

Arbuscular mycorrhizae in plant survival strategies

DAVID KOTHAMASI¹, RAMESH CHANDER KUHAD^{1*} & C.R. BABU²

¹*Department of Microbiology, University of Delhi South Campus, New Delhi 110 021, India;*

²*Department of Botany, University of Delhi, Delhi 110 007, India*

Abstract: Mycorrhizae have been associated with vascular plants since the Palaeozoic times. The colonization of terrestrial ecosystems by the ancestors of modern vascular plants was facilitated by symbiotic fungi similar to modern endomycorrhizae. Arbuscular Mycorrhizae (AM) comprise of over 150 species that are not host specific and form symbiotic associations with a wide range of host species. AM bestow a selective advantage on their host over competing non-host species by making available nutrients, providing defence against several pathogenic organisms and by influencing the composition of the microflora of the rhizosphere. However, the benefits that AM provides to its host come with a price tag. The plant has to forego up to 10-20% of its photosynthetic produce to maintain the fungus. This review discusses the conditions under which forming an AM association would be a competitively advantageous strategy for the host plant.

Resumen: Las micorrizas han estado asociadas a las plantas vasculares desde el Paleozoico. La colonización de ecosistemas terrestres por los ancestros de las plantas vasculares modernas fue facilitado por hongos simbióticos similares a las endomicorrizas modernas. Las micorrizas arbusculares (MA) comprenden más de 150 especies que no presentan especificidad de hospedero y que forman asociaciones simbióticas con una amplia gama de especies hospederas. Las MA confieren una ventaja selectiva a su hospedero sobre especies competidoras no hospederas haciendo disponibles algunos nutrientes, representando un desafío para varios organismos patógenos, e influenciando la composición de la microflora de la rizosfera. Sin embargo, los beneficios que proporcionan las MA a su hospedero tienen marcado un precio. La planta tiene que prescindir de hasta 10 ó 20% de sus productos fotosintéticos para mantener al hongo. En esta revisión se discuten las condiciones en las que la formación de una asociación MA podría ser una estrategia competitivamente ventajosa para la planta hospedera.

Resumo: As micorrizas têm estado associadas às plantas vasculares desde o Paleozóico. A colonização dos ecossistemas terrestres pelos ancestrais das plantas vasculares modernas foi facilitada por fungos simbióticos semelhantes às endomicorrizas modernas. As micorrizas arbusculares (AM) compreendem para cima de 150 espécies que não têm hospedeiros específicos e formam associações simbióticas com uma larga gama de espécies hospedeiras. As AM conferem uma vantagem selectiva aos seus hospedeiros sobre as espécies não hospedeiras por lhes disponibilizarem nutrientes, proporcionando defesa contra vários organismos patogénicos e por influenciarem a composição da microflora da rizosfera. Contudo, os benefícios que as AM proporcionam aos seus hospedeiros têm um preço. A planta tem que ceder cerca de 10-20% da sua produção fotossintética para manter os fungos. Esta revisão discute as condições sob as quais a formação de uma associação AM representa uma vantagem competitiva para a planta hospedeira.

Key words: Arbuscular mycorrhiza, competition, cost, mycorrhizosphere, stress, succession.

* *Corresponding Author:* Ramesh Chander Kuhad. Tel. 011-4107576; Fax: 011-6885270, 6886427; E-mail: micro@dusc.ernet.in

Introduction

Growth in plant communities is often governed by the availability of nutrients such as P and N. In contrast, C is growth-limiting element in fungal communities. It was but obvious for natural selection to have favoured the development of symbiotic associations between plants and fungi. Plants provide C to fungal symbionts and the fungi transfer nutrients from the soil to the host (Kumar *et al.* 1999; Pierzynski *et al.* 2000; Read 1990; Sen 2000). Mycorrhizae have been associated with vascular plants since the Palaeozoic era (Taylor 1990). The colonization of land by the ancestors of modern vascular plants seems to have been hastened by the origin of symbiotic associations between these plants and some phycomycetous fungi similar to those of modern endomycorrhizae (Malloch *et al.* 1980; Phipps & Taylor 1996; Simon *et al.* 1993). Arbuscular mycorrhizae (AM), the most prevalent plant-fungus association, comprise about 150 species, belonging to the order Glomales of Zygomycotina (Morton & Bentivenga 1994; Myrold 2000; Perry *et al.* 1989; Schenk 1981; Simon 1996). AM are one of the few plant-fungus associations with a fossil record (Taylor 1990) and are believed to have assisted vascular plants in their growth and survival (Simon *et al.* 1993).

AM are present in most soils and are generally not considered to be host specific. However, population sizes and species composition are highly variable and influenced by plant characteristics and a number of environmental factors such as temperature, soil pH, soil moisture, P and N levels, heavy metal concentration (Boddington & Dodd 1999), the presence of other microorganisms, application of fertilizers and soil salinity (Barea & Azcon-Aguilar 1983; Bationo *et al.* 2000). Species and strains of AM differ in their ability of tolerance to physical and chemical properties of soil (Abbot & Robson 1991), as a result they also differ in their effectiveness in improving plant growth.

Most angiosperm families form AM. It is believed that plants growing in aquatic, water logged and saline habitats usually do not form mycorrhizae (Malloch *et al.* 1980). However, Kothamasi *et al.* (unpublished data) have found AM colonization in the mangrove plants of Great Nicobar Island, India. Among the monocots, Cyperaceae and Juncaceae often do not form my-

corrhizal associations (Powell 1975). However, the presence of AM has been reported in some members of Cyperaceae of Venezuelan savannahs (Lovera & Cuenca 1996). In the dicots, Brassicaceae, Chenopodiaceae, Proteaceae, Restionaceae, Zygophyllaceae, Lecythidaceae, Sapotaceae and all families of Centrospermae do not form mycorrhizae (Tester *et al.* 1987). Infection may be reduced in plants growing in the vicinity of non-mycorrhizal plants especially of Cruciferae (Tester *et al.* 1987). Families rich in glucosinates predominantly lack mycorrhizae. This could be because of inhibitory action of these chemical substances on fungal growth (Malloch *et al.* 1980; Vierheilig *et al.* 2000). In *Brassica*, the stimuli necessary for the penetration and development of arbuscules is lacking and the plants do not provide any nutritional benefits to the fungus (Glenn *et al.* 1985). Although recent reports reveal AM colonization in wild crucifers, in each case colonization appeared only in the dead cortical cells and none of them formed arbuscules (DeMars & Boerner 1995a; Vierheilig *et al.* 2000).

AM form the connecting link between the biotic and geochemical portions of the ecosystem (Miller & Jastrow 1994). Mycorrhizae aid the plant in better growth by assisting it in absorbing useful nutrients from the soil, in the competition between plants and in increasing the diversity of a given area. A number of reviews have appeared recently on AM, particularly dealing with the application of AM in agriculture. Information on the role of AM in plant adaptations has been scattered and the present review deals with the critical appraisal of the role of AM in plant community dynamics, nutrient mobilization and overcoming both abiotic and biotic stresses.

AM and plant community dynamics

AM fungi are known to infect a wide range of host species. They have a large geographical distribution (Malloch *et al.* 1980), being found even in the Arctic tundras and the Antarctic region (DeMars & Boerner 1995b; Gardes & Dahlberg 1996). Unlike most ectomycorrhizal species, AM are not host specific. This enables them to form associations with a large number of plant species.

Grime *et al.* (1987), in a classic experiment involving several grass and herbaceous species dem-

onstrated that experimental set-ups inoculated with mycorrhizae had greater plant diversity than uninoculated set-ups. AM form hyphal links between plants of different species (Perry *et al.* 1989). These links could be involved in the transfer of nutrients between plants. At the plant community level, AM hyphae form a network-the *wood-wide web* (Fig. 1) that facilitates carbon exchange between the host and the symbiont, uptake of nutrients and their movement between plants linked by the AM hyphae (Fitter *et al.* 1998; Helgason *et al.* 1998; Newman 1988; Newman *et al.* 1994; Sen 2000). Mycorrhizae owing to their role in nutrient cycling, keep more nutrients in the biomass and in doing so increase the productivity of the ecosystem (Newman 1988). Mycorrhizal links between seedlings and mature trees may help the seedlings in establishing themselves by providing them with the required nutrients (Newman 1988; Newman *et al.* 1994).

AM fungi regulate plant communities by affecting competition, composition and succession (Allen & Allen 1984; Kumar *et al.* 1999). Limited resources and the struggle of the plants for a share of these is the primary selection pressure operating on plant species (St. John & Coleman 1983). In competition between plants, mycorrhizae in the soil favour the growth of one species and are detrimental to other competing species. Fitter (1977)

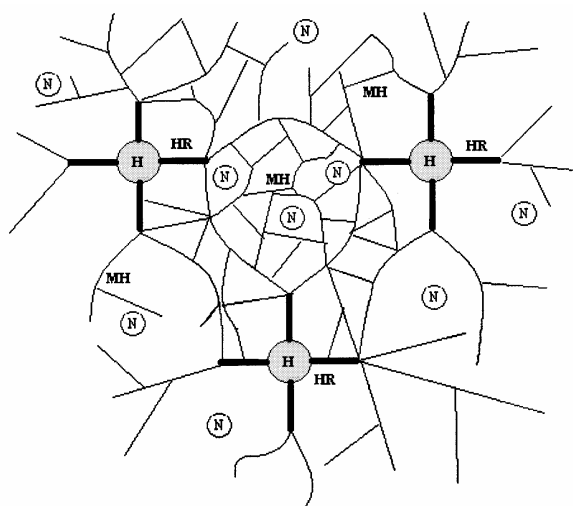


Fig. 1. The web formed by the AM hyphae (MH) forms bridges between host plants (H) of different species that permits nutrients exchange. The spread of the hyphae beyond the absorptive range of the host root (HR) aids in uptake of nutrients (N) from distant patches.

demonstrated this in a competition between two grasses *Lolium perenne* and *Holcus lanatus*. Inoculation with mycorrhizae favoured the growth of *H. lanatus*. This was an indirect effect as infection with mycorrhizae reduced the root length of *L. perenne* by 40%. AM may regulate competition between plants by making available to mycorrhizal plants, resources that are not available to non-mycorrhizal neighbours (Allen & Allen 1984). AM symbiosis increases intraspecific competition (Facelli *et al.* 1999). As a result, density of individuals of a single species would be reduced thereby allowing the co-existence of individuals of different species. This would lead to an increase in species diversity.

Mycorrhizae govern species composition in communities by influencing plant fitness at the establishment phase. AM prevent non-mycorrhizal plants from growing in soils colonised by them. This has a selective advantage for the fungus. Maintaining a high proportion of compatible host species at the expense of non-compatible species provides the fungus with an undisturbed carbon supply (Francis & Read 1994).

Succession is a chain of predictable processes whose course is influenced by nutrient availability. Mycorrhizae, owing to their role in nutrient uptake, may play an important part in determining the rate and direction of the process (Smith & Read 1997a). They influence the outcome of succession by amending the composition of species or by affecting species diversity (Gange *et al.* 1990).

Mycorrhizal propagules lose their vigour in a bare ground. Regions where the existing vegetation has been disturbed usually have enriched soils because of a pulse of N and P produced due to mineralization of residues left by the previous communities. This disturbed soil is first colonized by non-mycorrhizal families like Brassicaceae and Polygonaceae, which capitalize on the sudden flux of nutrients (Smith & Read 1997a). With the dwindling of the initial pool of nutrients, the non-mycorrhizal species of the pioneer stages are replaced first by the facultative and finally by the obligate mycotrophs (Smith & Read 1997a; Kumar *et al.* 1999). Succession is determined to a large extent by the quality and quantity of mycorrhizal spores present in the soil and by build-up of mycorrhizal networks capable of rapidly colonizing any newly germinating plant. It should be pointed out here that the mycorrhizal types involved in the final stages of succession are different under dif-

ferent climatic regimes. The dominant type of mycorrhiza changes from AM to ecto- and ericoid mycorrhiza as succession progresses from grassland to deciduous forest, boreal forest and heath along the gradient from warm-dry to cold-wet climates (Pankow *et al.* 1991).

The above pattern of succession seems to be true in temperate regions. In tropical countries like India, mycorrhizal plants act as pioneer species. It has been reported that mycorrhizal species like *Adhatoda vasica*, *Solanum xanthocarpum*, *Sporobolus* sp. and *Desmostachya* sp. form the pioneer vegetation in alkaline wastelands (Janardhanan *et al.* 1994). Babu *et al.* (unpublished data) have similarly found that mycorrhizal grass species have been the first to colonize fly ash mounds.

The functioning of plant communities depends to a large extent on decomposition, which makes nutrient elements available to the plant (Zhu & Ehrenfeld 1996). Decomposition is essentially carried out by the soil biota (bacteria, fungi, nematodes, arthropods, annelids), which breaks down the litter and organic matter of the soil. The external mycelium of both ectomycorrhiza and AM interact with these organisms. Some soil organisms have been found to feed on AM spores (Fitter & Garbaye 1994). By bringing about changes in the abundance and activity of decomposers, mycorrhizal fungi are believed to hasten the process of decomposition and thereby the nutrient cycling (Zhu & Ehrenfeld 1996).

AM and nutrient mobilization

An important role played by the AM fungi in plant growth is the absorption of nutrients from the soil and making them available to the plants (Hooker & Black 1995; Goicoechea *et al.* 2000). Nitrogen, phosphorus and potassium are the important nutrient elements required by plants for their growth. AM assist in nutrient uptake by exploring the soil beyond the range of roots (Miller & Jastrow 1994; Torrisi *et al.* 1999). Extraradical AM hyphae augment the uptake of nutrients from up to 12 cm away from the root surface (Cui & Caldwell 1996b). Hyphae may increase the availability of nutrients like N or P from locked sources by decomposing large organic molecules (George *et al.* 1995).

Phosphorus

Mycorrhizal fungi are known to develop bridges connecting the root with the surrounding soil particles to improve both nutrient acquisition by the plant and soil structure (Bethlenfalway 1992; Miller & Jastrow 1994). Unlike N₂-fixing bacteria that function as biological fertilizers, AM fungi do not add P to the soil. They only improve its availability to the plant. There is evidence that phosphatase activity is higher in the rhizosphere around AM than in non-mycorrhizal roots (Dodd *et al.* 1987).

The network of AM hyphae help in the uptake of nutrient ions like P that are not mobile (Miller & Jastrow 1994; Roldan-Fajardo 1994). The interdependence of mycorrhizal colonization and P acquisition by plants has been extensively studied (Azcón 1994; Ebel *et al.* 1994). P uptake is enhanced with the increase in root colonization by mycorrhizae. A system of barter operates, the colonized plant provides photosynthate to the AM, in return, its extraradical hyphae make more P available to the host (Merryweather & Fitter 1995a). AM colonization is determined by P availability in the soil. At low P concentrations there is high colonization and at high concentration there is low colonization. Plants rely more on AM when growing in soils deficient in P (Augé *et al.* 1994; Bationo *et al.* 2000; Merryweather & Fitter 1995b). Depriving a plant in its natural environment of mycorrhizae on a long-term basis can also reduce P acquisition (Merryweather & Fitter 1996).

In soils with a heterogeneous distribution of P, AM fungal hyphae deliver a uniform amount of P from distant rich and nearby uniform patches. Non-mycorrhizal plants are not very efficient in obtaining P from heterogeneous environment. However, in uniform patches there is no difference in P uptake by mycorrhizal and non-mycorrhizal plants (Cui & Caldwell 1996a). It has been found that plants that are non-mycorrhizal invest more in their vegetative tissues like shoots and roots (Allen 1982). In contrast, in mycorrhizal plants, the functions of the roots are taken over by the AM hyphae thereby permitting the host plant to invest its resources in reproductive organs.

Nitrogen

Nitrogen occurs in the soil predominantly in the form of nitrate and ammonia, which are water soluble and readily available for absorption (Tobar *et al.* 1994). Studies with labelled N have revealed

that AM increase N uptake by plants (Bijbijen *et al.* 1996; Faure *et al.* 1998; Mädder *et al.* 2000). AM fungal hyphae have been credited with the uptake and transfer of large amounts of N from the soil to the host (Hodge *et al.* 2000; Johansen *et al.* 1996). However, there is little reciprocal transfer of N from the plant to the fungi, which makes uptake and assimilation of N by the symbiont essential for its growth (Bijbijen *et al.* 1996). As has been mentioned previously, AM form underground hyphal links between plants. N transfer between plants by means of such links is possible (Read 1990). This mode of transfer is of little significance in soils with abundant N. However, in deficient areas and pioneer communities, inter-plant exchange may be occurring in associations involving mycorrhizal legumes and non-legumes in N (Haystead *et al.* 1988). Using labelled ^{15}N , Frey & Schüep (1993) demonstrated that N flows from *Trifolium alexandrinum* to *Zea mays* via AM fungal network. AM are also believed to enhance N_2 -fixation by symbiotic legumes by increasing root and nodule biomass, N_2 -fixation rates, root-N absorption rates, and plant N and P content (Olesniewicz & Thomas 1999).

Other nutrients

AM has been implicated to have a role in the uptake of other macronutrients. It has been reported to be involved in the uptake of K. In coach grass, 10% of total K uptake is mediated by the AM hyphae (Marshner & Dell 1994). AM hyphae have also been reported to be involved in the uptake of nutrients like S, Mg, Zn, Cu, Ca and Na (Bürkert & Robson 1994; Diaz *et al.* 1996; Galli *et al.* 1994; Smith *et al.* 1994).

AM and stress

AM facilitate better survival of plants under stress conditions through a boost 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, pathogen attack, metal pollution and grazing is briefly described.

Water

Stress due to conditions of drought is one of the major factors limiting plant growth. Improved plant nutrition increases drought resistance when faced with different levels of water stress (Nelson & Safir 1982). AM improve the uptake of nutrients like N and P in water stressed conditions (To-bar *et al.* 1994). Scarcity of water in soil is conveyed to the shoots by means of a non-hydraulic chemical signal that is relayed from the dehydrating roots to the aerial shoots by the transpiration system. This signal is believed to be a hormonal factor most probably abscisic acid (Davies & Zhang 1991; Hartung & Slovik 1991). The response is expressed by the leaves in terms of stunted growth and decreased stomatal conductance (Augé *et al.* 1994; Davies & Zhang 1991). AM alters this non hydraulic root-to-shoot signalling of soil drying by eliminating the leaf response (Augé *et al.* 1986 a). Mycorrhizal plants avoid drought to some degree by enhanced water uptake in soils with low water content (Augé *et al.* 1994). The extraradical AM hyphae increase the absorptive surface area of the roots (Hampp *et al.* 2000). This reduces the resistance to water uptake (Allen 1982). In soybean, AM have been found to reduce resistance to water uptake by 41% (Safir *et al.* 1972). Augé *et al.* (1986b) reported increased water uptake in rose plants colonized by two *Glomus* species. The fungal hyphae span the gap formed between the root and the soil when they shrink away from each other in dry conditions (Graham *et al.* 1971). However, increase in water uptake by AM was not found in *Citrus* plants subjected to drought stress (Graham *et al.* 1971).

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 a new environment in their zone of influence, AM 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). There are, however, a few reports that suggest the contrary (Dehne 1982). 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 healthy soils. However, uncolonized soybeans grown in infested soils suffered reduced growth (Zambolim & Schenck 1983). Mycorrhizal tobacco and alfalfa are reported to be resistant to a plethora of fungal pathogens like *Phytophthora megasperma*, *Pyrenochaeta terrestris*, *Fusarium oxysporum*, *Pythium ultimum* etc. (Kaye *et al.* 1984; Schenk 1981). Mycorrhizal tomato plants are found to be less susceptible to *Phytophthora* than non-mycorrhizal plants (Cordier *et al.* 1996; Trotta *et al.* 1996). It is believed that the amount of root tips influence the infecting ability of *Phytophthora* as the encystment of zoospores preferentially occurs behind the root tip. Mycorrhizal plants put out fewer roots and this allows them to tolerate pathogens better than non-mycorrhizal plants (Trotta *et al.* 1996). However, AM do not seem to afford tolerance against pathogens where host-pathogen interactions are vigorous (Bäath & Hayman 1984). Resistance to pathogens accorded by AM to host is not always the case. Plants that are benefited by AM colonization also seem susceptible to pathogen attack (Bäath & Hayman 1983). AM plants are subject to greater disease intensity when attacked by viruses. Viral multiplication and susceptibility of plants to viral attacks is higher in AM plants (Dehne 1982). Tomato plants inoculated with *Glomus* sp. and tobacco mosaic virus had more severe symptoms than non-mycorrhizal plants infected by the virus (Jabbaji-Hare & Stobbs 1984). Similar responses were found in mycorrhizal *Citrus* plants infected with citrus leaf rugose virus (Nemec & Myhre 1984). However, unlike other fungal endoparasites, AM play no role in transmitting viral infection between plants (Jabbaji-Hare & Stobbs 1984). The barter of substances between AM and the host cell is characterised by a high P metabolism and high concentrations of nucleic acids and proteins. The enhanced nucleic acid and protein production fosters viral multiplication leading to a better spread over the whole plant (Dehne 1982).

The impact of AM on pathogenic bacteria is not well documented. Mycorrhizal tomato plants infected with *Pseudomonas syringae* pv. *syringae* have been reported to be tolerant to the pathogen (Fitter & Garbaye 1994; Ravnskov *et al.* 1999). The growth of *P. flourescens* was found to be inhibited

by *Glomus intraradices* (Linderman 1994). AM seems to provide protection to host plants against root nematode attack. When nematode resistant and susceptible cultivars of cotton were inoculated with *Gigaspora margarita* and *Meloidogyne incognita*, the presence of the mycorrhizae countered the damage to the susceptible cultivar by the nematode (Hussey & Roncadori 1982). AM associations have been reported to have a suppressive effect on parasitic cyst and root nematodes. However, the nematodes also may retard the development of the fungal arbuscules and spores (Pinchot *et al.* 1996).

Several mechanisms have been proposed to explain the protection extended by AM 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). Unlike the ectomycorrhiza, antibiotic production has not been found in the AM. They afford protection or tolerance by different means. Increased root thickenings may act as deterrent. Chemical differences have been found between AM and non-AM plants. Amino acid content, particularly arginine has been found to be high in AM plants. Arginine and root extracts of mycorrhizal plants reduced chlamydospore production in *Thielaviopsis basicola*. AM 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. This very factor may also cause greater susceptibility of AM plants to diseases. As what is good for the endophyte is also good for the pathogen (Dehne 1982). Mycorrhizal fungi are believed to induce low activation of antimicrobial phenyl propanoid metabolism in roots. This accumulation of phenolics or their precursors protects the mycorrhizal plants from pathogens or prepares them to react faster by releasing defence phenolics (Morandi 1996). It has been reported that induced resistance of AM sweet orange to *Phytophthora* root-rot disease does not appear to operate unless a P nutritional advantage is conferred on the AM plant (Graham & Egel 1988). From the above discussion it is apparent that while AM may protect some plants against some pathogens, in others it may increase the severity of disease. The AM interaction with

the pathogen depends to a large extent on the host and the pathogen concerned (Bäath & Hayman 1983).

Toxic metals

The interaction between AM and heavy metals and the possible effect of these fungi in improving the tolerance of plants to toxicity has been the subject of several studies (Díaz *et al.* 1996). The importance of AM in alleviating heavy metal toxicity of plants varies from host to host. While in some plants protection by AM is apparent, in others enhanced metal uptake inhibits plant growth (Gadd 1993; Martino *et al.* 2000). The AM colonising the root cortex might absorb toxic metals from the plant tissues onto its own cells. In *Pteridium aquilinum*, AM hyphae colonising the root cortex contained higher amounts of metal than the host cytoplasm. Al, Cd, Fe, Ti were found concentrated in polyphosphate granules (Turnau *et al.* 1993). These authors suggested that the AM hyphae by sequestering the potentially toxic elements into the polyphosphate granules might be acting as metal filters in the plant. Metallothiones have been found in some AM species that chelated metals like Cd (Galli *et al.* 1994). Inoculation with AM fungi has been found to protect the plant from the toxicity of Pb and Zn, but the degree of protection varies depending on the plant fungus combination (Díaz *et al.* 1996). However, in areas with high metal concentrations, AM may inhibit plant growth by enhanced metal uptake from the soil (Galli *et al.* 1994).

Different strains of AM fungi have different sensitivity to metal toxicity. Therefore, the AM strain colonising a plant determines its ability to withstand toxicity (Díaz *et al.* 1996; Gildon & Tinker 1981). 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 adaptation of the AM involved to the presence of toxic metals (Nelson & Safir 1982). AM could play an important role in restoration of soils contaminated with heavy metals by affording protection to plants from them (Nelson & Safir 1982). However, one should not forget that presence of high concentration of heavy metals might affect the colonisation (Heggo *et al.* 1990; Kaomen *et al.* 1990).

Salinity

Plants growing in saline soils are subjected to two physiological stresses. Firstly, 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). AM have been shown by several workers to occur naturally in saline environments (Allen & Cumingham 1983; Ho 1987; Pond *et al.* 1984) despite the comparatively low mycorrhizal affinity of many halophytic plants (Brundett 1991). Kothamasi *et al.* (unpublished data) have found AM populations in mangroves of Tropical Great Nicobar island, India. AM have been shown to decrease yield losses of plants in saline soils (Pfeiffer & Bloss 1988; Pond *et al.* 1984; Poss *et al.* 1985). The protection offered could be due to the increased uptake of P that would offset the effects of salinity causing ions.

Herbivore grazing

Grazing by herbivores is a big drain on the energies of the plant. Defence against herbivores is a costly affair, reducing investment in plant growth and reproduction by 30-50% (Gates 1975). As both mycorrhizae and herbivores are dependent on the plant for carbohydrates they are bound to interact. Catherine & Witham (1994) reported that herbivore grazing reduced colonization by AM. This could affect the community structure. If herbivory reduces mycorrhizal colonization in a plant species, it might become a poor competitor and consequently decrease in abundance relative to species not affected. According to them, AM also seemed to affect the herbivores. AM plants influence the growth, mortality and fecundity of insects. Rabin and Pacovsky (1995) reported retarded larval growth and pupal development in fall army worm (*Spodoptera frugiperda*) and corn earthworm (*Heliothis zea*) larvae fed on mycorrhizal soybeans of both susceptible and resistant cultivars. AM fed larvae weighed 40% less, took longer to pupate and the average pupal weight was reduced by 17%. The mortality of *H. zea* increased by 15%. The causes could be the presence of a toxin, an antifeedant of plant or fungal origin or even altered nutrient status (Rabin & Pacovsky 1995). The exact mechanism needs to be investigated. Studies in this area

would yield valuable data. It would be interesting to see if AM also influence vertebrate herbivores.

AM and mycorrhizosphere

Rhizosphere is defined as the thin layer of soil adhering to a root system after shaking has removed the loose soil (Atlas & Bartha 1993). It differs from the surrounding soil in having a higher pH, lower water potential, lower partial pressure of oxygen, higher partial pressure of CO₂ and higher amounts of soluble carbohydrates. The high concentration of carbohydrates (root exudates) augments the microbial population per gram soil by 2-3 orders of magnitude in the rhizosphere than the surrounding soil (Garbaye 1991). It supports a variety of endophytes, exopathogens, parasitic pathogens mycorrhizal fungi and growth inhibiting deleterious rhizobacteria (Linderman 1988; Tawarayama *et al.* 1996).

Rhizosphere of mycorrhizal roots is referred to as mycorrhizosphere. AM use some of the root exudates and modify root functions. Microbial communities in the mycorrhizosphere differ from those in the rhizosphere community because of AM influences on the nature of root exudates (Kumar *et al.* 1999; Perry *et al.* 1989). AM hyphae cause the aggregation of the soil particles (Filion *et al.* 1999; Hooker & Black 1995; Linderman 1988), which increase the rate of movement of water and nitrates from the bulk soil to the root surface (George *et al.* 1995). Microbes flourish in these aggregates. The microflora in the mycorrhizosphere of the AM hyphae are selected over the soil microbes. These microbes influence the mycorrhizal uptake of water and nutrients. The microbial interactions in the mycorrhizosphere involve a number of bacteria and fungi that influence plant growth. These include the facultative anaerobes, extracellular chitinase producers, phosphate solubilizers, siderophore producers, antibiotic producers, pathogen suppressors, plant growth promoters, exopathogens and mycorrhizal suppressors. The hyphal strands extend the limits of the mycorrhizosphere beyond the boundaries of the non-mycorrhizal roots. The extraradical AM hyphae are nutritionally dependent on the host photosynthate, but their biomass is regulated by soil microbes and edaphic factors like pH, texture, fertility and pesticide content (Linderman 1988).

The water and nutrient uptake of the plant is governed to a large extent by the fungal symbionts. The symbionts themselves are in a close interaction with the microbes of the mycorrhizosphere (Hampp *et al.* 2000). To complete the circle, these microorganisms are in turn dependent on the host plant through its symbionts. A key factor that determines the survival of a plant in a nutrient deficient soil, is its ability to mobilise insoluble P by the release of alkaline phosphatases, mycorrhizal fungi are not necessarily more efficient than the root itself. Bacteria of the mycorrhizosphere play an important role in mobilising nutrients (Garbaye 1991; Linderman 1988). Some microbes are believed to actually establish a symbiotic association with the root, although the mechanisms involved have not been elucidated. Together with antagonists, these helpers contribute to the regulation of mycorrhizal development and thus to the adaptability of the plant. The relationship between plants and their soil involves a living interface, the mycorrhizosphere, which should be considered as an integral part of the root, determining most of its functions (Garbaye 1991).

The cost of AM

The benefits that accrue to the plant from mycorrhizal associations come with a price tag. It has been estimated that up to 10-20% of the total C fixed by the plant (Table 1) is used for maintaining the fungus (Fitter 1991; Marschner & Dell 1994; Smith & Read 1997 b). According to the resource allocation principle, the organism has a finite pool of resources and different end uses must compete for that pool (Read 1990). C used by the fungus, cannot be used for growth and reproduction of the host. This C loss must be offset by enhanced photosynthesis if mycorrhizal association has to be economical for the plant (Fitter 1991). The elevated uptake of nutrients like P by mycorrhizae can boost the rate of photosynthesis and thereby repay the C used by it (Sivak & Walker 1986; Smith & Read 1997 b). *Glomus intraradices* dramatically increased P uptake from soils in *Citrus* plants. Mycorrhizal *Citrus* grown in low P conditions showed higher photosynthetic rates than non-mycorrhizal plants grown in the same conditions (Eissenstat *et al.* 1993).

Table 1. Costs to plants of AM infection (Fitter 1991).

Biomass of mycorrhizal fungus	Up to 20% of root biomass: take 10% as typical figure
Cost of growth and maintenance of mycorrhizal fungus	1-10% of fungal biomass = 0.01-1.0% of root biomass
Root maintenance costs	ca 1.5% root biomass
Therefore cost of mycorrhizal fungus	≈ root maintenance cost

When limited nutrient availability retard photosynthesis and growth, the C cost of producing absorbing organs is high (Smith & Read 1997 b). The cost of constructing a unit length of fine root is proportional to volume and diameter (200 μm). In contrast, hyphal diameter (2-20 μm) is less by more than 2 orders of magnitude (Fitter 1997; Smith & Read 1997 b). Therefore, at least 100 times the length of hyphae can be constructed for a given investment of resources. The hyphae extend the zone that can be exploited for immobile nutrients (like P) by several mm. The gain extended to the plant is proportional to the root diameter. This determines the difference in cost between growing more roots to obtain nutrients or allocating the task to the fungal hyphae (Fitter 1997). However, when P is in plenty, absorption by the roots is efficient and maintaining mycorrhizae under such conditions is an unwarranted expense (Graham & Abbot 2000; Smith & Read 1997b).

Conclusions

The intimate relation that has existed between AM and plants since the Palaeozoic has led to interaction at the ecological, physiological and molecular levels. Around 95% of the modern day vascular plants are mycorrhizal, making this association of fundamental importance in all ecosystems. The fungi are involved in all survival requirements of the plants ranging from nutrient acquisition and defence against pathogens to competition with other plants. Their involvement bestows large selective advantages to the host and thus influences the composition of the plant community. Owing to their role, AM can be labelled as critical linkage species of a plant community.

Acknowledgements

The authors thank C.S.I.R. for the award of Senior Research Fellowship to David Kothamasi and Mr. Manoj Kumar for typing the manuscript.

References

- Abbot, L.K. & A.D. Robson. 1991. Factors influencing the occurrence of vesicular arbuscular mycorrhizae. *Agriculture, Ecosystem and Environment* **35**: 120-150.
- Allen, E.B. & M.C. Allen. 1984. Competition between plants of different successional stages; mycorrhizae as regulators. *Canadian Journal of Botany* **62**: 2625-2629.
- Allen, E.B. & G.L. Cumingham. 1983. Effects of vesicular arbuscular mycorrhizae on *Distichlis spicata* under three salinity levels. *New Phytologist* **93**: 227-236.
- Allen, M.F. 1982. Influence of vesicular arbuscular mycorrhizae on water movement through *Bouteloua gracilis* (HBK) Lag ex. Steud. *New Phytologist* **91**: 191-196.
- Atlas, R.M. & R. Bartha. 1993. Interactions between microorganisms and plants. pp. 69-102. *In: Microbial Ecology, Fundamentals and Applications*. III edition. The Benjamin/Cummings publishing Inc., USA.
- Augé, R.M., X. Duan, R.C. Ebel & A.J.W. Stodola. 1986a. Non hydraulic signaling of soil drying in mycorrhizal maize. *Planta* **193**: 74-82.
- Augé, R.M., K.A. Shekel & R.L. Wample. 1986b. Osmotic adjustment in leaves of VA mycorrhizal and non mycorrhizal rose plants in response to drought stress. *Plant Physiology* **82**: 765-770.
- Augé, R.M., X. Duan, R.C. Ebel & A.J.W. Stodola. 1994. Non hydraulic signalling of soil drying in mycorrhizal maize. *Planta* **193**: 74-82.
- Azcón, R. 1994. The role of arbuscular mycorrhizal fungi on nitrogen nutrition and metabolism by plants. *Mycorrhiza News* **6**: 1-5.
- Bäåth, E. & D.S. Hayman. 1983. Plant growth responses to vasicular arbuscular mycorrhiza. XIV. Interactions with *Verticillium* wilt on tomato plants. *New Phytologist* **95**: 419-426.
- Bäåth, E. & D.S. Hayman. 1984. No effect of VA mycorrhizae on red core diseases of strawberry. *Transactions of the British Mycological Society* **82**: 534-536.

- Barea, J.M. & C. Azcón-Aguilar. 1983. Mycorrhizae and their significance in nodulating nitrogen fixing plants. *Advances in Agronomy* **36**: 1-54.
- Bationo, A., S.P. Wani, C.L. Biielders, P.L.G. Vlek & A.U. Mokwanye. 2000. Crop residue and fertilizer management to improve soil organic carbon content, soil quality and productivity in the desert margins of West Africa. pp. 117-145. *In*: R. Lal, J.M. Kimble & B.A. Steward (eds.) *Advances in Soil Science. Global Climate Change and Tropical Ecosystems*. CRC Press, LLC Washington DC, USA.
- Bethlenfalway, G.J. 1992. Mycorrhizae and crop productivity. pp. 1-28. *In*: G.J. Bethlenfalway & R.G. Linderman (eds.) *Mycorrhizae in Sustainable Agriculture*. ASA special Publication, Madison WI.
- Bijbijen, J.N., S. Urquiaga, M. Ismaili, B.J.R. Alves & R.M. Boddey. 1996. Effect of arbuscular mycorrhizae on uptake of nitrogen by *Brachiaria arrecta* and *Sorghum vulgare* from soils labelled for several years with ¹⁵N. *New Phytologist* **133**: 487-494.
- Boddington, C.L. & J.C. Dodd. 1999. Evidence that differences in phosphate metabolism in mycorrhizae formed by species of *Glomus* and *Gigaspora* might be related to their life cycle strategies. *New Phytologist* **142**: 531-538.
- Brundett, M. 1991. Mycorrhizae in natural ecosystems. *Advances in Ecological Research* **21**: 171-313.
- Bürkert, B. & A.D. Robson. 1994. ⁶⁵Zn uptake in subterranean clover (*Trifolium subterraneum* L.) by three vesicular-arbuscular mycorrhizal fungi in a root-free sandy soil. *Soil Biology and Biochemistry* **26**: 1117-1124.
- Catherine, A.G. & T.G. Witham. 1994. Interactions between above ground herbivores and the mycorrhizal mutualists of plants. *Trends in Ecology and Evolution* **9**:251-255.
- Cordier, C., S. Gianinazzi & V. Gininazzi-Pearson. 1996. Colonisation patterns of root tissues by *Phytophthora nicotianae* var. *parasitica* related to disease in mycorrhizal tomato. *Plant and Soil* **185**: 223-232.
- Cui, M. & M.M. Caldwell. 1996a. Facilitation of plant phosphate acquisition by arbuscular mycorrhizae from enriched to soil patches. I. Roots and hyphae exploiting the same volume. *New Phytologist* **133**: 453-460.
- Cui, M. & M.M. Caldwell. 1996b. Facilitation of plant phosphate acquisition by arbuscular mycorrhizae from enriched soil patches. II. Hyphae exploiting root-free soil. *New Phytologist* **133**: 461-467.
- Davies, W.J. & J. Zhang. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology* **42**: 55-76.
- Dehne, H.W. 1982. Interaction between vesicular mycorrhizal fungi and plant pathogens. *Phytopathology* **72**: 1115-1119.
- DeMars, B.G. & R.E.J. Boerner. 1995a. Arbuscular mycorrhizal development in three crucifers. *Mycorrhiza* **5**: 405-408.
- DeMars, B.G. & R.E.J. Boerner. 1995b. Mycorrhizal status of *Deschampsia antarctica* in the Palmer station area, Antarctica. *Mycologia* **87**: 451-453.
- Díaz, G., C. Azcón-Aguilar & M. Honrubia. 1996. Influence of vesicular arbuscular mycorrhizae on heavy metal (Zn and Pb) uptake on growth of *Lygeum spartum* and *Anthyllis cystisoides*. *Plant and Soil* **180**: 241-249.
- Dodd, J.C., C.C. Burton, R.G. Burns & P. Jeffries. 1987. Phosphate activity associated with the roots and rhizosphere of plants infected with vesicular arbuscular mycorrhizal fungi. *New Phytologist* **107**:163-172.
- Ebel, R.C., A.J.W. Stodola, X. Duan & R.M. Augé. 1994. Non hydraulic root-to-shoot signalling in mycorrhizal and non mycorrhizal sorghum exposed to partial soil drying or root severing. *New Phytologist* **127**: 495-505.
- Eissenstat, D.M., J.H. Graham, J.P. Syvertsen & D.L. Drouillard. 1993. Carbon economy of sour orange in relation to mycorrhizal colonisation and phosphorous status. *Annals of Botany* **71**: 1-10.
- Epstein, E. 1972. *Mineral Nutrition of Plants, Principles and Perspectives*. Wiley, New York.
- Facelli, E., J.M. Facelli, S.E. Smith & M.J. McLaughlin. 1999. Interactive effects of arbuscular mycorrhizal symbiosis, intraspecific competition and resource availability on *Trifolium subterraneum* cv. Mt. Barker. *New Phytologist* **141**: 535-547.
- Faure, S., J.B. Cliuquet, G. Thephary & J. Boucaud. 1998. Nitrogen assimilation in *Lolium perenne* colonized by the arbuscular mycorrhizal fungus *Glomus fasciculatum*. *New Phytologist* **138**: 411-417.
- Filion, M., M. St. Arnaud & J.A. Fortin. 1999. Direct interaction between the arbuscular mycorrhizal fungus *Glomus intraradices* and different rhizosphere microorganisms. *New Phytologist* **141**: 525-533.
- Fitter, A. 1997. Nutrient acquisition. pp. 51-72. *In*: M.J. Crawley (ed.) *Plant Ecology*. II Edition. Blackwell Science, London.
- Fitter, A.H. & J. Garbaye. 1994. Interaction between mycorrhizal fungi and other soil organisms. *Plant and Soil* **159**: 11-25.
- Fitter, A.H., J.D. Graves, N.K. Watkins, D. Robinson & C. Scrimgeour. 1998. Carbon transfer between

- plants and its control in networks of arbuscular mycorrhizas. *Functional Ecology* **12**: 406-412.
- Fitter, A.H. 1977. Influence of mycorrhizal infection on competition for phosphorous and potassium by two grasses. *New Phytologist* **79**: 119-125.
- Fitter, A.H. 1991. Costs and benefits of mycorrhizae: implications for functioning under natural conditions. *Experientia* **47**: 350-355.
- Francis, R. & D.J. Read. 1994. The contributions of mycorrhizal fungi to the determination of plant community structure. *Plant and Soil* **159**: 11-25.
- Frey, B. & H. Schüepp. 1993. A role of vesicular arbuscular (VA) mycorrhizal fungi in facilitating inter-plant N transfer. *Soil Biology and Biochemistry* **25**: 651-658.
- Gadd, G.M. 1993. Interactions of fungi with toxic metals. *New Phytologist* **124**: 25-60.
- Galli, U., H. Schüepp & C. Brunold. 1994. Heavy metal binding by mycorrhizal fungi. *Physiologia Plantarum* **92**: 364-368.
- Gange, A.C., V.K. Brown & L.M. Farmer. 1990. A test of mycorrhizal benefit in early successional plant community. *New Phytologist* **15**: 85-91.
- Garbaye, J. 1991. Biological interactions in the mycorrhizosphere. *Experientia* **47**: 370-375.
- Gardes, M. & A. Dahlberg. 1996. Mycorrhizal diversity in arctic and alpine tundra: an open question. *New Phytologist* **133**: 147-157.
- Gates, R.G. 1975. The interface between slugs and wild ginger: some evolutionary aspects. *Ecology* **56**: 391-400.
- George, E., H. Marschner & I. Jakobsen. 1995. Role for arbuscular mycorrhizal fungi in uptake of phosphorous and nitrogen from soil. *Critical Reviews in Biotechnology* **15**: 257-270.
- Gildon, A. & P.B. Tinker. 1981. A heavy metal tolerant strain of a mycorrhizal fungus. *Transactions of the British Mycological Society* **77**: 648-649.
- Glenn, M.G., F.S. Chew & P.H. Williams. 1985. Hyphal penetration of *Brassica* (Cruciferae) roots by a vesicular arbuscular mycorrhizal fungus. *New Phytologist* **99**: 463-472.
- Goicoechea, N., M.C. Antolin & M. Sanchez-diaz. 2000. The role of plant size and nutrient concentrations in associations between *Medicago*, and *Rhizobium* and/or *Glomus*. *Biologia Plantarum* **43**: 221-226.
- Graham, J.H. & L.K. Abbot. 2000. Wheat responses to aggressive and non-aggressive arbuscular mycorrhizal fungi. *Plant and Soil* **220**: 207-218.
- Graham, J.H. & D.S. Egel. 1988. *Phytophthora* root rot development on mycorrhizal and phosphorus fertilized non mycorrhizal *Citrus* under drought stress. *New Phytologist* **105**: 411-419.
- Graham, J.H., J.P. Syvertsen & M.L. Smith, Jr. 1971. Water relations of mycorrhizal and P-fertilized non mycorrhizal *Citrus* under drought stress. *New Phytologist* **15**: 411-419.
- Grime, J.P., M.L. Mackey, S.H. Hillier & D.J. Read. 1987. Floristic diversity in a model system using experimental microcosms. *Nature* **328**: 420-422.
- Hampp, R., U. Nehls & T. Wallenda. 2000. Physiology of mycorrhiza. pp. 223-254. In: K. Esser, J.W. Kadereit, U. Lüttge & M. Runge (eds.) *Progress in Botany. Vol 61. Genetics, Physiology, Systematics, Ecology*. Springer-Verlag, Berlin.
- Hartung, W. & S. Slovik. 1991. Physicochemical properties of plant growth regulators and plant tissues determine their distribution and redistribution: stomatal regulation by abscisic acid in leaves. *New Phytologist* **119**: 361-382.
- Haystead, A., N. Malajcuk & T.S. Grove. 1988. Underground transfer to nitrogen between pasture plants infected with vesicular arbuscular mycorrhizal fungi. *New Phytologist* **108**: 417-423.
- Heggo, A., J.S. Angle & R.L. Chaney. 1990. Effect of vesicular arbuscular mycorrhizal fungi on heavy metal uptake by Soybeans. *Soil Biology and Biochemistry* **22**: 865-869.
- Helgason, T., T.J. Daniell, R. Husband, A.H. Fitter & J.P.W. Young. 1998. Ploughing up the wood-wide web. *Nature* **394**: 431.
- Ho, I. 1987. Vesicular arbuscular mycorrhizae of halophytic grasses in Alvard desert of Oregon. *Northwest Science* **61**: 148-151.
- Hodge, A., D. Robinson & A.H. Fitter. 2000. An arbuscular mycorrhizal inoculum enhances root proliferation in, but not nitrogen capture from nutrient rich patches in soil. *New Phytologist* **145**: 575-584.
- Hooker, J.E. & K.E. Black. 1995. Arbuscular mycorrhizal fungi as a components of sustainable soil plant systems. *Critical Reviews in Biotechnology* **15**: 201-212.
- Hussey, R.S. & R.W. Roncadori. 1982. Vesicular arbuscular mycorrhizae may limit nematode activity and improve plant growth. *Plant Disease* **66**: 9-14.
- Jabbaji-Hare, S.H. & L.W. Stobbs. 1984. Electron microscopic examination of tomato roots coinfecting with *Glomus* sp. and tobacco mosaic virus. *Phytopathology* **74**: 277-279.
- Janardhanan, K.K., F. Abdul-Khaliq Naushin & K. Ramaswamy. 1994. Vesicular arbuscular mycorrhiza in an alkaline usar land ecosystem. *Current Science* **67**: 465-469.

- Johansen, A., R.D. Finaly & P.A. Olsson. 1996. Nitrogen metabolism of external hyphae of the arbuscular mycorrhizal fungus *Glomus intraradices*. *New Phytologist* **133**: 705-712.
- Kaomen, I., S.P. McGrath & K.E. Giller. 1990. Mycorrhizal infection of clover is delayed in soils contaminated with heavy metals from past sewage sludge applications. *Soil Biology and Biochemistry* **22**: 871-873.
- Kaye, J.W. F.L. Pflieger & E.L. Stewart. 1984. Interactions of *Glomus fasciculatum* and *Pythium ultimum* on green house grown Poinsettia. *Canadian Journal of Botany* **62**: 1575-1579.
- Kumar, A., Nivedita & R.S. Upadhyaya. 1999. VA mycorrhizae and revegetation of coal mine spoils: a review. *Tropical Ecology* **40**: 1-10.
- Linderman, R.G. 1988. Mycorrhizal interactions with the rhizosphere microflora. The mycorrhizosphere effect. *Phytopathology* **78**: 366-371.
- Linderman, R.G. 1994. Role of VAM in biocontrol. pp. 1-25. *In*: F.L. Pflieger & R.G. Linderman (eds.) *Mycorrhizae and Plant Health*. APS Press.
- Lovera, M. & G. Cuenca. 1996. Arbuscular mycorrhizal infection in Cyperaceae and Graminae from natural, disturbed and restored savannas in La Gran Sabana, Venezuela. *Mycorrhiza* **6**: 11-118.
- Mädler, P., H. Vierheilig, T. Boller, B. Streitwolf-Engel, Frey, P. Christie & A. Wiemken. 2000. Transport of ¹⁵N from a soil compartment separated by a polytetrafluoroethylene membrane to plant roots via the hyphae of arbuscular mycorrhizal fungi. *New Phytologist* **146**: 155-161.
- Malloch, D.W., K.A. Pirozynsky & P.H. Raven. 1980. Ecological and evolutionary significance of mycorrhizal symbiosis in vascular plants. *Proceedings of the National Academy of Sciences USA* **77**: 2113-2118.
- Marschner, H. & B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil* **159**: 89-102.
- Martino, E., K. Turnau, M. Girlanda, P. Bonfante & S. Perotto. 2000. Ericoid mycorrhizal fungi from heavy metal polluted soils, their identification and growth in the presence of Zinc ions. *Mycologia Research* **104**: 338-344.
- Merryweather, J. & A. Fitter. 1995a. Phosphorus and carbon budgets mycorrhizal contributions in *Hyacinthoides non-scripta* (L.) Chourad ex Rothm. under natural conditions. *New Phytologist* **129**: 619-627.
- Merryweather, J. & A. Fitter. 1995b. Arbuscular mycorrhiza and phosphorus as controlling factors in the life-history of *Hyacinthoides non-scripta* (L.) Chourad ex Rothm. *New Phytologist* **129**: 629-636.
- Merryweather, J. & A. Fitter. 1996. Phosphorus nutrition of an obligately mycorrhizal plant treated with fungicide benomyl in the field. *New Phytologist* **132**: 307-311.
- Miller, R.M. & J.D. Jastrow. 1994. Vesicular arbuscular mycorrhizae and biogeochemical cycling. pp. 189-212. *In*: F.L. Pflieger & R.G. Linderman (eds.) *Mycorrhizae and Plant Health*. APS Press.
- Morandi, D. 1996. Occurrence of phytoalexins and phenolic compounds in endomycorrhizal interactions and their potential role in biological control. *Plant and Soil* **85**: 241-251.
- Morton, J.B. & S.P. Bentivenga. 1994. Levels of diversity in endomycorrhizal fungi (Glomales, Zygomycetes) and their role in defining taxonomic and non taxonomic groups. *Plant and Soil* **159**: 47-59.
- Myrold, D.D. 2000. Microorganisms. pp. 409. *In*: D.E. Alexander & R.W. Fairbridge (eds.) *Encyclopedia of Environmental Science*. Kluwer Academic Publishers, The Netherlands.
- Nemec, S. & D. Myhre. 1984. Virus- *glomus etunicatum* interactions in citrus root stocks. *Plant Disease* **68**: 311-314.
- Nelson, C.E. & G.R. Safir. 1982. Increased drought tolerance of mycorrhizal onion plants caused by improved phosphorus nutrition. *Planta* **154**: 407-413.
- Newman, E.I. 1988. Mycorrhizal links between plants: their functioning and ecological significance. *Advances in Ecological Research* **18**: 243-270.
- Newman, E.I., C.L.N. Devoy, N.J. Easen & K.J. Fowles. 1994. Plant species that can be linked by VA mycorrhizal fungi. *New Phytologist* **126**: 115-121.
- Olesniewicz, K.S. & R.B. Thomas. 1999. Effects of mycorrhizal colonization on biomass production and nitrogen fixation of black locust (*Roina pseudoacacia*) seedlings grown under elevated atmospheric carbon dioxide. *New Phytologist* **142**: 133-140.
- Pankow, W., T. Boller & A. Wiemken. 1991. The significance of mycorrhizas for protective ecosystems. *Experientia* **47**: 391-394.
- Perry, D.A., M.P. Amaranthus, J.G. Borchers, S.L. Borchers & R.E. Brainerd. 1989. Bootstrapping in ecosystems. *Bioscience* **39**: 230-237.
- Pfeiffer, C.M. & H.E. Bloss. 1988. Growth and nutrition of guayule (*Parthenium argentum*) in a saline soil as influenced by vesicular arbuscular mycorrhiza and phosphorus fertilization. *New Phytologist* **91**: 211-220.
- Phipps, C.J. & T.N. Taylor. 1996. Mixed arbuscular mycorrhizae from the triassic of Antarctica. *Mycologia* **88**: 707-714.

- Pierzynski, G.M., J.T. Sims & G.F. Vance. 2000. *Soils and Environmental Quality*. II Edition. CRC Press. Washington DC. USA.
- Pinochet, J., C. Calvet, R.A. Camprub & C. Fernandez. 1996. Interactions between migrating endoparasitic nematodes and arbuscular mycorrhizal fungi in perennial crops - a review. *Plant and Soil* **185**: 183-190.
- Pond, E.C., J.A. Menge & W.M. Jarrell. 1984. Improved growth of tomato in salinized soil by vesicular arbuscular mycorrhizal fungi collected from saline soils. *Mycologia* **76**: 74-84.
- Poss, J.A., E.C. Pond, J.A. Menge & W.M. Jarrell. 1985. Effect of salinity on mycorrhizal onion and tomato in soil with and without additional phosphate. *Plant and Soil* **88**: 307-319.
- Powell, C.L. 1975. Rushes and sedges are non mycotrophic. *Plant and Soil* **42**: 481-484.
- Rabin, L.B. & R.S. Pacovsky. 1995. Reduced larval growth of two Lepidoptera (Nocturidae) on excised leaves of soybean infected with a mycorrhizal fungus. *Journal of Economic Entomology* **78**: 1358-1363.
- Ravnskov, S., O. Nybroe & I. Jakobsen. 1999. Influence of an arbuscular mycorrhizal fungus on *Pseudomonas fluorescens*, F 57 in rhizosphere and hyphosphere soil. *New Phytologist* **142**: 113-122.
- Read, D.J. 1990. Mycorrhizas in ecosystems- Natures response to the law of minimum. pp. 101-130. In: D.L. Hawksworth (ed.) *Frontiers in Mycology*. Fourth International Mycological Congress, Regensburg. CAB International.
- Roldan-Fajardo, B.E. 1994. Effect of indigenous arbuscular mycorrhizal endophytes on the development of six wild plants colonizing a semi-arid area in south east Spain. *New Phytologist* **127**: 115-121.
- Safir, G.R., J.S. Boyer & J.W. Gerdemann. 1972. Nutrient studies and mycorrhizal enhancement of water transport in soybeans. *Plant Physiology* **49**: 700-703.
- Schenk, N.C. 1981. Can mycorrhizae control root diseases. *Plant Disease* **65**: 230-234.
- Sen, R. 2000. Budgeting for the wood-wide web. *New Phytologist* **145**: 161-165.
- Simon, L. 1996. Phylogeny of the Glomales: Deciphering the past to understand the present. *New Phytologist* **133**: 95-101.
- Simon, L., J. Bonsquet, R.C. Levesque & M. Lalonde. 1993. Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature* **363**: 67-69.
- Sivak, M.N. & D.A. Walker. 1986. Photosynthesis *in vivo* can be limited by phosphate supply. *New Phytologist* **102**: 499-512.
- Smith, S.E., V. Gianinazzi-Pearson, R. Koide & G. Cairney. 1994. Nutrient transport in mycorrhizas: structure, physiology and consequences for efficiency of the symbiosis. *Plant and Soil* **159**: 103-113.
- Smith, S.E. & D.J. Read. 1997a. Growth and carbon economy of VA mycorrhizal plants. pp. 105-125. In: *Mycorrhizal Symbiosis*. II Edition. Academic Press, London.
- Smith, S.E. & D.J. Read. 1997b. The role of mycorrhizas in ecosystems. pp. 409-452. In: *Mycorrhizal Symbiosis*. II Edition. Academic Press. London.
- St. John, T.V. & D.C. Coleman. 1983. The role of mycorrhizae in plant ecology. *Canadian Journal of Botany* **61**: 1005-1013.
- Tawarayama, K., S. Watanabe, E. Yoshida & T. Wagaatsuma. 1996. Effect of onion (*Allium cepa*) root exudates on the hyphal growth of *Gigaspora margarita*. *Mycorrhiza* **6**: 57-59.
- Taylor, T.N. 1990. Fungal associations in terrestrial paleoecosystems. *Trends in Ecology and Evolution* **5**: 21-25.
- Tester, M., S.E. Smith & F.A. Smith. 1987. The phenomenon of "nonmycorrhizal" plants. *Canadian Journal of Botany* **65**: 419-431.
- Tobar, R., R. Azcon & J.M. Barea. 1994. Improved nitrogen uptake and transport from ¹⁵N-labelled nitrate by external hyphae of arbuscular mycorrhiza under water-stressed conditions. *New Phytologist* **126**: 119-122.
- Torrisi, V., G.S. Pattinson & P.A. McGee. 1999. Localized elongation of roots of cotton follows establishment of arbuscular mycorrhizas. *New Phytologist* **142**: 103-112.
- Trotta, A., G.C. Varese, E. Gnani, A. Fusconi, S. Sampb & G. Berta. 1996. Interactions between the soil borne root pathogen *Phytophthora nicotianae* var. *parasitica* and the arbuscular mycorrhizal fungus *Glomus mossae* in tomato plants. *Plant and Soil* **185**: 199-209.
- Turnau, K., I. Kottke & F. Oberwinkler. 1993. Elemental localization in mycorrhizal roots of *Pteridium aquilinum* (L.) Kuhn. collected from experimental plots treated with Cd dust. *New Phytologist* **123**: 313-324.
- Vierheilig, H., R. Bennett, G. Kiddle, M. Kaldorf & J. Ludwig-Müller. 2000. Differences in glucosinolate

- patterns and arbuscular mycorrhizal status of glucosinolate containing species. *New Phytologist* **146**: 343-352.
- Zambolim, L. & N.C. Schenck. 1983. Reduction of the effects of pathogenic root infecting fungi on soybean by mycorrhizal fungus *Glomus mossae*. *Phytopathology* **73**: 1402-1405.
- Zhu, W. & J.G. Ehrenfeld. 1996. The effects of mycorrhizal roots on litter decomposition, soil biota and nutrients in a spodosolic soil. *Plant and Soil* **179**: 109-118.