hepper CM (1983) The effect of nitrate and phosphate on the vesicular–arbuscular mycorrhizal infection of lettuce. New Phytol 93:389–399

Herring JR, Fantel RJ (1993) Phosphate rock demand into the next century: impact on world food supply. Nat Resour Search 2:226–246

Ho WC, Ko WH (1985) Effect of environmental edaphic factors. Soil Biol Biochem 17:167–170

Hobbie JE, Hobbie EA (2006) N-15 in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. Ecology 87:816–822

Hodge A, Fitter AH (2010) Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. Proc Natl Acad Sci U S A 107:13754–13759

Hodge A, Campbell CD, Fitter AH (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature 413:297–299

Illmer P, Schinner F (1992) Solubilization of inorganic phosphates by microorganisms isolated from forest soil. Soil Biol Biochem 24:389–395

Jakobsen I (1995) Transport of phosphorus and carbon in VA mycorrhizas. In: Varma A, Hock B (eds) Mycorrhiza. Springer, Berlin, pp 297–324

Jasper DA, Abbott LK, Robson AD (1989) Soil disturbance reduces the infectivity of external hyphae of vesicular-arbuscular mycorrhizal fungi. New Phytol 112:93–99

Johnson NC (1993) Can fertilization of soil select less mutualistic mycorrhizae? Ecol Appl 3:749–757

Kabir Z, O'Halloran IP, Widden P, Hamel C (1998) Vertical distribution of arbuscular mycorrhizal fungi under corn (*Zea mays* L.) in no-till and conventional tillage systems. Mycorrhiza 8:53–55

Kahiluoto H, Ketoja E, Vestberg M (2000) Promotion of utilization of arbuscular mycorrhiza through reduced P fertilization 1. Bioassays in a growth chamber. Plant Soil 227:191–206

Khan MS, Zaidi A, Wani PA (2007) Role of phosphate-solubilizing microorganisms in sustainable agriculture-a review. Agron Sustain Dev 27:29–43

Khan AA, Jilani G, Akhtar MS (2009) Phosphorus solubilising bacteria: occurance, mechanisms and their role in crop production. J Agric Biol Sci 1:48–58

Kim KY, Jordan D, McDonald GA (1998) *Enterobacter agglomerans*, phosphate solubilizing bacteria and microbial activity in soil: effect of carbon sources. Soil Biol Biochem 30:995–1003

Koide TR, Shreinner PR (1992) Regulation of vesicular arbuscular mycorrhizal symbiosis. Annu Rev Plant Physiol Plant Mol Biol 43:557–581

Kosuta S, Chabaud M, Lougnon G, Gough C, Dénarié J, Barker DG, Bécard G (2003) A diffusible factor from arbuscular mycorrhizal fungi induces symbiosis-specific MtENOD11 expression in roots of *Medicago truncatula*. Plant Physiol 131:952–962

Kosuta S, Hazledine S, Sun J, Miwa H, Morris RJ, Downie JA, Oldroyd GE (2008) Differential and chaotic calcium signatures in the symbiosis signaling pathway of legumes. Proc Natl Acad Sci U S A 105:9823–9828

Kucey RMN (1983) Phosphate solubilizing bacteria and fungi in various cultivated and virgin Alberta soils. Can J Soil Sci 63:671–678

Kucey RMN (1988) Effect of *Penicillium bilaji* on the solubility and uptake of P and micronutrients from soil by wheat. Can J Soil Sci 68:261–270

Kucey RMN, Janzen HH, Legget ME (1989) Microbial mediated increases in plant available phosphorus. Adv Agron 42:199–228

Lapeyrie F (1988) Oxalate synthesis from soil bicarbonate by the mycorrhizal fungus *Paxillus involutus*. Plant Soil 110:3–8

Lin XG, Feng YZ, Zhang HY, Chen RR, Wang JH et al (2012) Long-term balanced fertilization decreases arbuscular mycorrhizal fungal diversity in an arable soil in north China revealed by 454 pyrosequencing. Environ Sci Technol 46:5764–5771

Liu YJ, Shi GX, Mao L, Cheng G, Jiang SJ et al (2012) Direct and indirect influences of 8 yr of nitrogen and phosphorus fertilization on *Glomeromycota* in an alpine meadow ecosystem. New Phytol 194:523–535

López-Ráez JA, Charnikhova T, Gómez-Roldán V et al (2008) Tomato strigolactones are derived from carotenoids and their biosynthesis is promoted by phosphate starvation. New Phytol 178:863–874

Matsumura A, Taniguchi S, Yamawaki K, Hattori R, Tarui A, Yano K, Daimon H (2013) Nitrogen uptake from amino acids in maize through arbuscular mycorrhizal symbiosis. Am J Plant Sci 4:2290–2294

Matsumura H, Umezawa K, Takeda K, Sugimoto N, Ishida T, Samejima M, Ohno H, Yoshida M, Higarashi K, Nakamura N (2014) Discovery of a eukaryotic pyrroloquinoline quinone dependent oxidoreductase belonging to new auxiliary activity family in the database of carbohydrate-active enzymes. PLoS One 9:e104851

McGonigle TP, Miller MH (1996) Mycorrhizae, P absorption and yield of maize in response to tillage. Soil Sci Soc Am J 60:1856–1861

Michelsen A, Schmidt IK, Sleep D (1996) Leaf 15^N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53–63

Miller MH (2000) Arbuscular mycorrhizae and the phosphorus nutrition of maize: a review of Guelph studies. Can J Plant Sci 80:47–52

Miller RM, Jastrow JD (1992) The role of mycorrhizal fungi in soil conservation. In: Behtlenfalvay GJ, Linderman RG (eds) Mycorrhizae in sustainable agriculture. ASA Special Publication 54. ASA, Madison, pp 29–44

Miller MH, McGonigle TP, Addy HD (1995) Functional ecology of vesicular-arbuscular mycorrhizas as influence by phosphate fertilization and tillage in an agricultural ecosystem. Crit Rev Biotechnol 15:241–255

Mohammadi GR, Chatrnour S, Jalali-honarmand S, Kahrizi D (2015) The effects of planting arrangement and phosphate biofertilizer on soybean under different weed interference periods. Acta Agric Slov 105:313–322

Morton JB (1990) Species and clones of arbuscular mycorrhizal fungi (*Glomales*, *Zygomycetes*): their role in macro and micro evolutionary processes. Mycotaxon 37:493–515

Motsara MR, Bhattacharyya PB, Srivastava B (1995) Biofertilizers their description and characteristics. In: Biofertilizer technology, marketing and usage, a sourcebook- cum-glossary, fertilizer development and consultation organisation 204–204, A Bhanot Corner, 1–2 Pamposh Enclave, New Delhi, 110048, pp 9–18

Nagy R, Drissner D, Amrhein N, Jakobsen I, Bucher M (2008) Mycorrhizal phosphate uptake pathway in tomato is phosphorus-repressible and transcriptionally regulated. New Phytol 181:950–959

Nahas E (1996) Factors determining rock phosphate solubilization by microorganism isolated from soil. World J Microb Biot 12:18–23

Nair MG, Safir GR, Siqueira JO (1991) Isolation and identification of vesicular-arbuscular mycorrhiza-stimulatory compounds from clover (*Trifolium repens*) roots. Appl Environ Microbiol 57:434–439

Navazio L, Moscatiello R, Genre A, Novero M, Baldan B, Bonfante P, Mariani P (2007) A diffusible signal from arbuscular mycorrhizal fungi elicits a transient cytosolic calcium elevation in host plant cells. Plant Physiol 144:673–681

Oehl F, Sieverding E, Ineichen K, Ris EA, Boller T, Wiemken A (2005) Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. New Phytol 165:273–283

Ogbo FC (2010) Conversion of cassava wastes for biofertilizer production using phosphate solubilizing fungi. Bioresour Technol 101:4120–4124

Oláh B, Brière C, Bécard G, Dénarié J, Gough C (2005) Nod factors and a diffusible factor from arbuscular mycorrhizal fungi stimulate lateral root formation in *Medicago truncatula* via the DMI1/DMI2 signalling pathway. Plant J 44:195–207

Ozanne PG (1980) Phosphate nutrition of plants – general treatise. The role of phosphorus in agriculture. In: Khasawneh FE, Sample EC, Kamprath EJ (eds) American Soc Agron Crop Sci Soc America, Soil Sci Soc America, Madison, pp 559–589

Park JH, Bolan N, Megharaj M, Naidu R (2011) Isolation of phosphate solubilizing bacteria and their potential for lead immobilization in soil. J Hazard Mater 185:829–836

Peters S (2002) Mycorrhiza 101. Reforestation Technologies International, Salinas

Raghuwanshi R (2012) Opportunities and challenges to sustainable agriculture in India. NEBIO 3:78–86

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47:376–390

Read DJ, Leake JR, Langdale AR (1989) The nitrogen nutrition of mycorrhizal fungi and their host plants. In: Boddy L, Marchant R, Read DJ (eds) Nitrogen, phosphorous and sulphur utilization by fungi. Cambridge University Press, New York, pp 181–204

Redecker D, Kodner R, Graham LE (2000) Glomalean fungi from the Ordovician. Science 289:1920–1921

Rillig MC, Wright SF, Eviner VT (2002) The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant Soil 238:325–333

Rodriguez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol Adv 17:319–339

Same BI, Robson AD, Abbott LK (1983) Phosphorus, soluble carbohydrates and endomycorrhizal infection. Soil Biol Biochem 15:593–597

Siqueira JO, Safir GR, Nair MG (1991) Stimulation of vesicular-arbuscular mycorrhiza formation and growth of white clover by flavonoid compounds. New Phytol 118:87–93

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic/Elsevier, New York

Smith FA, Grace EJ, Smith SE (2009) More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. New Phytol 182:347–358

Son CL, Smith SE (1995) Mycorrhizal growth responses: interaction between photon irradiance and phosphorus nutrition. New Phytol 108:305–314

Stamford NP, Silva JA, Freitas ADS, Araujo Filho JT (2002) Effect of sulphur inoculated with *Acidithiobacillus* in a saline soil grown with *Leucena* and *mimosa* tree legumes. Bioresour Technol 81:53–59

Stribley DP, Read DJ (1976) The biology of mycorrhiza in the ericaceae VI. The effects of mycorrhizal infection and concentration of ammonium nitrogen on growth of cranberry (*Vaccinium macrocarpon* Ait.) in sand culture. New Phytol 77:63–72

Subha Rao NS (1982) Advances in agricultural microbiology. In: Subha Rao NS (ed) Oxford and IBH Publ Co, pp 229–305

Thomson BD, Robson AD, Abbott LK (1986) Effects of phosphorus on the formation of mycorrhizas by *Gigaspora calospora* and *Glomus fasciculatum* in relation to root carbohydrates. New Phytol 103:751–765

Tisdall JM (1994) Possible role of soil microorganisms in aggregation in soils. Plant Soil 159:115–121

Treseder KK (2004) A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol 164:347–355

Tsai SM, Phillips DA (1991) Flavonoids released naturally from alfalfa promote development of symbiotic *Glomus* spores in vitro. Appl Environ Microbiol 57:1485–1488

Van Elsas JD, Van Overbeek LS, Fouchier R (1991) A specific marker pat for studying the fate of introduced bacteria and their DNA in soil using a combination of detection techniques. Plant Soil 138:49–60

Van Veen JA, Leonard S, Van Overbeek LS, Van Ellsas JD (1997) Fate and activity of microorganisms introduced into soil. Microbiol Mol Biol R 61:121–135

Venkateswarlu B, Rao AV, Raina P, Ahmad N (1984) Evaluation of phosphorus solubilization by microorganisms isolated from arid soil. J Indian Soc Soil Sci 32:273–277

Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586

Weidmann S, Sanchez L, Descombin J, Chatagnier O, Gianinazzi S, Gianinazzi-Pearson V (2004) Fungal elicitation of signal transduction-related plant genes precedes mycorrhiza establishment and requires the dmi3 gene in *Medicago truncatula*. Mol Plant Microbe Interact 17:1385–1393

Whiteside MD, Treseder KK, Atsatt PR (2009) The brighter side of soils: quantum dots track organic nitrogen through fungi and plants. Ecology 90:100–108

Whiteside MD, Digman MA, Gratton E, Treseder KK (2012) Organic nitrogen uptake by arbuscular mycorrhizal fungi in a boreal forest. Soil Biol Biochem 55:7–13

Wright SF, Upadhyaya A (1998) A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant Soil 198:97–107

Wright SF, Starr JL, Paltineau IC (1999) Changes in aggregate stability and concentration of glomalin during tillage management transition. Soil Sci Soc Am J 63:1825–1829

Yang WQ, Goulart BL, Demchak K, Li Y (2002) Interactive effects of mycorrhizal inoculation and organic soil amendments on nitrogen acquisition and growth of highbush blueberry. J Am Soc Hortic Sci 127:742–748

Yoneyama K, Xie X, Kusumoto D, Sekimoto H, Sugimoto Y, Takeuchi Y, Yoneyama K (2007a) Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. Planta 227:125–132

Yoneyama K, Yoneyama K, Takeuchi Y, Sekimoto H (2007b) Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. Planta 225:1031–1038

Zaidi A, Khan MS, Ahemad M, Oves M (2009) Plant growth promotion by phosphate solubilizing bacteria. Acta Microbiol Immunol Hung 56:263–284