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Role of arbuscular mycorrhizal fungi (AMF) in global sustainable development

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Abstract: Mycorrhizal symbiosis is a highly evolved mutually beneficial relationship that exists between Arbuscular Mycorrhizal Fungi (AMF) and most of the vascular plants. The majority of the terrestrial plants form association with Vesicular Arbuscular Mycorrhiza (VAM) or Arbuscular Mycorrhizal fungi (AMF). This symbiosis confers benefits directly to the host plant's growth and development through the acquisition of Phosphorus (P) and other mineral nutrients from the soil by the AMF. In addition, their function ranges from stress alleviation to bioremediation in soils polluted with heavy metals. They may also enhance the protection of plants against pathogens and increases the plant diversity. This is achieved by the growth of AMF mycelium within the host root (intra radical) and out into the soil (extra radical) beyond. Proper management of Arbuscular Mycorrhizal fungi has the potential to improve the profitability and sustainability of agricultural systems. In this review article, the discussion is restricted to the mycorrhizal benefits and their role in sustainable development.

Keywords: Arbuscular Mycorrhizal fungi, Sustainable development, Growth improvement, Nutrient uptake

INTRODUCTION

During the past four decades, we have witnessed the doubling of human population and a concurrent doubling of food production. Plant nutrition has played a key role in the dramatic increase in meeting the demand for and supply of food. Increase in crop production has been made possible through the use of commercial man-made fertilizers. The consumption of Nitrogenous (N) fertilizer has increased almost nine fold and that of Phosphorus (P) more than four fold. The tremendous increase of N and P fertilizers in addition to the introduction of highly productive and agricultural systems has allowed these developments to occur at relatively low costs (Schultz et al., 1995). But the increasing use of fertilizers and highly productive system have also created environmental problems such as deterioration of soil quality, surface water and ground water as well as air pollution, reduced biodiversity and suppressed ecosystem function (Schultz et al., 1995; Socolow, 1999).

Environmental pollution resulting from greater nutrient availability can be either direct or indirect. Directly, misuse and excessive or poorly managed use of fertilizers can result in leaching, volatilization, acidification and denitrification. Indirectly, the production (use of fossil fuel in Haber-Bosch process) and transport (combustion of fossil fuel) of fertilizer result in air- borne carbon dioxide and nitrogen pollution, which will be eventually deposited into terrestrial ecosystems. inexpensive and attractive alternatives. One problem with the use of these sources of plant nutrition is their high content of heavy metals which may have adverse effects on crop growth, crop consumers or microorganism in soil or rhizosphere (Giller *et al.*, 1998; Graham, 2000). Consequently, these sources are unfit for human consumption if the heavy metal content is not drastically reduced.

The most limiting nutrients for plant growth are N and P. Although soil may contain vast amount of either nutrients, most of them are not readily available for the plant use. Most of N is tied into soil organic matter. Even after fertilization, plants have to compete with soil microbes for easily available soluble N but problem with P are different. In acidic soils, even when phosphorus fertilizer is added in substantial quantities, it becomes non available as fertilizers P precipitates with iron or aluminum whereas in alkaline soils P precipitates as calcium phosphates (Hinsinger, 2001). Accordingly, P limitation may be a difficult problem to overcome through the addition of P-containing fertilizers.

So, the recent increase in crop yields and food production in developed countries have been achieved by intensive agricultural practices. These increase, however have not come without tremendous environmental costs. In developing countries, the problems are different. The lack of fertilizers and adequate agricultural practices do not allow intensive crop production and a vast segment of the population remains undernourished. Clearly, there is

Community wastes and sewage sludge provide

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an urgent need for sustainable agricultural practices on a global level. In the developed world a reduction of energy and environmental costs is necessary. In developing countries, efficient, sustainable practices are needed to allow cost efficient production of adequate nutrition for the growing populations. To overcome the ecological problems resulting from the loss of plant nutrients and to increase crop yields in the absence of resources for obtaining costly fertilizers, microscopic organisms that allow more efficient nutrient use or increase nutrient availability can provide sustainable solutions for present and future agricultural practices.

Since microbes provide unique and indispensable transformation in the biological cycle of the soil and provide plants with essential nutrients, Arbuscular mycorrhizal fungi (AMF) fall into this group, associating with the majority of terrestrial plants, providing them with nutrients and protection from environmental stress. By understanding the role of mycorrhizae in cropping systems, it will further improve the manipulation of agronomic strategies and planning to maximize the benefits derived from mycorrhizal association and, thus, improving plant growth.

The term "Mycorrhiza" was coined by Frank (1885) who was fairly certain that these symbiotic plant-fungus associations were required for the nutrition of both partners. According to Brundrett (2004) mycorrhizas occur in a specialized plant organ where intimate contact results from synchronized plant-fungus development.

CATEGORIES OF AMF

There are two main types of AMF given by Gallaud (1905) as Arum and Paris type. In mycorrhizal plants with Paris associations, hyphae grow as coils within cells, while those with Arum type have colonies that expand primarily by linear growth along longitudinal air channels between cortex cells.

TYPES OF MYCORRHIZAE

Mycorrhizae are primarily categorized based on the type of fungi involved and changes in the morphogenesis of fungi and roots (Harley and Smith, 1983). These are grouped as follows:

Ectomycorrhizae: It is characterized by the presence of hyphal plexus between root cortical cells producing a net like structure called 'Hartig net'. The fungal partner in an ectomycorrhizae most frequently belongs to the Basidomycota though in some cases, it an ascomycete. **Endomycorrhizae:** Endomycorrhizae are characterized by the fungal hyphae which penetrate the cortical cells of host root tissues. It comprises of both septate and aseptate fungi. They do not have external sheath and the hyphae are present intracellularly as well as intercellularly within roots. This type of association occurs in all agronomic crops and basically falls in three categories (Wilcox, 1991): (i) Ericaceous mycorrhizae, (ii) Orchidaceous mycorrhizae, (iii) Arbuscular mycorrhizal fungi.

Ericaceous mycorrhizae: This type of association is found in plants of the order Ericales. Arbuscules are not formed. This is further divided into 3 types: (i) Ericoid mycorrhizae, (ii) Arbutoid mycorrhizae, (iii) Monotropoid mycorrhizae

Orchidaceous mycorrhizae: Mycorrhizal fungi penetrate the host cells and form intracellular hyphal coils called peloton coil. Majority of orchid Mycobionts are member of Basidiomycota, e.g. *Armillaria, Rhizoctonia, Tulasnella* etc. A striking exception has been the fungal partners of *Epipaltis spp. Wilcoxina* and *Phialophora* are potential mycorrhizal ascomycetes in orchids (Bidartondo *et al.*, 2004).

AMF: These Fungi are characterized by the presence of intracellular hyphae in the primary cortex which form vesicles and arbuscular later on. Arbuscules are so named by Gallaud (1905) because they look like trees. Vesicles are thin-walled or thick-walled globose to subglobose, irregular shaped structures. AMF are found in all angiospermic families, except some families such as Betulaceae, Urticaceae, Commelinaceae, Cyperaceae and Polygonaceae. Earlier, the name Vesicular Arbuscular Mycorrhizal (VAM) fungus was used, but since not all the groups produce vesicles, the term AMF is preferred (Friberg, 2001). Some of the important genera are Glomus, Acaulospora, Gigaspora, Scutellospora, Enterophospora and Sclerocystis.

Ectendomycorrhiza: Ectendomycorrhizae term was first coined by Melin in 1923. It is an intermediate type of association and showing features of both Ecto and Endomycorrhizae (Harley, 1989). Mantle is thin or lacking. It is having both intracellular as well as intercellular hyphae in cortical region of roots. *Alnus* sp, *Salix* spp, *Populus* spp and *Eucalyptus* spp. can have both Endomycorrhizal and Ecto-mycorrhizal associations (Chilvers *et al.*, 1987).

CLASSIFICATION OF AMF

The monograph of Gerdemann and Trappe (1974) gave a classification system and provided an orderly framework within which scientists could conduct research work. Since then, the most taxonomic efforts have concentrated more on the description of new species than on the evolution of taxonomic relationships. Nicoloson and Gerdemann (1968) divided the fungi into two groups of Endogone, one forming extrametrical azygospore/zygospore but producing intrametrical vesicles. Gerdemann and Trappe (1974) divided the old Endogone sensulate into seven genera including three nonmycorrhizal genera (*Endogone, Modicella and*

Glaziella) and four mycorrhizal genera (*Glomus*, *Sclerocystsis*, *Gigaspora* and *Acaulospora*). They were all placed in Endogonaceae, Endogonales and Zygomycetes. Trappe and Schenck (1982) recognized another mycorrhizal genus *Entrophospora*. Walker (1986) added *Scutellospora* having dropped *Sclerocystsis* from the total five mycorrhizal fungal genera. Thaxter (1992) and Gerdemann and Trappe (1974) originally placed members of the Endogonaceae in the order Mucorales (Zygomycetes). Its association with plants, aseptate hyphae, and reproductive structures which ranged from asexual chalmydospores and azygospores to sexual zygospores and a propensity for sporocarp development constituted the logic of this placement.

Morton and Benny (1990) placed the five genera into three families i.e., Glomaceae, Acaulosporaceae, Gigasporaceae and two suborders i.e., Glomineae and Gigasporaineae, both of them were placed in new order Glomales. Recently, Morton and Benny (2001) recognized two new families with two new generas, the Archaeosporaceae having *Archaeospora* and Paraglomaceae having *Paraglomus*. But recently some more genera of AMF like *Racocetra*, *Kuklospora*, *Pacispora*, *Otospora*, *Geosiphon*, *Ambispora* and *Intraspora* have also been included (Schußler *et al.*, 2001).

DIVERSITY OF AMF GENERA

In India, 106 species of 6 dominant genera of AMF have been reported which are more abundant in cultivated than in non-cultivated lands. These fungi are represented by 60 species of *Glomus*, 14 species of *Acaulospora*, 12 species of *Gigaspora*, 15 species of *Scutellospora*, 3 species of *Entrophospora*, 2 species of *Sclerocystis* (Gupta and Mukerji, 2001).

SIGINIFICANCE OF AMF

AMF in soil fertility: Many thousands of experiments have shown that AMF can overcome nutrient limitation to plant growth by enhancing nutrient acquisition (Clark and Zeto, 2000). Most studies have investigated P uptake but mycorrhizae have been implicated in the uptake of other essential nutrients also. The increase in inorganic nutrient uptake in mycorrhizal plants is mainly because fungal hyphae provide the large surface area for nutrient acquisition to external root surface as compared to uninfected roots. As the fungal mycelium grows through soil, it scavenges for mineral nutrients and is able to make contact with uninfected roots, sometimes of different host species. The small extra-radical mycelium compared to roots which allows penetration into some crystalline minerals, aggregates and organic matter with smaller pores than could be exploited by root alone. Unavailable forms of phosphate can be solubilized with the secretion of enzymes also (Joner and Johansen, 2000).

a) Phosphorus uptake: Phosphorus is a major plant nutrient required in relatively large amounts and plays a vital role in all biological functions in energy transfer through the formation of energy-rich phosphate esters and is also an essential component of macromolecules such as nucleotiodes, phospholipids and sugar phosphates (Marschner, 1995). The most important benefits of mycorrhizae are the increase in the phosphorus uptake by the plant. The general process of phosphorus uptake consists of three sub-processes; (i) absorption from soil by AMF hyphae, (ii) translocation along the hyphae from external to internal (root cortex) mycelia, (iii) the transfer of phosphate to cortical root cells (Barea, 1991).

The various mechanisms proposed to account for enhanced nutrient uptake include (i) increased exploration of soil; (ii) increased translocation of phosphorus into plants through arbuscules; (iii) modification of root environment; (iv) efficient utilization of P within plants; (v) efficient transfer of P to plant roots; and (vi) increased storage of absorbed P. Uptake of phosphate by roots is much faster than diffusion of ions to the absorption surfaces of the root (Bhat and Kaveriappa, 2007). This causes phosphate depletion zone around the roots. The extensive extrametrical hyphae of AMF extend out into the soil for several centimeters so that it bridges the zone of nutrient depletion. Thus, the plant is able to exploit microhabitats beyond the nutrient depleted area where rootlets and root hair cannot thrive (O'keefe and Sylvia, 1992). AMF phosphatases are able to mineralize organic P sources. Alkaline phosphatase activity is related to phosphate metabolism of fungus as it is present within the fungal vacuoles where polyphosphate granules were observed. The polyphosphate granules in fine branches of arbuscules are broken down by enzymatic activities releasing inorganic phosphorus in the cytoplasm.

b) Nitrogen uptake: Nitrogen is needed for the formation of amino acids, purines, pyrimidines and, is thus, indirectly involved in protein and nucleic acid synthesis. AMF associated plants have increased nitrogen content in shoots. A number of mechanisms are suggested for this effects, namely (i) improvement of symbiotic nitrogen fixation; (ii) direct uptake of combined nitrogen by mycorrhizal fungi; (iii) facilitated nitrogen transfer, a process by which a part of nitrogen fixed by nodulated plants benefits the non-nodulated plants; (iv) increased enzymatic activities involved in nitrogen metabolism like pectinase, xyloglucanase and cellulose which are able to decompose soil organic matter (Barea, 1991). The hyphae of AMF have the tendency to extract nitrogen and transport it from the soil to plants. They contain enzymes that breakdown organic nitrogen and contain nitrogen reductase which alters the forms of nitrogen in the soil. AM improves growth, nodulation and nitrogen fixation

in legume-*Rhizobium* symbiosis. They also uptake NH⁺ readily from soil which forms the larger fraction of available nitrogen in many natural ecosystems. In soils where nitrate is the dominant nitrogen source, AMF have only a minor influence in acquisition of nitrogen by plants (Johnson et al., 1992). AMF hyphae improve nitrogen transfer in communities, since the network of AM mycelia links different plant species growing nearby and helps overlap the pool of available nutrients for these plants. According to McFarland et al. (2010) more than 50% of plant N requirement is supplied by mycorrhizal association. Mycorrhizal inoculation enhanced activities of nitrate reductase, glutamine synthetase and glutamine synthase in the roots and shoots of mycorrhizal corn (Zea mays L.) as reported by Subramanian and Charest (1999). Recently, a plant ammonium transporter, which is activated in the presence of AMF has been identified and indicated that the way by which N is transferred in plant may be similar to P transfer (Guether et al., 2009).

c) Supply of organic mineral nutrients: Although many mycorrhizal fungi can access inorganic forms of N and P, some litter-inhabiting mycorrhizal fungi produce proteases and distribute soluble amino compounds through hyphal networks into the root (Read *et al.*, 1989). Recently, *Glomus* has been shown to transport the amino acids glycine and glutamine into wheat (Hawkins *et al.*, 2000).

d) Micronutrients: The extrametrical hyphae of AMF take up and transport potassium (K), calcium and sulphates and AM colonization affects the concentration and amounts of K in shoots. AM plants accumulate large quantities of some micronutrients (Zn, Cu, Co) under conditions of low soil nutrient availability (Faber et al., 1990). The absorption is attributed to the uptake and transport by external hyphae due to wider exploration of soil volume by extended extrametrical hyphae. Uptake and concentration of manganese (Mn) in plants may not be affected by AM and more often it may be lower in AM plants, thus contributing to higher Mn tolerance in plants. The enhanced iron (Fe) uptake may be due to specific Fe chelators. The uptake of iron (Fe) from low concentration solutions is due to the siderophores formed by AMF (Szaniszlo et al., 1981).

UPTAKE OF WATER

AMF also play an important role in the water economy. The AMF association improves the hydraulic conductivity of the roots and improves water uptake by the plants or otherwise alters the plant physiology to reduce the stress response to soil drought (Safir and Nelson, 1985). Mycorrhizal plants show better survival than non–mycorrhizal plants in extreme dry conditions. It reveals that mycelial network extends deeper and wider in the soil in search of water and nutrients. The permeability of cell membrane to water may also be altered by mycorrhizal colonization though the improved phosphorus nutrition and colonization by AMF can improve the drought resistance of plants (Osonubi et al., 1991; Sylvia and Williams, 1992). Under conditions of drought stress, AMF exert their influence by increasing the transpiration rate and lowering stomatal resistance or by altering the balance of plant hormones (Huang et al., 1985). The change in leaf elasticity due to AMF inoculation improves water and turgor potential of leaf and also increase root length and depth (Ellis et al., 1985; Kothari et al., 1990) and may also influence water relations and therefore, the drought resistance of the plants. The probable reasons for the enhanced water and nutrient uptake rates by mycorrhizal plants which can be due to better distribution of absorbing hyphal network, more favorable geometry of hyphae in comparison to roots, greater surface area and faster extension rate, increased functional longevity, chemical alteration in soil rhizosphere, altered rhizosphere microbial population, uptake kinetics, greater hydraulic conductivities, lower transportation rates per unit leaf area, extraction of water from soil to lower water potentials and more rapid recovery form water stress.

SOIL AGGREGATION AND SOIL STABILIZATION

Disturbances in ecosystem affect the physical, chemical and biological processes in the soil. AMF help in the binding of soil particles and improve soil aggregation and soil conservation (Dodd, 2000). Arbuscular mycorrhizal fungi are also known to enhance soil fertility, as they produce glomalin which upon accumulation in soil, along with the AMF hyphae forms micro aggregates and finally macro aggregates and, thus, acts as a backbone for soil aggregation and soil stabilization directly. It also releases exudates in the soil and thus promotes aggregate stability and also boost up other microorganism growth (Johnson *et al.*, 2002).

ROLE OF VAM FUNGI IN WASTELAND RECLAMATION

AMF have a great potential in the recovery of disturbed lands and these can be used in reclamation of wastelands. Inoculation with AM fungi can improve the growth and survival of desirable revegetation species. Colonization with AMF can cause a beneficial physiological effect on host plant in increasing uptake of soil phosphorus (Gerdemann, 1975). Nicoloson (1967) suggested that plant growth in wastelands could be effectively improved by incorporating AMF. It has been suggested that many plants may require mycorrhizal infection in order to survive on disturbed land. The absorptive surface area contributed by soil mycelium allows phosphorus uptake from a much greater volume. Host growth is also enhanced particularly in phosphorus-deficient soils (Mosse, 1973). AM fungi have been conclusively shown to improve revegetation of coal spoils, strip mines, waste areas, road sites and other disturbed areas (Jha *et al.*, 1994). Addition of AMF provides a nutritional advantage to associated plants in addition to providing possible resistance to low pH, heavy metal toxicants and high temperature. Presence and utilization of AMF has markedly increased the success of rehabilitation to these moisture deficient zones.

Pre-inoculation of nursery seedlings with appropriate mycorrhizal fungi would benefit in revegetation of disturbed mined land. Rani *et al.* (1998 a b,1999 and 2001) from our laboratory had worked on the effect of *Glomus mosseae*, *G. fasciculatum* along with *Rhizobium* and *Trichoderma* on better biomass yield of *Prosopis cineraria* and *Acacia nilotica* and reported further that coinoculation with AM and *Rhizobium* resulted in maximum growth and best nodulation.

ROLE OF AMF IN AGRICULTURE

The AMF symbiosis has also been shown to contribute substantially to soil conservation via its role in the formation of water-stable soil aggregates by the extrametrical hyphae. These aggregates are crucial for creating and maintaining a macroporous, water permeable soil structure, which is prerequisite for erosion resistance and also necessary for efficient nutrient cycling.

The profuse use of phosphate fertilizers and chemicals causes pollution problems and health hazards. So the use of AMF is being encouraged in agriculture. The exploitation of mycorrhizal fungi is not easy because large scale production of AMF on field scale is not yet possible. But there is a possibility of mass production of AMF by means of appropriate crop and soil management practices. More farm management practices can influence the types of AMF found in agriculture soils. Apart from effects of fertilizer application on AMF, other practices like crop rotation, minimal cultivation, monoculture, tillage, organic amendments, and application of biocides affects the AMF (Kaur and Mukerji, 1999) Mycorrhizal symbiosis plays an important role in the tropical agricultural crops because in tropical region, the soil is phosphorus deficient. Mosse (1973) reported that 75% of the phosphorus applied to the crops is not utilized by them but get converted to forms unavailable to plants.

a) Crop dependency on mycorrhiza: The relative dependency on AMF for nutrient uptake in crop plants depend on root factors such as surface area, root hair abundance and length, growth rate, response to soil conditions and exudations (Smith and Read, 1997). Crops such as corn (*Zea mays*) and flax (*Linum usitatissiumum*) are highly dependent on AMF to meet their early phosphorus requirements. Legumes, beans and potatoes

also benefit significantly from mycorrhizae. Barley, wheat and oat benefit from mycorrhizal symbiosis.

b) Crop rotation: A crop rotation is a system of growing crop plants in a repeated defined sequence.Crop rotation is a tool for managing nutrient supply, weeds, pests and diseases. It is well known that the preceding crop will affect the growth of the subsequent crop. This phenomenon, known as the 'rotation effect', cannot be explained entirely by nutritional effects and other factors such as AMF may play an important role in the success of crop rotation. It has been well established that the AMF activity is decreased by non mycorrhizal fungi host plants and highly mycorrhizal host crop increase AMF inoculum potential of the soil and colonization of the subsequent crops (Karasawa et al., 2002). An increase in AMF colonization and growth in maize occurred following sunflower (Helianthus annuus, mycorrhizal) when compared to corn following mustard (nonmycorrhizal). Here non mycorrhizal plants in the rotation reduce the rate of AMF colonization in following crops. Gavito and Miller (1998) also observed delayed AMF colonization of corn (Zea mays) following canola (Brassica napus); a non-mycorrhizal host species, when compared to the colonization of corn following the AMF host species bromegrass (Bromus spp.) and alfalfa (Medicago sativa). The corn following canola had significantly lower AMF colonization for upto 62 days after planting after which the colonization was equal to that following an AMF host species. These observations suggest that AMF populations can be built up and the inhibitory effect of a non-mycorrhizal crop can be reversed after cropping with a mycorrhizal crop (Gavito and Miller, 1998).

c) Phosphorus fertility: The benefits of AMF are greatest in systems where P in the soil is low. As the level of P available to plants increases, the plant tissue phosphorus also increases and the plant carbon investment in mycorrhizae is not economically beneficial to the plant (Grant *et al.*, 2001). Encouragement of mycorrhizal symbiosis may increase early uptake of phosphorus, improving crop yield potential without starter P fertilizer application (Grant *et al.*, 2005).

d) **Seedling establishment:** AMF also play an important role in successful reforestation and there are several reports of increased establishment of many of forest seedlings in the field, like *Quercus rubra* (Dickie *et al.*, 2001). In a study conducted by Ramos-Zapata *et al.* (2006) on establishment of *Desmoncus orthacanthos* along with inoculation of AM fungi resulted in a three fold increase in survival of seedlings in the field.

ALLEVIATION OF ENVIRONMENTAL STRESS

AMF are able to alter plant physiological and morphological properties in a way by which plant can

handle the stress (Miranasari *et al.*, 2008). AM fungi facilitate better survival of plants under stress conditions through a boost up in uptake of nutrients particularly P, Zn, Cu and water. They make the host resilient to adverse conditions created by unfavourable factors related to soil or climate. The role played by these fungi in alleviating the stress on the plant due to drought, metal pollution, salinity and grazing is briefly described.

a) Water stress: Water stress is a major agricultural constraint in the semi-arid tropics. It is well known to have a considerable negative impact on nodule function. It inhibits photosynthesis and disturbs the delicate mechanism of oxygen control in nodules. The latter is essential for active nitrogen fixation. AMF symbiosis can protect host plants against detrimental effects caused by water stress. Quilambo (2000) reported that inoculation with indigenous inoculants resulted in increased leaf and root growth and prevented the expected increase in root to shoot ratio and root–weight ratio that is normally observed under phosphorus deficient and water stress conditions in peanut.

AMF improve the uptake of nutrients like N and P in water stressed conditions (Tobar et al., 1994). Water scarcity in soil is conveyed to the shoots by means of non-hydraulic chemical signal that is relayed from the dehydrating roots to the aerial shoots by the transpiration system. The response is expressed by the leaves in terms of stunted growth and decreased stomatal conductance. AMF alters this non-hydraulic root-to-shoot signaling of soil drying by eliminating the leaf response (Auge et al., 1986). The extraradical AMF hyphae increase the absorptive surface area of the roots (Hampp et al., 2000) which in turns reduces the resistance to water uptake. Hence, the role played by AMF in alleviating water stress of plants has been investigated and it appears that drought resistance is enhanced. An increase reliance on AMF for nutrient uptake can frequently be detected. Hence, AMF help to alleviate the water stress conditions. b) Bioremediation: The activity of soil microorganisms and microbial processes is reduced by the pollution caused by heavy metals. The high toxicity of heavy metals to the soil microbes and microbiological processes, associated to the long term effects in the soil, are recognized as important facts. All microorganisms including AMF show resistance to heavy metals by 'tolerance' when the organism survives in the presence of high internal metal concentrations, or by 'avoidance' when the organism is able to restrict metal uptake. The use of plants to remove toxic metals from soils (phytoremediation) is emerging as a potential strategy for cost-effective and environmentally sound remediation of contaminated soils.

AMF have been reported to evolve strategies which can alleviate heavy metal threats in mixed culture systems and thus, from the food chains (Kramer, 2005), which involve immobilization of metal compounds, precipitation of polyphosphate granules in the soil, adsorption of chitin in the fungal cell wall and finally chelation of heavy metal in the AMF (Gaur and Adholeya, 2004). Mycorrhizal colonization of plant roots can reduce translocation of heavy metals to shoots by binding of the heavy metals to the cell walls of the fungal hyphae in roots. In this way, mycorrhizae can help higher plants to adapt and survive in contaminated habitats. The existence of synergistic effects of saprobe fungi such as Fusarium concolor and Trichoderma koningii on plant root colonization by AMF and on the effectiveness of AMF on plant resistance to heavy metals in soil has been proved (Wang et al., 2007). Kothamasi (2001) suggested that the AM hyphae, by sequestering the potentially toxic elements into the polyphosphate granules, might be acting as metal filters in the plant. Different strains of AM fungi have different sensitivity to metal toxicity. Therefore, the AMF strain colonizing a plant determines its ability to withstand toxicity (Diaz et al. 1996). The abundance of the external hyphae produced by the fungus may be involved in capturing the metal by the fungi and thereby leading to plant protection. This would, however, depend on the ecological adaptations of the AM involved to the presence of toxic metals (Nelson and Safir, 1982). Glomus caledonium seems to be a promising mycorrhizal fungus for bioremediation of heavy metal contaminated soil (Liao et al., 2003).

c) Salinity stress: Salinization of soil is a serious problem and is increasing steadily in many parts of the world, in particular in arid and semi-arid areas (Giri et al., 2003; Al-Karaki, 2006). AMF can help to overcome the problem of salinity stress. Plants growing in saline soils are subjected to physiological stresses. The toxic effects of specific ions such as Na and Cl present in saline soils, which disrupt the structure of enzymes and other macromolecules, damage cell organelles, disrupt photosynthesis and respiration, inhibit protein synthesis and induce ion deficiencies (Epstein, 1972). AMF have been found to occur naturally in saline environments despite the comparatively low mycorrhizal affinity of many halophytic plants. AMF can protect some nonhalophytic plants against yield losses in moderately saline soils. Possible mechanisms include the stimulation of root growth, improved plant nutrition (Al- Karaki, 2000) and increased synthesis of plant polyols in mycorrhizal plants. AMF help in improved acquisition of phosphorus, nitrogen and other growth promoting nutrients which are helpful for the normal growth of plants in saline soil. d) Effect of fungicide: A large number of fungicides have been shown to have detrimental effects on arbuscular mycorrhizal (AMF) fungi (Trappe et al., 1984). Fungicides may affect AMF directly through the soil or indirectly through systemic responses in the plant. External hyphae could be expected to be more sensitive to the direct effects of fungicides than internal hyphae as the root surface may protect the latter (Kjoller and Rosendahl, 2000). Sreenivasa and Bagyaraj (1989) had studied the effect of a total of nine fungicides on root colonization with VA mycorrhizal fungi and observed a reduction from 10 to 20% of root infection percentages when the recommended level of fungicides was used. Mycorrhizal colonization, however, was reduced in field plots through applications of the fungicide benomyl as a soil drenches (O'Connor *et al.*, 2002).

HERBIVORE GRAZING

Kothamasi (2001) suggested that grazing by herbivores is a big drain on the energies of the plant. As both mycorrhizae and herbivores are dependent on the plants for carbohydrates they are bound to interact. Catherine and Witham (1994) reported that herbivore grazing reduced colonization by AMF. This could affect the community structure.

INCREASED RESISTANCE TO ROOT PATHOGENS

AM are intimately associated with their host plants, particularly the roots. Therefore, an interaction between the symbionts and plant pathogens is bound to occur. By creating new environments in their zone of influence, AMF contribute to the proliferation of specific microorganisms, a few of them interact with pathogens by antibiosis, competition and parasitism (Filion et al., 1999). Plants are subject to attack by various organisms ranging from fungi, bacteria, viruses and nematodes. Mycorrhizal plants usually suffer less damage from infection than non -mycorrhizal plants (Dehne, 1982; Filion et al., 1999). Soybean colonized with Glomus mosseae grown in soils infested with pathogenic Macrophomina phaseolina, Fusarium solani and Rhizoctonia solani had growth greater or comparable to plants grown in without AMF inoculated soils. Mycorrhizal tobacco and alfalfa are reported to be resistant to a plethora of fungal pathogens like Phytophthora megasperma, Pyrenocheata terrestris, Fusarium oxysporum, Pythium ultimum etc. (Kaye et al., 1984; Schenk, 1981).

Several mechanisms have been proposed to explain the protection extended by AMF to host plants against attack by pathogens. Mycorrhizal root tissues are more lignified than non-mycorrhizal ones, particularly in the vascular region. This restricts the endophyte to the cortex. The same mechanism may hold back the invading organism too (Dehne, 1982) increasing root thickenings, and causing chemical differences. Amino acid content, particularly arginine has been found to be high in AM plants. AMF altered physiology of roots may prevent penetration and retard the development of nematodes (Schenk, 1981). Some authors have suggested that improved nutrition may protect the plant against pathogens. Mycorrhizal fungi are believed to induce high activation of antimicrobial phenyl propanoid metabolism in roots. It has been reported that induced resistance of AMF sweet orange to *Phytophthora* root–rot disease does not appear to operate unless a P nutritional advantage is conferred on the AMF plant (Graham and Egel, 1988).

ROLES IN ECOSYSTEM

The ecology of mycorrhizal fungi is not well documented (Abbott and Gazey, 1994; Francis and Read, 1995). Hence, conclusions are mostly drawn from short–term studies with a small range of partnerships often under experimental conditions.

a) Carbon cycling: Significant amount of carbon flows through mycorrhizal mycelia to different components of soils. Production of glycoproteins such as glomalin that are involved in the formation and stability of soil aggregates may have also an important influence on other microorganisms associated with the AMF mycelium (Johansson *et al.*, 2004).

b) Effects on plant community and ecosystem: The floristic diversity and productivity of plant community have been shown to depend upon the presence of species rich assemblage of AMF species (Van der Heijden *et al.*, 1998). Increasing fungal diversity resulted in greater species diversity and higher productivity. The mechanism behind these effects is likely to be differential effects of specific plant fungus.

BIOHARDENING TOOL

The technique of using AM fungi in micropropagation has been applied recently for clonal selection in woody plants (Salamanca et al., 1992). The inoculation of AMF to nursery plants has been proved both necessary and feasible and it has been extended to micropropagated plants (Adholeya et al., 2005). Salamanca et al. (1992) studied mycorrhizal inoculation of micropropagated woody legumes used in revegetation programmes for desertified Mediterranean ecosystem. Inoculation of micropropagated plantlets with active culture of AMF appeared to be critical for their survival and growth (Yadav et al., 2011). This avoids 'transient transplant shock' and stunted growth on transfer in the field. Endomycorrhization can modify root architecture to give a root system which is better adapted for uptake of mineral nutrients and water as well as increasing hormone production and resistance to pesticides and root pathogens. Micropropagated plantlets inoculated with AM spores increases the survival rate and growth in potted conditions.

INCREASING VASE LIFE OF ORNAMENTAL FLOWERING PLANTS

Vase life is an important consideration of choosing flowers. The longevity or potential of vase life of flower is determined by environmental conditions under which the flowers are produced and post harvest factors such as increase in the activity of peroxidase enzyme, increase in level of ethylene and due to tissue deterioration caused by microbes in the vase solution.

Colonization by mycorrhizal fungi has been shown to increase the vase life of cut flowers (Wen, 1991; Wen and Chang, 1995) but the mechanism involved is still unknown. Some of the reasons of having better and prolonged vase-life of cut flowers in mycorrhizal inoculated plants can be because of better vascular development by mycorrhizal fungi (Wen, 1991; Chang, 1994) or due to decreased ethylene production. Besmer and Koide (1999) also attributed the increased vase-life of cut flowers of Antirrhium majus to the reduction of ethylene production in mycorrhizal plants. Parish (1968) suggested that increase in peroxidase activity is one of the most reliable indicators of maturity. Enhanced peroxidase activity was associated with an increase in the level of peroxides and free radicals, which reacted with cellular constituent (Fridovich, 1975).

AMF inoculated plants show less increase in peroxidase activity because AMF increase the activity of antioxidative enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Blilov *et al.*, 2000). Also, these anti-oxidative enzymes constitute an important primary defense mechanism of cells against superoxide free radicals generated under stress condition (Bowler *et al.*, 1992).

PHYSIOLOGICAL AND BIOCHEMICAL PARAMETERS

a) Photosynthesis: AM fungi may function as a metabolic sink causing basipetal mobilization of photosynthates to roots thus providing a stimulus for greater photosynthetic activity (Bevege *et al.*, 1975). Increase in activity of hormones like cytokinin and gibberellin could elevate photosynthetic rates by stomatal opening influencing ion transport and regulating chlorophyll levels (Allen *et al.*, 1982). AMF symbiosis need carbon source from symbiotic partner synthesized by the process of photosynthesis and upto 20% of the total photoassimilates substances can be transferred to the fungal partner (Graham, 2000). AMF are known to enhance the uptake of phosphorus (P) from the soil which, in turn, has an important role as energy carrier during photosynthesis.

b) Production of growth hormones: Plants with mycorrhiza exhibit higher content of growth regulators

like cytokinins and auxins as compared to nonmycorrhizal ones. AMF colonized roots show changes in root morphology by getting much thicker and carry fewer root hairs. Hormone accumulation in the host tissue is affected by mycorrhizal colonization with changes in the levels of cytokinins, abscissic acid, gibberellins like substances. The effect of AMF on photosynthesis and host morphology could also be hormonal. *Glomus mosseae* has been shown to synthesize phytohormones. c) Alters soil enzyme activity: Enzyme activity is often used as an index of total microbial activity in the soil as well as its fertility (Dhruva Kumar *et al.*, 1992) and is also useful in the study of changes caused in soil due to land degradation.

Xyloglucanases, a hydrolytic enzyme is involved in the penetration and development of AM fungi in plant roots (Garcia-Garrido et al., 2002); esterase indicates catabolic activity in the soil, directly correlated with microbial activity of soil; phosphatases include acid as well as alkaline phosphatase that helps in release of inorganic phosphorus from organically bound phosphorus returned to soil (Kumar et al., 1992); chitinases are known to catalyses degradation of chitin, a major component of most fungal cell wall and are also known to enhance defense mechanism, thus helps in providing protection against diseases; trehalose catalyses the hydrolysis of trehalose which is known to be a very common signal in plant symbiosis (Mellor, 1992). Peroxidase enzyme activity increases in diseases and injured plant tissue but AM symbiosis is known to retard this enzyme activity by enhancing root penetration and colonization.

Inoculation with AMF *G. vessiforme* enhanced soil proteinase, polyphenoloxidase, urease and saccharase activities compares with control in watermelon (Zhao *et al.*, 2010). AM fungi are known to alter the soil enzymes activity and, thus, increase plant establishment and transport problems.

AMF IN WEED CONTROL

Sustainable system targeting *Striga* management can be achieved by the AM fungi inoculation technique. Several reports have suggested that AM fungi can change the nature/composition of weed communities in mixed culture system in a variety of ways, including changing the relative abundance of mycotrophic weeds species (colonized by AMF) and non-mycorrhizal species (non-colonized).

As an example, Witch weed i.e. *Striga hermonthica* (Del.) Bent. Scrophulariaceae have been found to seriously affect cereal production in many tropical countries. Infection of *Striga* resulted in a significant reduction in cereal grain yield between 20-100%. AMF could provide a new means of ecologically based weed management by affecting the fruiting of weed communities. According to Lendzemo (2004), *Striga* performance in the presence of AMF was negatively impacted with reduced and/or delayed germination, attachment and emergence.

Conclusion

With greater interests and a consensus on the need to promote sustainable development, mycorrhiza have an important role to play in reducing the harmful effects of agricultural inputs like fertilizers for improving plant growth and pesticides, fungicides, insecticides in controlling several diseases. It is a cost-effective and non-destructive means of achieving high productivity leading to establishment of a viable, low-input farming system. It is highly likely that, in the near future, crop production constraints in the world will be circumvented by technologies based on biological processes like mycorrhiza. Commercial mycorrhizal products are available in different forms including tablets, granules, powder and liquid. By using AMF we may explore several ways in which it can offer a more holistic approach to addressing different environmental issues, including 'carbon-neutral' energy, ecologically sustainable land management, disease management and CO₂ sequestration.

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REFERENCES

- Abbott, L.K. and Gazey, C. (1994). An ecological view of the formation of VA mycorrhizas. *Plant and Soil*, 159: 69-78.
- Adholeya, A., Tiwari, P. and Singh, R. (2005). *Commercial production of AMF inoculum and its inoculation strategies*.
 In: S. Declerck and A. Verma, (Eds.), Root-organ culture of mycorrhizal fungi (pp 5-7), USA.
- *Al-Karaki, G.N. (2000). Growth of mycorrhizal tomato and mineral acquisition under salt stress. *Mycorrhiza*, 10: 51-54.
- Al-Karaki, G.M. (2006). Nursery inoculation of tomato with arbuscular-mycorrhizal fungi and subsequent performance under irrigation with saline water. *Scientia Horticulture*, 109: 1-7.
- Allen, M.F., Moore, T.S. and Christensen, M. (1982). Phytohormone changes in altered levels of gibberellin-like substances and abscisic acid in the as affected by vesiculararbuscular mycorrhizae. *Plant and Soil*,121-130.
- Auge, R.M., Schekel, K.A. and Wample, R.L. (1986). Greater leaf conductance of well-watered VA mycorrhizal rose plants is not related to phosphorus nutrition. *New Phytol.*, 103: 107-116.
- Barea, J.M. (1991). Vesicular-arbuscular mycorrhizae as modifiers of soil fertility. *Adv. Soil Sci.*, 15: 1-40.
- Besmer, Y.L. and Koide, R.T. (1999). Effect of mycorrhizal colonization and P on ethylene production by snapdragon (*Antirrhinum majus* L.) flower. *Mycorrhiza*, 9: 161-166.
- Bevege, D.I., Bowen, G.D. and Skinner, M.F. (1975).

Comparative carbohydrate physiology of ecto and endomycorrhizas. In: F.E. Sanders, B. Mosse and P.B. Tinker (Eds.), Endomycorrhizas (pp 149-175), Academic Press, New York.

- Bhat, P.R. and Kaveriappa, K.M. (2007). Effect of AM fungi on the growth and nutrition uptake in some endemic Myristicaceae members of the Western ghats, India. In: M. Tiwari. and S.C. Sati (Eds.), The Mycorrhizae: Diversity, Ecology and Application (pp 295-309), Daya Pub. House, Delhi.
- Bidartondo, M.I., Burghardt, B. and Gebauer, G. (2004). Changing partners in the dark: Isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. *Proceedings of the Royal Society*, 271:1799-1806.
- Blilov, I.P., Bueno, J.A., Ocampo and Garcia-Garrido, J. (2000). Introduction of catalase and ascorbate peroxidase activities in tobacco roots inoculated with the arbuscular mycorrhizal *Glomus mosseae*. *Mycol. Res.*, 104: 722-725.
- Bowler, C., Van Montagu, M. and Inze, D. (1992). Superoxide dismutase and stress tolerance. *Ann. Rev. Plant Physiol. and Plant Mol. Biol.*, 43: 83-116.
- Brundrett, M. (2004). Diversity and classification of mycorrhizal associations. *Biol. Rev.*, 79: 473-495.
- Catherine, A.G. and Witham, T.G. (1994). Interactions between above ground herbivores and the mycorrhizal mutualists of plants. *Trends in Ecology and Evolution*, 9: 251-255.
- Chang, D.C.N. (1994). What is the potential for management of vesicular-arbuscular mycorrhizae in horticulture? In: A.D. Robson, L.K Abbott and N. Malajczuk (Eds.), Management of mycorrhizas in agriculture, horticulture and forestry, (pp 187-190). Kluwer, Dordrecht.
- Chilvers, G.A., Laperyrie, F.F. and Horan, D.P. (1987). Ectomycorrhizal vs. endomycorrhizal fungi with in the same root systems. *New Phytol.*, 97: 441-448.
- Clark, R.B. and Zeto, S.K. (2000). Mineral acquisition by arbuscular mycorrhizal plants. *J. Plant Nutr.*, 23: 867-902.
- Dehne, H.W. (1982). Interaction between vesicular mycorrhizal fungi and plant pathogens. *Phytopathology*, 72: 1115-1119.
- Dhruva Kumar, J.H.A., Sharha, G.D., Mishra, R.R. (1992). Soil microbial population numbers and enzyme activities in relation to altitude and forest degradation. *Soil Biol. Biochem.* 24: 761–767.
- Diaz, GC., Azcon, Aguilar and Honrubia, M. (1996). Influence of vesicular-arbuscular mycorrhizae on heavy metal (Zn and Pb) uptake on growth of *Lygeum spartum* and *Anthylis cystisoides*. *Plant and Soil*, 180: 241-249.
- Dickie, I.A., Koide, R.T. and Fayish, A.C. (2001). Vesicular-Arbuscular Mycorrhizal infection of *Quercus rubra* seedlings. *New Phytologist*, 151(1): 257-264.
- Dodd, J.C. (2000). The role of arbuscular mycorrhizal fungi in natural ecosystems. *Outlook on Agriculture*, 29(1): 55-62.
- Ellis, J.R., Lassen, H.J. and Boosalis, M.G. (1985). Drought resistance of wheat plants incubated with vesicular arbuscular mycorrhizae. *Plant and Soil*, 86: 369-378.
- Epstein, E. (1972). *Physiological genetics of plant nutrition*. In Epstein E. (Ed.), Mineral Nutrition of Plants (pp 325-344), Principles and Prospectus, New York.
- Feber, B.A., Zasoki, R.J., Burau, R.G and Urio, K. (1990). Zinc uptake by corn as affected by vesicular arbuscular mycorrhizae. *Plant and Soil*, 129: 121-130.

- Filion, M.M., St. Arnaud and Fortin, J.A. (1999). Direct interaction between the arbuscular mycorrhizal fungus *Glomus intraradices* and different rhizosphere microorganisms. *New Phytologist*, 141: 525-533.
- Francis, R. and Read, D.J. (1995). Mutualism and antagonism in the mycorrhizal symbiosis with special reference to impacts on plant community structure. *Can. J. Bot.*, 73:1301-1309.
- Frank, A.B. (1885). Ueber die auf wurzelsymbiose beruhende Ernahrung gewisser Baume durcha Unterirdische pilze. Ber. Dtsch. *Bot. Ges.*, 3: 128-145.
- Friberg, S. (2001). Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on Niger Inland delta, Mali, West Africa. *CBN Skriftserie*. 3: 53-80.
- Fridovich, I. (1975). Superoxide dimutase. Annu. Rev. Biochem., pp: 44:147-159.
- Gallaud, I. (1905). Etudes surles mycorrhizes endophytes. *Rev. Gen. Bot.*, 17:5.
- Garcia-Garrido, J.M., Ocampo, J.A. and Garcia-Romera, I. (2002). *Enzymes in the arbuscular mycorrhizal symbiosis*.
 In: R. Burns and R. Dick, (Eds.), Enzymes in the environment: activity, ecology and application (pp 125-151), Marcel Dekker, New York.
- Gaur, A. and Adholeya, A. (2004). Prospects of arbuscular mycorrhizal fungi in phytoremediation of heavy metal contaminated soils. *Current Sci.*, 86: 528-534.
- Gavito, M.E and Miller, M.H. (1998). Early phosphorus nutrition, mycorrhizae development, dry matter partitioning and yield of maize. Plant and Soil, 199:177–186.
- Gerdemann, J.W. (1975). *Vesicular-arbuscular mycorrhizae*. In: Torrey, J.G. and Clarkson, D.T. (Eds.), The Development and Function of Roots (pp 575-591), Academic Press, London.
- Gerdemann, J.W. and Trappe, J.M. (1974). Endogonaceae in the Pacific Northwest. *Mycologia Mem.*, **5**: 1-76.
- Giller, K.E., Witter, E. and McGrath, S.P. (1998). Toxicity of heavy metals to microorganisms and microbial processes in agriculture soils: a review. *Soil Biol. Biochem.*, 30: 1389-1414.
- Giri B., Kapoor, K. and Mukerji, K.G (2003). Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass and mineral nutrition of *Acacia auriculiformis*. *Biol. Fert. Soils*, 38: 170-175.
- Graham, J.H. (2000). Assessing cost of arbuscular mycorrhizal symbiosis in agrosystems. In: G.K. Podila and D.D. Donds (Eds.), Current Advances in Mycorrhizae Research (pp 127-140), APS Press, St Paul.
- Graham, J.H. and Egel, D.S. (1988). *Phytophthora* root rot development on mycorrhizal and phosphorus fertilized on mycorrhizal Citrus under drought stress. *New Phytologist*, 105: 411-419.
- Grant, C.A., Bittman, S., Montreal, M., Plenchette, C. and Morel, C. (2005). Soil and fertilizer phosphorus: Effects on plant P supply and mycorrhizal development. *Can. J. Plant Sci.*, 85: 3-14.
- Grant, C.A., Flaten, D.N., Tomasiewicz, D.J., Sheppard, S.C. (2001). The importance of early season phosphorus nutrition. *Can. J. Plant Sci.*, 81: 211-224.
- Guether, M., Balestrini, R., Hannah, M., He, J., Udvardi, M.K. and Bonfante, P. (2009). Genome-wide reprogramming of

regulatory networks, transport, cell wall and membrane biogenesis during arbuscular mycorrhizal symbiosis in *Lotus japonicus*. *New Phytologist*, 182(1): 200-212.

- Gupta, R. and Mukerji, K.G. (2001). Microbial technology. A.P.H. Publishing Crop, New Delhi. pp: 233.
- Hampp, R., Mertz, A., Schaible, R., Schwaigerer, M. and Nehls, U. (2000). Distinction of *Araucaria angustifolia* seeds from different locations in Brazil by a specific DNA sequence, *Trees*, 14: 429-434.
- Harely, J.L. and Smith, S.E. (1983). Mycorrhiza Symbiosis, Academic Press, London, pp : 483.
- Harley, J.L. (1989). The significance of mycorrhiza. *Mycol. Res.*, 92: 129-139.
- Hawkins, H.J., A. Johansen and G. George (2000). Uptake and transport of organic and inorganic nitrogen by arbuscular mycorrhizal fungi. *Plant and Soil*, 226: 275-285.
- Hinsinger, P. (2001). Bioavailability of trace elements as related to root induced chemical changes in the rhizosphere. In: GK. Gobran, W.W. Wenzel, E. Lombi (Eds.), Trace elements in the rhizosphere (pp 25-41), CRC Press LCC, Boca Raton Florida, USA.
- Huang, R.S., Smith, W.K. and Yost, R.E. (1985). Influence of vesicular-arbuscular mycorrhizae on growth, water relation and leaf orientation in *Leucaena leucocephala* (Linn.) De wit. *New Phytol.*, 99: 229-243.
- Jha, D.K., Sharma, G.D. and Mishra, R.R. (1994). Ecology of Vesicular-Arbuscular Mycorrhiza. In: A.B. Prasad and R.S. Bilgrami (Eds.), Microbes and Environments (pp 199-208), Narendra Publishing House.
- Johansson, J., Paul, L. and Finlay, R.D. (2004). Microbial interactions in the mycorhizosphere and their significance for sustainable agriculture. *Microbial. Ecol.*, 18:1-13.
- Johnson, D., Leake, J.R., Ostle, N., Ineson, P. and Read, D.J. (2002). In situ 13CO2 pulse-labelling of upland grasslands demonstrates a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. *New Phytologist*, 153: 327-334.
- Johnson, N.C., Tilman, D. and Wedin, D. (1992). Plant and soil control on mycorrhizal fungal communities. *Ecology*, 73: 2034-2042..
- Karasawa, T.Y., Kasahara, M. and Takebe (2002). Differences in growth responses of maize to preceding cropping caused by fluctuation in the population of indigenous arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, 34: 851-857.
- Kaur, M. and Mukerji, K.G. (1999). The application of vesicular arbuscular mycorrhizal fungi in afforestation. In:
 A. Singh and K.R. Aneja (Eds.), From Ethanomycology to Fungal Biotechnology (pp 213-224), Plenum Press, New York.
- Kaye, J.W., Pfleger, F.L. and Stewart, E.L. (1984). Interactions of *Glomus fasciculatum* and *Pythium ultimumon* green house grown Poinsettia. *Can. J. Botany*, 62:1575-1579.
- Kjoller, R. and Rosendahl, S. (2000). Effects of fungicides on arbuscular mycorrhizal fungi: differential responses in alkaline phosphatase activity of external and internal hyphae. *Biol. Fert. Soil*, 31: 361-365.
- Kothamasi, D., Kuhad, R.C and Babu, C.R. (2001). Arbuscular mycorrhizae in plant survival strategies. *International Society* for Tropical Ecology, 42(1):1-13.

- Kothari, S.K., Marschner, H. and Romheld, V. (1990). Direct and indirect effects of VA mycorrhizal fungi and rhizosphere microorganisms on acquisition of mineral nutrients by maize (*Zea mays* L.) in a calcareous soil. *New Phytol.*, 116: 637-645.
- Kramer, U. (2005). Phytoremediation: novel approaches to cleaning up polluted soils. *Current Opinion in Biotechnology*, 16: 133-141.
- Kumar, D.J.H.A., Shasha, G.D. and Mishra, R.R. (1992). Soil microbial population numbers and enzyme activities in relation to latitude and forest degradation. *Soil Biol. Biochem.*, 24: 761-767.
- Lendzemo, V.W. (2004). The tripartite interaction between sorghum, *Striga hermonthica* and arbuscular mycorrhizal fungi. Ph.D thesis, Wageningen University, Wageningen, The Netherlands.
- Liao J.P., Lin, X.G., Cao, Z.H., Shi, Y.Q. and Wong, M.H. (2003). Interactions between arbuscular mycorrhizae and heavy metals under sand culture experiment. *Chemosphere*, 50(6): 847-853.
- Marschner, H. (1995). Mineral nutrition of higher plants, 2nd Edn. Academic Press, London.
- McFarland, J., Ruess, R., Keilland, K., Pregitzer, K., Hendrick, R. and Allen, M. (2010). Cross-ecosystem comparisons of in situ plant uptake of amino acid-N and NH₄⁺. *Ecosystems*, 13:177–193.
- Melin, E. (1923). Experimentelle Untersuchungen iber die Konstitution und Okologie der Mykorrhizen von *Pinus* silvestris L. and *Picea abies* (L.) Karst. Mykol Untersuch, 2: 73-331.
- Mellor, R.B. (1992). Is trehalose asymbiotic determinant in symbiosis between higher plants and microorganisms? *Symbiosis*, 12:113-129.
- Miransari, M., Bahrami, H.A., Rejali, F. and Malakouti, M.J. (2008). Using arbuscular mycorrhiza to alleviate the stress of soil compaction on wheat (*Triticum aestivum* L.) growth. *Soil Biology and Biochemistry*, 40(5):1197-1206.
- Morton, J.B. and Benny, GL. (2001). Two new families of Glomales, Archaeosporaceae and Paraglomaceae, with two new genera *Archaeospora* and *Paraglomus*, based on concordant molecular and morphological characters. *Mycologia*, 93: 181-195.
- Morton, J.B. and Benny, GL. (1990). Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): New order, Glomales two new suborders Glomineae and Gigasporineae and two new families, Acaulosporaceae and Gigasporaceae with emendation of Glomaceaea. *Mycotaxon*, 37: 471-491.
- Mosse, F.E. (1973). Advance in the study of vesiculararbuscular mycorrhizae. *Ann. Rev. Phytopath.*, 72: 1125-1132.
- Nelson, C.E. and Safir, G.R. (1982). The water relations of well watered mycorrhizal and non mycorrhizal onion plants. Journal Am. Soc. Mortc. Sci., 107: 271-276.
- Nicolson, T.H. and Gerdemann, J.W. (1968). Mycorrhiza *Endogone* species. *Mycologia*, 60: 313-325.
- Nicolson, T.H. (1967). Vesicular-arbuscular mycorrhizal: a universal plant symbiosis. Sci. Prog., (Oxford), 55:561.
- O'Conner, P.J., Smith, S.E. and Smith, E.A. (2002). Arbuscular mycorrhizas influence plant diversity and community structure in semi-arid herbland. *New Phytol.*, 154(1): 209-

218.

- O' Keefe, D.M. and Sylvia, D.M. (1992). Chronology and mechanism of phosphorus uptake by mycorrhizal sweet potato plants. *New Phytol.*, 122: 651-659.
- Osonubi, O., Mulongoy, K., Awotoye, O.O., Atayese, M.O. and Okali, D.V.V. (1991). Effect of Ectomycorrhizal and vesicular arbuscular mycorrhizal fungi on drought tolerance of four leguminous woody seedlings. *Plant and soil*, 136: 131-143.
- Parish, R.W. (1968). Studies on senescing tobacco leaves disc with special reference to peroxidase. The effect of cutting and inhibition of nucleic acid and protein synthesis. *Planta*. 82:1-13.
- Quilambo, O.A. (2000). Functioning of peanut (*Arachis hypogaea* L.) under nutrient deficiency and drought stress in relation to symbiotic associations. Ph.D thesis. University of Groningen, the Netherlands.Van Denderen B.V., Groningen. ISBN 903671284X.
- Ramos-Zapata, J.A., Orellana, R. and Allen, E.B. (2006). Establishment of *Desmoncus orthacanthos Martius* (Arecaceae): Effect of inoculation with arbuscular mycorrhizae. *Revista De Biologia Tropica*, 54(1):65-72.
- Rani, P., Aggarwal, A. and Mehrotra, R.S. (1998a). Establishment of nursery technology through *Glomus* mosseae, *Rhizobium* sp. and *Trichoderma harzianum* on better biomass yield of *Prosopis cinararia* Linn. *National Academic Sciences*, Allahabad, 68 (B), III and IV: 301-305.
- Rani, P., Aggarwal, A. and Mehrotra, R.S. (1998b). Growth responses in Acacia nilotica inoculated with VAM fungi (Glomus fasciculatum), Rhizobium sp. and Trichoderma harzianum. J. Mycopath. Res., 36 (1): 13-16.
- Rani, P., Aggarwal, A. and Mehrotra, R.S. (1999). Growth responses in Acacia nilotica inculated with VAM fungi (Glomus mosseae), Rhizobium sp. and Trichoderma harzianum. Indian Phytopath., 52 (2): 151-153.
- Rani, P., Aggarwal, A. and Sharma, D. (2001). Improvement in biomass yield of *Prosopis cineraria* through VAM. *Rhizobium* sp. and *Trichoderma harzianum*. Adv. Plant Sci., 14(2): 593-596.
- Read, D.L., Leake, J.R. and Langdale, A.R. (1989). The nitrogen nutrition of mycorrhizal fungi and their host plants. In: L. Boddy, R. Marchant and D.J. Read (Eds.), Nitrogen, Phosphorus and Sulphur Utilization by Fungi (pp181-204), *Cambridge University Press*, Cambridge.
- Safir, G.R and Nelson, C.E. (1985). VA-mycorrhizas plant and fungal water relations, In: Proc 6th North. Am. Conf. on Mycorrhiza, (Eds.) R. Molina, Corvallis. 471.
- Salamanca, C.P., Heera, M.A. and Barea, J.M. (1992). Mycorrhizal inoculation of micropropagated woody legumes used in revegetation programmes for desertified Mediterranean ecosystems. *Agronomie*, 12: 869-872.
- Schenk, N.C. (1981). Can mycorrhizae control root diseases? *Plant diseases*, 65: 230-234.
- Schußler, A., Schwarzott, D. and Walker, C. (2001). A new fungal phylum, the Glomeromycota: phylogeny and evolution. *Mycol Res.*, 105(12): 1413-1421.
- Schultz, R.C., Colletti, J.P., Isenhart, T.M., Simkins, W.W., Mize, C.W. and Thompson, M.L. (1995). "Design and Placement of a Multi-species Riparian Buffer Strip System", *Agroforestry system*, 29:1-16.

- Smith, S.E and Read, D.J. (1997). Vesicular-arbuscular mycorrhizas. In: Mycorrhizal Symbiosis 2nd Edn., Academic Press, London. 9-160.
- Socolow, R.H. (1999). Nitrogen management and the future of food: Lessons from the management of energy and carbon. Proceeding of the National Academy of Sciences USA 96: 6001-6008.
- Sreenivasa, M.N. and Bagyaraj, D.J. (1989). Use of pesticide for mass production of vesicular-arbuscular mycorrhizal inoculum. *Plant and Soil*, 119: 127-132.
- Subramanian, K.S. and Charest, C. (1999). Acquisition of N by external hyphae of an arbuscular mycorrhizal fungus and its impact on physiological responses in maize under drought-stressed and well watered condition. *Mycorrhiza*, 9: 69-75.
- Sylvia, D.M. and Williams, S.E. (1992). Vesicular-arbuscular mycorrhizae and environmental stress. In: R.G. Lindermann and G.J. Bethlenflavay (Eds.), Mycorrhizae in sustainable agriculture, American Society of Agronomy (pp 101-124), Madisn. Wisc. Special Publication No. 54.
- Szaniszlo, P.J., Powell, P.E., Reid, C.P.P. and Cline, GR. (1981). Production of hydroxamate siderophore iron chelators by Ectomycorrhizal fungi. *Mycologia*, 73: 1158-117.
- Thaxter, R. (1922). A revision of the Endogoneae. *Proc. Am. Acad. Arts Sci.*, 57: 292-348.
- Tobar, R.M., Azcon, R. and Barea, J.M. (1994). Improved nitrogen uptake and transport from 15N-labelled nitrate by external hyphae of arbuscular mycorrhiza under waterstressed conditions. *New Phytologist*, 126: 119-122.
- Trappe, J.M. and Schenck, N.C. (1982). Taxonomy of the fungi endomycorrhizae. A. Vesicular arbuscular mycorrhizal fungi (Endogonsles). In: N.C. Schenck (Ed.), Methods and principles of mycorhizal research (pp 1-10), St. Paul, Minn., American Phytopathological Society.

- Trappe, J.M., Molina, R. and Castellano, M. (1984). Reactions of mycorrhizal fungi and mycorrhiza formation to pesticides. *Ann. Rev. Phytopath.*, 22: 331-359.
- Van der Heijden, M.G.A, Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf- Engel, R. Boller, Weimken, T.A. and Sanders, I.R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, **396**: 69-72.
- Walker, C. (1987). Current concepts in the taxonomy of the Endogonaceae. Proceedings of the 7th NACOM. IFAS, University of Florida, Gainesville, Fla.
- Wang, M.Y., Xiai, R.X., Wu, Q.S., Liu, I.H. and Hu, L.M. (2007). Influence of arbuscular mycorrhizal fungi on microbes and enzymes of soils from different cultivated densities of red clover. *Annals of Microbiology*, 57(1):1-7.
- Wen, C.L. (1991). Effect of temperature and *Glomus* sp on the growth and cut flower quality of micropropagated *Gerbera jamesoni*. M. S. thesis, National Taiwan University, Taiwan.
- Wen, C.L. and Chang, D.C.N. (1995). Effects of temperature and *Glomus* sp. on the cut flower quality of micropropagated *Gerbera jamesoni*. Memories of the College of Agriculture, National Taiwan University, 35:75-91.
- Wilcox, H. (1991). *Mycorrhizae*. In: Y. Waisel, A. Eshel and U. Kafkati (Eds.), The Plant Root: The Hidden Half (pp 731-765), Marcel Dekker, New York.
- Yadav, K., Singh, N. and Aggarwal, A. (2011). Influence of arbuscular mycorrhiza (AM) fungi on survival and development of micropropagated *Acorus calamus* L. during acclimatization. *Journal of Agricultural Technology*, 7(3): 775-781.
- Zhao, M., Li, M., and Liu, R.J. (2010). Effect of arbuscular mycorrhizae on microbial population and enzyme activity in explant soil used for watermelon production. *International Journal of Engineering, Sciences and Technology*, 2(7):17-22.