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Arbuscular Mycorrhizal Fungi Promoting Phosphorus Uptake in plants

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ABSTRACT: Arbuscular mycorrhizal fungi (AMF) are most widespread endosymbionts that show a mutualistic association with the majority of terrestrial plants. AMF are known to play a key role in the growth and development of host plant, mainly by enhancing water as well as soil nutrient uptake. Most of the soil nutrients like Nitrogen, phosphorous etc., although present in large amounts are either highly immobile or least available to plants, but quite essential for plant growth and development. AMF aids plants in the uptake of such immobile essential soil nutrients. Phosphorous (P) is one of such essential and critical soil nutrient, making around 0.2% of the plant dry matter. Phosphorous being very much immobile and poorly soluble becomes one of the difficult soil nutrient for plants to uptake. Recent studies have reckoned AMF to be highly beneficial for soil fertility that emphatically helps in phosphorous uptake. In this review paper consolidation of literature is made about the mutualistic symbiosis of AMF and plants for the uptake of phosphorous.

Key words: AMF, Phosphorus, Plant Growth, Nutrient Uptake

INTRODUCTION

In nature, association is a wonted phenomenon occurring over a wide range but understanding beneficial associations is a bit difficult task for biologists, ecologists and agronomists to elaborate as the processes like evolution, natural selection, extinction may aid selfish performances (West *et al.*, 2007; Harcombe, 2010; Rainey & De Monte, 2014). So for finding a solution to this problem a strategic theoretical along with empirical efforts have been made by carrying experiments, investigations on a wide range of organisms on both specie as well as symbiotic species (Keller and Chapuisat, 1999; Griffin *et al.*, 2004; Douglas, 2008). It is quite astonishing that symbiotic associations between AM fungi and roots of higher plants though being 450 million years old (Smith and Read, 2008) although not being fully unzipped (Walder *et al.*, 2012, 2015) as yet have been recently described (Bever *et al.*, 2009; Kiers *et al*., 2011). The symbiotic associations of plant roots and fungi have fascinated many generations of biologists, however these associations in the late 1880's were given the name Mycorrhiza—derived from the Greek for fungus-root (Frank, B. 1885). The most widespread and certainly most significant mutualism between plants and fungi is the root symbiosis, termed as Arbuscular Mycorrhizal Fungi (AMF). These fungal endosymbionts, are nearly universal in their association with flowering plants, including some agriculturally important crop species (Jeffries, P. *et. al.*, 2003). Recently, Arbuscular mycorrhizal fungi (AMF) were placed in a new monophyletic group, the phylum *Glomeromycota*, which probably originated nearly 1,400–1,200 million years ago, from the same ancestral group as the *Basidiomycota* and *Ascomycota* (Schussler *et. al*., 2001) and is much older than the primitive land plants. AMF are important biotrophic organisms, consorted with about 80% of land plants. The arbuscular mycorrhiza is the most extensively spread mycorrhizal association which exists in ecosystems all over the world developing a close link between plants and the rhizosphere (Harley and Smith, 1983; Trappe, 1987; Allen, 1996; Smith and Read, 1997). In this symbiotic association the fungi obtains carbon from their host plants, while assisting the plants in the uptake of highly immobile and poorly soluble phosphorus and other mineral nutrients from soil (Auge, 2001). This association is beneficial to plants as phosphorus being a major essential nutrient is important for plant growth and development, is highly immobile, AMF eases the way for the uptake of P into the host plant.

In the roots of higher plants arbuscular mycorrhizal (AM) symbiosis is extensively spread where it plays a crucial role in nutrient cycling as well as in shielding plants against environmental stresses (Varma and Hock, 1998). Thus, AMF may have played an important role in promoting the colonization of land by plants (Simon *et. al.,* 1993; Remy *et.al.,* 1994; Redecker, 2000, Heckman *et. al.,* 2001). Phosphorus is an essential macronutrient that serves multiple functions, as a key structural element in phospholipids, nucleic acids and several enzymes and coenzymes in all organisms. It plays an important role in enzyme regulation, energy metabolism, signal transduction cascades and activation of metabolic intermediates. It is also involved in various important plant biochemical processes. Therefore, maintenance of cellular phosphorus homeostasis as well as a reliable source of phosphorus is essential for sustenance of life. In most of the soil conditions, comparing phosphorous with other major nutrients, it is the least mobile, poorly soluble and least available to plants and is therefore a major limiting factor for plant growth and development. Even in well-fertilized soils, the P concentration is usually less than 50 ppb in the soil solution. The rate of absorption of phosphate by growing roots is greater than the rate of soil phosphate diffusion, resulting in the formation of depletion zone at the root system level consequently, restricts the supply of phosphorus to the plant (Marschner, 1995; Smith and Read, 1997).

Promotion of arbuscular mycorrhizal associations in the early growing stages may increase phosphorus uptake by crops, resulting in the improvement of crop yield potential and in replacing plethoric phosphorous applications as fertilizer. Use of fertilizers under existing agricultural practices have shown reduction in the effective nutrient use by plants mainly because of the nutrient transformations along with natural chemical sorption. For instance, on applying phosphorous fertilizer to the field, almost 90% of the phosphorous either due to its transformation on binding with Ca, Al and Fe- bearing soil mineral surfaces or due to process of leaching, becomes unavailable to plants (Doolette and Smernik, 2011; Randriamanantsoa *et al.,* 2013). Concerning situations arise in soils having greater phosphorous binding volume, as under such conditions phosphorous transmittal to plant needs higher P input compared to its output in harvested crops (MacDonald *et al.,* 2011), drastically leading to quite lower phosphorous use efficiency in agricultural fields applied with phosphorous fertilizer. For compensating this phosphorous, a well-organized strategy is employed by adopting enhanced AMF. AMF association enhances the plant growth by improving the uptake of nutrients like nitrogen, phosphorus and also micronutrients (Goussous and Mohammad, 2009; Shuab *et al*., 2014; Lone *et al*., 2015a, 2015b, 2016; Shuab *et al*., 2016). The close interaction between the symbiotic partners in mycorrhizal association is based on bidirectional nutrient bartering and, as such, is often constructive for both organisms: the fungus accumulates photosynthetic carbohydrates from the host plant, in return compensates the host plant by increasing soil-borne nutrient acquisition especially phosphate. Thus, persuasive phosphorous management practices, either using efficient fertilizers or boosting revitalized mycorrhizal associations can not only avoid the negative effects of phosphorous fertilizers on environmental quality but can also elevate the economics of crop production (Grant *et. al*., 2005).

Phosphorus Deficiency and its effect

Nitrogen is a major constituent of the most important plant substances. After nitrogen, phosphorous (P) is considered as a second most essential macronutrient ensuring normal plant growth and proper functioning. On around 40% of worlds arable soil, phosphorous is known to be a limiting factor for plant growth and development (Vance, 2001). Adequate phosphorus allows various processes to operate at optimum rates and progress of the plant growth and development at an optimum level. When phosphorus is limiting, the noticeable effects are reduction in leaf expansion and leaf surface area, as well as on the number of leaves. Shoot growth is more influenced than root growth leading to decrease in root shoot dry weight ratio. However, root growth is also abridged by phosphorous paucity, leading to fewer root mass for absorption of water and nutrients (Bates and Lynch, 1996). Usually, phosphorus deficiency delays the processes of carbohydrate utilization, while carbohydrate production through photosynthesis continues. This ultimately results in accumulation of carbohydrates and development of dark green coloured leaf (Singh and Singh, 2006). In some plants like tomato and corn, phosphorous deficient leaves develop a purple colour. In phosphorous deficient plants, phosphorus is translocated to active meristematic tissues from older tissues, resulting in foliar deficiency symptoms appearing on the older (lower) portion of the plant. Nonetheless, apart from loss of yield such symptoms due to phosphorus deficiency are rarely observed in the field. Other effects of phosphorus deficiency include reduced quality of forage, fruit, grain crops and vegetable, stunted growth, delayed maturity and decreased disease resistance. Under phosphorous deficient conditions, sugars can accumulate and account for development of anthocyanin pigments, producing a reddish-purple color. Usually such symptoms only prevail on extremely phosphorus deficient soils.

However, reddish-purple color does not always reveal phosphorus deficiency but may be a normal plant characteristic as such coloring may also be inferred by other factors such as insect damage which causes interruption of sugar transport to the grain. Phosphorus is often credited as a row-applied starter fertilizer for enhancing early growth. In 1980s, University of Nebraska starter fertilizer studies showed early growth response to phosphorus in less than 40 percent of the test fields (Penas, 1989).

Phosphorous: Uptake and regulation

Plants absorb phosphate from the external soil solution in the form of orthophosphates, but can also absorb certain forms of organic phosphorous (P). Soil phosphorous is in equilibrium with phosphate sorbed onto soil minerals and colloids, which maintains low concentrations of phosphate in soil solution whilst buffering the amount of phosphate in solution. Phosphorous ion being slightly immobile, through diffusion is taken into root cells.

Phosphorus (P) exists in both inorganic (Pi) as well as in organic (Po) forms, like nitrogen, through the process of mineralization organic (P) can be converted to inorganic (Pi). Inorganic (Pi) may be held very firmly in crystal lattices of largely insoluble forms such as various Ca, Fe, and Al phosphates and may also be chemically bonded to the surface of clay minerals. Labile P exchange occurs rapidly with the soil solution and is viewed as being in isotopic equilibrium with it. Inorganic phosphorous (Pi) in soils having pH 6.5 is readily available for plant use. At lower pH the reduced solubility of Fe and Al phosphates regulates the solution concentration however at higher pH reduced solubility of Ca phosphates becomes important. The availability of these sources of phosphorous (P), wholly and solely depends on the rhizosphere pH, any change in this pH may result to either increase or decrease in phosphorous availability to plants. Furthermore, the production of chelating compounds such as organic anions (example citrate and oxalate) enhances the availability of P from some sources (Marschner, 1995).

The magnitude of the phosphorous (P) uptake depends on numerous soil factors including the size of labile pool and buffering capacity, which affect the solution concentration in bulk soil, together with the characteristic which influences diffusion coefficient. This includes the pH, solution concentration, the redox potential and ionic strength of the soil solution as well as the water content and other factors that affect the tortuosity of the diffusion path. On comparing with these soil factors, the effect of root radius and root absorbing capacity (influenced by K_m and V_{max} of the uptake system) on rate of uptake are relatively small. However, smaller the diameter of the absorbing structures smaller is the depletion affect and the greater the importance of absorbing capacity. Root hairs effectively extend the diameter of the absorbing surface of the root beyond the depletion zone and have a significant effect on P uptake, especially if they are long (Claarsen and Barber 1976; Clarkson, 1985; Schweiger and Jakobsen, 1999 a; Jakobsen *et.al,* 2005 a). Presence of phosphorous in the soil and its uptake into the plants from both natural as well as fertilizer sources under the influence of transformed phosphorous in soils remains a point of efficacious research (Bu¨nemann *et al*., 2008). General agreement is that the several transformed forms of Pi including those of phosphates of Ca, Fe etc., get accessed by both AMF associated plants and the non-mycorrhizal plants (Marschner, 1995; Frossard *et al.,* 2011). However, in arbascular mycorrhizal associations the fungi grow extensively to form well developed hyphal network that absorbs inorganic phosphorus (Pi). Each individual hyphae having smaller diameter than roots and root hairs get easy access to narrower soil pores, hence increase the soil volume explored (Drew *et al.,* 2003; Smith and Read, 2008; Schnepf *et al*.,2011). Mycorrhizal plants absorb the soil Phosphorus (P) faster and more completely than non-mycorrhizal plants because the distance of diffusion for any HPO_4^{2-} or $H_2PO_4^{+}$ ion in the soil solution have almost always been shorter to the nearest hypha than to the nearest root.

Phosphorous Transport via Apoplastic and Symplastic mode

The apoplasm "dead space" comprises of root walls, the cortical cells and the open spaces between these tissues. Apoplasm consists of interlaced fibers forming an open latticework in roots that acts for filtering soil solution and increase the path length over which phosphate ions must diffuse to the underlying uptake sites on the plasmalemma. The cell wall fibers are having net negative charge that repels anions like phosphate ions in solution, confining there transfer through larger pores within apoplasm. The movement of these anions is further repelled by the negatively charged hydroxyl ion associated with the mucilage that is excreted around the roots. The net effect of these repulsions results into movement of phosphate that may be impeded within the apoplast, further modifying the concentration of phosphate at the outer surface of the plasma lemma, distinctly in the inner cortical cells.

Symplast, a continuous system of protoplasts linked by plasmodesmata, is the inner side of the plasma membrane of a cell. Plasmodesmata act as a channel that allows flow of small as well as large molecules.

Uptake of phosphate into the root symplasm involves transport from concentrations less than 2 µM in the surrounding apoplasm across the membrane to the cytoplasm.

Whilst soil solution concentrations rarely exceed 10µM and are typically less than 2 µM (Bieleski, 1973), cytosolic Pi concentration are within the millimolar range (Mimura *et al.,* 1996). Both AMF as well as plants accumulate inorganic phosphorous (Pi) against a considerable electrochemical gradient. Successful phosphate anion transfer to root cells demands overcoming of the strong electrochemical gradient which is facilitated by the net negative charge associated with inner plasma lemma together with the millimolar concentrations of phosphorus across cytoplasm and apoplasm. Therefore, phosphate (P) ion transport across the plasmalemma needs a high-affinity, energy driven transport mechanism. Apart from this, the negative potential difference generated across plasma membrane of fungi and plant cell drives the accumulation of more phosphorus anions against it. The driving force for inorganic phosphorous (Pi) influx is the proton gradient generated at the expense of ATP using P-type H^+- ATPase pump (Ullrich-Eberius *et al*., 1984; Daram *et al*., 1998**)**. Consequently, the huge membrane potential difference with a negative potential of the cytoplasm (−150 to −200 mV) allows cotransport of inorganic phosphorous (Pi) and other anions with protons in a secondary transport process. Weisenseel *et al*., (1979) measured H^+ currents entering the root hair tip of barley, whereas Kochian *et al*. (1992) measured H^+ influx and efflux, former near the tip and later at the basal region of root hairs from *Limnobium stoloniferum*. Outcome of these studies on the localization of H^+-ATPase activity in root hairs are backed by immunolocalization of the protein in rhizodermal cells (Parets-Soler *et al*., 1990) and histochemical localization of H^+-ATPase gene expression in root hairs (Moriau *et. al*., 1999).

Mechanisms underlying for the release of Pi from the fungus that it absorbs from the soil to the interfacial apoplast are obscure, however plant phosphorous uptake is well understood. AMF infected root cortical cells, show exclusively AM-Inducible plant PiT genes that are different from those involved in the direct uptake pathway (Bucher, 2007; Javot *et al*., 2007). These PiTs are present in all of the potentially AMF associated plants investigated so far, regardless of their responsiveness to AM fungal colonization. Moreover, enzyme H+-ATPases actively facilitates Pi uptake by energizing the plasma membrane of plant surrounding the intra cellular fungal structures (Smith and Read, 2008). Potentially, phosphorus uptake via both direct and AMF pathways are independent and general assumption is that in AMF colonized plants, AMF pathway provides an extra contribution to the overall phosphorous absorption via direct pathway (Smith and Smith, 2011). However, advanced physiological and molecular research's reject such assumptions as there is a complex interplay resulting into highly variable contributions of the two phosphorous uptake pathways. Dual isotope labeling can be used to know about the relative contributions of AM and direct phosphorous uptake pathway, where one of the phosphorous radioisotope is added to a hyphal compartment and other to a compartment accessible to both hyphae and roots (Pearson and Jakobsen, 1993). Outcome of such approach is that the AM pathway is involved in the phosphorous uptake and may also show its impact on the plants that on AMF colonization do not show any better growth.

Specific transporter mediated Symbiotic phosphate transfer in AMF

Root cells selectively take up phosphorous from soil ranging from micro to submicromolar external concentrations and w1000-fold higher concentrations that generate inside the cell. Being highly energy dependent, this uptake process of soil phosphorus is mediated by the concerted activities of specialized membrane proteins which includes phosphate transporters and proton-ATPases. In phosphorous uptake pathway, the view regarding the involvement of several phosphate transporters is strongly supported. The fully sequenced *Arabidopsis* and rice genomes, as well as extensive sequencing of genomic and cDNA clones from other plant species have facilitated the identification of many plant phosphate transporters. Molecular- genetic studies strongly support the view that different phosphate transporters are involved in the different uptake pathways. Corresponding genes were shown either to be constitutively expressed or up regulated under phosphate-deficient conditions (Daram, P. *et al.*, 1998; Liu, C.M. *et al*., 1998; Liu, H. *et al.*, 1998; Leggewie, G. *et al*. 1997; Zimmermann, P. *et al*. 2003) or to be induced upon AM fungal colonization. Several constitutively expressed genes were shown to be expressed at the rhizodermal level, including root hairs and around the root tip. The identification of gene encoding a plant Pi transporter (StPT3) which was upregulated in AM roots of potato provided the first insight into the molecular mechanism for transfer of phosphorus at the symbiotic interface of colonized cortical cells (Rausch, C. *et al.*, 2001).

Recent study has indicated that different members of the Pht1 family of Pi transporters are involved in the direct pathway of plant Pi uptake, at the level of the root epidermis, and in the AM-uptake pathway involving fungal and plant structures (Smith, F.W. *et al*., 2003; Karandashov and Bucher, 2005; Nagy *et al.*, 2005). Two AMF phosphate transporters GvPT and GiPT from *Glomus versiforme* and *Glomus intraradices*, respectively (Harrison, M.J. and Van Buuren, M.L. 1995, Maldonado-Mendoza, I.E. *et al*. 2001) form a common clade with transporters identified in fungal species from the Basidiomycota and Ascomycota. At least two members of this clade (PHO84 and GvPT) exhibit high affinity towards phosphate, with Km values of 8 mM and 18 mM, respectively (Harrison, M.J. and Van Buuren, M.L. 1995; Maldonado-Mendoza, I.E. *et al*. 2001; Bun-Ya, M. *et al*. 1991).The GvPT and GiPT genes are predominantly expressed in the extraradical fungal mycelium exposed to micromolar phosphate concentrations (Maldonado-Mendoza, I.E. *et al*. 2001), so their encoded proteins are likely to participate in phosphate uptake at the fungus–soil interface. Absorbed phosphate is subsequently incorporated into nucleic acids, phospholipids and other phosphorylated molecules or is condensed into polyphosphate. The phosphate-containing compounds are then translocated to the intraradical mycelium (Smith and Read, 1997; Ezawa, T. *et al*. 2003, Viereck, N. *et al*. 2004). Phosphate ions passing through the fungal plasma membrane inside roots probably follow a concentration gradient; their transfer through the membrane could be facilitated by ion-specific carriers, pumps or channels. The released phosphate is subsequently transferred into plant cortex cells through plant phosphate transporters, the ultimate step in the 'mycorrhizal' uptake pathway. Expression studies performed with different tissues of mycorrhizal potato, rice and *Medicago truncatula* plants allowed the identification of four AMF inducible plant phosphate transporters – StPT3, StPT4, ORYsa; Pht1;11 and MtPT4, which are probably involved in the transfer of the uptake of fungus-delivered phosphate in colonized plant cells (Rausch, C. *et al*. 2001, Harrison, M.J. *et al.* 2002, Paszkowski, U. *et al*. 2002). Activation of the 'mycorrhizal' uptake pathway is therefore characterized by the induction of mycorrhiza-specific phosphate transporters and (partial) down regulation of the 'direct' uptake pathway phosphate transporters (Liu, H. *et al.* 1998, Rausch, C. *et al.* 2001, Paszkowski *et. al.,* 2002). Most of the phosphorus can be taken up via the 'mycorrhizal' uptake pathway (Smith, *et al*. 2003; Smith, *et al*. 2004), it can be hypothesized that mycorrhiza-upregulated plant phosphate transporters play a pivotal role in plant productivity and fitness in most natural and agricultural ecosystems.

Model for Reciprocal action of Carbon and Phosphorous transition in AM fungi

AMF forms a mutualistic association with most of plants where fungi accumulates Carbon supply from the host plant and in return compensates by enhancing soil nutrient acquisition especially by making poorly mobile and less soluble phosphorous ions available to the host plant through hyphal uptake (Smith and Read, 2008; Karasawa *et al*., 2012). Nevertheless, hosting AMF by plants involves a complex series of interactions with several hosts and multiple fungal strains and for associations both fungi and plants choose better partners that provide more resources (Bever *et al*., 2009; Keirs *et al*., 2011). Modern researches carried on AMF have very well shown that mycorrhizal fungi in the association, besides forming part of soil biomass by its protruding hyphae in the soil, also forms a below ground Carbon reservoir (Högberg and Högberg 2002, Meyer *et al*., 2010, Olsson *et al*., 1999). In addition to this mycorrhiza plays a key role in several other processes that include the transportation, degradation and uptake of soil nutrients like N and P from soil through different tactics and their supply to the host plant in castling of the photosynthate (Courty *et al.*, 2010, Fellbaum *et al.*, 2012, Whiteside *et al.*, 2012). Hence for a sustainable growth and development along with reducing the disastrous effects of environmental change on agriculture, forestry and horticulture, planned strategy has to be employed for the utilization and application of AMF that will ultimately provide a boost for our agricultural and other productions (Verbruggen *et al.*, 2010, Johnson *et al.*, 2013). The carbon demand of fungus on root colonization can comprise a considerable cost to the host plant, as marked by the contracted growth at high Phosphorous levels (Peng *et al.*, 1993). This also signifies that there is a close relationship between external phosphorous supply and the tuning of carbon distribution to the fungal associate in the AMF symbiosis. Within the symbiosis it has been traced out that the increase in carbohydrate availability simulates carbon flux across mycocrrhizal interface and at the same time alters the uptake, allocation and transfer of phosphorous. Outcome of other studies along with these findings (Solaiman and Saitlo, 2001; Bücking and Heysar, 2003) suggest that exchange of carbon from host plant for phosphorous in soil may be concurrent.

According to a model proposed by Bücking and Shachar, (2005) for the reciprocal interaction between carbon and phosphorous in AMF, extra radical mycelium (ERM) actively absorbs inorganic phosphorous and later enters metabolically active phosphorous pool in cytoplasm. From there it gets translocated to the mycorrhizal root in the form of short chain polyP. Phosphorous uptake via extra radical mycelium (Maladonado-Mendoza *et al.,* 2001) and efflux of phosphorous into the interfacial apoplast (Bücking and Heyer, 2000) are regulated by intracellular metabolically active phosphorous concentration within the hyphae. A steady flow of inorganic phosphorous across the interfacial apoplast to the mycorrhizal roots of host plant and its shift to the sinks will: (i) Enhance plant growth and photosynthetic activity (ii) Improve the transfer of carbohydrates to the mycorrhizal roots and (iii) Allows sucrose efflux through the plant plasma membrane into the interfacial apoplast. Within interfacial apoplast of Plants, enzyme acid invertase hydrolyzes the sucrose to glucose and fructose, which can be absorbed by the Intra Radical Mycelium(IRM). The activity of invertase is regulated by the pH, thereby stimulated by the activity of the H^+-ATPases, whose activity and gene expression is enhanced by an AM infection and by the sucrose concentration (Murphy *et al*., 1997; Blee and Anderson, 2002). Mycorrhizal fungus uptakes hexoses and consequently convert these hexoses to fungal carbohydrates such as trehalose and glycogen (Shachar-Hill *et al*., 1995; Bago *et al*., 2003) via hexose-phosphates driven by a polyP-hexokinase (Cappacio and Callow, 1982) or other hexokinases will increase the remobilization of polyP (Solaiman and Saito, 2001). The remobilization of polyP will enhance the intracellular inorganic phosphorous concentration in the hyphae (Bücking and Heyser, 2003), and thereby allow inorganic phosphorous efflux through the fungal plasma membrane into the interfacial apoplast. The increased transfer of glycogen and triacylglycerol (TAG) to the extra radical mycelium would provide the necessary energy for active uptake processes from the soil and the carbon skeletons for an extension of the extra radical mycelium to get access to new phosphorou resources. For measuring carbon (C)-phosphorus(P) exchange in the host plant and two mycorrhizal partners across soil phosphorous gradient, Baoming and Bever (2016) developed a triple isotopic labeling method (^{14}C, ^{32}P, and ^{33}P) inside a split-root design. It was found that more carbon content was allocated to the AMF by the host plant, resulting into increments in the phosphorous/unit plant carbon also there was quite reduction in the strength of preferential allocation of carbon from the host plant to the AMF while increasing soil P availability.

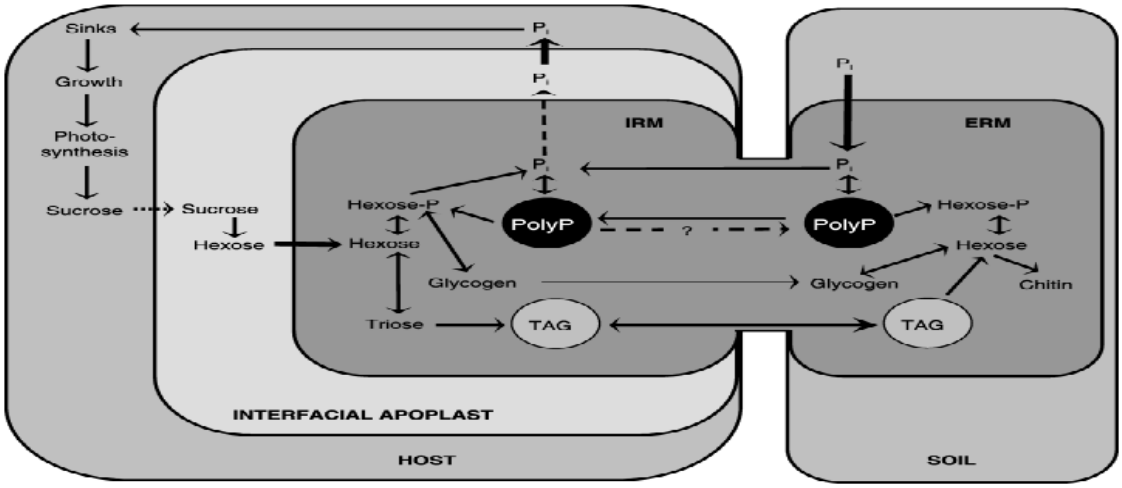

Fig. 1. Illustration of a model for the interaction between phosphate (P) and carbohydrate exchange in the arbuscular mycorrhizal (AM) symbiosis. Bold arrows, active uptake processes; broken arrows, passive efflux processes. ERM, extraradical mycelium; IRM, intraradical mycelium; polyP, polyphosphates; TAG, triacylglycerol (Bücking and Shachar, 2005).

CONCLUSION

The phosphorus nutrition of plants is mainly controlled by phosphorus dynamics in the soil, rhizosphere and plant continuum. Given the importance of phosphorus to plants, chemical fertilizers are being used over a long period of time, however chemical fertilizers have adverse toxic effects on the production potential of the land and the ultimate consumers of the products.

Toxic residues of agricultural chemicals entering the human diet are of major concern today. Excessive use of chemical fertilizers causes environmental pollution both at the manufacturing and application sites. It is therefore most necessary to reduce the dependence on chemical inputs in agriculture. This is possible only through eco-friendly approaches of farming system. Besides other biotechnological interventions, the arbuscular mycorrhiza fungi associated with plants under varied edapho-climatic conditions could be explored and screened for efficient symbionts. Phosphorous being very much immobile and poorly soluble becomes one of the difficult soil nutrients for plants to uptake. AMF by means of complex hyphal network aids plants in the uptake of such immobile essential soil nutrients, as phosphorous is one of such essential and critical soil nutrient, making around 0.2% of the plant dry matter.

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