

Mycorrhiza-mediated phosphorus use efficiency in plants

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Abstract

Phosphorus is the second most important plant nutrient after nitrogen that is critical for plant growth, it contributes up to about 0.2% dry mass. It can become deficient in different agro ecological conditions. In soil, it may be present in relatively large amounts, but it is one of the most difficult nutrients for plants to acquire. Much of it is poorly available because of the very low solubility of phosphates of iron, aluminium, and calcium, leading to soil solution concentrations of 10 μM or less and very low mobility. Plants have evolved a range of strategies that increase either soil solution phosphorus uptake capacity or availability in soil. The most exceedingly common of these strategies worldwide is inoculation of plant roots by arbuscular mycorrhizal fungi. Inoculation can promote plant growth by enhancing phosphate uptake from soil, particularly when the supply of phosphorus limits growth.

Key words: arbuscular mycorrhiza, phosphorus use efficiency, plant nutrition.

Abbreviations: AM, arbuscular mycorrhiza; C_{\min} , minimum soil solution nutrient concentration; I_{\max} , maximum uptake; K_m , Michaelis constant; P, phosphorus; P_o , orthophosphate; PEI, phosphorus efficiency index; PUE, phosphorus use efficiency.

Introduction

Continuing food production in intensive agriculture systems requires application of adequate amounts of phosphorus (P) on agricultural fields in order to sustain crop yields. On the other hand, there is a great need to improve the efficiency of this finite and non-renewable resource and also reasonable use of P resources in agriculture. Presently, phosphate production is about 133 Mt globally and dominated by four countries: the USA, Russia, Morocco, and China, which collectively utilize about 75% of the world's phosphate rock (Stewart et al. 2005). Phosphate rock is a finite non-renewable resource and the depletion of phosphate rock reserves is difficult to predict. However, if future consumption continues at the 5-year average mine production rate that occurred between 1997 and 2001, the global peak in phosphorus production is predicted to occur around 2030 (Cordell et al. 2009). The estimated world reserves would last about 90 years, while USA reserves would last only 25 years. However, low P availability limits plant growth on many soils across the world and is a common constraint to agricultural productivity, particularly in developing countries where access to P fertilizers is restricted (Lynch 2007).

In agriculture the excessive use of fertilizers and manures may result in diffuse P losses to surface and groundwater by erosion, surface runoff, and subsurface leaching (Buczko, Kuchenbuch 2007). P fertilizers, derived predominantly from rock phosphate, are used in intensive agricultural systems to overcome soil P deficiency, and thus make a

significant contribution to current global food production and security. However, rock phosphate reserves are a finite, non-renewable resource and there is renewed concern for more sustainable and equitable use of P resources in agriculture and a need to improve the efficiency with which P fertilizers are used in different agricultural systems (Bouwman et al. 2009; Cordell et al. 2009; Van Kauwenbergh 2010; Richardson et al. 2011). Total soil P typically ranges from 100 to 2000 mg kg^{-1} soil, which corresponds to about 350 to 7000 kg ha^{-1} P on an area basis, although only a small fraction of this P is available for crop uptake (Morel 2002). Removal of P by crops may vary between 3 to 30 kg ha^{-1} ; hence crop production will gradually diminish available soil P in the absence of external P application.

Why is phosphorus important?

Phosphorus is the second most important macronutrient, second to nitrogen, that is crucial for the stability and continued existence of life. P is an integral component of ATP and ADP molecules, phospholipids and nucleic acid, which are important in cellular membranes, and provides compounds for photosynthesis in plants and respiration in animals. There are many elementary and principal roles of P in many plant physiological processes, such as photosynthesis, utilization of sugar and starch, and energy transfer. Aside from this vital metabolic role, P is an indispensable structural component of numerous molecules, including nucleic acids, which are the building blocks of genes and chromosomes in the cell nucleus

and are obligatory for cell division and formation of meristematic tissues (Tisdale et al. 1985). For maximum yield, plants are in need for an ample amount of P from the very early stages of growth (Grant et al. 2005). Therefore, direct availability of P determines plant growth, and limited supply of P results in crop yield loss (Hinsinger 2001). A regular insufficient early-season P supply can limit crop yield and thus P fertilizer is commonly applied to ensure that sufficient P is available to optimize crop production.

Phosphorus dynamics in rhizosphere

The rhizosphere is the critical zone of interactions among plants, soils, and microorganisms. Plant roots can greatly modify the rhizosphere environment through their various physiological activities, particularly regarding exudation of organic compounds such as mucilage, organic acids, phosphatases, and some specific signalling substances, which are key drivers of various rhizospheric processes (Rakshit et al. 2002a). The chemical and biological processes in the rhizosphere not only determine mobilization and acquisition of soil nutrients as well as microbial dynamics, but also control nutrient use efficiency of crops, and thus intensely influence crop productivity (Hinsinger et al. 2009; Richardson et al. 2009a; Wissuwa et al. 2009; Zhang et al. 2010). Due to its low solubility and mobility in soil, P can be rapidly depleted in the rhizosphere by root uptake, resulting in a gradient of P concentration in a radial direction away from the root surface (Rakshit, Bhadoria 2009). In spite of total soil P content usually exceeding the plant requirements, the low mobility of soil P can restrict its availability to plants. Soluble P in the rhizosphere soil solution should be replaced 20 to 50 times per day by P delivery from bulk soil to the rhizosphere to meet plant demand (Marschner 1995). Therefore, P dynamics in the rhizosphere are mainly controlled by plant root growth and function, and are also highly related to physical and chemical properties of soil (Neumann, Romheld 2002). Because of the unique properties of P in soil, such as low solubility, low mobility, and high fixation by the soil matrix, the availability of P to plants is mainly controlled by two key processes:

- (i) spatial availability and acquisition of P in terms of plant root architecture as well as mycorrhizal association;
- (ii) bioavailability and acquisition of P controlled by rhizosphere chemical and biological processes.

Key role of phosphorus during early crop growth

The significance of sufficient P availability during early crop growth has been reported in different crop species (Grant et al. 2005). It has been reported that enhanced early-season P nutrition in maize increased dry matter at early stages partitioned to the grain at later development stages (Parewa et al. 2010). Likewise, in wheat and barley, P supply during

earlier growth had superior effect on final grain yield than P supply in later stages (Smith et al. 2011). Plenet et al. (2000) reported a greater difference in dry matter accumulation of maize under P deficiency during early stages of growth. The above ground dry matter accumulation was observed to be severely reduced (up to 60%) during early stages of maize growth, while there were only slight differences on dry matter accumulation at harvest and grain yield. The effect of early P deficiency on decline in shoot growth occurs because of slight stimulation of root growth (Mollier, Pellerin 1999). The initial reduction in growth related to P deficiency has an ultimate effect on the final crop yield, which is experienced by the crop throughout the remaining of the growing period.

Phosphorus use efficiency and plant growth

Nutrient efficiency is mainly considered as dry matter produced per unit nutrient element concentration in dry matter (Godwin, Blair 1991), which can also be termed as the internal nutrient requirement. However, there is much controversy concerning the concept of nutrient use efficiency, as it can be defined in different ways. Considering yield parameters, efficiency with regard to a specific mineral nutrient, is the capability of any species or cultivar of producing dry matter, in a soil limiting in that particular nutrient element. (Buso, Bliss 1988). Agronomic efficiency is defined as the total harvestable amount per unit of growth limiting nutrient element applied in the soil (Caradus, Woodfield 1990). External efficiency is the sum of nutrient content in soil primarily taken up by plants to produce a certain fraction of whole dry matter produced (Fohse et al. 1988). Some researchers have used the term nutrient efficiency ratio, which is calculated as the reciprocal of the nutrient concentration in the whole plant (Gourley et al. 1994). Other workers have used the term nutrient uptake efficiency (Buso, Bliss 1988). Uptake efficiency is defined in terms of total uptake per plant or specific uptake per unit root length (Marschner 1995).

Internal P management, like the effects of P stress on yield components and the way the plant distributes the acquired P among shoot organs, varies widely between genotypes (Sattelmacher et al. 1994). However, even greater genetic variation has been found in traits for acquisition of nutrients by roots (Lynch, Beebe 1995). Root morphological characters, such as root length, surface area, root radius, and density of root hairs, are regarded as having primary importance for P-uptake efficiency (Sattelmacher et al. 1994). Root morphology is determined not only by genetic but also by environmental factors, including soil P availability (Hajabbasi, Schumacher 1994). Plasticity of the root system can be exploited for developing P efficient cultivars. Nuruzzaman et al. (2005) hypothesized that P-acquisition efficiency in plant species varies with their rhizosphere volume and chemistry.

The second component of uptake efficiency is root physiological activity such as differing uptake kinetics, i.e. I_{\max} , K_m and C_{\min} , which result in different nutrient uptake rates per unit root and time (Steingrobe, Classen 2000). Plants differ in P-absorbing capacity of their roots, and even inter-specific variations have been found (Nielsen, Barber 1978; Krannitz et al. 1991). The parameter found to differ most among genotypes is the maximum net influx, I_{\max} (Claassen 1990) and plants are considered efficient when I_{\max} is high. However, when soil P availability is low, the rate limiting step in P uptake is its transport to the root surface and a high I_{\max} is useless (Jungk, Claassen 1997). Other mechanisms or traits that affect specific uptake efficiency include chemical mobilization of nutrients by root exudates, induced pH changes in the rhizosphere and AM associations (Marschner 1995). Nutrient-efficient species possess either morphological or physiological characteristics that facilitate higher nutrient uptake and/or better nutrient utilization, or are able to chemically influence the rhizosphere with a consequent improved nutrient availability (Sattelmacher et al. 1994). Bhadoria et al. (2001) found high P efficiency of groundnut in the field resulted from a high P influx, present even at low P concentrations in soil solution. In contrast, Bhadoria et al. (2004) found that groundnut is incapable of obtaining high P influx in nutrient solution at low P concentration. This indicates that some other mechanism must come into play to increase P influx under field conditions, for example, chemical mobilization of P bound to the soil solid by root exudates (Ae et al. 1990), or cell wall components (Ae et al. 2001) or contribution of AM (Marschner 1995).

When a plant is P deficient, two factors control plant growth. One is the rate of P absorption or P influx. The other is the ratio of dry mass increase to P content increase, which can be thought of as the efficiency with which P is used to produce dry matter, the P-use efficiency (PUE; Haynes et al. 1991; Koide 1991). The PUE is expected to vary according to tissue type. Seeds, for example, often have lower PUE than stems, because seeds require more P to produce a given dry mass than do stems. Variation in PUE also occurs among plant species (Christie, Moorby 1975; Haynes et al. 1991), and as a consequence of variation in P availability and mycorrhizal colonization (Haynes et al. 1991; Koide, 1991).

Factors affecting phosphorus use efficiency

The two following factors control the rate of P absorption or P influx into roots.

(i) The quantity of various nutrients, available for plant, including C, N, P etc., determine the capability of the root surface area (root morphology) to absorb P from the soil, and controls P absorption by the plant, all else being equal. The more P held by the plant (its internal P reserve; Bloom et al. 1985), the more can be used to produce root surface

area in order to acquire P from the soil. Therefore, the most critical of these nutrient elements under the control of the plant is P itself.

(ii) The efficiency with which the internal P reserve is used to absorb P from the soil. There is no immediate negative consequence to inefficient use of a non-limiting resource, simply because it is available in non-limiting amounts.

However, immediate benefit is a consequence of more efficient use of plant P, because P is the limiting resource. Koide et al. (1999) defined the efficiency with which the internal P reserve is used to absorb P from the soil as the phosphorus efficiency index (PEI). The PEI is analogous to the 'efficiency index of dry weight production' (Blackman 1919), which determines how efficiently the plant's current dry mass is used to gain more mass. It can often be expressed as the relative growth rate. Similarly, PEI is defined as a measure of how efficiently the plant's internal P reserve is used to gain more P (Hunt 1990). Thus, phosphorus influx into roots is a function of both plant P content and PEI, and accordingly, growth rate is a function of the PUE, the P content and the PEI.

Mycorrhiza plays a role in phosphorus transport

P is critical for plant growth and makes up about 0.2% of dry mass, but it is one of the most difficult nutrients for plants to acquire. In soil, it may be present in relatively large amounts, but much of it is poorly available because of the very low solubility of phosphates of iron, aluminium, and calcium, leading to soil solution concentrations of 10 mM or less and very low mobility (Ryan, Graham 2002; Ryan et al. 2005). In consequence, uptake of orthophosphate (P_i) by root epidermal cells including root hairs leads to lower P_i concentrations in the rhizosphere, as replacement does not keep pace with uptake. Plants and fungi take up P as negatively charged P_i ions ($H_2PO_4^-$), which possess additional problems, because the concentration in cells is about 1 000-fold higher than in the soil solution and the cell membrane has an inside-negative electric potential. P_i uptake, therefore, requires metabolic energy and involves high-affinity transporter proteins (Bucher 2007).

Accordingly, plants have evolved a range of strategies that increase either P_i uptake capacity or availability of P_i in soil. The most widespread of these strategies worldwide is AM symbiosis (Cheng et al. 2011; Lambers et al. 2011). AM symbioses are widespread in the plant kingdom and contribute significantly to plant P nutrition and growth in natural ecosystems. Association of AM may improve P uptake from soil (Smith et al. 2011). AM fungi are ecologically significant because they form relationships in and on the roots of a host plant in a symbiotic association so that mycorrhizas, not roots, are the chief organs of nutrient uptake by plants (Bagayoko et al. 2000). Mycorrhizas form a critical link between the aboveground plant and the soil by

influencing plant nutrient cycling (Rakshit et al. 2002a) and soil structure (Korb et al. 2003). AM fungi colonize most agricultural species (exceptions include *Brassica* spp. and *Lupinus* spp.) and have an important role in the P nutrition of many farming systems worldwide, especially on soils with low available P (Smith, Smith 2011; Smith et al. 2011). However, the advantages of increased P-uptake and growth over comparative, non-mycorrhizal plants at low P diminish with increasing soil P availability (Rakshit et al. 2002a; Rakshit et al. 2002b). There is often little advantage in growth at soil P levels necessary for near maximum plant growth rates in intensive agricultural systems (Simpson et al. 2011). In some instances, growth rates of AM plants are less at high soil P than those of comparative nonmycorrhizal plants (Johnson et al. 1997). The ability of AM to enhance host-plant uptake of relatively immobile nutrients, in particular P and Zn (Balakrishnan, Subramanian 2012), and their requirement for up to 20% of host photosynthate for establishment and maintenance, is well accepted (Graham 2000; Subramanian et al. 2008; Subramanian et al. 2009). It has generally been recognized that the effect of AM symbiosis associated with host plants is beneficial, because growth and development of the plants are stimulated, drought tolerance increases and the association has a high potential for agriculture (Rakshit et al. 2002b) and land reclamation (Liu, Li 2000). As a result of these characteristics, AM fungi have been expected to promote plant growth in degraded and denuded lands (Yokoyama et al. 2005; Rakshit et al. 2008). The most publicized benefit of mycorrhiza is the improved growth rate, often shown in experimental comparisons of mycorrhizal and non-mycorrhizal plants through its inoculation (Subramanian, Charest 2007). Plant benefits with this association under nutrient-poor conditions increasing phosphorus uptake by the host plant (Koide 1991). Miller et al. (1995) and coworkers reported an interesting case where disturbance of an arable, no-till soil resulted in reduced AM development and subsequently less absorption of P by seedlings of maize in the field. Neumann and George (2004) concluded that mycorrhizal colonization seems to increase P uptake from dry soil.

Plants grown at high P in the presence of mycorrhizae accumulated only 88% of biomass of plants grown at high P in absence of mycorrhizae, indicating that mycorrhizae can reduce plant growth when not contributing to the symbiosis. Although a beneficial role of mycorrhizal symbiosis has been frequently observed, there have been cases reported where mycorrhizal inoculation has led to a decrease in plant productivity, particularly in AM plants (Jifon et al. 2002; Schroeder, Janos 2004). The results of Correa et al. (2006) showed that plants react differently to ectomycorrhiza formation, depending on their stage of development, leaf area, their initial nutritional status, and the amount of nitrogen supplied.

Plant response to AM inoculation is extremely variable

both among and within species. Inoculation by AM have a wide range of effects on different plant species in relation to P nutrition in different situations. The effectiveness of AM fungi *Gigaspora margarita* in increasing plant growth was observed to be closely correlated with colonised root length (Rohyadi et al. 2004). Generally, the development of AM inoculation seemed to follow a three phase growth curve i.e. a lag phase, a phase of rapid growth and a phase of constancy or plateau phase with increase age of plants (Saif 1986). Upon mycorrhizal inoculation, increase in shoot growth is generally lower at the initial stage, and then increases rapidly with age of plants (Bethlenfalvay, Linderman 1992). Ma et al. (2006) found that root inoculation and the number of proliferating spores increased with increasing levels of peat. Mycorrhizal plants deplete phosphate to lower levels and to a much larger soil volume per unit root length than nonmycorrhizal plants (Allen 1991). Influx of P in roots colonized by AM fungi can be three to five times that in nonmycorrhizal roots (Smith, Read 1997). Jakobsen (1986) reported a two to three times increase in influx of P to roots of pea and clover plants, respectively, due to the effect of mycorrhiza.

Mechanism of P uptake by mycorrhiza: increased surface area

The external hyphae of AM extend from the root surface to the soil beyond the P depletion zone and have access to a greater volume of undepleted soil than the root alone (Jakobsen 1986; Lambers 2006; Lambers et al. 2011). Some hyphae may extend more than 10 cm from root surfaces (Jakobsen et al. 2005) which is further than most root hairs. Also, the small diameter of hyphae (20 to 50 μm) allows access to soil pores that cannot be explored by roots. Therefore, a root system forming a mycorrhizal network will have a greater effective surface area (Lambers et al. 2008) for absorbing nutrients and exploring a greater volume of soil than nonmycorrhizal roots. In one study, the volume was calculated to be at least 100 times greater with mycorrhizal association than in its absence (Sieverding 1991). Moreover, mycorrhizal colonization may induce formation of lateral roots or increase root branching (Lynch 2007; Rakshit, Bhadoria 2009), further increasing the volume of soil explored.

Mycorrhizal plants can absorb more P at lower concentration in the soil solution than nonmycorrhizal plants (Lynch, Brown 2001; Rakshit, Bhadoria 2009). One possible explanation is that mycorrhizal hyphae have a higher affinity (lower K_m) for P than roots (Zhu et al. 2010). But this phenomenon is not necessary for explaining improved P uptake by mycorrhizal roots. Barber (1984) explained that there is a very limited concentration gradient around hyphae (i.e., minimal depletion zone) since the radius of hyphae is much smaller than that of roots plus root hairs (0.005 mm versus 0.15 mm). Hence, P concentration

in soil solution around hyphae is always higher than in the P depletion zone around roots, and hyphae may absorb more P in low P soil even without having a higher affinity for P.

Mechanism of P uptake by mycorrhiza: biochemical modification of rhizosphere

Several researchers worldwide proposed rhizospheric microbial inoculants as integral and indispensable components of integrated nutrient management systems (Adesemoye, Kloepper 2009; Harvey et al. 2009; Khan et al. 2010), particularly regarding their ability to increase the availability of P for crops (Kucey, Leggett 1989; Bowen, Rovira 1999; Jakobsen et al. 2005). Mycorrhizae play a considerable role in alteration of the biochemical environment (Rakshit, Bhadoria 2009) and in the physiological characteristics of the rhizosphere, which can improve P accessibility in the rhizosphere (Richardson 1994; Whitelaw 2000; Jakobsen et al. 2005; Harvey et al. 2009; Richardson et al. 2009a; Khan et al. 2010; Richardson, Simpson, 2011). Mycorrhiza was shown to induce increased proton efflux or pCO₂ activity around the rhizosphere, lowering pH to around 6.3 (Rigou, Mignard 1994) resulting in greater solubilization of P (Kucey, Leggett 1989; Bowen, Rovira 1999), predominantly in neutral to calcareous soils (Bago, Azcon-Aguilar 1997). Citric acid and siderophores produced by mycorrhizae can enhance bioavailability of P supply in the soil more specifically in the case of Fe- or Al-bound P in acidic soils (Haselwandter 1995; Cress et al. 1986; Richardson, Simpson 2011). Furthermore, mycorrhizae has been reported to produce alkaline phosphatases, which can mobilize P from organic sources, and a low rate of this can have a long-term impact on mobilizing phosphate (Tarafdar, Marschner 1994). The hydrolysis of organic P by extracellular phosphatases secreted by mycorrhizae, excretion of protons, hydroxyls and organic anions (Rakshit, Bhadoria 2007), and modifications of the redox potential around mycelium and roots of the mycorrhizal association might also hasten the release of P ions from soil to solution (Hinsinger 2001). Alteration in rhizospheric pH is also associated with the soil-buffering capacity, microbial activities, and plant genotypes. (Raghothama, 1999; Hinsinger et al. 2003; Vance et al. 2003). These different mechanisms play a significant role, especially in response to phosphorus mobilization (Lambers et al. 2011).

Organic anion exudation in the rhizospheric environment plays a vital role in the bioavailability of soil P (Hinsinger 2001; Roelofs et al. 2001). Mycorrhiza releases organic anions such as citrate, malate and oxalate, which can occupy sorption sites that might otherwise mobilize P, or replace P in the sparingly soluble complexes with aluminium, iron and calcium (Richardson et al. 2011). Thus it can enhance availability of P into soil solution (Khademi et al. 2009; 2010; Richardson et al. 2011), which might be

accountable for the greater release of organic forms of soil P (Wei et al. 2010). Mycorrhiza is also reported to produce carboxylates, which influence ligand exchange, ligand-promoted dissolution of P-bearing minerals such as Fe/Al oxides, and thus having a significant contribution in P mobilization. However, carboxylate induces alteration in surface charges on clays, and complexation of P with Al/Fe oxides have not been much discussed yet by researchers (Neumann et al. 1999; Wang et al. 2010). It has been found that the Al-activated malate transporter mediates malate exudation (Hoekenga et al. 2006) and that the extrusion transporter mediates citrate exudation (Magalhaes et al. 2007), and both may confer resistance to complexation of P with Al/Fe.

Role of mycorrhiza in crops

AM fungi are associated with improved growth of many plant species due to increased nutrient uptake, production of growth promoting substances, tolerance to drought, salinity and transplant shock and synergistic interaction with other beneficial soil microorganisms such as N-fixers and P-solubilizer. Symbiotic association of plant roots with VA-fungi often result in enhanced growth because of increased acquisition of P and other low mobility mineral nutrients (Table 1). Advantages of AM symbiosis over the non-mycorrhizal state of the same plant genotype are inextricably associated with root architecture, in that plants with extensive, branched root systems, very fine roots and long root hairs tend to show relatively low improvement in growth when they are mycorrhizal, even in low P soils (Condrón 2004; Cherr et al. 2006; Fageria 2007; Simpson et al. 2011). AM symbioses have a mixed reputation worldwide as a means of improving crop growth, particularly under high soil P conditions. The reason for this is the lack of obvious nutritional benefits to the crop, or a apparent 'parasitic' effect that constrains crop yield under high soil P conditions. Consequently, it has been suggested that there may be benefits to production by managing crop rotations to reduce AM fungi (Richardson et al. 2011). From a P-use efficiency perspective, the challenge is to increase the utilization of organic P for plant production, either as a consequence of modified agronomic practices (Simpson et al. 2011) or by using plants or microorganisms capable of enhancing the mineralization of organic P (Richardson et al. 2009a; Richardson et al. 2009b).

Conclusions

Scientific evidence gathered so far in this review indicates that mycorrhiza is likely to have a significant impact on plant nutrient uptake, particularly phosphorus, its allocation and cycling. However, the responses of plant species richness and plant production to P-limitation can only be understood when the interactions of this limitation

Table 1. Phosphorus-uptake responses of some agricultural crops to mycorrhizal inoculation (indigenous/externally added)

Crop	Mycorrhizal inoculation	Response	Experimental set up	Reference
Maize	<i>Glomus intraradices</i>	Grain yield increased by 41%	Pot / field experiment with red sandy loam soil	Ananthi et al. 2011
Wheat	<i>Glomus mosseae</i> , <i>Glomus deserticola</i> , <i>Gigaspora gergaria</i>	Shoot P content increased by 6 to 54% with 79.5 to 109% dependency. <i>G. mosseae</i> had the largest effect on plant growth and other physiological parameters	Efficiency of AM fungi in enhancing growth and mineral content of wheat plants in saline soil	Abdel-Fattah, Asrar 2012
Maize	<i>Glomus intraradices</i>	Recorded 9% better growth and yield attributes and grain	Influence of iron application and AM inoculation in calcareous sandy clay loam soil (pH 7.58)	Archana et al. 2012
Green gram	<i>Glomus fasciculatum</i> , <i>Glomus mosseae</i>	Grain yield (by 14.8 and 13.5%) and grain P content was significantly increased (by 21.95 and 20.97%), respectively	Field experiment in typical alfisols with silty clayloam, containing different levels of N, AM and <i>Rhizobium</i>	Bhat et al. 2011
Kinnow	<i>Glomus manihotis</i> , <i>Glomus mosseae</i> , <i>Gigaspora gigantea</i>	Increased foliar P concentration by 43.21, 12.35 and 111.52%, respectively	Field study	Shamshiri et al. 2012
Rice and mung bean	<i>Glomus caledonium</i>	Improved formation of mycorrhizas by intercropping increased total P uptake by 57% in rice, and total P and N acquisition by 65 and 64%, respectively, in mung bean	Method of plastic film and nylon net partition and tracing ¹⁵ N transfer between the intercropped upland rice and mung bean to allow penetration with and without a barrier of nylon net of fungal hyphae, assayed the effect on nutrient acquisition and biomass	Li et al. 2009
Maize, sorghum, millet, mash bean, mung bean	Indigenous mycorrhiza	Crops showed 3 to 101% increase in shoot dry matter with inoculation of AM fungi. Significant increase of plant P uptake for 63, 80, 75, 166 and 50% for the respective crops	Pot experiment with Tarnab soil, sandy loam, mixed hyperthermic UdicHaplustepts containing low P concentration for 70 days	Sharif et al. 2011
Wheat	<i>Glomus mosseae</i>	Grain yield increased by 25.9%	Field experiment with seed priming and soil inoculation	Kumar et al. 2011a
Strawberry	<i>Glomus clarum</i> , <i>Glomus caledonium</i>	Fruit yield increased by 17.8%	Soilless substrate was drip irrigated with different P concentrations and inoculated with AM in unheated greenhouse	Cekic, Yilmaz 2011
Maize	<i>Glomus mosseae</i>	Seed yield increased by 21.53%	Field experiment with sandy loam sand	Mobasser, Moradgholi 2012
Cape gooseberry	<i>Glomus</i> sp., <i>Acaulospora</i> sp., <i>Entrophospora</i> sp.	AM fungi alleviated and compensated for the growth limitations imposed by saline conditions	Field experiment with clay loam sand with pH 5.59 and EC 5.65 dS m ⁻¹	Miranda et al. 2011
Alfalfa	<i>Gigaspora rosea</i> , <i>Glomus intraradices</i> + <i>Gigaspora rosea</i> , <i>Glomus etunicatum</i> + <i>Glomus intraradices</i>	Water use efficiency, root and shoot dry weight significantly increased. Maximum water use efficiency, shoot and root weight was achieved with dual inoculation	Pot experiment with sterilized soil at two water regimes	Khan et al. 2007

Table 1. (continued)

Crop	Mycorrhizal inoculation	Response	Experimental set up	Reference
Beet, lettuce, velvetleaf	<i>Glomus intraradices</i>	Increased P content by 150% in lettuce and 160% in velvetleaf. No significant effect on PEI and P content in beet. Significant decrease in PUE for lettuce, no effect for velvetleaf and beet	Pot experiment with soil / sand mixture	Koide et al. 2000
Peach	<i>Glomus mosseae</i> , <i>Glomus versiforme</i> , <i>Paraglomus occultum</i>	Plant height, stem diameter, shoot, root and total dry weight significantly increased by 30.3, 17.2, 34.4, 64.5 and 45.4%, respectively with inoculation of <i>G. mosseae</i> , 11.8, 10.9, 19.4, 31.2% and 23.5% with <i>G. versiforme</i> , and 6.4, 1.9, 12.1, 24.8 and 16.8% with <i>P. occultum</i> . Inoculation elevated K, Mg, Fe and Zn content in leaves and roots, Ca content in leaves, Cu and Mn content in roots	Pot experiment with autoclaved substrate	Wu et al. 2011
Wheat	<i>Glomus fasciculatum</i>	Significant increased grain yield by 21.6, 13.3, and 17.5% for AM, <i>Azotobacter</i> , and AM + <i>Azotobacter</i> , respectively	Field study using seed inoculation with AM and <i>Azotobacter</i> at different levels of irrigation	Hasanpour et al. 2012
Maize	–	Grain yield increased by 18.1%	Experimental soil calcareous with sandy loam texture (pH 7.58)	Amanullah et al. 2011
Chickpea, barley	<i>Glomus</i> spp. (<i>G. intraradices</i> , <i>G. mosseae</i> , <i>G. claroideum</i> , <i>G. microgregatum</i> , <i>G. caledonium</i> , <i>G. etunicatum</i>)	Positive effects on nutrient status of chickpea and barley grown under moderate soil nutrient supply. Better response in chickpea in respect to nutrient concentration, and in barley in respect to dry matter accumulation. No effect on growth	Field with a low soil availability of P	Farzaneh et al. 2011
<i>Jatropha curcas</i>	<i>Glomus aggregatum</i> , <i>Glomus macrocarpum</i> , <i>Glomus mosseae</i> , <i>Glomus fasciculatum</i> , <i>Glomus intraradices</i> , <i>Glomus etunicatum</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora delicata</i> , <i>Gigaspora margarita</i> , <i>Scutellospora pellucida</i>	Low soil P content enhanced AM spore population and inoculation in roots. Highly significant dependence on plant growth	Field study with two different soil types, black cotton soil (pH 7.5) and red-murumy soil (pH 6.1)	Jamaluddin, Singh 2006
Pearl millet, sorghum, cow pea	<i>Glomus mossae</i>	AM application increased P concentration in shoots by 170%	Experiments in acid sandy soils (pH 5.6) deficient in P	Bagayoko et al. 2000

with multiple other abiotic resources and biotic interactions are taken into consideration. To increase sustainability of agriculture, plant adaptations to low P concentrations in soils can be attained by using mycorrhiza. With rising prices for P fertilizers, the use of mycorrhiza and the breeding of cultivars with adapted root systems or exudation strategies are possible tools in maintaining or increasing productivity.

References

- Adesemoye A.O., Klopper, J.W. 2009. Plant-microbes interactions in enhanced fertilizer-use efficiency. *Appl. Microbiol. Biotechnol.* 85: 1–12.
- Ae N., Arihara J., Okada K., Yoshihara T., Johansen C. 1990. Phosphorus uptake by pigeon pea and its role in cropping systems of Indian subcontinent. *Science* 248: 447–480.
- Ae N., Shen R., Otani T. 2001. The significance of the root cell wall in phosphorus uptake. In: Ae N., Arihara J., Okada K., Srinivasan A. (eds) *Plant Nutrient Acquisition: New Perspectives*. Tokyo, Springer-Verlag, pp. 251–275.
- Allen M.F. 1991. *The Ecology of Mycorrhizae*. Cambridge University Press, Cambridge. 184 p.
- Amanullah M.M., Ananthi T., Subramanian K.S., Muthukrishnan P. 2011. Influence of mycorrhiza, nitrogen and phosphorus on growth, yield and economics of hybrid maize. *Madras Agric. J.* 98: 62–66.
- Ananthi T., Amanullah M.M., Subramanian K.S. 2011. Influence of fertilizer levels and mycorrhiza on root colonization, root attributes and yield of hybrid maize. *Madras. Agric. J.* 98: 56–61.
- Archana J., Amanullah M.M., Manoharan S., Subramanian K.S. 2012. Influence of iron and arbuscular mycorrhiza inoculation on growth and yield of hybrid maize in calcareous soil. *Madras. Agric. J.* 99: 65–67.
- Bagayoko M., George E., Romheld V., Buerkert A. 2000. Effect of mycorrhizal fungi and phosphorus on growth and nutrient uptake of millet, cowpea and sorghum on a West African soil. *J. Agric. Sci.* 135: 399–407.
- Bago B., Azcon-Aguilar C. 1997. Changes in the rhizospheric pH induced by arbuscular mycorrhiza formation in onion (*Allium cepa* L.). *Z. Pflanz. Bodenkunde* 160: 333–339.
- Balakrishnan N., Subramanian K.S. 2012. Mycorrhizal symbiosis and bioavailability of micronutrients in maize grain. *Maydica* 57: 129–138.
- Barber S.A., 1984. *Soil Nutrient Bioavailability. A Mechanistic Approach*. John Wiley and Sons, New York, USA. 398 p.
- Bethlenfalvay G.J., Linderman R.G. 1992. *Mycorrhizae in Sustainable Agriculture*. American Society of Agronomy Inc. Wisconsin, USA.
- Bhadoria P.B.S., Singh S., Claassen N. 2001. Phosphorus efficiency of wheat, maize and groundnut grown in low phosphorus-supplying soil. *Plant. Nutr.* 92: 530–531.
- Bhadoria P.S., Dessougi H.E., Liebersbach H., Claassen N. 2004. Phosphorus uptake kinetics, size of root system and growth of maize and groundnut in solution culture. *Plant Soil* 262: 327–336.
- Bhat M.L., Bangroo S.A., Ali T., Yadav S.R.S., Aziz M.A. 2011. Combined effects of rhizobium and vesicular arbuscular fungi on green gram (*Vigna radiata* L. Wilczek) under temperate conditions. *Res. J. Agric. Sci.* 2: 17–20.
- Blackman V.H. 1919. The compound interest law and plant growth. *Ann. Bot.* 33: 353–360.
- Bloom A.J., Chapin F.S.III, Mooney H.A., 1985. Resource limitation in plants: An economic analogy. *Annu. Rev. Ecol. System.* 16: 363–392.
- Bouwman A.F., Beusen A.H.W., Billen G., 2009. Human alteration of the global nitrogen and phosphorus soil balances for the period 1970–2050. *Global Biogeochem. Cycles* 23: GB0A04.
- Bowen G.D., Rovira A.D. 1999. The rhizosphere and its management to improve plant growth. *Adv. Agron.* 66: 1–102.
- Bucher, M., 2007. Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. *New. Phytol.* 173: 11–26.
- Buczko U., Kuchenbuch R.O., 2007. Phosphorus indices as risk-assessment tools in the USA and Europe – a review. *J. Plant Nutr. Soil Sci.* 170: 445–460.
- Buso G.S.C., Bliss F.A., 1988. Variability among lettuce cultivars grown at two levels of available phosphorus. *Plant Soil* 111: 67–73.
- Caradus J.R., Woodfield D.R. 1990. Estimates of heritability for and relationships between root and shoot characters of white clover. I. Replicated clonal material. *Euphytica* 46: 203–209.
- Cekic C., Yilmaz E. 2011. Effect of arbuscular mycorrhiza and different doses of phosphorus on vegetative and generative components of strawberries applied with different phosphorus doses in soilless culture. *African J. Agric. Res.* 6: 4736–4739.
- Cheng L., Bucciarelli B., Shen J., Allan D.L., Vance C.P. 2011. Update on white lupin cluster roots acclimation to phosphorus deficiency. *Plant. Physiol.* 156: 1025–1032.
- Cherr C.M., Scholberg J.M.S., McSorely R. 2006. Green manure approaches to crop production: a synthesis. *Agron. J.* 98: 302–319.
- Christie E.K., Moorby J. 1975. Physiological responses of semiarid grasses. I. The influence of phosphorus supply on growth and phosphorus absorption. *Austr. J. Agric. Res.* 26: 423–436.
- Condron L.M. 2004. Phosphorus – surplus and deficiency. In: Schjonning P., Christensen B.Y., Elmholt S. (eds) *Managing Soil Quality – Challenges in Modern Agriculture*. CAB International, Wallingford, pp. 69–84.
- Cordell D., Drangert J.O., White S., 2009. The story of phosphorus: Global food security and food for thought. *Global Environ. Change* 19: 292–305.
- Correa A., Strasser R.J., Martins-Loucao M.A., 2006. Are mycorrhiza always beneficial? *Plant Soil* 279: 65–73.
- Cress W.A., Johnson G.V., Barton L.L. 1986. The role of endomycorrhizal fungi in iron uptake by *Hilaria jamesii*. *J. Plant Nutr.* 9: 547–556.
- Fageria N.K., 2007. Green manuring in crop production. *J. Plant. Nutr.* 30: 691–719.
- Farzaneh M., Vierheilig H., Lössl A., Kaul H.P. 2011. Arbuscular mycorrhiza enhances nutrient uptake in chickpea. *Plant Soil Environ.* 57: 465–470.
- Fohse D., Claassen N., Jungk A. 1988. Phosphorus efficiency of plants. I. External and internal P requirement and P uptake efficiency of different plant species. *Plant Soil.* 110: 101–109.
- Gamal M.A.F., Abdul-Wasea A.A. 2012. Arbuscular mycorrhizal fungal application to improve growth and tolerance of wheat (*Triticum aestivum* L.) plants grown in saline soil. *Acta Physiol. Plant.* 34: 267–277.
- Godwin D.C., Blair G.J. 1991. Phosphorus efficiency in pasture species: A comparison of white clover accessions. *Austr. J. Agric. Res.* 42: 531–540.
- Gourley C.J.P., Allan D.L., Russsele M.P. 1994. Plant nutrient efficiency: A comparison of definitions and suggested

- improvement. *Plant Soil* 158: 29–37.
- Graham J.H. 2000. Assessing cost of arbuscular mycorrhizal symbiosis in agroecosystems. In: Podila G.K., Douds D.D. (eds) *Current Advances in Mycorrhizae Research*. APS Press, StPaul, pp. 127–140.
- Grant C., Bittman S., Montrea M., Plenchette, C., Morel C., 2005. Soil and fertilizer phosphorus: Effects on plant P supply and mycorrhizal development. *Can. J. Plant Sci.* 85: 3–14.
- Hajabbasi M.A., Schumache T.E., 1994. Phosphorus effects on root growth and development in two maize genotypes. *Plant Soil* 158: 39–46.
- Harvey P.R., Warren R.A., Wakelin S.A., 2009. Potential to improve root access to phosphorus: the role of nonsymbiotic microbial inoculants in the rhizosphere. *Crop. Pasture Sci.* 60: 144–151.
- Hasanpour J., Panahi M., Sadeghi P.M.M., Arabsalmani K., 2012. Effect of inoculation with VA mycorrhiza and azotobacter on grain yield, LAI and protein of wheat on drought stress condition. *Int. J. Agric. Sci.* 2: 466–476.
- Haselwandter K., 1995. Mycorrhizal fungi: Siderophore production. *Crit. Rev. Biotechnol.* 15: 287–291.
- Haynes B., Koide R.T., Elliott G. 1991. Phosphorus uptake and utilization in wild and cultivated oats *Avena* sp. *J. Plant Nutr.* 14: 1105–1118.
- Hinsinger P. 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root induced chemical changes: a review. *Plant Soil* 237:173–195.
- Hinsinger P., Bengough A.G., Vetterlein D., Young I.M. 2009. Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant Soil* 321: 117–152.
- Hinsinger P., Plassard C., Tang C., Jaillard B. 2003. Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. *Plant Soil* 248: 43–59.
- Hoekenga O.A., Maron L.G., Pineros M.A., Cancado G.M.A., Shaff J. 2006. AtALMT1, which encodes a malate transporter, is identified as one of several genes critical for aluminum tolerance in Arabidopsis. *Proc. Natl. Acad. Sci. USA* 103: 9738–9743.
- Jakobsen I. 1986. Phosphorus inflow into roots of mycorrhizal and non mycorrhizal peas under field conditions. In: Gianinazzi-Pearson V., Gianinazzi S. (eds) *Physiological and Genetic Aspects of Mycorrhiza*. INRA, Paris. pp. 317–322.
- Jakobsen I., Leggett M.E., Richardson A.E. 2005. Rhizosphere microorganisms and plant Phosphorus Uptake. In: Sims J.T., Sharpley A.N. (eds) *Phosphorus, Agriculture and the Environment*. American Society for Agronomy, Madison, pp. 437–494.
- Jamaluddin Singh A.K. 2006. Studies on arbuscular mycorrhizal fungi associated with *Jatropha curcas* L. *Myco. News* 18: 12–14.
- Jifon J.L., Graham J.H., Drouillard D.L., Syvertsen J.P. 2002. Growth depression of mycorrhizal *Citrus* seedlings grown at high phosphorus supply is mitigated by elevated CO₂. *New Phytol.* 153: 133–142.
- Johnson N.C., Graham J.H., Smith F.A., 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* 135: 575–585.
- Johnson N.C., Pflieger F.L. 1992. Vesicular-arbuscular mycorrhizae and cultural stress. In: Bethlenfalvay, G.J., Lindennan, R.G. (eds) *Mycorrhizae in Sustainable Agriculture*. Am. Soc. Agron. Special PubHcalion 54, Am. Soc. Agron, Madison, pp. 71–99.
- Jungk A., Claassen, N. 1997. Ion diffusion in soil-root system. *Adv. Agron.* 61: 53–110.
- Khademi Z., Jones D.L., Malakouti M.J., Asadi F. 2010. Organic acids differ in enhancing phosphorus uptake by *Triticum aestivum* L. – Effects of rhizosphere concentration and counter ion. *Plant Soil* 334: 151–159.
- Khademi Z., Jones D.L., Malakouti M.J., Asadi F., Ardebili M. 2009. Organic acid mediated nutrient extraction efficiency in three calcareous soils. *Austr. J. Soil Res.* 47: 213–220.
- Khan I.A., Mirza S.N., Ayub N., Nizami M. 2007. Yield and water use efficiency (WUE) of *Medicago sativa* as influenced by vesicular arbuscular mycorrhizae (VAM). *Pakistan J. Agric. Sci.* 44: 456–460.
- Khan M.S., Zaidi A., Ahemad M., Oves M., Wani P.A. 2010. Plant growth promotion by phosphate solubilising fungi – current perspective. *Arch. Agron. Soil Sci.* 56: 73–98.
- Koide R.T. 1991. Nutrient supply, nutrient demand and plant response to mycorrhizal infection. *New Phytol.* 117: 365–386
- Koide R.T., Dickie I.A., Goff M.D. 1999. Phosphorus deficiency, plant growth and the phosphorus efficiency index. *Funct. Ecol.* 13: 733–736.
- Koide R.T., Goff M.D., Dickie I.A. 2000. Component growth efficiencies of mycorrhizal and nonmycorrhizal plants. *New Phytol.* 148: 163–168.
- Korb J.E., Johnson N.C., Covington W.W. 2003. Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments. *J. Appl. Ecol.* 40: 101–110.
- Krannitz P.G., Aarssen L.W., Lefebvre D.D. 1991. Relationships between physiological and morphological attributes related to phosphate uptake in 25 genotypes of *Arabidopsis thaliana*. *Plant Soil* 133: 169–175.
- Kucey R.M.N., Leggett M.E. 1989. Increased yields and phosphorus uptake by Westar canola (*Brassica napus* L.) inoculated with a phosphate-solubilizing isolate of *Penicillium bilaji*. *Can. J. Soil Sci.* 69: 425–432.
- Kumar A., Sharma K.D., Gera R. 2011. Arbuscular mycorrhizae (*Glomus mosseae*) symbiosis for increasing the yield and quality of wheat (*Triticum aestivum*). *Indian J. Agric. Sci.* 81: 478–480.
- Kumar D., Rakshit A., Parewa H.P., Kumar P. 2011. Nutrient use efficiency in different crop species – A review. *Environ. Ecol.* 29: 2098–2105.
- Lambers H., Finnegan P.M., Laliberte E., Pearse S.J., Ryan M.H., Shane M.W., Veneklaas E.J. 2011. Phosphorus nutrition of Proteaceae in severely phosphorus-impooverished soils: Are there lessons to be learned for future crops? *Plant. Physiol.* 156: 1058–1066.
- Lambers H., Raven J.A., Shaver G.R., Smith S.E., 2008. Plant nutrient-acquisition strategies change with soil age. *Trends Ecol. Evol.* 23: 95–103.
- Li Y., Ran W., Zhang R., Sun S., Xu G. 2009. Facilitated legume nodulation, phosphate uptake and nitrogen transfer by arbuscular inoculation in an upland rice and mung bean intercropping system. *Plant Soil* 315: 285–296.
- Liu R.J., Li X.L. 2000. Function and mechanism of mycorrhiza. In: Liu R.J., Li X.L. (eds) *Arbuscular Mycorrhizae and its Application*. Science Press, Beijing, pp. 98–145.
- Lynch J.P. 2007. Roots of the second green revolution. *Austr. J. Bot.* 55: 1–20.
- Lynch J.P., Beebe S.E. 1995. Adaptation of beans (*Phaseolus vulgaris* L.) to low phosphorus availability. *Hort. Sci.* 30: 1165–1171.
- Lynch J.P., Brown K.M., 2001. Topsoil foraging-an architectural adaptation of plants to low phosphorus availability. *Plant Soil* 237: 225–237.
- Magalhaes J.V., Liu J., Guimaraes C.T., Lana U.G.P., Alves V.M.C.

2007. A gene in the multidrug and toxic compound extrusion (MATE) family confers aluminum tolerance in sorghum. *Nature Gen.* 39: 1156–1161.
- Miller R.M., Reinhardt D.R., Jastrow J.D. 1995. External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* 103: 17–23.
- Miranda D., Fischer G., Ulrichs C. 2011. The influence of arbuscular mycorrhizal colonization on the growth parameters of cape gooseberry grown in a saline soil. *J. Soil. Sci. Plant. Nutr.* 11: 18–30.
- Mollier A., Pellerin S. 1999. Maize root system growth and development as influenced by phosphorus deficiency. *J. Exp. Bot.* 50: 487–497.
- Mobasse H.R., Moradgholi, A. 2012. Mycorrhizal bio-fertilizer applications on yield seed corn varieties in Iran. *Ann. Biol. Res.* 3: 1109–1116.
- Morel C. 2002. Characterization phytodisponibilité soil P by modeling the transfer of phosphate ions between soil and solution. Habilitation searches. INPL-ENSAIA Nancy, 80 p.
- Ma N., Kazuhira Y., Marumoto T. 2006. Promotion of host plant growth and infection of roots with arbuscular mycorrhizal fungus *Gigaspora margarita* by the application of peat. *Soil Sci. Plant Nutr.* 52: 162–167.
- Neumann E., George E., 2004. Colonisation with the arbuscular mycorrhizal fungus *Glomus mosseae* (Nicol. & Gerd.) enhanced phosphorus uptake from dry soil in *Sorghum bicolor* (L). *Plant Soil* 261: 245–255.
- Neumann G., Romheld V., 2002. Root-induced changes in the availability of nutrients in the rhizosphere. In: Waisel Y., Eshel A., Kafkafi U. (eds) *Plant Roots: The Hidden Half*. Marcel Dekker, New York, pp. 617–649.
- Neumann G., Massonneau A., Martinoia E., Romheld V. 1999. Physiological adaptation to phosphorus deficiency during proteoid root development in white lupin. *Planta* 208: 373–382.
- Nielsen, N.E., Barber, S.A., 1978. Differences among genotypes of corn in the kinetics of P uptake. *Agron. J.* 70: 695–698.
- Nuruzzaman M., Lambers H., Bolland M.D.A., Veneklaas E.J. 2005. Phosphorus benefits of different legume crops to subsequent wheat grown in different soils of Western Australia. *Plant Soil* 271: 175–187.
- Parewa H.P., Rakshit A., Rao A.M., Sarkar N.C., Raha P. 2010. Evaluation of maize cultivars for phosphorus use efficiency in an Inceptisol. *Int. J. Agric. Environ. Biotechnol.* 3: 195–198.
- Plenets D., Mollier A., Pellerin S.I. 2000. Growth analysis of maize field crops under phosphorus deficiency. II. Radiation use efficiency, biomass accumulation and yield components. *Plant Soil* 224: 259–272.
- Raghothama K.G. 1999. Phosphate acquisition. *Annu. Rev. Plant Physiol. Mol. Biol.* 50: 665–693.
- Rakshit A., Bhadoria P.B.S. 2007. An indirect method for predicting activity of root exudates in field grown maize and groundnut in a low P soil. *J. Indian Soc. Soil. Sci.* 55: 493–499.
- Rakshit A., Bhadoria P.B.S. 2009. Influence of arbuscular mycorrhizal hyphal length on simulation of P influx with the mechanistic model. *African J. Microbiol. Res.* 3: 1–4.
- Rakshit A., Bhadoria P.B.S., Das D.K. 2002. An overview of mycorrhizal symbioses. *J. Interacad.* 6: 570–581.
- Rakshit A., Sarkar N.C., Sen D. 2008. Influence of organic manures on productivity of two varieties of rice. *J. Central Eur. Agric.* 9: 629–634.
- Rakshit A., Bhadoria P.B.S., Mittra B.N. 2002. Nutrient use efficiency for bumper harvest. *Yojana*, Delhi, May 2002, 12–15.
- Richardson A.E. 1994. Soil microorganisms and phosphorus availability. In: Pankhurst C.E., Doube B.M. Gupta V.V.S.R., Grace P.R. (eds) *Management of the Soil Biota in Sustainable Farming Systems*. CSIRO Publishing, Collingwood, pp. 50–62.
- Richardson A.E., Simpson R.J. 2011. Soil microorganisms mediating phosphorus availability. *Plant Physiol.* 156: 989–996.
- Richardson A.E., Barea J.M., McNeill A.M., Prigent-Combaret C. 2009a. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant Soil* 321: 305–339.
- Richardson A.E., Hocking P.J., Simpson R.J., George T.S. 2009b. Plant mechanisms to optimise access to soil phosphorus. *Crop. Pasture Sci.* 60: 124–143.
- Richardson A.E., Lynch J.P., Ryan P.R., Delhaize E., Smith F.A. 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant Soil* 349: 121–156.
- Rigou L., Mignard E. 1994. Factors of acidification of the rhizosphere of mycorrhizal plants. Measurement of pCO₂ in the rhizosphere. *Acta. Bot. Gall.* 141: 533–539.
- Roelofs R.F.R., Rengel Z., Cawthray G.R., Dixon K.W., Lambers H. 2001. Exudation of carboxylates in Australian Proteaceae: chemical composition. *Plant Cell. Environ.* 24: 891–904.
- Rohyadi A., Smith F.A., Murray R.S., Smith S.E. 2004. Effects of pH on mycorrhizal colonisation and nutrient uptake in cowpea under conditions that minimise confounding effects of elevated available aluminium. *Plant Soil* 260: 283–290.
- Ryan M.H., Graham J.H. 2002. Is there a role for arbuscular mycorrhizal fungi in production agriculture? *Plant Soil* 244: 263–271.
- Ryan M.H., van Herwaarden A.F., Angus J.F., Kirkegaard J.A. 2005. Reduced growth of autumn-sown wheat in a low-P soil is associated with high colonisation by arbuscular mycorrhizal fungi. *Plant Soil* 270: 275–286.
- Saif S.R. 1986. Vesicular-arbuscular mycorrhizae in tropical forage species as influenced by season, soil texture, fertilizers, host species and ecotype. *Angew. Bot.* 60: 125–139.
- Sattelmacher B., Horst W.J., Becker H.C. 1994. Factors that contribute to genetic variation for nutrient efficiency of crop plants. *Z. Pflanzenernahr Bodenkult.* 157: 215–224.
- Schroeder M.S., Janos D.P. 2004. Phosphorus and intraspecific density alter plant responses to arbuscular mycorrhizas. *Plant Soil* 264: 335–348.
- Shamshiri M.H., Usha K., Singh B. 2012. Growth and nutrient uptake responses of kinnow to vesicular arbuscular mycorrhizae. *ISRN Agronomy* 2012: Article ID 535846.
- Sharif M., Ahmad E., Sarir M.S., Muhammad D., Shafi M., Bakht J. 2011. Response of different crops to arbuscular mycorrhiza fungal inoculation in phosphorus-deficient soil. *Commun. Soil Sci. Plant Anal.* 42: 2299–2309.
- Simpson R.J., Oberson A., Culvenor R.A., Ryan M.H., Veneklaas E.J., 2011. Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. *Plant Soil* 349: 89–120.
- Smith S.E., Read D.J. 1997. *Mycorrhizal Symbiosis*. Academic Press, San Diego.
- Smith S.E., Read D.J. 2008. *Mycorrhizal Symbiosis*. 3rd Ed., Academic Press, London.
- Smith S.E., Smith F.A. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to

- ecosystem scales. *Annu. Rev. Plant Biol.* 62: 227–250.
- Smith S.E., Jakobsen I., Gronlund M., Smith F.A. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiol.* 156: 1050–1057.
- Steingrobe B., Classen N. 2000. Potassium dynamics in the rhizosphere and efficiency of crops. *J. Plant Nutr. Soil Sci.* 163: 101–106.
- Stewart W., Hammond L., Kauwenbergh S.J.V. 2005. Phosphorus as a Natural Resource. In: Sims J.T., Sharpley A.N. (eds). *Phosphorus: Agriculture and the Environment*. American Society of Agronomy, USA.
- Subramanian K.S., Charest C. 2007. Arbuscular mycorrhiza and drought management of crops In: Montano N.M., Camargo-Ricalde S.L., Garcia-Sanchez R., Monroy-Ata A. (eds) *Arbuscular Mycorrhizae in Arid and Semi-Arid Environments*. The National Institute of Ecology-Mexico, Mundi Prensa, Madrid, Spain.
- Subramanian K.S., Bharathi C., Jegan R.A. 2008. Response of maize to mycorrhizal colonization at varying levels of zinc and phosphorus. *Biol. Fertil. Soils* 45: 133–144.
- Subramanian K.S., Tenshia V., Jayalakshmi K. 2009. Biochemical changes and zinc fractions in arbuscular mycorrhizal fungus (*Glomus intraradices*) inoculated and uninoculated soils under differential zinc fertilization. *Appl. Soil Ecol.* 43: 32–39
- Tarafdar J.C., Marschner H. 1994. Phosphatase activity in the rhizosphere and hyphosphere of VA-mycorrhizal wheat supplied with inorganic and organic phosphorus. *Soil Biol. Biochem.* 26: 387–395
- Tisdale S.L., Nelson W.L., Beaton J.D. 1985. *Soil Fertility and Fertilizers*. 4th Ed. Macmillan, New York.
- Van Kauwenbergh S.J. 2010. World phosphate rock reserves and resources. International Fertilizer Development Center, Muscle Shoals. http://pdf.usaid.gov/pdf_docs/PNADW835.pdf.
- Vance C.P., Stone C.U., Allen D.L. 2003. Phosphorus acquisition and use critical adaptations by plants for securing a non renewable resource. *New Phytol.* 157: 423–447.
- Wang B., Yeun L.H., Xue J.Y., Liu Y., Ane, Qiu Y.L. 2010. Presence of three mycorrhizal genes in the common ancestor of land plants suggests a key role of mycorrhizas in the colonization of land by plants. *New Phytol.* 186: 514–525.
- Wei L., Chen C., Xu Z. 2010. Citric acid enhances the mobilization of organic phosphorus in subtropical and tropical forest soils. *Biol. Fertil. Soils* 46: 765–769.
- Whitelaw M.A. 2000. Growth promotion of plants inoculated with phosphate-solubilizing fungi. *Adv. Agron.* 69: 99–152.
- Wissuwa M., Mazzola M., Picard C. 2009. Novel approaches in plant breeding for rhizosphere-related traits. *Plant Soil* 321: 409–430
- Wu Q.-S., Li G.-H., Zou Y.N. 2011. Roles of arbuscular mycorrhizal fungi on growth and nutrient acquisition of peach (*Prunus persica* L. Batsch) seedlings. *J. Anim. Plant Sci.* 21: 746–750.
- Yokoyama K., Tateishi T., Saito M., Marumoto T. 2005. Application of a molecular method for the identification of a *Gigaspora margarita* isolate released in a field. *Soil Sci. Plant Nutr.* 51: 125–128.
- Zhang Q., Blaylock L.A., Harrison M.J. 2010. Two *Medicago truncatula* half-ABC transporters are essential for arbuscules development in arbuscular mycorrhizal symbiosis. *Plant Cell* 22: 1483–1497.
- Zhu J., Zhang C., Lynch J.P. 2010. The utility of phenotypic plasticity for root hair length for phosphorus acquisition. *Funct. Plant Biol.* 37: 313–322.