



REVIEW ARTICLE

A CRITICAL REVIEW ON ARBUSCULAR MYCORRHIZAL FUNGI AND SOIL
PROPERTIES IN NATURAL SYSTEMS

* Saranya, K and Kumutha, K

Department of Agricultural Microbiology, Directorate of Natural Resource Management, Tamil Nadu
Agricultural University, Coimbatore, Tamil Nadu, India- 641 003.

ARTICLE INFO

Article History:

Received 12th February, 2011
Received in revised form
19th March, 2011
Accepted 27th April, 2011
Published online 14th May 2011

Key words:

AM fungi, soil,
Nutrients and phosphorous (P)

ABSTRACT

Soil properties are governed by biotic and abiotic components including land use management. Hyphae of arbuscular mycorrhizal fungi (AMF) are considered to be primary soil nutrient promoters and there is a positive correlation between AMF hyphae and soil fertility in natural systems. Both past and recent evidences prove that, these symbiotic fungi are present in most terrestrial ecosystems especially in tropics and play a major role in both the growth of plants and important ecosystem processes. AM has a cementing capacity to maintain soil health. Acquisition of minerals by AM in the soil ensures increased crop productivity. This paper traces the role of AM on soil physical, chemical, biochemical and biological properties that influence the sustainable agriculture.

© Copy Right, IJCR, 2011, Academic Journals. All rights reserved.

INTRODUCTION

AM symbiosis is often associated with improved plant growth. This enhanced growth has been attributed to nutritional and non-nutritional effects of AM fungi. AM effects the evolution of the plant, microbial communities, soil nutrient status and structure at long term. Direct, short-term AM influences such as pathogen antagonism, alleviation of drought and heavy metal stresses, competition against ruderals and enhancement of photosynthetic rates and phytohormone levels (Allen *et al.*, 1980) are well-established. Frequently observed is an increased uptake of less mobile nutrients, especially P, but also ammonium (NH₄⁺), Cu and zinc (Zn), potassium (K), calcium (Ca) and sulfur (S) (Bethlenfalvay *et al.*, 1989). AM also promotes symbiotic N fixation (Barea *et al.*, 1987) even if this may be related to improved P nutrition. Enhanced uptake of P is most often responsible for the growth increase of plants due to mycorrhization (Abbott and Robson, 1984). Up to 80% of the plant P, 60% of Cu and 25% of Zn can be delivered by external AMF hyphae extending as much as 12 cm from the root surface (Li *et al.*, 1991; Marschner and Dell, 1994). AMF hyphae form a network within the soil and between plants. This network distributes C and nutrients. It supplies energy for soil processes, extending the rhizosphere to the much larger mycorrhizosphere.

Influence of AM on Soil properties

i) Physical changes

Mycorrhizae are multifunctional in agro-ecosystems (Newsham *et al.*, 1995), potentially improving physical

(through the external hyphae), chemical (through enhanced nutrient uptake) and biological soil qualities increasing the soil stability (Figure 1). The mycorrhizal role in maintaining soil structure is important in all ecosystems (Ryan and Graham, 2002). Soil aggregation is one of the components of soil structure. Mycorrhizal fungi contribute to soil structure by growth of external hyphae into the soil to create a skeletal structure that holds soil particles together; creation by external hyphae of conditions that are conducive for the formation of microaggregates; enmeshment of micro aggregates by external hyphae and roots to form macroaggregates and directly tapping carbon resources of the plant to the soils (Miller and Jastrow, 2000). This direct access will influence the formation of soil aggregates, because soil carbon is crucial to form organic materials necessary to cement soil particles. Hyphae of AM fungi may be more important in this regard than hyphae of saprotrophic fungi due to their longer residence time in soil. Fungal hyphae are among the most important agents in soil aggregate stabilization among the soil biota, although effects of roots, soil bacteria and fauna are clearly significant as well (Degens, 1997). A new factor of presumably great importance in soil aggregation was discovered: glomalin (Wright and Upadhyaya, 1996). Glomalin produced by AMF and its concentration in aggregates (Wright and Upadhyaya, 1998) and soil (Rillig *et al.*, 2001) correlate with the percentage of water-stable aggregates. The direct effect of glomalin was much stronger than the direct effect of AMF hyphae themselves, suggesting that this protein is involved in a very important hyphal mediated mechanism of soil aggregate stabilization, atleast for the 1–2 mm size class of aggregates (Rillig *et al.*, 2001, 2002; Rillig, 2004). The extraradical hyphae also interact with components of the rhizosphere

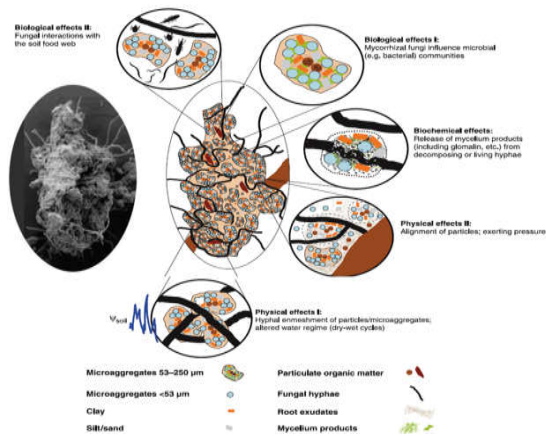


Figure 1: Overview of various mechanisms that are hyphal mediated and influences the formation or stabilization of soil

microbiota and together they contribute to the formation of water-stable aggregates which are critical for a good soil structure. In agricultural systems, the formation and maintenance of soil structure may be influenced by soil properties, root architecture, management practices (tillage, fertilization) and it now appears, characteristics of AMF and AMF-host compatibility. The extraradical hyphae of AMF and roots may be viewed as a 'sticky string bag' wherein hyphae and roots entangle and enmesh soil particles to form macro aggregate structures (Miller and Jastrow, 2000).

ii) Chemical changes

Mycorrhizae also have biochemical and physiological characteristics which differ from those of roots which can enhance P availability. They can acidify the rhizosphere through increased proton efflux or pCO_2 enhancement (Rigou and Mignard, 1994), which can mobilize P (Bago and Azcon-Aguilar, 1997), particularly in neutral or calcareous soils. In acidic soils, where phosphorus is mainly bound with Fe or Al, excretion of chelating agents (citric acid and siderophores) by mycorrhizae can enhance bioavailable P supply of the soil.

Acquisition of Minerals in the soil by AM

Phosphorous nutrition

The various forms of P compounds present in soils are broadly categorized into inorganic and organic P. Their relative distribution in soil depends upon various factors including the type of vegetation, fertilizer history, microbial activity and cultivation and soil type. Inorganic P (P_i) occurs in soil solution, adsorbed onto the soil surfaces or precipitated as discrete minerals as Fe and Al phosphates in acid soils and as Ca and Mg phosphates in alkaline and calcareous soils. The relative distribution and plant availability of these forms depends mainly on soil pH. Though inorganic P in soil solution constitutes only a small proportion of total P (<1%), plants derive most of their immediate P requirements from this source. Organic P occurs both as soluble P in soil solution, and as insoluble P adsorbed onto soil particles or as a component of soil organic matter (Anderson, 1980). Generally, organic P is mineralized either by simple autolysis or through enzymatic dephosphorylation in soil (Cosgrove, 1977). The addition of

soluble P as fertilizer increases the concentration of P initially in soil solution followed by a decrease. The process of removal of P from soil solution is generally termed phosphate 'fixation' or 'retention' (Bache, 1964). This process is initially rapid but then becomes slower with time and involves both inorganic sorption, precipitation and organic immobilization reactions. The solubility of fixed P however declines with time.

P uptake

The AM especially benefit plants grown in soils where P is likely to limit plant growth. This may be explained primarily by the increased soil volume explored by AM hyphae relative to that of root hairs of non-AM plants (Bolan, 1991; Jakobsen, 1995). A reduced effectiveness of AM colonization of roots often occurs when soluble soil P levels increase (Abbott and Robson, 1984; Bolan, 1991; Marschner and Dell, 1994). The AM hyphae normally transport P located at greater distances from the root than do non-AM roots. For example, the soil P depletion zone away from roots for non-AM white clover (*Trifolium repens*) plants was ~ 10 mm compared to > 20 mm for *Glomus* (*G. mosseae*) plants (Li *et al.*, 1991). In other studies, the soil P depletion zone for *G. mosseae*-white clover was > 110 mm (Li *et al.*, 1991) and > 80 mm for *Acaulasporea* (*A. laevis*) - subterranean clover (*Trifolium subterraneum*) (Jakobsen *et al.*, 1992b) for plants grown in containers with hyphae only compartments (fine screens separating compartments). Hyphal uptake of P also depended on the spread as well as the rate of hyphal spread (Jakobsen, 1995). For example, *A. laevis* hyphae spread 81 mm after four weeks in soil, while in two other fungi (*Glomus* sp.), hyphae spread only 31 mm (Jakobsen *et al.*, 1992a). Even though hyphae from *Glomus* sp. spread less than *A. laevis*, the *Glomus* sp. was more effective than *A. laevis* near the roots (0-10 mm) (Jakobsen *et al.*, 1992a, b). In addition, it has been estimated that 80% of plant P could possibly be supplied by AM hyphae from as far as 100 mm distance when root exploitation has been restricted (Li *et al.*, 1991).

Increased availability of less soluble sources of P to plants has been attributed to AM. For example, AM plants received more P and grew better than non-AM plants when sparingly soluble inorganic sources of P like Fe-, Al- and Ca-phosphates (Bolan *et al.*, 1987) and organic sources like RNA and phytate were applied to soil. The AM somehow may have been able to provide extended hyphal lengths to access more P or to facilitate conversion of sparingly soluble P compounds to available forms for enhanced host plant acquisition. Hyphae of AM may excrete ethylene (Ishii *et al.*, 1996), flavonoids (Ishii *et al.*, 1997), volatile substances (Koske, 1982), and growth regulating compounds (Barea and Azcon-Aguilar, 1982) like cytokinins to stimulate growth and potentially increase hyphal growth. Formation and / or excretion of organic substances by AM hyphae or AM-roots to soluble non-available forms of P might be important to facilitate host plant access to available P (Bolan, 1991). Oxalic acid has been reported to be produced by ectomycorrhizal fungi, but production of organic acids such as oxalic or citric to solubilize sparingly soluble P sources has not been reported for AM. Both AM and non-AM maize (*Zea mays*) had similar concentrations of organic acids, reducing sugars, and amino acids in exudates when solubilizing substances were sought in AM studies (Azaizeh *et al.*, 1995).

Good evidence that AM hyphae produce substances to solubilize P has yet to surface. However, enhanced solubilization of P could be facilitated by other accompanying micro-organisms (Azcon-Aguilar and Barea, 1992).

The availability of soil P may be altered by changes in rhizosphere pH (Bolan, 1991; Marschner, 1991). Increasing soil pH usually increases the availability of Al- and Fe-phosphates and decreases the availability of Ca-phosphates. Excretion of H⁺ at root surfaces is prevalent under many plant growth conditions (Marschner *et al.*, 1986; Marschner, 1995), and changes in rhizosphere pH after symbiotic AM colonization by roots have been proposed (Gianinazzi-Pearson and Azcon-Aguilar, 1991). Rhizosphere soil pH decreased when AM white clover was grown in soil with NH₄-N because of enhanced plant uptake of NH₄-N (Li *et al.*, 1991). *Glomus mosseae*-sorghum (*Sorghum bicolor*) grown with low P had greater P uptake when grown in soil with added NH₄-N than with added NO₃-N, and both sources of N decreased soil pH (Ortas *et al.*, 1996). However, soil pH increased with NO₃-N as plants aged. *Glomus mosseae* onion (*Allium cepa*) grown in soil with added NH₄-N decreased rhizosphere soil pH and NO₃-N increased soil pH during early (30-day-old) plant growth; NO₃-N decreased soil pH when plants were older (60-day-old) (Bago and Azcon-Aguilar, 1997). However, no growth medium promoted pH changes occurred when *G. mosseae* hyphae were grown under axenic conditions with added NH₄-N (Bago and Azcon-Aguilar, 1997).

Solubilization of sparingly soluble soil P compounds might occur through increased activity of exocellular enzymes such as phosphatase (or phytase) in the rhizosphere / hyphosphere of AM-roots or AM hyphae (Tarafdar and Jungk, 1987). Rhizosphere soil often has a higher activity of phosphatase than bulk soil (Dodd *et al.*, 1987). Even though external root surfaces have extensive acid alkaline phosphatase activity, particularly under low or P deficient conditions, which could potentially solubilize organic P, AM hyphae and AM-roots could also contribute considerable acid phosphatase activity to the hyphosphere and soil (Thiagarajan and Ahmad, 1994). Improved and unimproved maize and soybean (*Glycine max* = improved and *Glycine soja* = unimproved) cultivars had higher root phosphatase activities when roots were colonized by *Gigaspora (Gi.) margarita* and *G. intraradices* compared to non-AM plants, and *Gi. margarita* roots generally had higher phosphatase activity than *G. intraradices* roots (Khalil *et al.*, 1994). In addition, *G. pallidum*-cowpea (*Vigna unguiculata*) had higher root phosphatase activity than non-AM plants (Thiagarajan and Ahmad, 1994). Phosphatase activity of *G. mosseae* hyphae was effective in hydrolyzing organic P (Naphytate) to enhance P acquisition in wheat (*Triticum aestivum*) over non-AM plants. On the other hand, *G. invermaium* or *G. caledonium* hyphae had no influence on phosphatase activity in hyphal compartments of soil mixes, even though AM hyphae depleted inorganic P from these as well as from adjacent compartments where cucumber (*Cucumis sativus*) roots were. Phosphatase activity was not correlated with concentrations of labile organic P (organic matter) in soil extracts (Joner and Jakobsen, 1995).

Nitrogen nutrition

AMF has been shown to play an important role in plant N acquisition, when the major part of soil mineral N is present as

ammonium, which is less mobile because of absorption by clay minerals. A number of mechanisms were suggested and investigated to explain AM effect on N uptake using ¹⁵N labeled methodologies. The mechanisms included (i) the improvement of biological nitrogen fixation : an indirect activity based on the supply of PO₄ for N₂ fixation (Barca and Azcon-Aguilar, 1983), (ii) direct uptake of combined nitrogen by VAM (Frey and Schuepp, 1993), (iii) facilitated 'N transfer' a process by which part of nitrogen, a biologically fixed benefits the non fixing plants growing nearby (Hamel *et al.*, 1999) and (iv) enzymatic activities involved in N metabolism (Harley and Smith, 1983). The AM hyphae have the capacity to take up and transport N from soil to roots (Bago *et al.*, 1996). Information separating hyphal contribution from root acquisition of N has come from studies where hyphae were separated from roots using compartments. Mesh screens are placed in soil to allow hyphae – but not roots – to penetrate across compartments, or fine screens so that hyphae could not penetrate across compartments. The source of N is usually added to the hyphal or non-hyphal compartment(s) to study N movement (usually as ¹⁵N) and accumulation in plants tissue. Initial studies with *G. mosseae* celery (*Apium graveolens*) have indicated that AM plants obtained higher ¹⁵N from either organic or inorganic sources of N than non-AM plants, even though both AM and non-AM plants had equal amounts of P (Ames *et al.*, 1983). In addition, AM hyphae could effectively deplete soil of both NH₄-N and NO₃-N : N uptake and translocation by hyphae appeared to be regulated by host plant demand for N (Johansen *et al.*, 1994). The AM hyphae increased soil N pool size, and used soil N sources which were less available to and / or used available N more efficiently than non-AM plants. These results also separated direct (uptake and transport of N) and indirect (P-mediated demand for N) acquisition of N.

Considerable research has been conducted on the benefits of AM to legumes and consequent enhancement of N nutrition. For example, AM enhance nodulation and N₂-fixation in legumes (Barea and Azcon-Aguilar, 1980; Barea *et al.*, 1987; 1989). Adequate supply of P to roots and nodules was also required for optimum N₂-fixation (Barea, 1991). *Glomus mosseae* – soybeans had higher numbers of nodules, higher dry matter and lower nodule specific mass and activity compared to non-AM plants with comparable P concentrations (Brown *et al.*, 1988). It relates also indirectly to N₂ fixation in several tripartite symbiosis. As a component of rhizosphere, AM fungi can remain in dynamic interaction with other symbiotic microorganisms and free living heterotrophs. Tripartite interactions between AM fungi-*Rhizobium*-legume is one of the most studied system where in Mycorrhizal partner helps better nodulation and N₂ fixation through improved P uptake. Experiments involving use of ¹⁵N have clearly demonstrated that AM inoculation enhanced biological nitrogen fixation in soybean – *Rhizobium* – AM symbiosis (Kumutha and Santhakrishnan, 2000) casuarinas – Frankia – AM symbiosis, mulberry – *Azospirillum* – AM symbiosis (Kumutha *et al.*, 2006).

Although AM can absorb both NO₃⁻ and NH₄⁺ forms of nitrogen, but since NO₃⁻ is much more mobile it is also in great demand by plants, the soil surrounding root can also be deficient in NO₃⁻, absorption of NH₄⁺ -N is preferred. Experimental evidences are reported for the hyphal uptake of

NO_3^- by *G. intraradices* (Bago *et al.*, 1996), where as Villegas *et al.* (1996) reported a preference for NH_4^+ uptake. When investigating the key enzymes of N metabolism in this symbiosis, it has been observed the increased activities of glutamine synthetase (GS) and nitrate reductase (NR) activities in mycorrhizal roots, suggesting that AM fungus assimilates both NO_3^- and NH_4^+ (Subramanian, 1999), facilitated nitrogen transfer is a process by which part of the nitrogen, as biologically fixed by nodal plants, benefits the non fixing plants growing nearby as in cases of intercropping. Pastures and agroforestry intercropping system are also benefited by sharing a part of nitrogen fixed by legume – *Rhizobia*.

Application of Consortia comprising of *G.fasciculatum*, *Azospirillum brasilense* and phosphate solubilizing *Bacillus* significantly increased the dry matter production, N & P uptake by 21, 34 and 60 percent over control in neem. Not only the growth enhancement but also resulted the significant increase in survival of *Azospirillum* as well as PSB even after 90 days of application. AM hyphae can improve N transfer, since the network of AMF mycelium can link different plant species growing nearby and overlap the pool of available nutrients for these plants. The different degree of mycotrophy of fixing and non fixing plants, mostly legumes and graminaceous crops affect AM status in mixed cropping in comparison with pure standard consequently influence the role of AM in N transfer.

AM and Trace elements

Two micro nutrients like zinc and copper have been shown to be consistently at higher concentration in AM plants. These micronutrients may not be as readily translocated from roots to shoots as P and distribution in roots and shoots depends on soil P level. Enhanced acquisition of Zn and Cu in shoots was reduced when P was increased in soil, although an enhanced acquisition of these nutrients occurred even at high levels of soil P. The report says the contribution of hyphae to enhanced acquisition of Zn in *G. messeae* maize was calculated to be 48% of total plant Zn (Kothari *et al.*, 1991). Compared to non AM plants, root Zn was 22% higher in AM plants, indicating that Zn transport from hyphae to roots and roots to shoots was enhanced. Enhance Cu acquisition followed similar trends and it closely followed the increase in dry matter. Several plants grown on long fallowed fields often exhibited Zn deficiency and added Zn or AM overcame the deficiency to indicate that AM could replace Zn under some conditions (Timmer and Leydon, 1980; Thompson, 1996). Increase in Cu and Zn content was reported with the inoculation of selected AM fungi viz., *Acaulospora laevis*, *Gigaspora margarita* and *Glomus mosseae* in *Acacia nilotica* (Reena and Bagyaraj, 1990) and also in *Leucaena leucocephala* (Habte and Aziz, 1991). It has been observed in our laboratory that *Glomus fasciculatum* was found to be dominant in the rhizosphere of neem and it was observed to be more suitable for inoculation which enhanced dry weight, uptake of N, P, K, Cu and Zn significantly over other inoculants. Followed by the studies with triple inoculation of *Glomus fasciculatum*, *Azospirillum* and *Phosphobacterium* significantly increased the dry weight and uptake of nutrients viz., N, P, K, Zn, Cu, Fe and Mn in neem seedlings (Kalavathy, 1995). AMF increase the uptake of any nutrient that move to plant roots by diffusion. It has

been demonstrated that hyphal translocation of Zn from soil to the plant is influenced by P nutrition at high P levels, plants were unable to obtain Zn because of suppression of AM infection and the elements of hyphal translocation.

The information on acquisition of the macronutrient cations (K, Ca, Mg) by AM plants has been relatively inconsistent in that increases, no effects and decreases have been reported. Acquisition of K, Ca and Mg was considerably more enhanced in AM plants grown in acidic then in alkaline soils when colonized with selected AM isolates. Acidic soils are generally low in cationic basis, which are often limiting to plants grown in such soils. Limiting acidic soil may also change the effectiveness of AM isolates for acquisition of macronutrient cations and change the predominant active AM species associated with plants (Siqueira *et al.*, 1990). In contrast to AM plants grown in acidic soil, those grown in natural to alkaline soils generally have limited enhancement of K, Ca and Mg acquisition. This also depends on the AM isolate and plant species or type of plant. Isolates of AM differed in enhancing acquisition of K, Ca and Mg in AM sorghum grown at different temperatures *G. macrocarpum* > *G. intraradices* = *G. fasciculatum* (Raju *et al.*, 1990). Thus, AM isolates can modify K, Ca and Mg acquisition in plant tissues regardless of soil nutrient status and the environmental conditions under which plants may be grown. Radiotracer (^{32}P) studies on P nutrition of AM inoculated plants, clearly showed the increase in specific activity of ^{32}P with lower concentrations of P at our laboratory (Pandiyarajan, 1994; Kumutha, 2001). The higher ^{32}P activity could be interpreted in terms of improved hyphal exploitation and competitive ability of the hyphae to absorb localized and dilute sources of P rather than non mycorrhizal plants. Increase in specific activity of ^{32}P may lead to an increase in %pdf and P uptake from fertilizer and soil. Besides increasing P uptake, a considerable increase (2-3 fold) in PUE of the phosphatic fertilizer was reported (Kumutha, 2001).

iii) Biochemical changes

Soil enzymatic activities have been described to establish indices of soil fertility, soil productivity and soil quality (Busto and Perez-Mateos, 1997). There have been many reports that AM fungi can increase soil enzyme activities, such as phosphatase (Kothari *et al.*, 1990; Mar Vazquez *et al.*, 2000), dehydrogenase, urease, protease and β -glucosidase (Caravaca *et al.*, 2003, 2004). The mechanisms on the enhancement of soil enzymatic activities may involve direct and indirect roles of AM fungi: (1) AM propagules themselves synthesize soil enzymes. It is reported that AM fungal hyphae can produce some hydrolytic enzymes (Varma, 1998); (2) mycorrhizal plants may release more root exudates containing soil enzymes than that of non-mycorrhizal plants because of the larger root system and/or improved nutrition and/or resistances to stress of mycorrhizal plants. Rao and Tak (2001) reported AM fungal inoculation resulted in enhanced plant growth, total uptake of N, P and many other nutrients, activities of dehydrogenase, phosphatases and nitrogenase in the rhizosphere in gypsum mine spoil; (3) AM fungi alter soil microbial communities in the rhizosphere directly or indirectly through changes in root exudation patterns or through fungal exudates, the so called “mycorrhizosphere effect” (Linderman, 1992). Mar Vázquez *et al.* (2000) reported mycorrhizal

colonization induced qualitative changes in the microbial population and enzyme activities in the rhizosphere of maize plants. On the other hand, soil phosphatase and urease are closely related to the P and N nutrition of plants. Thus, the enhancement of soil enzyme activities is one of the physiological and biochemical mechanisms involved in a mycorrhization effect on plant mineral nutrition.

iv) Soil microbial changes under mycorrhizal symbiosis

VAM and rhizosphere microorganisms can influence their mutual development which results in a symbiotic interaction. VAM fungi occupy inter and intracellular spaces inside the roots and establish a mutualistic association with host plant. Penetration of cortical cells by VAM fungi could provide a route of entry for bacteria into the endorhizosphere. VAM interactions with rhizosphere microorganisms have focused mainly on the introduction of organism involved in nutrient translocation such as free living associative nitrogen fixing bacteria viz., *Azotobacter*, *Azospirillum* or organism which can solubilize inorganic phosphatases (Azcon *et al.*, 1992). VAM fungi and rhizosphere microorganisms can also influence their development which results in synergistic interactions. The influence upon colonization by VAM fungus, on population of functional groups of rhizosphere and rhizoplane bacteria and actinomycetes associated with the roots of sweet corn and clover, varied significantly in both rhizosphere and rhizoplane, but had no effect on gram negative bacteria (Meyer and Linderman, 1986).

The positive interaction between *Azospirillum* and VAM fungi in the rhizosphere could be due to direct interaction between microorganisms or indirectly by their effect on the host plant physiology. The presence of VAM fungi causes increase in number and diversity of microorganisms in rhizosphere. Colonization of roots with VAM fungi stimulates inflow of sugars from shoot to root, that may alter C availability to the rhizosphere microorganisms. Rhizosphere interactions occur between AM fungi and other soil microorganisms with effects on plant nutrient balances, such as nitrogen-fixing bacteria and plant growth-promoting rhizobacteria (Paula *et al.*, 1993). Microbial interactions involving AMF appear to play a key role in ecological and biotechnological approaches to improving sustainability of soil-plant systems. Rhizosphere microorganisms can affect AM formation by acting on AM propagule germination and/or the establishment of entry points of the AM fungi in the roots. Conversely, by altering the quality and quantity of root exudates, AM symbiosis can modulate the activity and/or number of the microbial components in the soil surrounding the mycorrhizal root system, giving way to the so-called mycorrhizosphere (Azcon *et al.*, 1992). Specific types of organisms are able to establish relationships with mycorrhizal fungi which affect plant growth and health and also soil quality. AM have the potential to alter bacterial species composition in rhizosphere soil (Meyer and Linderman, 1986) and some bacteria can positively stimulate certain aspects of the symbiosis (Azcon and Barea, 1985). However, it is unknown whether microbial effects can be exerted directly on AM fungal hyphae. The length of AM hyphae may increase in response to a high content of soil organic matter and that in response to AM colonization the activity of acid phosphatase in soil may decrease. Increased alkaline phosphatase activity

in response to the presence of AM hyphae in root-free soil was seen only in one of three soil treatments and was therefore attributed to an interaction between mycorrhizal hyphae and other microorganisms producing phosphatases. VAM infection could cause changes not only in rhizosphere populations, but also in the activity of the microflora at the root surface and in the rhizoplane (Dodd *et al.*, 1987).

As AM fungi coexist and interact with plant growth promoting rhizobacteria (PGPR) in soils, changes in microbial community structure may also affect the function of AM fungi (Wang *et al.*, 2006). AM fungi in a larger context: as a link between plant and soil in the plant-soil continuum. Within this context, plant responses to AM fungi may be influenced, perhaps decisively, by the soil microflora and fauna with which the soil mycelia of AM fungi associate. Bethlenfalvay *et al.* (1999) reported the significant increase in bacterial numbers isolated from the water stable aggregate soil fraction in first 3 weeks of plant growth. As well as interacting with disease causing soil organisms AMF also interact with a whole range of other microorganisms in soils. Bacterial communities and specific bacterial strains promote germination of AM fungal spores and can increase the rate and extent of root colonisation by AM (Johansson *et al.*, 2004). Once the arbuscular symbiosis has developed, AM hyphae influence the surrounding soil, which has been termed the mycorrhizosphere (Linderman, 1988), resulting in the development of distinct microbial communities relative to the rhizosphere and bulk soil (Andrade *et al.*, 1997). Within the mycorrhizosphere AMF interact with beneficial rhizosphere microorganisms including free living N₂ fixing bacteria and general plant growth promoting rhizobacteria (Arias *et al.*, 1991). Large increases in yield over uninoculated controls have been observed with some PGPR though the interaction with PGPR can be antagonistic as well as synergistic and there seems to be a high degree of specificity between the plant, AMF and PGPR species involved in these interactions. The legume – *Rhizobium* symbiosis is strongly influenced by AMF and there is some evidence to suggest that legume nodules contain AMF communities quite distinct from those found in the roots of legumes. The *Rhizobium* symbiosis is dependent on high concentrations of P and so the enhanced P nutrition arising from the AM colonization can result in an increase in nodulation and N₂ fixation.

Conclusion

Thus, in a nutshell the role of AM in improving the properties of soil and to obtain good seedling survival and growth after inoculation has been widely recognized all over the world by farmers and agricultural officers. Mycorrhizal technology, therefore has assumed greater relevance in crop production. The practical application can lead to successful afforestation, additional soil management.

REFERENCES

- Allen, M.F., T.S. Moove and M. Christensen. 1980. Phytohormone changes in *Bentelona gravilis* infected by VA Mycorrhiza increases cytokinin in the host plant. *Can. J. Bot.*, 58: 371-375.
- Anderson, G. 1980. Assessing organic phosphorus ratios to evaluate the effects of vesicular – arbuscular mycorrhizae

- on nutrient uptake in unsterilized soils. *Biol. Fertil. Soils.*, 8: 293-297.
- Andrade, G., K.L. Mihara, R.G. Linderman, G.J. Bethlenfalvay. 1997. Bacteria from rhizosphere and hydrosphere soils of different arbuscular mycorrhizal fungi. *Plant Soil*, 192: 71-79.
- Arias, I., I. Koomen, J.C. Dodd, R.P. White, D.S. Hayman. 1991. Growth responses of mycorrhizal and nonmycorrhizal tropical forage species to different levels of soil phosphate. *Plant Soil*, 132: 253-260.
- Azcon, A.C. and J.M. Barea. 1985. Effect of soil microorganisms on formation of vesicular-arbuscular mycorrhizas. *Trans. Brit. Mycol. Soc.*, 84: 536-537.
- Azcon, R., C. Barea, J.M. Azcon-Aguilar. 1992. Vesicular-arbuscular mycorrhizal fungi in nitrogen-fixing systems. *Meth. Microbiol.*, 24: 391-416.
- Barea, J. M. and C. Azcon-Aguilar. 1982. Mycorrhizas and their significance in nodulating nitrogen-fixing plants. *Adv. Agron.*, 36: 1-54.
- Bethlenfalvay, G.J., I.C. Cantrell, K.L. Mihara and R.P. Schreiner. 1999. Relationships between soil aggregation and mycorrhizae as influenced by soil biota and nitrogen nutrition. *Biol. Fertil. Soils*, 28: 356-363.
- Bolan, N. S. 1991. A critical review on the role of phosphorus by plants. *Plant Soil*, 134: 189-207.
- Busto, M.D. and M. Perez-Mateos. 1997. Agronomic and detoxifying potential of soil enzymes: biotechnological perspectives on the application of immobilized enzymes in the soil environment. *Rec. Res. Dev. Biol. Biochem.*, 1: 47-62.
- Caravaca, F., M.M. Alguacil, R. Azcón, G. Díaz and A. Roldán. 2004. Comparing the effectiveness of mycorrhizal inoculation and amendment with sugar beet, rock phosphate and *Aspergillus niger* to enhance field performance of the leguminous shrub *Dorycnium pentaphyllum* L. *Appl. Soil Ecol.*, 25(2): 169-180.
- Caravaca, M.M., D. Alguacil, Figueroa, J.M. Barea and A. Roldan. 2003. Re-establishment of *Retama sphaerocarpa* as a target species for reclamation of soil physical and biological properties in a semi-arid Mediterranean area. *For. Ecol. Manage.*, 182: 49-58.
- Degens, B.P. 1997. Macro-aggregation of soils by biological bonding and binding mechanisms and the factors affecting these: A review. *Aust. J. Soil Res.*, 35: 431-459.
- Dodd, J.C., C.C. Burton, R.G. Burns and P. Jeffries. 1987. Phosphatase activity associated with the roots and the rhizosphere of plants infected with vesicular-arbuscular mycorrhizal fungi. *New Phytol.*, 107: 163-172.
- Dodd, J.C. and B.D. Thomson. 1994. The screening and selection of inoculant arbuscular mycorrhiza and ectomycorrhizal fungi. *Plant Soil*, 159: 149-158.
- Jakobsen, I, L. K. Abbott and A. D. Robson. 1992a. External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L. 1. Spread of hyphae and phosphorus inflow into roots. *New Phytol.*, 120: 371-380.
- Jakobsen, I, L. K. Abbott and A. D. Robson. 1992b. External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L. 2. Hyphal transport of ^{32}P over defined distances. *New Phytol.*, 120: 509-516.
- Johansson, J., L.R. Paul and R.D. Finlay. 2004. Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. *FEMS Microbiol. Ecol.*, 48: 1-13.
- Kothari, S.K., H. Marschner and V. Romheld. 1990. Direct and indirect effects of VA mycorrhizae and rhizosphere microorganisms on mineral nutrient acquisition by maize (*Zea mays* L.) in a calcareous soil. *New Phytol.*, 116: 637-645.
- Kumutha, K. 2001. Symbiotic influence of AM fungi and Rhizobacteria on Biochemical and nutritional changes in mulberry (*Morus alba* L.). Ph.D. thesis submitted to Tamil Nadu Agricultural University.
- Li, X. L., H. Marschner and E. George. 1991. Acquisition of phosphorus and copper by VA-mycorrhizal hyphae and root to shoot transport in white clover. *Plant Soil*, 136: 49-57.
- Linderman, R. 1988. Mycorrhizal interactions with the rhizosphere microflora: the mycorrhizosphere effect. *Phytopath.*, 78, 366-371.
- Mar Vázquez, S., R. César, Azcón and J.M. Barea. 2000. Interactions between arbuscular mycorrhizal fungi and other microbial inoculants (*Azospirillum*, *Pseudomonas*, *Trichoderma*) and their effects on microbial population and enzyme activities in the rhizosphere of maize plants. *Appl. Soil Ecol.*, 15: 261-272.
- Meyer, J. R. and R.G. Linderman. 1986. Selective influence on populations of rhizosphere or rhizoplane bacteria and actinomycetes by mycorrhizas formed by *Glomus fasciculatum*. *Soil Bio. Biochem.*, 18: 191-196.
- Miller, R.M. and J.D. Jastrow. 2000. Mycorrhizal fungi influence soil structure. In: Kapulnik, Y., Douds, D.D. (Eds.), *Arbuscular Mycorrhizas: Physiology and Function*. Kluwer Academic, Dordrecht, pp. 3-18.
- Newsham, K.K., A.H. Fitter and A.R. Watkinson. 1995. Multifunctionality and biodiversity in arbuscular mycorrhizas. *Trends Ecol. Evol.*, 10: 407-411.
- Paula, M.A., J.O. Siqueira, J. Dobereiner. 1993. Ocorrência de fungos micorrízicos vesicularbusculares e de bactérias diazotróficas na cultura da batata-doce. *Rev. Bras. Ci. Solo.*, 17: 349-356.
- Rao, A.V. and R. Tak. 2001. Influence of mycorrhizal fungi on the growth of different tree species and their nutrient uptake in gypsum mine spoil in India. *Appl. Soil Ecol.*, 17: 279-284.
- Rigou, L. and E. Mignard. 1994. Factors of acidification of the rhizosphere of mycorrhizal plants. Measurement of pCO₂ in the rhizosphere. *Acta Bot. Gall.*, 141: 533-539.
- Rillig, M.C., S.F. Wright and V. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. *Plant Soil*, 238: 325-333.
- Rillig, M.C. 2004. Arbuscular mycorrhizae and terrestrial ecosystem processes. *Ecol. Lett.*, 7: 740-754.
- Rillig, M.C., S.F. Wright, K.A. Nichols, W.F. Schmidt and M.S. Torn. 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant and Soil*, 233: 167-177.
- Ruiz-Lozano, J. M. and M. Gomez. 1995. Effects of arbuscular-mycorrhizal *Glomus* species on drought tolerance: physiological and nutritional plant responses. *Appl. Environ. Microb.*, 456-460.

- Ryan, M.H. and J.H. Graham. 2002. Is there a role for arbuscular mycorrhizal fungi in production agriculture? *Plant Soil*, 244: 263–271.
- Thiagarajan, T. R. and M.H. Ahmed. 1994. Phosphatase activity and cytokinin content in cowpea (*Vigna unguiculata*) inoculated with a vesicular – arbuscular mycorrhizal fungi. *Biol. Fert. Soils.*, 17: 51-56.
- Varma, A. 1998. Hydrolytic enzymes from arbuscular mycorrhizae. In: A. Varma and B. Hock, Editors, *Mycorrhiza: Structure, Function, Molecular Biology and Biochemistry*, Springer–Verlag Gmbh, Heidelberg, Germany, pp. 373–390.
- Wang, F.Y., X.G. Lin, R. Yin and L.H. Wu. 2006. Effects of arbuscular mycorrhizal inoculation on the growth of *Elsholtzia splendens* and *Zea mays* and the activities of phosphatase and urease in a multi-metal-contaminated soil under unsterilized conditions. *Appl. Soil Ecol.*, 31: 110-119.
- Wright, S.F. and A. Upadhyaya. 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. *Soil Sci.*, 161: 575–586.
- Wright, S.F. and A. Upadhyaya. 1998. A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. *Plant Soil*, 198: 97-107.
