Tropical and Subtropical Agroecosystems

REVIEW [REVISIÓN]

APPLICATIONS OF ARBUSCULAR MYCORRHIZAL FUNGI IN AGROECOSYSTEMS

[APLICACIÓN DE LAS MICORRIZAS ARBUSCULARES EN LOS AGROECOSISTEMAS]

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SUMMARY

Arbuscular mycorrhizal fungi belong to phylum Glomeromycota, which are main component of the soil microbiota in most agroecosystems and form symbiotic association with most of the plants. By forming an extended, intricate hyphal network, AM fungi can efficiently absorb mineral nutrients from the soil and deliver them to their host plants in exchange for carbohydrates. They facilitate nutrient uptake, particularly with respect to immobile nutrients, such as phosphorus and enhance tolerance to drought, disease resistance, building up a macroporous structure of soil that allows penetration of water and air and prevents erosion, enhance photosynthesis and reduce stresses during micropropagation. Thus the present review focuses on nutritional and non-nutritional benefits of arbuscular mycorrhizal fungi in agroecosystems.

Key words: AM fungi; mineral nutrients; micro-propagation; phosphorus; photosynthesis.

RESUMEN

Los hongos micorrizicos arbusculares pertenecen al phylum Glomearomycota, que son componente principal de la microbiota del suelo en la mayoría de los agroecosistemas y forman la asociación simbiótica con la mayoría de las plantas. Formando una red hifal extendida e intrincada; estos hongos pueden absorber eficientemente los nutrientes minerales del suelo y entregarlos a sus plantas huésped a cambio de carbohidratos. Facilitan la absorción de nutrientes, particularmente los elementos inmóviles, tales como fósforo; también son importantes en la tolerancia a la sequía, aumentan la estructura macroporosa del suelo que permite la penetración del agua y del aire y previene la erosion; aumentan la resistencia a enfermedades y la fotosíntesis y reducen el estrés durante la micro-propagación. El presente trabajo de revisión se centra en las ventajas nutricionales y no-nutricionales de los hongos micorrizicos arbusculares en agroecosistemas.

Palabras claves: Hongos micorrizicos arbusculares; nutrientes; minerales; micro-propagación; fósforo; fotosíntesis.

INTRODUCTION

Plants in natural ecosystem are mostly dependent on mycorrhizae for supply nutrients at adequate levels in order to sustain normal growth and reproduction. The mycorrhizas may also have often other less –direct influences on plant fitness and survival. These indirect mycorrhizal benefits that have been mostly reported include tolerance to various biotic or aboitic stresses (Brundrett, 1991). From all of these beneficial effects on plant performance and soil health, it is evident that arbuscular mycorrhizal (AM) fungi are crucial for the functioning of terrestrial ecosystems (Oehl *et al.,* 2003). Not only their presence but also their genetic and functional diversities are of importance: AM fungal diversity can be decisive for both plant community structure and ecosystem productivity (Oehl *et al., 2003*). Therefore, the application of AM fungi is of interest for the reclamation and revegetation of degraded lands, an aspect of particular interest in the tropics (Oehl *et al., 2003*). Modern intensive farming practices are evidently a threat for AM fungi, as indicated by studies of AM fungi performance in agro-ecosystems (Oehl *et al., 2003*). However, a recent study on the effects of conventional versus low-input agriculture reported that different management

practices did not affect AM fungal communities in an important way (Oehl *et al., 2003*). Arbuscular mycorrhizal species appeared to occur as rapidly or slowly sporulating ecotypes depending on the agricultural management practices (Oehl *et al., 2003*). This review gives an insight on the applications of AM fungi in agro-ecosystems.

NUTRITIONAL BENEFITS

Phosphorus

Phosphorus is one of the essential mineral nutrients for plants. The preferred form of phosphorus taken up by plants is ortho-phosphate (Vance, 2003). Due to the fact that phosphate (P) is generally not very mobile in soils, narrow depletion zones in the order of millimetres form around P-absorbing roots (Hinsinger *et al.*, 2005). Low phosphate concentrations in soil can be limiting for plant growth. Therefore, plants have developed mechanisms such as symbiotic relations with soil fungi, to increase their access to soil phosphate. Probably the most important symbiotic mechanism is the formation of mycorrhizas, mutualistic symbiotic associations between plant roots and specific soil fungi. Arbuscular mycorrhizal association usually increased the growth of the plants by enhancing the uptake of nutrient especially P (Abbott and Robson, 1982, Harley and Smith, 1983, Kucey *et al.*, 1989, Mosse, 1973, Tinker, 1978). Results from a greenhouse study that examined the effects of beneficial AM fungi on growth and nutrient uptake by grapevines in different soil types showed that 1) grapevines grown in red hill soils (Ultisols) are heavily dependent on mycorrhizal fungi to supply P needed for growth and ultimately the acquisition of other nutrients, 2) grapevines grown in more fertile valley soils (Mollisols) are less dependent on mycorrhizal fungi, yet can still benefit in terms of greater P uptake, depending on plant demand for P (i.e. growth rate), 3) native isolates of AM fungi are not necessarily better adapted to specific soils in promoting growth and nutrient uptake of grapevines (Schreiner, 2007). Strawberries (*Fragaria ×ananassa* Duch.) grown in alfisols of semiarid areas in India results in suboptimal yields. Low organic carbon and low phosphorus (P) availability, in addition to high P fixation, affects P availability drastically, even when it is applied externally. Inoculated plants had a significantly greater fruit yield when grown at 150 kg P·ha^{-1} and the yield was comparable with uninoculated plants grown at 200 kg P·ha^{-1}. The external P requirements were 71 kg·ha^{-1} for mycorrhizal and 106 kg·ha^{-1} for nonmycorrhizal strawberry plants to obtain 90% of the maximum fruit yield (Sharma and Adholeya, 2004). It has been often reported that the rate of uptake by mycorrhizal plants is faster than that by non-mycorrhizal roots (Sanders and Tinker, 1973, Smith *et al.*, 1985, Son and Smith, 1988). With

increasing level of soil P, mycorrhizal response on plant growth declines and may either abolished or leads to growth depressions (Peng *et al.,* 1993). The shift in root length: shoot dry weight ratio is a typical response to improved P nutrition in both mycorrhizal and non-mycorrhizal plants. In mycorrhizal plants, the P concentration per unit dry weight are higher and thus, the P use efficiency is lower than non-mycorrhizal plants (Marschner and Dell, 1994). This indicates that other growth factors (carbohydrates, mineral nutrients) become limiting or that in mycorrhizal root systems the feed-back regulation between nutrient uptake rates and shoot demand are less well-regulated than in non-mycorrhizal plant systems (Douds *et al.* , 1988). Effective P acquisition by the external hyphae is related to a) formation of polyphosphates in the hyphae and thus, maintaining low internal phosphate (Pi) concentrations b) the small hyphal diameter leading to a relatively larger volume delivering P per unit surface area compared to the root surface area (Jungk and Claassen, 1989) and correspondingly 2-6 times higher P influx rate per unit length of hyphae (Jakobsen *et al.,*1992) and production of extracellular acid phosphatases which catalyze the release of P from organic complexes in soil.

Phosphatases: represent a broad range of intracellular as well as soil accumulated activities that catalyze the hydrolysis of both esters and anhydrides of phosphoric acid (Spier and Ross, 1978). Phosphatase enzymes are also directly involved in the acquisition of phosphorus by plants. Their importance, however, is not always obvious. The proposition that plants with lower activities of root phosphatases may gain and use phosphorus more readily than plants with higher ones has been put forward by Mc Lachlan (1980) who found that acid phosphatase activity was lower in plants more efficient in P- uptake than grown under P-deficient conditions. Mycorrhizal colonization had been shown to influence root phosphatase activity.

Acid phosphatase may be associated with the growth and development of the fungus within the host tissue (Gianinazzi *et al.,* 1979) as well as with phosphorus acquisition in the rhizosphere. Joner and Jacobson (1995) reported that mycorrhizal colonization resulted in a lower activity of acid phosphatases. Information on the role of AM fungi in the production of extra cellular phosphatase and metabolization of organic –P (Po) are conflicting. The extra cellular phosphatase activity of the roots may be stimulated in the presence of easily hydrolysable substances (Tarafdar and Claassen, 1988) but repressed by non hydrolysable forms of P (Azcòn *et al.,* 1992). García-Gómez *et al.* (2002) reported that soluble and extractable root acid phosphatase activity (RAPA) was higher in *Glomus claroideum* inoculated *Carica papaya* L. plants. In another experiment, plants of rape, wheat and onion

were inoculated singly with *Glomus geosporum, G. mosseae,* and *G. monosporum* or were left uninoculated and were grown in sand with little available phosphorus. Here the root acid phosphatase activity levels were higher for plants inoculated with *G. geosporum* and *G. mosseae* than for control plants. Colonization by *G. monosporum* did not result in a similar increase in phosphatase activity, but plant growth was improved (Dodd *et al.,* 1987). Further, in greenhouse pot experiments conducted at the Universidad de la Frontera, Tamuco, Chile, seedlings of wheat cultivars, Dalcahue, Malihue, Carahue and Naofen were grown in the typical low phosphorus volcanic soil of South Chile with and without 300 kg of phosphorus pentaoxide per hectare and harvested at 21, 42, 63, 84, and 96 days after planting. The AM colonization was similar among all genotypes. The AM root colonization was increased up to 63 days before decreasing up to 84 days after planting. Root surface acid phosphatase activity did not differ significantly among cultivars and the enzyme was significantly influenced by phosphorus. When plants were grown without phosphorus fertilizer, maximum enzyme activity was reached at 63 days for Carahue and Dakahue and 43 days for Naofen and Malihue. Phosphatase activity was highest at 21 days but quickly declined in the later samplings (Rubio *et al.* ,1990).

Alkaline phosphatase activity specific to AM fungi have been reported (Bertheau, 1977). This enzyme activity is closely linked to both the mycorrhizal growth stimulation and the arbuscular phase of the colonization and there is strong evidence that it is of fungal origin (Gianinazzi – Pearson and Gianinazzi, 1978). Gianinazzi – Pearson and Gianinazzi (1978) have proposed that this AM fungal specific alkaline phosphatase would play in polyphosphate breakdown since ultra-cytochemical studies revealed that alkaline phosphatase activity was localized in the vacuoles of mature arbuscules (Gianinazzi *et al.,* 1979). Studies conducted at the Indian Institute of Horticultural Research (Hessaraghatta, Bangalore, India) on phosphatase activity in *Carica papaya* L. roots showed that inoculation with AM fungi enhanced the activity of both root surface acid and alkaline phosphatases (25%−114%). Here, the acid phosphatase activity was much greater than alkaline phosphatase activity. Plants inoculated with *Glomus mosseae* showed better activity than those with *G. fasciculatum* (Mohandas 1990). In studies conducted by Fries *et al.* (1998), maize (*Zea mays* cv. *Great Lakes 586*) plants were grown under five different levels of soil phosphorus, either in the presence or absence of formononetin or the AM fungus, *Glomus intraradices.* Formononetin treatment enhanced colonization of the root by *G. intraradices* and partially overcame inhibition of AM fungal colonization by high soil

phosphorus concentrations. ACP (acid phosphatase) and ALP (alkaline phosphatase) activities were closely related to the level of fungal colonization in maize roots. ACP activity in maize roots responded more to soil phosphorus availability than ALP activity (38% more). These results suggest that ACP was involved in the increased uptake of phosphorus from the soil, while ALP may be linked to active phosphate assimilation or transport in mycorrhizal roots. Thus, soil phosphorus directly affected a number of enzymes essential in host–endophyte interplay, while formononetin enhanced fungal colonization (Fries *et al.,* 1998). In studies conducted on *Terminalia arjuna*, grown in polythene bags in sterilized soil treated with *Glomus mosseae*, *G. fasciculatum,* and rock phosphate separately, or in various combinations results showed that acid phosphatase activity increased to a maximum in *G. fasciculatum* roots followed by *G. mosseae* + phosphorus and *G. mosseae* + *G. fasciculatum* treated roots. The acid phosphatase activity in shoots was maximum in *G. mosseae* + phosphorus treated plants. All other combinations had reduced acid phosphatase activity. Alkaline phosphatase activity was considerably lower than the acid phosphatase activity in the roots and shoots of all the AM fungi treated *Terminalia* plants. Alkaline phosphatase activity was maximum in roots of *G. fasciculatum* + phosphorus and in shoots of *G. mosseae* + phosphorus, followed by phosphorus treated plants. Positive correlation was noted between acid phosphatase activity and phosphorus concentration (Bhadraiah *et al.,* 1999).

Phosphatase activity may be detected in several ways, histochemically e.g. by precipitating a Fast Blue RR salt with P from alpha-naphtyl acid phosphate to indicate metabolically active cells or cell component (Tisserant *et al.* ,1993), as qualitative visualization employing e.g. phenolphthalein phosphate activity (Trolldenier, 1992) , or as a quantitative measurement of hydrolysis of a substrate either, measured as disappearance of substrate or as formation of one of the two resulting products. Since its introduction three decades ago (Tabatabai and Bremner, 1969) the use of *P*-nitrophynyl phosphate (pNPP) as a substrate in quantitative measurement of endogenous soil phosphatase and extracellular phosphatase of plant and micro-organism has dominated due to its convenience.

Nitrogen

Nutrient acquisition via the fungal partner involves transfer across two interfaces: one between the soil and the extraradical mycelium (ERM) of the AM fungus and one between the intraradical mycelium (IRM) of the AM fungus and the root cortex cells. Soil-to-plant nitrogen transport by the ERM of AM fungi was first demonstrated using compartmented pots where ^{15}N-labeled nitrogen sources were applied

to soil containing the ERM (Ames *et al.* ,1983, Johansen *et al.* ,1992, Frey and Schüepp 1993). The ERM can take up ammonium (NH_4^+), nitrate (NO_3^-), and amino acids (Ames *et al.* ,1983, George *et al.* ,1992, Frey and Schüepp 1993, Johansen *et al.* ,1994, Tobar *et al.* ,1994, Bago *et al.* ,1996, Hawkins *et al.* ,2000, Toussaint *et al.* ,2004, Govindarajulu *et al.* , 2005) and nitrogen uptake from root-free compartments (RFCs) could account for as much as 30% to 80% of total plant nitrogen uptake in compartmented growth systems (Frey and Schüepp, 1993, Johansen *et al.* ,1994). High nitrogen uptake ability by AM fungi was confirmed using *in vitro* model systems (Govindarajulu *et al.,* 2005). Nitrogen uptake by AM fungi has focused mostly on legumes. When AM fungi improve the P-nutrition of the host plant there may be a corresponding increase in nodulation, N_2 fixation and growth (Robson *et al.,* 1981). Enhancement effects of AM fungi on the N contents in nodulated legumes are not only derived from N_2 fixation but in part through higher uptake of soil N (Azcòn and Barea, 1992). However, mobility of NO_3^- being high and that of NH_4^+ being relatively low, an important contribution of the external hyphae to the N nutrition of the host plant can be expected from $NH_4 - N$ rather than $NO_3 - N$ uptake. Other studies have demonstrated that AM fungi were able to metabolize inorganic N (Ho and Trappe, 1975; Ames *et al.,* 1983, Smith *et al.,* 1985). Also hyphal transport of N between individual plants can be substantial (Newman *et al.* ,1992) and may play a role in competition between plants as well as N cycling between species sharing same type of AM fungi (Marschner and Dell, 1994).

Other macronutrients

Little is known on the role of AM fungi in the uptake of K, Ca, Mg and S. Although for arbuscular mycorrhizae there are many results on effect of colonization on concentrations and amount of K in shoots, these results are inconsistent and difficult to interpret (Sieverding and Toro, 1988). Remarkable difference in growth response of soyabean to AM fungal inoculation with different geographic isolates of *Glomus mosseae* seemed to be more related to improved K rather than P-nutrition of the host plant (Bethlenfalvay *et al.,* 1989). Higher levels of K were noted in sorghum colonized by *Glomus fasciculatum* (Raju *et al.,* 1987) and in *Eupatorium odoratum* colonized with *Glomus macrocarpus* (Sieverding, 1983).

By supplying radioisotopes ^{45}Ca, $^{35}SO_4$, a certain capacity of the external hypae of AM fungi for uptake and transport to the host root has been shown for Ca (Rhodes and Gerdemann, 1975) and $SO_4 -S$ (Cooper and Tinker, 1978). Compared to P, the uptake and transport rates particularly of Ca were very low. It has

been suggested that polyphosphate granules could serve as the means for the hyphal transport of Ca (White and Brown, 1979). However, due to the necessity to maintain very low cytosolic free Ca^{2+} concentration, delivery loaded polyphosphates to the arbuscules would be harmful to their functioning. In view of the high mobility of Ca^{2+} and SO_4^{2-} in the soil, a substantial contribution of the hyphal delivery to the host is not likely undermost circumstances. For Mg, direct experimental evidence for uptake and transport in mycorrhizal hyphae is either lacking or inconclusive (Kothari *et al.,* 1990 a,b).

In an study, vegetative pistachio seedlings (*Pistacia vera* L.cv. *Ravar*) were inoculated with *Glomus intraradices*, *Glomus etunication*, *Glomus microaggregatum* and *Glomus mosseae* at different levels of phosphorus (0, 18.6, 27.8 and 37 mg P2O5 /kg soil, as triple super phosphate source) as compared to non-mycorrhizal treatment. In this experiment, AM fungi increased Ca, P, K, Mg and Zn, concentrations in root dry matter and also translocation of P, K and Zn from roots to above ground organs. Further, AM inoculated onion had greater concentrations of P and K in shoot tissues, P in bulb tissues, and greater P, Ca, Mg, Na, K, Zn, and Fe total uptake than nonmycorrhizal plants at intermediate soil salinity (Ojala *et al.,* 1983). Growth and nutrient uptake of *Euterpe oleracea* seedlings was significantly improved by inoculation of effective AM fungi. Here, inoculation with *S. gilmorei* resulted in increment of 92% in total plant height, 116% in stem diameter, 361% in dry matter production, 191% in N, 664% in P, 46% in K, 562% in Ca, 363% in Mg and 350% in Zn contents in comparison to uninoculated controls (Chu, 1999). Further, leaflets of inoculated Lychee (*Litchi chinensis* Sonn.) plants reported higher concentrations of P, K, Cu, Zn and lower concentrations of Ca, Mg and Mn as compared to control plants (Janos *et al.,* 2001).

Micronutrients

Several reports exist on the enhancement of Zn and Cu uptake by AM plants can be attributed to the uptake and transport in external hyphae to the host plant (Kothari *et al.,* 1991 a and b). Increased uptake for Zn and Cu were noted for sorghum colonized by *Glomus fasciculatum* (Raju *et al.,* 1987) and cotton colonized by *Gigaspora calospora* and *Glomus intraradices* (Smith and Roncadri, 1986). The hyphal contribution of *Glomus mosseae* in total uptake ranged from between 16 and 25% for Zn and 13 to 20% for P in maize grown in calcareous soil. In same soil, Li *et al.* (1991) demonstrated that the delivery of Cu from the hyphal compartment ranged from 52 to 62% of the total Cu uptake under restricted rooting space.

In contrast, Mn uptake and concentrations in plants are some times not affected, but more often are lower in AM plants (Lambert and Weidensaul, 1991). The decrease in Mn concentrations is most likely an indirect effect caused by the changes induced by the AM fungi in the rhizosphere micro-organisms in general and decrease in population of Mn reducers in particular (Kothari *et al.,* 1991b). The role of AM fungi on Boron (B) of host plant is either lacking or inconclusive. Arbuscular mycorrhizal fungi may decrease B concentration in host plants (Kothari *et al.,* 1991 a and b). Plants have varying mechanisms for mobilizing, chelating and reducing ferric (Fe) in order to facilitate uptake (Marschner, 1986). Treeby (1992) indicated that AM fungi may facilitate the Fe uptake in acidic but not in alkaline soils.

NON NUTRIENT BENEFITS

Photosynthesis

Since growth stimulation is often associated with AM colonization and it seems likely that important metabolic processes such as photosynthesis would also be stimulated (Allen *et al.,* 1981, Johson *et al.,* 1982). Johnson (1984) and Nemec and Vu (1990) reported improved photosynthetic rates in *Citrus aurantium* L. inoculated with *Glomus intraradices* as compared to un-inoculated plants. Similarly Johnson *et al.,* (1982) reported increased photosynthesis and greater stomatal conductance in mycorrhizal *Citrus sinensis* L.

Lösel and Cooper (1979) observed a greater translocation of photosynthates to root of mycorrhizal onion and suggested that this could reflect increased photosynthesis by leaves of the mycorrhizal plants. Levy and Krikun (1980) observed improved photosynthesis of mycorrhizal *Citrus* plants following water uptake suggesting that the improvement was associated with stomatal regulation. Increase in transpiration and photosynthetic rates and chlorophyll concentrations in the grass, *Bouteloua gracilis* was reported by Allen and Allen (1981). Higher P-levels in leaf tissue of AM host plants have as been suggested as the primary reason for high photosynthetic rates (Lösel and Cooper, 1979). Yano-Melo *et al., (*1999) reported that *Glomus clarum* and *Glomus etunicatum* enhanced growth, photosynthesis and transpiration rates of *Musa* sp. and these effects were due to improved P-nutrition. Also, with increased respiratory losses (Snellgrove *et al. ,*1982) from the mycorrhizal symbiont, AM fungi may function as metabolic sink causing basipetal mobilization of photosynthates to roots (Bevege *et al. ,*1975), thus providing stimulus for greater photosynthetic activity (Frier, 1977, Herold, 1980). In addition, enhanced levels of cytokinin (Allen *et al.,* 1980) were found in association with AM colonization. Increase of such hormones especially cytokinins, could alleviate photosynthetic rate by stomatal opening (Incoll and Whitelam, 1977) influencing iron transport (Van Stevennick, 1976) and regulating chlorophyll levels (Richmond and Lang, 1957, Stetler and Laetsch, 1965). Nemec and Vu (1990) reported that inoculation of sour orange with *Glomus intraradices* accounted for improved photosynthetic CO_2 fixation, which was consistent with increase in chlorophyll and RuBPlase activity. Similarly, Wu and Xia (2006) reported that *Citrus tangerine* seedlings inoculated with *Glomus versiforme* had higher photosynthetic rates than corresponding control seedlings. In another study, Fay *et al.* (2006) reported that AM colonization of barley (*Hordeum vulgare* L. cv. *Manitou*) by *Glomus mosseae* resulted in enhancement of maximum photosynthetic rate at the lowest P level and was associated with a higher stomatal conductance, but was not related to increased leaf P or to changes in photon yield or the ratio of variable (*FV*) to maximum (*FM*) chlorophyll fluorescence.

Drought resistance

Plant colonized by AM fungi can tolerate and recover more rapidly from soil water deficits than plants without AM fungi (Allen and Boosalis, 1983, Bildus *et al.,*1986, Henderson and Davies, 1990). Johnson and Hummel (1985) reported increased resistance to drought and transplant stress by Carrizo citrange seedlings inoculated with *Glomus intraradices* as compared to un-inoculated ones. The tolerance of lettuce plants (*Lactuca sativa* L. cv. *Romana*) to drought stress differed with the AM fungal isolate with which the plants were associated. Seven fungal species belonging to the genus *Glomus* were studied for their ability to enhance the drought tolerance of lettuce plants. These fungi had different traits that affected the drought resistance of host plants. The ranking of AM fungal effects on drought tolerance, based on the relative decreases in shoot dry weight, was as follows: *Glomus deserticola > Glomus fasciculatum > Glomus mosseae > Glomus etunicatum > Glomus intraradices > Glomus caledonium > Glomus occultum*. In this comparative study specific AM fungi had consistent effects on plant growth, mineral uptake, the CO_2 exchange rate, water use efficiency, transpiration, stomatal conductance, photosynthetic phosphorus use efficiency and proline accumulation under either well-watered or drought-stressed conditions. The ability of the isolates to maintain plant growth effectively under water stress conditions was related to higher transpiration rates, levels of leaf conductance, proline concentration, N, and P contents. Differences in proline accumulation in leaves among the fungal symbioses suggested that the AM fungi were able to induce different degrees of osmotic adjustment (Ruiz-Lozano *et al.,* 1885).

A variety of mechanism may help to ameliorate drought stress in mycorrhizal plants thereby enhancing plant recovery after drought. Mycorrhizal plants sometimes increase root length density or alter the root system morphology, enabling colonized plants to explore more soil volume and extract more water than non colonized plants during the drought (Davies *et al.,* 1996). It has been suggested that mycorrhizal hyphae may directly enhance root water uptake, providing adequate water to preserve physiological activity in plants, particularly under severe drought conditions (Allen, 1982, Faber *et al.,* 1991). Extramatrical hyphae can also bind soil to roots and maintain better root-soil contact during drought and facilitate water uptake (Davies *et al.,* 1992). Augé *et al.* (1986) reported that mycorrhizal colonization enhanced stomatal control in rose plants and reduced water loss during drought. Improved drought tolerance and better recovery by mycorrhizal plants is often related to improved P uptake (Fitter, 1985, Graham *et al.,* 1987, Nelson and Safir 1982a and b). Mycorrhizal fungi have been shown to improve osmo-regulation in tissue of colonized plants by increasing leaf tissue solute concentration (Allen and Boosalis, 1983). The AM fungi may induce increase in the level of soluble proteins which contribute to plant tolerance to stresses, such as drought (Ruiz-Lozano and Azcon, 1995, Subramanian and Charest, 1998). Sugar accumulation in mycorrhizal maize plants had been reported under drought conditions (Subramanian *et al.,* 1997). Higher levels of sugar may improve the ability of the plants to withstand drought stress and recover after the condition is restored (Kameli and Lösel, 1993).

Disease resistance

Arbuscular mycorrhizal fungi can reduce plant root disease symptoms and pathogen populations in soil through mechanisms that are not well understood (Schönbeck, 1979, Dehne, 1982, Graham, 1986, Caron, 1989, Perrin, 1990, Lindermann, 1994). The action has been attributed to improvement of plant nutrition, stimulation of host plant disease resistance mechanisms, direct interaction with pathogens and indirect effect through changes in soil microflora (St-Arnaud *et al.,* 1995). The synthesis of chemical compounds implicated in physical or chemical resistance to pathogen infection has been observed in response to mycorrhizal colonization (Baltruschat and Schönbeck, 1975, Krishna and Bagyaraj, 1983, Morandi *et al.,* 1983, Lieberei and Feldmann, 1989, Grandmaison *et al.,* 1993). Increased phenolic metabolism in plant roots has been suggested as a part of mechanism involved in the biocontrol (Morandi *et al*., 1984). Mycorrhizal fungi are able to cause an accumulation of phenolics, in particular phytoalexins and associated flavinoids and isoflavinoids in the roots of their host plants. Conjugate isoflavinoids that are not toxic and that accumulate at higher levels in mycorrhizal roots could serve as storage form of phytoalexins which could be easily hydrolyzed in case of pathogen attack (Morandi *et al.,* 1984). For example, when tomato plants were inoculated with *Glomus mosseae,* the damage caused by *Fusarium oxysporum* f. sp. *lycopersici* was considerably reduced (Dehne and Schonbeck, 1975). Such tolerance, due to mycorrhizal association may be imparted by one or more of the following mechanisms: alterations in the physiology of the host, improvement of the plant nutritional status, anatomical changes and production of phenolic compounds (Baltruschat and Schonbeck, 1972; Ling-Lee *et al.,* 1977; Dehne *et al.,* 1978; Krishna and Bagyaraj, 1983; Morandi *et al.* ,1984). Of these the production of phytoalexins is considered to be an important mechanism of disease resistance in plants (Morandi *et al.,* 1984).

The beneficial effects of the AM symbiosis result from a complex molecular dialogue between the two symbiotic partners and some processes occurring in this dialogue are known to be mediated by phytohormones on the plant side. Thus, phytohormones have been proposed as" suitable candidates for signalling between plants and AM fungi", and it is tempting to speculate in the autoregulation of mycorrhization (Meixner *et al.,* 2005). The elevated jasmonic acid (JA) levels occurring upon mycorrhization may enhance the defence status of mycorrihizal tissues, which were shown to be less sensitive to secondary infection by pathogens (Cordier *et al.,* 1998). The role of mycorrhiza in plant defense was carried out by modulating endogenous JA levels via overexperension or suppression of JA biosynthetic genes, thus it is tempting to speculate that JA serves as endogenous signal in mycorrhiza-induced resistance (Pozo and Azcon-guilar, 2007). On the other hand, it has been suggested that plant defense responses mediated by salicylic acid (SA) are involved in the regulation of enteric endophytic colonization (Iniguez *et al.,* 2005). Exogenous SA application delays mycorrhizal colonization, it is plausible that AM fungi repress SA-dependent defense responses in the host in order to achieve a compatible interaction (Dumas-Gaudot *et al., 2000*). In the case of mycorrhizal plants, such attenuation could explain the delay in systemic accumulation of PR-proteins upon treatement with SA or analogs (Shaul *et al.,* 1999). Moreover, interaction between AM fungi (*Glomus etunicatum*) and SA had the highest effect on infection of *Fusarium* wilt and disease severity in tomato was reduced by 70% (Ozgönen *et al.,* 2001).

Further, the potential of AM fungi to alleviate nematode induced plant stress has been widely investigated because of their ability to increase root growth and nutrient absorption. Numerous studies have reported to increase host tolerance or resistance

in many plant –nematode systems especially fruit crops viz., *Citrus* (Smith and Kaplan, 1988; Ó Bannon *et al.,* 1979) cherry (Pinochet *et al.,* 1995), banana (Umesh *et al.,* 1988), apple (Utkhede *et al.,* 1992) etc. Umesh *et al.* (1988) reported suppression or reduction of burrowing endophyte *Radopholus similes* by *Glomus fasciculatum* in banana (*Musa acuminata* Colla.). They attributed following reasons for the disease resistance:1) Arbuscular mycorrhizal colonization of roots mechanically preventing nematode penetration and establishment 2) Increased plant vigour masking the nematode damage 3) increased nutritional status of roots 4) increased sugar content in the roots and 5) other physiological and anatomical alterations in the host.
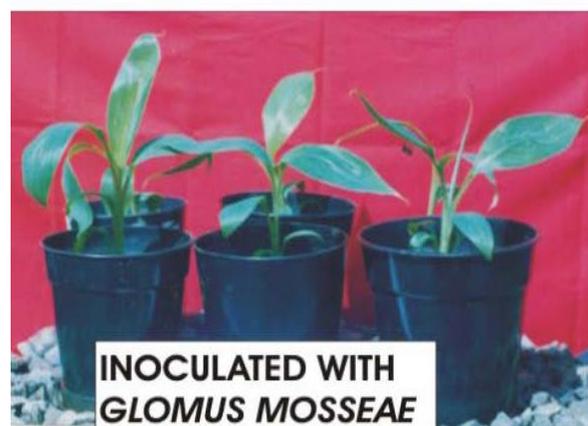
Micro-propagation (Plate 1)

Among other applications, micropropagation is used to produce certified stock for nurseries. The plants produced with this method are free from any microorganisms, including symbiotic ones which are necessary in nutrients and water uptake and provide some protection against certain biotic and abiotic stresses. Thus, a reintroduction of symbiotic micro-organisms is needed to facilitate a smooth plant transition from pro-tective *in vitro* conditions to the field (Sbrana *et al.,* 1994, Monticelli *et al.,* 2000, Taylor and Harrier 2000, Borkowska 2001). The mycorrhization technology has been used during the last years in a number of micropropagated crops in order to improve their survival rate and growth during *post vitro* stages (Schubert and Lubraco, 2000, Rai, 2001, Borkowska, 2002, 2005). Mycorrhizal fungi help to recover the biological activity and physical properties of a soil and they are active in mobilizing minerals (Camprubi *et al.*, 1993, Diaz and Honrubia, 1993, Calvet *et al.,* 2001). Thus, arbuscular mycorrhizas are important in establishment and subsequent growth of crops, especially those cultured in intensive agriculture systems, where soil structure, chemistry and microflora is frequently degraded (Borkowska *et al. ,*2008). Early mycorrhizal inoculation and colonization of tissue cultured plantlets of plant species has been reported to reduce transplant shock during acclimatization, thus increasing plant survival and establishment rates. Also micro-propagated plantlets that were inoculated with arbuscular mycorrhiza have enhanced plant quality, nutrient uptake and plant growth (Estrada – Luna *et al. ,*2000, Ravolanirina *et al. ,*1989 a and b, Branzanti *et al. ,*1992, Schübert *et al. ,*1992, Azcón- Aguilar *et al. ,*1994, Lovato *et al. ,*1994, Rapparini *et al. ,* 1994, Vesteberg and Estaún 1994). Arbuscular mycorrhizal fungi can induce morphological modifications in the host plant root system (Berta *et al.,* 1993, Atkinson *et al.,* 1994). A more branched root system has been in observed in mycorrhizal plants of different herbaceous

and woody species (Amijee *et al.,* 1989, Berta *et al.,* 1990, Schellenbaum *et al.,* 1991). Recent work suggested that some of the effects of mycorrhizal symbiosis are likely to be due to direct influence on root system rather than to the effect of the AM fungus in improving mineral nutrition (Hooker *et al.,* 1992, Berta *et al.,* 1995). Furthermore, some fungal effects on morphogenesis could be induced by metabolites or hormones (Fortuna *et al.,* 1998). The development of an efficient root system is particularly important in micro-propagated plants, where the AM fungi could have a positive effect not only by inducing rapid development of a functioning root system but also through benefits on plant growth in subsequent period (Atkinson *et al.,* 1994).
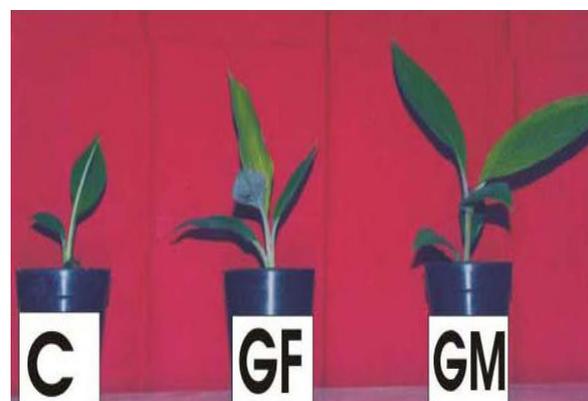
(A)

(B)

Plate 1. A) Response of micro-propagated tissue cultured banana to inoculation with AM fungi (C-Control; GF- Inoculated with *Glomus fasiculatum,* GM- Inoculated with *Glomus mosseae*).
B) Micro-propagated tissue cultured banana inoculated with *Glomus mosseae.*

Soil aggregation and stabilization

Soil aggregation is a complex, hierarchical process mediated by both biotic and abiotic factors (Tisdall and Oades, 1980). Aggregation is essential to maintaining soil porosity, allowing gas exchange and water infiltration, and facilitating biogeochemical cycling (Diaz-Zorita et al., 2002). Soil structure is also crucial to the success of sustainable agriculture and erosion resistance. Over one-third of the world's arable land was damaged by erosion over the last 40 yr (Pimentel et al., 1995) and much of the focus of sustainable agriculture has shifted towards managing for well-aggregated soils. Hyphae of AM fungi are considered to be primary soil aggregators for several reasons: the extraradical hyphae of AM fungi have a significant biomass in most soils (Rillig and Allen, 1999), as obligate biotrophs these fungi do not need to compete with saprobes for soil carbon and AM fungal hyphae are more resistant to fungivory than saprobic fungi (Klironomos and Kendrick, 1996). Arbuscular mycorrhizal fungi may stabilize soils up to 5 months after their host's death (Tisdall and Oades, 1980). A positive correlation between AM fungal hyphae and aggregate stabilization in natural systems is described by Miller and Jastrow (1990) and Jastrow et al., (1998). Rillig et al., (2002) described significant indirect effects of AM fungal hyphal length on waterstable aggregate (WSA) stabilization via the production of glomalin-related soil protein (GRSP) in a natural grassland system.

Little is known about the effects of different AM fungal taxa on aggregate stabilization. Schreiner et al., (1997) tested the WSA forming ability of three AM fungal species on soybean (*Glycine max*). The authors found that *Glomus mosseae* stabilized aggregates in the 2– 4 mm size class significantly more than *Glomus etunicatum* and *Gigaspora rosea* , but there were no differences between species in the 1–2 mm or 0.25–1 mm size classes. Plants with dense, fibrous root systems (such as grasses) assist aggregate formation (Oades, 1993, Amézketa, 1999). Similarly, hyphal characteristics may contribute to aggregation ability. An AM fungus with dense hyphal clusters may hold soil particles together better than diffuse hyphae, but this hypothesis has never been tested. The idea of an aggregation 'specialist' is attractive to agriculture as well as to applications in ecosystem restoration. If a species of AM fungi is promoted due to its WSA stabilization properties, independent of plant host or soil type, it could be used to inoculate crops or other soils with poor water aggregate stability (Piotrowski et al., 2004).

The effects of arbuscular mycorrhizal fungi on the stability of agricultural soils was provided by the pioneering work of Tisdall and Oades (1979), who demonstrated the importance of soil hyphae of arbuscular mycorrhizal fungi in determining the level of water-stable aggregation. Thomas *et al., (*1986) demonstrated that onion roots colonized by *Glomus macrocarpum* increased the aggregation of a calcareous silty – clay loam as compared to non-host plant. Later studies by, Thomas *et al.* (1993), reported that roots and external hyphae contributed equally to water- stable soil aggregation and that both of them had an additive effect on soil aggregation process. Rothwell (1984) suggested that the reactions between root phenolics and glucosamine residues in AM hyphal walls could be a stabilizing mechanism for soil aggregates. Also hyphal fragments of AM fungi and dead AM spore and sporocarps may act as nucleation sites in the formation of soil-aggregates, by supplying substrate to the microbial community. Differences in the hyphal density and morphology among AM fungi isolates may account for divergent soil properties. Morphological restrictions of different AM fungi could result in the colonization of different micro-sites within soil that may enhance aggregation whenever multiple fungi are colonizing the soil. Since the spatial distribution of soil hyphae can vary among fungal species (Jakobsen et al., 1992), an increase in the overall hyphal density of AM mycelium around the roots may result from multiple AM fungal colonization's, compared to single species. Alternately, different AM fungi may produce different types and/or amounts of soil binding agents and the interaction of these agents within the aggregates may result in synergistic soil stability. Thus little is known about the mechanisms of AM fungal mediated soil aggregation, but it seems to result from binding of small particles into micro-aggregates and the entanglement of microaggregates into macroaggregates. The ability of AM fungi to extract water from small pores within the soil matrix may also contribute to the stabilization of soil aggregates by entanglement and cementing mechanisms.

CONCLUSIONS

Thus, most our knowledge about mycorrhizal benefits comes from studies of crops and forage plants. Many crops may be expected to be facultatively mycorrhizal because they have ruderal ancestors and were selected for rapid growth in high fertility soils. However, tropical crops and forage species often grow in acidic, highly infertile soils and they are highly dependant on arbuscular mycorrhizae as they have so many benefits to confer. Many modern agronomic practices are disruptive to mycorrhizal symbiosis. There is great potential for low input agriculture to manage the system in a way that promotes mycorrhizal symbiosis. Most agricultural crops can perform better and are more productive when well colonized by AM fungi. The ability of the same AM fungi to colonize many species of plants has ecological implications. Plants of different species can be linked underground to a

common mycelial network. One plant may provide the photosynthate carbon for the establishment of the mycelial network which another plant of a different species can utilize for mineral uptake. This implies that arbuscular mycorrhizae are able to balance below ground intra–and interspecific plant interactions. Mycorrhizae diversity has been shown to increase plant species diversity as the potential number of associations increases. Dominant arbuscular mycorrhizal fungi can prevent the invasion of non-mycorrhizal plants on land where they have established symbiosis and promote their mycorrhizal hosts.

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