

Review

The vesicular-arbuscular mycorrhizal symbiosis

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Vesicular-arbuscular mycorrhiza fungi are associated with the majority of the terrestrial plants. Their function ranges from stress alleviation to bioremediation in soils polluted with heavy metals. However, our knowledge about this symbiosis is still limited. For the semi-arid tropics, where some African countries are located, there is a great possibility of using mycorrhizas as a biological tool for sustainable agriculture. This review gives an overview on the mycorrhizal benefits and recommends some management practices for the semi-arid Africa conditions.

Key words: Arbuscular mycorrhizal fungi, endomycorrhizas, soil fungi, symbiosis, vesicular arbuscular mycorrhiza.

INTRODUCTION

Mycorrhiza is the mutualistic symbiosis (non-pathogenic association) between soil-borne fungi with the roots of higher plants (Sieverding, 1991). Two types of mycorrhiza are known today: ecto- and endomycorrhizas. The ectomycorrhizas are characterized by an extracellular fungal growth in the root cortex. They are more common in temperate and boreal forest trees and number over 5000 species mainly within the Basidiomycetes (Sieverding, 1991). Some tropical trees such as pine and eucalyptus plants, however, have also been found to form ectomycorrhizal associations. The endomycorrhizas are characterized by inter- and intracellular fungal growth in root cortex, forming specific fungal structures, referred to as vesicles and arbuscles. This characteristic growth gives the endomycorrhiza the alternate name, vesicular arbuscular mycorrhiza. It is the most widely distributed association in plants. About 80% of all terrestrial plant species form this type of symbiosis (Smith and Read, 1997) and 95% of the world's present species of vascular plants belong to families that are characteristically mycorrhizal (Quilambo, 2000).

The arbuscular mycorrhizal fungi (AMF) belong to taxonomic order called Glomales, which currently

comprises 6 genera (Figure 1). Because they are the most common underground symbiosis and have important agricultural applications this review will focus on the vesicular-arbuscular mycorrhiza.

The vesicular-arbuscular mycorrhizas (VAM)

Kilronomos and Kendrick's statement (1993) that "we may know less that we think about mycorrhizas, since we have consistently based broad hypotheses and conclusions on studies of a small number of taxa" emphasizes the great diversity of VAM. They are found in a wide range of habitats usually in the roots of angiosperms, gymnosperms and pteridophytes. They also occur in the gametophytes of some mosses, lycopods and Psilotales which are all rootless (Mosse et al., 1981; Pocock and Duckett, 1985). Recently, they were also found in aquatic plants (Beck-Nielsen and Madsen, 2001).

There are plants, however, that have been shown to be mycorrhiza free, such as Proteaceae (Nicholson, 1967; Brundrett et al., 1996), Cruciferae, Zygophyllaceae

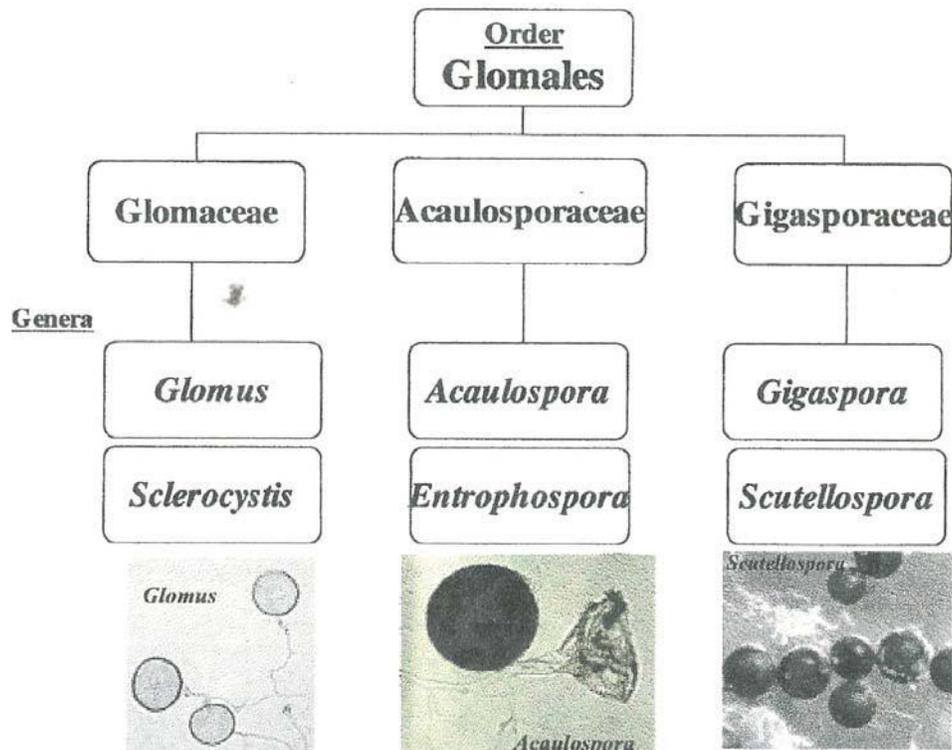


Figure 1. The current taxonomy of AMF with examples of the large spores produced by different genera in soil. From Dodd (2000).

(Varma 1998) Dipterocarpaceae, Betulaceae, Myrtaceae and Fagaceae (Nicholson, 1967). Although Cactaceae, Chenopodiaceae, Cyperaceae, Amarantaceae and Juncaceae were thought to be mycorrhiza free , most of the species were found to be infected under natural stressed rangeland conditions (Neeraj et al., 1991). The reason why some plants do not form mycorrhizas is not fully known, but it may be related to the presence of fungitoxic compounds in root cortical tissue or in root exudates. It may also be due to interactions between the fungus and the plant at the cell wall and (or) middle lamella level (Tester et al., 1987). High concentrations of salicylic acid have been found to reduce mycorrhization (Medina et al., 2003), meaning that plants with a genetic basis for high salicylic acid content have evolved to be mycorrhiza free.

Despite the great diversity of African plants few have been described in relation to their mycorrhizal associations. Because VAM ameliorate and increase tolerance to adverse soil conditions, influence response to severe climatic conditions and have compatibility with different hosts, they increase plant productivity and are important for natural and managed ecosystems (Brundrett et al., 1996). Recent evidence by Koide and Dickie (2002) has shown that AMF increase reproduction (via both male and female functions) and offspring survival.

While evidence of mycorrhizal benefit from “pot trials” has become steadily more convincing, evidence from

parallel field experiments is remarkable for its inconsistent results (Fitter, 1985). In some field studies, mycorrhizal infection has been shown to increase plant growth and survival, but there are many accounts of null or even negative effects (McGonigle and Fitter, 1988).

Despite these data, the functioning of arbuscular mycorrhiza in the field, in particular at ecosystem level, is attracting increasing attention (Allen, 1991; Brundrett, 1991). Benefits from AMF seem to be confined to particular growth periods (Johnson et al., 1997), namely the seedling stage (Gange et al., 1990, 1993) and during reproduction (Koide et al., 1994; Wilson and Hartnett, 1998).

The presence of mycorrhizas in aquatic plants was firstly reported by Sondergaard and Lindegaard (1977). Since then mycorrhiza have been found in aquatic macrophytes colonizing lakes and streams (Beck-Nielsen and Madsen, 2001). In submerged African plants AMF colonization has not been convincingly demonstrated. At the Ganges river, mangroves and plants known as non-mycotrophic under natural conditions, were found to be mycorrhizal (Sengupta and Chaudhuri, 2002).

The presence of AMF in freshwater wetlands (Miller, 2000), indicates that the biology and ecology of this association deserves further research, especially with respect to the role of fungi in plant nutrition and tolerance of habitat conditions. Stevens et al. (2002) supported the hypothesis that in inundated conditions, AMF had little

effect on plant response to P supply. They suggested that AMF association may be uncoupled at relatively high levels of P supply.

VAM AND SOIL FERTILITY

Three main components are involved in VAM association: 1) the soil, 2) the fungus and 3) the plant (Figure 2). The fungal component involves, the fungal structure within the cell of the root and the extraradical mycelium in the soil. The last may be quite extensive

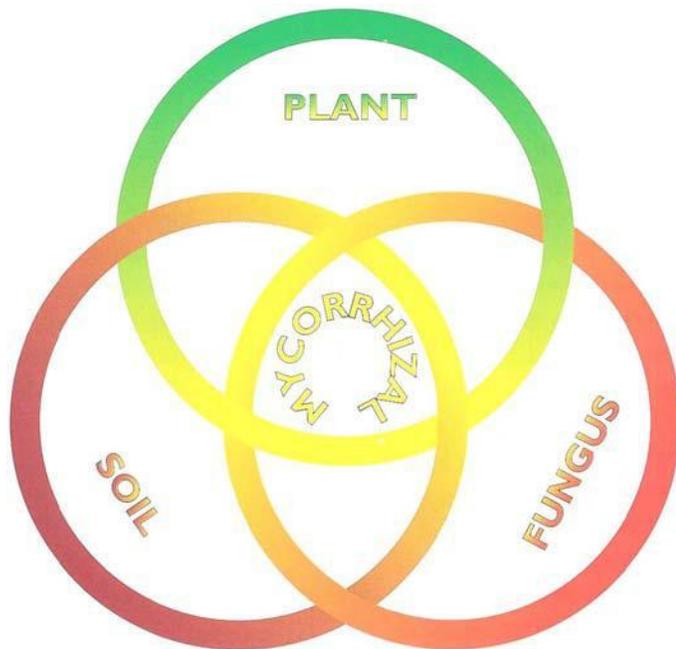


Figure 2. Mycorrhizal association, showing the interactions between fungus, plant and soil. From Brundrett et al. (1996).

Table 1. Effects of VAM in nutrient's absorption.

Nutrient	References
Phosphorus	Harley and Smith (1983), Al-Karaki and Al-Radad (1997), Chandreshekara et al. (1995)
Nitrogen	
Potassium	Liu et al. (2002)
Magnesium	Liu et al. (2002)
Copper	Gildon and Tinker (1983), Li et al. (1991)
Zinc	Faber et al. (1990), Gildon and Tinker (1983), Chen et al. (2003), Jamal et al. (2002)
Calcium	Liu et al. (2002)
Iron	Caris et al. (1998)
Cadmium	Guo et al. (1996) Gonzalez et al. (2002)
Nickel	Jamal et al. (2002), Guo et al. (1996)
Uranium	Rufyikiri et al. (2002)

under some conditions, but does not form any vegetative structures (Smith and Read, 1997). Its primary function is the absorption of resources from the soil. The increased efficiency of mycorrhizal roots versus nonmycorrhizal roots is caused by the active uptake and transport of nutrients by mycorrhizae. Mycorrhizae are described as improving the absorption of several nutrients as indicated in (Table 1).

Inoculation with *Glomus mosseae* not only affected plant growth and nutrition in *Medicago sativa*, but also enhanced the activity of *Rhizobium meliloti* when it was applied as an inoculant (Azcón-Aguilar et al., 1979).

AMF have been shown to improve productivity in soils of low fertility (Jeffries, 1987) and are particularly important for increasing the uptake of slowly diffusing ions such as PO_4^{3-} (Jacobsen et al., 1992), immobile nutrients such as P, Zn and Cu (Lambert et al., 1979; George et al., 1994; George et al., 1996; Ortas et al., 1996; Liu et al., 2002) and other nutrients such as Cadmium (Guo et al., 1996). Under drought conditions the uptake of highly mobile nutrients such as NO_3^- can also be enhanced by mycorrhizal associations (Ázcón et al., 1996; Subramanian and Charest, 1999).

In legume plants the importance of AMF symbiosis has been attributed to high P requirements on the nodulation and N_2 fixation process which requires enhanced P uptake (Barea and Ázcón-Aguilar, 1983). Improved P nutrition has been shown to increase in infertile and P-fixing soils of the tropics (Dodd, 2000).

Mycorrhizal fungi can also improve absorption of N from NH_4^+ -N mineral fertilizers, transporting it to the host plant (Ames et al., 1983; Johansen et al., 1993). Its transport and absorption can also increase biomass production in soils with low potassium, Calcium and Magnesium (Liu et al., 2002).

EFFECTS OF VAM ON DROUGHT AND SALINITY STRESS

Drought stress is a major agricultural constraint in the semi-arid tropics. It is known to have a considerable negative impact on nodule function (Sprent, 1971). Drought inhibits photosynthesis and disturbs the delicate mechanism of oxygen control in nodules. The latter is essential for active nitrogen fixation (Goicoechea et al., 1995).

AMF symbiosis can protect host plants against detrimental effects caused by drought stress (Ruiz-Lozano et al., 1999; Sanchez-Diaz and Honrubia, 1994). Quilambo (2000) reported that inoculation with an indigenous inoculant resulted in increased leaf and root growth and prevented the expected increase in root to shoot ratio and root-weight ratio that are normally observed under phosphorus deficient and drought stress conditions in peanut. In watermelon (*Citrullus lunatus* Thunb.) mycorrhizal colonization was found to improve

not only the plant yield and water use efficiency, but also the quality of the fruit (Kaya et al., 2003).

Several mechanisms have been proposed to explain the protection of AMF symbiosis, such as changes in plant hormones (Allen et al., 1982; Barea and Azcón-Aguilar, 1982; Danneberg et al., 1992; Goicoechea et al., 1995), increased leaf gas exchange and photosynthetic rate (Ruiz-Lozano et al., 1996a); direct hyphal water uptake from the soil and transfer to the host plant (Hardie, 1985; Faber et al., 1991; Ruiz-Lozano and Azcón, 1995), enhanced activity of enzymes involved in anti-oxidant defence (Ruiz-Lozano et al., 1996b), nitrate assimilation (Ruiz-Lozano and Azcón, 1996), enhanced water uptake through improved hydraulic conductivity and increasing leaf conductance and photosynthetic activity (Koide, 1985; Dell-Amico et al., 2002), osmotic adjustment (Augé et al., 1986) and changes in cell-wall elasticity (Augé et al., 1987; Sanchez-Diaz and Honrubia, 1994).

Often mycorrhizal improvement of drought tolerance occurs via drought avoidance. It can be a function of the often observed improved acquisition of phosphorus, nitrogen and other growth promoting nutrients by AMF plants (Augé et al., 2001).

According to Fitter (1988) the influence of AMF on water uptake and transport may be a secondary consequence of enhanced host phosphorus nutrition, although these effects are not consistent (Davies et al., 2002).

AMF can also reduce the impact of environmental stresses such as salinity (Ruiz-Lozano et al., 1996a). In *Azadirachta indica* with increased salinity level, there was a decrease in percent of root infection by AMF (Pande and Tarafadar, 2002).

VAM FUNGI, POLLUTANTS, HERBICIDES AND PESTICIDES

Work with AMF strains tolerant to heavy-metal has provided evidence for their rapid adaptation to contaminated soils. Joner and Leyval (1997) found that cadmium-tolerant *Glomus mosseae* isolates AMF were responsible for uptake, transport and immobilization of cadmium. Copper (Cu) was absorbed and accumulated in the extraradical mycelium of three AMF isolates, as observed in a study with *Glomus spp.* (Gonzalez-Chávez et al., 2002). Other references indicated resistance of arbuscular mycorrhizal fungi to aluminium. Soil aluminum normally causes significant reduction in tissue Calcium and Magnesium concentrations (Cumming and Ning, 2003).

Glomus caledonicum seems to be a promising mycorrhizal fungus for bioremediation of heavy metal contaminated soil (Liao et al., 2003). Ruffykiri et al. (2002) found that AM fungus could uptake and translocate uranium towards the roots. At varying zinc levels, mycorrhizal colonization increases zinc absorption and

accumulation in the roots. This may help to explain the alleviation of zinc toxicity at high concentrations (Chen et al., 2003). Mycorrhizae were found to ameliorate the toxicity of trace metals in polluted soils growing in soybean and lentil plants (Jamal et al., 2002).

In *Cynara cardunculus* mycorrhiza survived to pesticide employed in commercial nursery and enhanced wild carroon plant productivity (Marin et al., 2002). Mycorrhizal colonization, however, was reduced in field plots through applications of the fungicide benomyl as a soil drench (O'Connor et al., 2002).

Restoration of degraded areas using VAM fungi

The soils of disturbed sites are frequently low in available nutrients and lack the nitrogen-fixing bacteria and mycorrhizal fungi usually associated with root rhizospheres (Cooke and Lefor, 1990). As such, land restoration in semi-arid areas faces a number of constraints related to soil degradation and water shortage (Whisenant, 1999; Valejo et al., 2002a, b). As mycorrhizae may enhance the ability of the plant to cope with water stress situations associated to nutrient deficiency and drought (Schreiner et al., 1997), mycorrhizal inoculation with suitable fungi has been proposed as a promising tool for improving restoration success in semi-arid degraded areas (Pigott, 1982).

By stimulating the development of beneficial microorganisms in the rhizosphere (Pennington, 1986), the use of VAM-infected plants could reduce the amount of fertilizer needed for the establishment of vegetation and could also increase the rate at which the desired vegetation becomes established by stimulating the development of beneficial microorganisms in the rhizosphere (Pennington, 1986). Degraded soils are common targets of revegetation efforts in the tropics, but they often exhibit low densities of AMF fungi (Michelsen and Rosendahl, 1990). This may limit the degree of mycorrhizal colonization in transplanted seedlings and consequently hamper their seedling establishment and growth in those areas. Soil inoculation with *G. mosseae* has significantly enhanced plant growth and biomass production in limestone mine spoils (Rao and Tak, 2002).

Root pathogens

The phenomenon of AMF protecting plants from root pathogens is known from studies involving root-infecting pathogens e.g. *Phytophthora parasitica* or *Fusarium sp.*, root-invading nematodes (Dodd, 2000) and horticultural and agricultural species such as tomato (*Lycopersicon esculentum* Mill.), alfalfa (*Medicago sativa* L.) (Dehne and Schonebeck, 1979), and in grasses (Newsham et al., 1995). *G. mosseae* induced local and systemic resistance to *P. parasitica* and was effective in reducing

symptoms produced by this pathogen (Pozo et al., 2002). Larsen and Bodker (2001), however, found that in severely infected root cortical tissue *Glomus mosseae* had reduced energy reserves and biomass and did not protect the plant from the biotrophic pathogen, *Aphanomyces euteiches*. In wheat, high levels of colonization by AMF did not protect crop roots from damage by root pathogens Ryan et al. (2002).

Plant diversity and soil aggregation

Van der Heidjen et al. 1998) have provided evidence that diversity of AMF determines plant community structure through the response of individual plant species to this diversity. AMF diversity is the major factor in the maintenance of plant biodiversity and ecosystem stability and function. Several studies show that AMF alters plant community structure by affecting the relative abundance of plant species and plant-species diversity (Grimme et al., 1987; Gange et al., 1990; Sanders and Koide 1994). Interplant transport of assimilates from the dominant canopy species via a common mycorrhizal network to subordinate plant species, has been suggested as a mechanism by which AMF affect the floristic diversity of plant communities (Grimme et al., 1987). Another mechanism by which AMF may affect plant community structure is the differential growth response of plant species to colonization by AMF, the so called "mycorrhizal dependence" (Gederman, 1975; Plenchete et al., 1983; Habate and Manjunath, 1991).

The species composition and diversity of AMF communities has the potential to determine plant population and plant community structure. The fact that plant species vary in the degree of response to AMF species has important implications for growth of individual plant species. In turn, this will affect a plant's ability to coexist with other plant species in a community (Van der Heidjen et al., 1998). On the other hand, established mycorrhizal plants may serve as important sources of inoculum for initially nonmycorrhizal, conspecifics, which may affect regeneration and could contribute to patchy distributions of species within the community (Koide and Dickie, 2002).

VAM MANAGEMENT AND PERSPECTIVES

The main areas in which the benefits of introducing inoculant AMF into a plant growth system will accrue, are those in which they are lacking indigenous inoculum of AMF. These include sterilised soils or post *in vitro* plant micro-propagation, buried, extremely fertilised, degraded areas (Dodd, 2000) or rooting of pepper cuttings (Thanuja et al., 2002). It is widely accepted that plants with highly branched root system (Gramineae) are less mycotrophic (less dependent on the fungi for normal

growth) than those with coarser roots (e.g. cassava, onion). Root branching determines plant dependence on the symbiosis.

Soils under low-input management show higher VAM fungus spore populations than soils under conventional management (Galvez et al., 2001; Douds et al, 1993, 1995). Early colonizing sand dunes species are non-mycorrhizal, whereas the later seral grasses are colonized with AMF (Nicolson, 1960).

Survival of AMF in soil may be affected by the presence or absence of crops and by the crop being grown (Troeh et al., 2003). The same author also reported differences related to crop succession. Fallow on fields had less spores than cultivation of corn followed by soybean, independently of the cultivars of corn or soybean. In cowpeas, inoculation and amendment with organic manure resulted in increased growth and yield (Muthukumar and Udayan, 2002). Inoculation with AMF and addition of composted grape pomace was beneficial to plants. This has been interpreted as the result of mycorrhizal fungus enhancing P uptake through extraradical hyphae. Such uptake increases nutrient-use efficiency (Linderman and Davis, 2002).

In some cases, composted municipal waste addition and mycorrhizal inoculation were effective tools in programmes for revegetation of shrub species in semi-arid mediterranean areas (Caravaca et al., 2003a). The use of native mycorrhizal as a potential source of AM inoculum was considered a preferential strategy for ensuring the successful re-establishment of native shrub species in semi- arid degraded soil (Caravaca et al., 2003b). Bell et al. (2003) found that the susceptibility of Acacia seedlings to colonization by AMF appeared to be seasonal. Colonization increased with increasing daytime temperatures and and daylength.

Despite the beneficial effects of AMF, their activity may be greatly limited by soil fumigation, non- responsive plant varieties, or rotations based primarily on non-mycorrhizal crops or crops of low AMF dependency. Salicylic acid contents in the plant reduced mycorrhization, suggesting that enhanced salicylic acid levels in plants delay AMF root colonisation. Although salicylic acid affect AMF root colonization, it has no effect on the potential of plants to be colonized by AMF (Medina et al., 2003).

Manipulation of agricultural systems to favour AMF colonization must occur only if there is a clear evidence that AMF make a positive contribution to yield or are vital for maintenance of ecosystem health and sustainability (Ryan et al., 2002).

A summary of publications devoted to the agricultural and environmental benefits of mycorrhiza is available at <http://www.mycorrhiza.ag.utk.edu>. Despite a high number of publications on VAM covering a variety of topics, the issues which most concern african countries such as drought and increased crop growth and yield are the least addressed. Under the conditions of many African countries, where no effective isolates are available and

occurrence and distribution of AMF are still unknown, pot trials are an important step for correct management of indigenous AMF. These trials must be designed to determine basic characteristics, such as host-fungus specificity interaction and competitiveness between AMF and, effectiveness of the AMF under possible environmental stresses, well-watered, drought stress, salinity, N and P deficiency conditions. Cheap and mass production of VAM inoculum will represent a significant step in its use in African agriculture.

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