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Review

The vesicular-arbuscular mycorrhizal symbiosis

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Vesicular-arbuscular mycorrhiza fungi are associated with the majority ot the terrestrial plants. Their function ranges from stress alleviation to bioremediation in soils polluted with heavy metals. However, our knowlwdge 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 recomends 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 (Siverding, 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 symboisis (Smith and Read, 1997) and 95% of the world's present species of vascular plants belong to families that are charcteristically 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 agriculatural applications this review will focus on the 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 pterydophytes. 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 Proteacea (Nicholson, 1967; Brundrett et al., 1996), Cruciferae, Zygophyllaceae

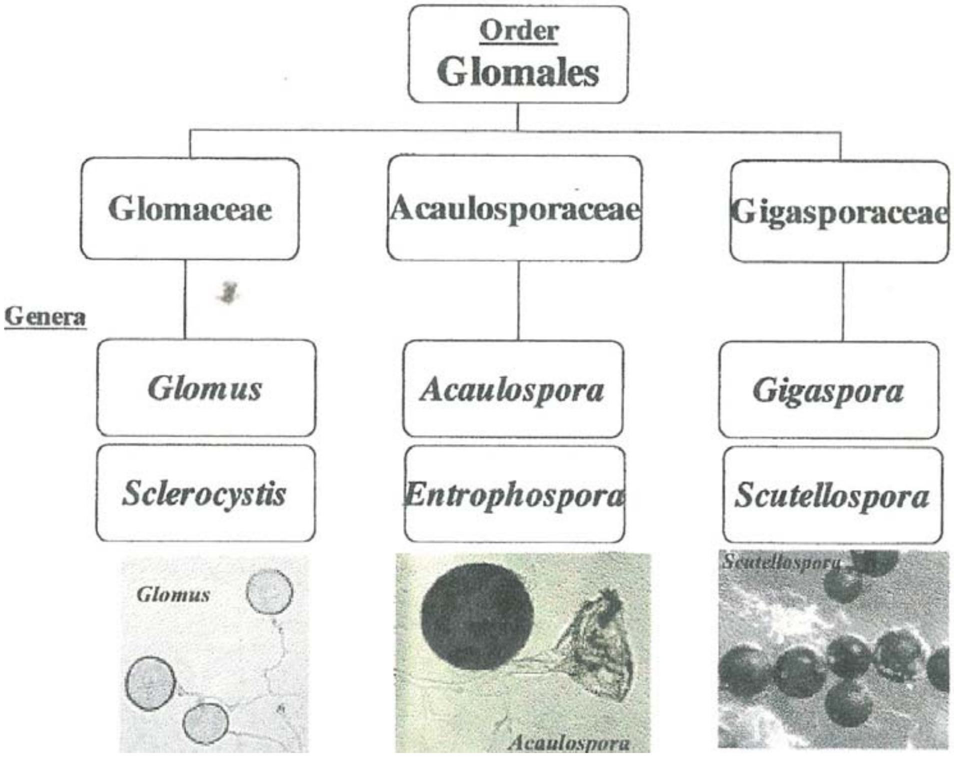

Figure 1. The current taxonomy of AMF with examples of the large spores produced by different genera in soil. From Dodd (2000).

(Varma 1998) Dipterocaceae, Betulaceae, Myrtaceae and Fagacaeae (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 salycilic acid have been found to reduce mycorrhization (Medina et al., 2003), meaning that plants with a genetic basis for high salycilic acid content have evolued 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 functioining 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-Nilsen and Madsen, 2001). In submerged African plants AMF colonization has not been not convincingly demonstratated. 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 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 absortion of several nutrients as indicated in (Table 1).

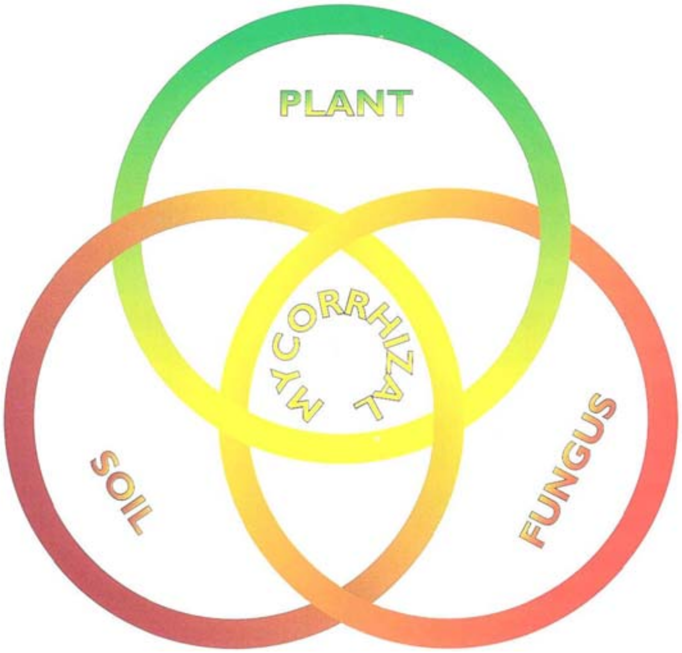

Figure 2. Mycorrhizal association, showing the interactions between fungus, plant and soil. From Brundrett et al. (1996).

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)

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), imobile 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 mechanims 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 Ázcón, 1995), enhanced activity of enzymes involved in anti-oxidant defence (Ruiz-Lozano et al., 1996b), nitrate assimilation (Ruiz-Lozano and Ázcón, 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 imobilization 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). Rufykiri 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 carrdoon 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 degradated 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 constrains related to soil degradation and water shortage (Whisenant, 1999; Valejo et al., 2002a, b). As mycorrhizae may enhance the ability of the plant to scope with water stress situtations 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 sucess 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 horticulutural and agricultural species such as tomato (*Lycopersicum 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 mecahnism 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 Heijden 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 intrepreted 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 mediteranean areas (Caravaca et al., 2003a). The use of native mycorrhizal as a potenntial 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 avariety 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 occurence and distribuition 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 environmanetal 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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REFERENCES

Al-Karaki GN, Al-Raddad A (1997). Effects of arbuscular fungi and rought stress on growth and nutrient uptake of two wheat genitypes diffrering in their drought resistance. Mycorrhiza 7:83-88.

Allen MF (1991). The ecology of mycorrhizae. Cambridge University Press, Cambridge

Allen MF, Moore TS, Christensen M (1982). Phytohormone changes in Bouteolua gracils infected by vesicular-arbuscular mycorrhizae. II. Altered levels of gibberellin-like substances and abscisic acid in the host plant. Can. J. Bot. 60:468-471.

Ames RN, Reid CPP, Porter L, Cambardella C (1983). Hyphal uptake and transport of nitrogen from two ^{15}N-labelled sources by *Glomus mosseae*, a vesicular-arbuscular mycorrhizal fungus. New Phytol.95:381-396.

Augé RM, Schekel KA, Wample RL (1986). Greater leaf conductance of well-watered VA mycorrhizal rose plants is not related to phosphorus nutrition. New Phytol. 103:107-116.

Augé RM, Schekel KA, Wanple RL (1987). Rose leaf elasticity changes in response to mycorrhizal colonization and drought acclimation. Physiol. Plant. 70:175-182

Augé, RM, Stodola, Ann J.W, Tims JE, Saxton AM (2001). Moisture retention properties of a mycorrhizal soil. Plant Soil 230:87-97.

Azcón R, Gomes M, Tobart R (1996). Physiological and nutritional responses by Lactuca sativa L. to nitrogen sources and mycorrhizal fungi under drought stress conditions. Biol. Fert. Soils 22:156-161.

Azcón-G de Aguilar C, Azcón R, Barea JM (1979). Endomycorrhizal fungi and Rhizobium as biological fertilisers for Medicago sativa in normal cuntivation. Nature 279: 325-236

Baligar AC, Bennet OL (1986). Outlook on fertilizer use efficiency in the tropics. Fert. Res.10:83-96.

Barea JM, Azcón-Aguilar C (1982). Production of plant growth regulating substances by vesicular-arbuscular mycorrhizal *Glomus mosseae*. Appl. Environ. Microbiol. 43:810-813.

Barea JM, Azcon-Aguilar C (1983). Mycorrhizas and their significance in nodulating nitrogen-fixing plants. Adv. Agron. 36:1-54.

Beck-Nielsen D, Madsen T V (2001) Occurrence of vesicular-arbuscular mycorrhiza in aquatic macrophytes from lakes and streams. Aquatic Bot. 71: 141-148.

Bell J; Wells S, Jasper DA, Abbott LK (2003). Field inoculation with arbuscular mycorrhizal fungi in rehabilitation of mine sites with native vegetation, including Acacia sp. Aus. System. Bot. 16(1): 131-138.

Boddington CI, Dodd JC (2000). The effect of agricultural practices on the development of indigenous arbuscular mycorrhizal fungi.I. Filed studies in an Indonesian ultisdol. Plant Soil 218:137-144.

Brundrett M (1991). Mycorrhizas in natural ecosystem. *In*: Macfayden, Begon, M and Fitter AH (eds). Advances in Ecological Research vol 21, pp.171-173, Academi Press London.

Brundrett M, Beegher N, Dell B, Groove T, Malajczuk N (1996) Working with mycorrhizas in Forestry and Agriculture. ACIAR Monograph 32. 374+xp. ISBN186320 181 5

Caravaca F, Barea JM, Palenzuela J, Figueroa D, Alguacil MM, Roldan A (2003a). Establishment of shrub species in a degraded semiarid site after inoculation with native allocthhonous arbuscular mycorrhizal fungi. Appl. Ecol. 22(2): 103-111.

Caravaca F, Figueroa D, Azcon-Aguilar C, Barea JM, Roldan A (2003b). Medium-term effects of mycorrhizal inoculation and composed municipal waste addition on the establishment of two Mediterranean shrub species under semi-arid field conditions. Agric. Ecosys. Environ. 97(1-3):95-105.

Caris C, Hoerdt W, Hwkins HJ, Roenheld V, George E (1998). Studies on the iron transport by arbuscular mycorrhizal hyphae from soil to peanut and sorghum plants. Mycorrhiza 8:35-39.

Ceccarelli S, Grando S (1996). Drought as a challenge for the plant breeder. Plant Growth Regul. 20:149-155.

Chandreshekara CP, Patil VC, Sreenivasa MN (1995). VA-mycorrhiza mediated P effect on growth and yield of sunflower (Helianthus annus L.) at different P levels. Plant Soil 176:325-328.

Chen BD, Li XL, Tao HQ, Christie P, Wong MH (2003). The role of arbuscular mycorrhiza in zinc uptake by red clover growing in calcareous soil spiked with various quantities of zinc. Chemosphere 50(6): 839-846

Cooke JC, Lefor MW (1990) Comparison of veiscular-arbuscular mycorrhizae in plants from disturbed and adjacent undisturbed regions of a costal salt marsh in Clinto, Connecticut, USA. Environ. Manage. 14 (1): 212-137.

Cumming Jr, Ning J (2003). Arbuscular mycorrhizal fungi enhence aluminium resistance of broomsedge (*Andrpongon virginicus* L). J. Exp. Bot. 54(386):1477-1459.

Danneberg G, Latus C, Zimmer W, Hundeshagen B, Schneider-Poetsch HJ, Bothe H. (1992). Influence of vesicular-arbuscular mycorrhiza on phytohormeone balances in maize (*Zea mays* L.). J. Plant Physiol. 141:33-39.

Davies Jr FT, Portugal-Olalde V, Aguilera-Gomez-L, Alvarado MJ; Ferrera-Cerrato RC, Bouton TW (2002). Alleviation of drought stress of Chile ancho pepper (*Capsicum annuum* cv San Luis) with arbuscular mycorrhiza indigenous to Mexico. Scientia Horticulturae 92: 347-359.

Dehne HW, Schonebeck F (1979). Untersuchungen zum einfluss der endotrophen mycorrhiza auf planzenkrankheiten. I. Ausbreitung von *Fusarium oxysporum* f. sp.*lycopersici* in tomaten. Phytotologische Zeitshrift 95:104-110.

Dell'Amico J, Torrecillas A, Rodriguez P, Morte, A, Sanchez-Blanco MJ (2002). Responses of tomato plants associated with the arbuscular mycorrhizal fungus *Glomus clarum* during drought and recovery. J. Agric. Sci. 138:387-393.

Dodd JC (2000) The role of arbuscular mycorrhizal fungi in agro-and natural ecossystems. Outlook on Agriculture 29 (1):55-62.

Douds DD, Galvez L, Janke R, Wagoner P (1995) Effect of tillage and farming system upon populations and distribution of veiscular-arbuscular mycorrhizal fungi. Agric. Ecosys. Environ. 52:111-118.

Douds DD, Janke RR, Peters (1993). VAM fungus spore populations and colonization of roots of maize and soybean under conventional and low-input sustainable agriculture. Agric. Ecosys. Environ 43:325-335.

Faber BA, Zasoski RJ, Burau RG, Uriu K (1990). Zinc uptake by corn as affected by vesicilar-arbuscular mycorrhizae. Plant Soil:121-130.

Faber BA, Zasoski RJ, Munns DN, Schakel K (1991). A method for measuring hyphal uptake in mycorrhizal plants. Can. J. Bot. 69:87-94.

Fitter AH (1985) Functioning of vesicular-arbuscular mycorrhizas under field conditions. New Phytol. 99:237-263.

Fitter AH (1988). Water relations of red clover Trifolium pratense L., as affected by VA mycorrhizal infection and phosphorus supply before and during drought. J. Exp. Bot. 39:595-604.

Galvez, L , Jr. Douds DD, Drinkwater LE, Wagoner P (2001). Effect of tillage and farming system upon VAM fungus populations and mycorrhizas and nutrient uptake of maize. Plant Soil 228:299-308.

Gange AC, Brown VK, Farmer LM (1990). A test of mycorrhizal benefit in an early successional plant coumnity. New Phytol. 115:85-91.

Gange AC, Brown VK, Sinclair GS (1993) Vesicular-arbuscular mycorrhizal fungi: a determinat of plant community structure in early successino. Funct. Ecol. 7:616-622.

Gederman JW (1975). Vesicular-arbuscular mycorrhizae.pp 575-591. In: J.C. Torey and D.P Clarkson (eds). The development and function of roots. Academic Press, NY, USA.

George E, Gorgus E, Schmeisser A, Marschner H (1996). A method to measure nutrient uptake from soil by mycorrhizal hyphae. *In* Mycorrhizas in Integrated System from Genes to plant Development (eds) Azcon-Aguilar and JM Barea). Luxembourg. European Community.

George E; Romheld V, Marschner H (1994). Contribution of mycorrhizal fungi to micronutrient upteke by plants. *In* Biochemistry of Metal Micronutrients in the Rhizosphere (eds) J.A. Monthey, D.E Crowley and D.G.Luster pp93-109. Boca raton FL CRC Press.

Gildon A, Tinker PB (1983). Interactions of vesicular-arbuscular mycorrhizal infection and heavy metals in plants. I. The effects of heavy metals on the development of vesicular-arbuscular mycorrhizas . New Phytol. 95:247-261.

Goicoechea N, Doleza K; Antolin MC, Strand M, Sanchez-Diaz M (1995). Influence of mycorrhizae and *Rhizobium* on cytokinin content in drought stressed alfalafa. J. Exp. Bot. 46:1543-1549.

Gonzalez-Chavez C, D'Haen J, Vangronsveld J, Dodd JC (2002). Copper soprtion and accumulation by the extraradical mycelium of different Glomus spp (arbuscular mycorrhizal fungi) isolated from the same polluted soil. Plant Soil 240(2):287-297.

Grimme JP, Mackey ML, Hillier SA, Read DJ (1987). Floristic diversity in a model system using experimental micrososmos. Nature 328:420-422.

Guo Y; George E, Marschner H (1996). Contribution of an arbuscular mycorrhizal fungus to uptake of Cadmnium and Nickel in bean by maize plants. Plant Soil 184:195-205.

Habate M, Manjunath A (1991). Categories of vesicular-arbuscular mycorrhizal dependency of host species. Mycorrhiza 1:3-12.

Hardie K (1985). The effect of removal of extraradical hyphae on water uptake by vesicular-arbuscular mycorrhizal plants. New Phytol. 101:677-684.

Harley JL, Smith SE (1983). Mycorrhizal symbiosis. Academic Press, London UK.

Jacobsen I, Abbott LK, Robson A (1992). External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trofoluim subterraneum* L. I. Spread of hyphae and phosphorus inflow into roots. New Phytol. 120:371-380.

Jamal A, Ayub N, Usman M, Khan AG (2002). Arbuscular mycorrhizal fungi enhance zinc and nickel uptake from contaminated soil by soybean and lentil. Int. J. Phytoremed. 4(3):203-221.

Jeffries P (1987). Use of mycorrhiza in agriculture. Crit. Rev. Biotechnol. 5:319-357

Johanssen A, Jakobsen I, Jessen ES (1993). External hyphae of vesicular-arbuscular mycorrhizal fungi associated with Trifolium subterraneum L. 3. Hyphal transport of 32P and 15N. New Phytol. 124:61-68.

Johnson NC, Graham JH, Smith FA (1997). Functioning of mycorrhizal associations along the mutualism-parasitism continuum New Phytol. 135:575-585.

Johnson NC, Pfleger FL (1992). VA mycorrhizas and cultural stresses. In Mycorrhizas in Sustainable Agruclture. Ed GJ Betlhenfalvay. Wisconsis, Madison,USA

Joner EJ, Levylal C (1997). Uptake of roots by roots and hyphae of Glomus mosseae/Trifolium subterraneum mycorrhiza from soil amenede with high and low concentrations of cadmium. New Phytol. 135:53-360.

Kaya C, Higgs D, Kirnak H, Tas I (2003). Mycorrhizal colonization improves fruit yield and water use efficiency in water melon (Citrullus lanatus Thunb) grown under well-watered and water-stresse3d conditions. Plant Soil 253(2):287-292.

Kilronomos JN, Kendrick WB (1993) Research on mycorrhizas: trends in the past 40 years as expressed in the "MYCOLIT"database. Newt Phytol. 125:595-600.

Koide R (1985). The nature of growth depressions in sunflower caused by vesicular arbuscular infection. New Phytol. 99:449-462.

Koide RT, Dickie IA (2002). Effects of mycorrhizal fungi on plant populations. Plant Soil 244 (1-2): 307-317.

Koide RT, Shumway DL, Mabon SA (1994). Mycorrhizal fungi and reproduction of field populations of Abutilon theophrasti Med. (Mlavaceae). New Phytol. 126:123-130.

Lal R (1997) Long term tillage and maize monoculture effects on a tropical Alfisol in western Nigeria. Soil Tillage Res. 42:161-174.

Lambert DH; Baker DE, Cole H Jr. (1979). The role of mycorrhizae in the interactions of phosphorus with zinc, copper and other elements. Soil Sci. Soc. Am. J. 43:976-980.

Larsen J, Bodker L (2001). Interactions between pea rootimg-inhabiting fungi examined using signature fatty acids. New Phytol.149:487-493.

Li, X.-L, George E, Marschner H (1991). Extension of the phosphorus depletion zone in VA-mycorrhizal white clover in a calcareous soil. Plant Soil 136:41-48.

Liao JP, Lin XG, Cao ZH, Shi YQ, Wong MH (2003). Interactions between arbuscular mycorrhizae and heavy metals under sand culture experiment. Chemosphere 50 (6): 847-853.

Linderman RG, Davis EA (2002). Vesicular-arbuscular mycorrhiza and plant growth response to soil amendment with composed grape pomace or its water extract. Phyton-Annales Botanicae 11(3): 446-450.

Liu A, Hamel C, Elmi A, Costa C, Ma B, Smith DL (2002). Concentrations of K, Ca and Mg in maize colonised by arbuscular mycorrhizal fungi under field conditions. Can. J. Soil Sci. 82(3): 271-278.

Marin M, Ybarra M, Fe A, Garcia-Ferriz L (2002). Effect of arbuscular mycorrhizal fungi and pesticides on *Cyanara cardunculatus* growth. Agricultural and Food Science in Finland 11 (3): 245-251.

McGonigle TP, Fitter AH (1988). Geowth and phosphorus inflows of *Trifolium repens* L. with a range of indigenous vesicular-arbuscular fungi. New Phytol. 108:59-66.

Medina MJH, Gagnon H, Piche Y, Ocampo JA, Garrido JMG, Vierheilig H (2003). Root colonization by arbuscular mycorrhizal fungi is affected by the salicilic acid content of the plant. Plant Sci. 164(6); 993-998.

Michelsen A, Rosendhal S (1990). The effect of VA mycorrhizal fungi, phosphorus and drought stress on the growth of *Acacia nilotica* and *Leucaena leucocephala* seedlings. Plant Soil 133:79-83.

Miller SP (2000). Arbuscular mycorrhizal colonization of semi-aquatic grasses along a wide hydrologic gradient. New Phytol.145:143-155.

Mosse B, Stribley DP, Le Tacon F (1981). Ecology of mycorrhizae and mycorrhizal fungi. Adv. Microbiol. Ecol. 2:137-210.

Muthukumar T, Udaiyan K (2002). Growth abd yield of cowpea as influenced by changes in arbuscular mycorrhiza response to organic manuring. J. Agron. Crop Sci. 188(2):123-132.

Neeraj, Shankar A, Mathew J, Varma AK (1991). Occurrence of VA mycorrhizae within Indian semi-arid soild. Biol. Fert. Soils 11:140-144.

Newsham KK, Fitter AH, Watkison AR (1995). Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. J. Ecol. 83:991-1000.

Nicolson TH (1967). Vesicular-arbuscular mycorrhiza-a universal plant symbiosis. Sci. Prog. 55:561-581.

Nicolson TH (1960) Mycorrhizae in the Graminae. II. Development in different habitats particularly sand dunes. Can. J. Soil Sci. 43:132-145.

O'Connor PJ, Smith SE, Smith EA (2002). Arbuscular mycorrhizas influence plant diversity and community structure in semi-arid herbland. New Phytol. 154(1):209-218.

Ortas I, Harries P.J, Rowell DI (1996). Enhanced uptake of phosphorus by mycorrhizal sorghum plants as influenced by form of nitrogen. Plant Soil 184:255-264.

Pande M, Tarafadar JC (2002). Effects of phosphorus, salinity and moisture on VAM fungal association in neem (*Azadirachta indica* L.). Symsbiosis 32 (3):195-209.

Pennington JC (1986) Feasibility of using mycorrhizal fungi for enhancement of plant establishment on degraded material disposal sites; A literarature review. Miscellaneous Paper D-86-3. US Army Engineer Waterways Experiment Station, Vicksburg, Mississipi, USA.

Pigott CD (1982). Survival of mycorrhizas formed by Centroccocum geophilum in dry soils. New Phytol. 92:513-517.

Plenchette CA, Fortin A, Forlan N (1983). Growth response of several plant species to mycorrhiza in a soil of moderate P-fertility. I. Mycorrhizae aunder field conditions. Plant Soil 70:199-203.

Pocock K, Duckett JG (1985) On the occurrence of the branched and swollen rhizoids in Britisg hepatics: their relationships with the substratum and association with fungi. New Phytol. 99: 281-304.

Pozo MJ, Cordier C, Dumas-Gaudot E (2002). Lozalized versus systemic effect of arbuscular mycorrhiszal fungi on defence responses to Phytophthora infection in tomato plants. J. Exp. Bot. 53(368):525-534.

Quilambo OA (2000). Functioning of peanut (*Arachis hypogaea* L.)under nutrient deficiency and drought stress in relation to symbiotic associations.PhD thesis. University of Groningen, the Netherlands. Van Denderen B.V., Groningen.ISBN 903671284X.

Rao AV, Tak R (2002). Growth of different tree species and their nutrient uptake in limestone mine spoil as influenced by arbuscular mycorrhizal (AM)-fungi in Indian arid zone. J. Arid Environ.. 51(1):113-119.

Rufykiri G, Thiry Y, Wang L, Delvaux B, Declerck S (2002). Uranium uptake and translocation by the arbuscular fungus, Glomus intraradices, under root-organ culture conditions. New Phytol. 156(2):275-281.

Ruiz-Lozano JM, Azcon R (1996). Mycorrhizal colonization and drought stress as factors affecting nitrate reductase activity in lettuce plants. Agric. Ecosys. Environ. 60:175-181.

Ruiz-Lozano JM, Azcon R, Gomez M (1996a). Alleviation of salt stress by arbuscular mycorrhizal Glomus species in Lactuca sativa plants . Physiol. Plant. 98:767-772.

Ruiz-Lozano JM, Azcón R, Plama JM (1996b). Superoxide dismutase activity in arbuscular mycorrhizal *Lactuca sativa* plants subjected to drought stress. New Phytol. 134:327-333.

Ruiz-Lozano JM, Roussel H, Gianinazzi S, Gianinazzi-Perason V (1999). Defense genes are differentially induced by a mycorrhizal fungus and *Rhizobium* sp. in a wild-type and symbiosis-defective pea genotypes. Mol. Plant-Microbe Interact. 12:976-984.

Ryan MH, Norton RM, Kirkegaard JA, McCormick KM, Knights SE, Angus JF (2002). Increasing mycorrhizal colonisation does not improve growth and nutrition of wheat on vertsols in south-eastern Australia. J. Agric. Res. 53(10):1173-1181.

Sanchez-Diaz M, Honrubia M (1994). Water relations and alleviation of drought stress in mycorrhizal plants. *In* Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems (S.Gianninazi and H. Schuepp (eds). Pp167-178. Birkhauser Verlag, Basel, Switzerland. ISBN 3-7643-5000-8.

Sanders IR, Koide RT(1994). Nutrient acquisition and community structure in co-occuring mycortrophic and non-mycotrophic old-field annuals. Funct. Ecol. 8:77-84.

Schreiner RP, Mihara KL, McDaniel H, Bethlenfalvay GJ (1997). Mycorrhizal functioning influence plant and soil functions and interactions. Plant Soil 188:199-209.

Sengupta A, Chaudhuri S (2002). Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. Mycorrhiza 12(4); 169-174.

Sieverding E (1991) Vesicular-arbuscular mycorrhiza management in tropical agrosystems. Technical Cooperation, Federal Repuplic of Germany Eschborn. ISBN 3-88085-462.

Smith SE, Read DJ (1997) Mycorrhizal symbiosis. Academic Press, Inc San Diego California. ISBN 0-12-652840-3.

Sondergaard M and Lindegaard S (1977) Vesicular-arbuscular mycorrhizae in some aquatic vascular plants. Nature 268: 232-233.

Sprent JI (1971). The effect of water stress on nitrogen-fixing root nodules. I. Effects on the physiology of detached soybean nodules. New Phytol. 70:9-16.

Stevens KJ, Spender SW, Petersen RL (2002). Phosphorus, arbuscular mycorrhizal fungi and performannce of the wetland *Lythrum salicaria* L. under inundated conditions. Mycorrhiza 12(6):277-283.

Subramanian KS, Charest C (1999). Acquisition of N by external hyphae of an arbuscular mycorrhizal fungus and its impact on physiological responses in maize under drought-stressed and well-watered conditions. Mycorrhiza 9:69-75.

Tester M, Smith SE, Smith FA (1987). The phenomenon of “nonmycorrhizal plants”. Can. J. Bot. 65:419431.

Thanuja TV, Hedge RV, Sreenivasa MN (2002). Induction of rooting and root growth in black pepper cuttings (Piper nigrum L.) with inoculatioon of arbuscular mycorrhizae . Scientia Horticulture. 92(3-4):339-346.

Troeh ZI, Loynachan TE (2003). Endomycorrhizal fungal survival in continuous corn, soybean and fallow. Agron. J. 95(1):224-230.

Vallejo VR, Serrasloses I, Cortina J, Seva JP, Valdecantos A, Vilagrosa A. (2000a). Restoration for soil protection after disturbances. In: Trabaud L (eds). Life and Ecosystems in the Mediteranean. WIT Press, Southhampton pp301-344.

Vallejo VR, Serrasloses I, Cortina J, Seva JP, Valdecantos A, Vilagrosa A. (2000b). Restoration strategies and actions in Mediterranean degraded lands. In: Enne, G, Zanolla Ch, Peter D. (eds). Desertification in Europe: Mitigation strategies, land use Planning, Oofice for Official Publications of the European Communities, Luxembourg, pp. 221-233.

Van der Heijden MGA, Boller T, Wiemken A, Sanders JA (1998) Different arbuscular mycorrhizal fungal species are potential determinats of plant community strucuture. Ecology 79 (6): 2082-2091.

Varma A (1998). Functions and Application of Arbuscular Mycorrhizal Fungi in Arid and semi-Arid Soils. *In*: Mycorrhiza: Structure, Function, Molecular Biology and Biotechnology. A. Varma and B. Hock (eds). 2nd edition. Library of Congress Cataloging-in-Publication Data. ISBN 3-540-63981-0.

Whisenant SG (1999). Repairing Damaged Wildlands. Cambridge University Press, Cambridge 312 p.

Wilson GWT, Hartnett DC (1998). Interspecific variation in plant responses to mycorrhizal colonization in talgrass prairie. Am. J. Bot. 85:1732-1738.