

## Mycorrhiza: Fungus and Plant Root Symbiosis in the Functioning of Natural Ecosystems

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### ABSTRACT

Mycorrhiza are global associations including diverse morphological, functional and evolutionary categories. Almost all the plant species of natural vegetation and the agricultural crop plants of the tropics live in mycorrhizal association with fungi. Vesicular arbuscular mycorrhizal associations (VAM), which are also called arbuscular mycorrhiza (AM) or glomeromycotan mycorrhiza (GM), are the most widespread and common root-fungus associations. Mycorrhizal fungi are better than roots at acquiring poorly mobile phosphate from the soil, which they exchange with their host plant for their sole source of carbon. In addition to their role in phosphate acquisition, AMF have other potential benefits to plants like the uptake of important nutrients such nitrogen, protection against root pathogens, water acquisition and the mediation of pollution effects. Current review discusses the biology of mycorrhiza in relation to mutualistic relationship with plants in natural eco-system.

**Keywords:** Fungi, Root, Mycorrhiza, Vesicles, Arbuscules

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### INTRODUCTION

It was Frank (1885), who gave the name “mycorrhiza”. Kelley (1931) incorporated the second “r” in the word “mycorrhiza”. According to Nehls *et al.* (2001) and Pfeffer *et al.* (2001) mycorrhiza differ primarily from other plant-fungus associations because they are close associations where exchange of materials takes place between living cells. Janse (1897) called the intramatrical spores “vesicules” and Gallaud (1905) called the other commonly observed intracellular structures “arbuscules”. In general, arbuscules are used to define VAM associations. According to McGonigle *et al.* (1990) and Toth *et al.* (1990) their abundance is usually correlated with the degree of colonization of young roots by VAM fungi.

Arbuscules are short-lived structures that are often not in attendance or hard to see due to rootage and pigments in field-collected roots. There is discrepancy in naming these mycorrhizas appropriately as arbuscular mycorrhizal association. The recognition that not all fungi formed vesicles led to the proposal that this symbiosis should be renamed arbuscular mycorrhiza. Nowadays the term arbuscular mycorrhiza has now become a trend, however the term vesicular-arbuscular mycorrhiza (VAM) is as accurate as arbuscular mycorrhiza (AM). The present review discuss the biology of mycorrhiza, its nomenclature and its mutualistic

association with plant roots. The article discuss the species concept in relation to systematics of mycorrhiza and its significance in the natural eco-systems.

## 1. Discovery and Description

Early on mycorrhizal quantification was achieved by clearing the roots by heating in KOH and staining fungal cell walls with trypan blue in lactophenol (Phillips and Hayman 1970). However, this stain does not differentiate between active and inactive or dead cells of the fungal hyphae (Singh 2005). Probably the most popular method for quantification of mycorrhization is based on the line intersect technique devised by Newman (1966). Giovannetti and Mosse (1980) compared various methods of mycorrhizal quantification, which led to greater acceptance of the line intersect method. Mycorrhizas are complex symbioses and the fungi involved in it produce a variety of structures within the root. Quantification of these structures viz. hyphae, arbuscules, and vesicles was standardized by the method proposed by McGonigle *et al.* (1990). The extraction of spores from soil is essential for their classification. It was made possible by wet sieving and decanting method, a method commonly used to extract nematodes from soil and adapted to arbuscular mycorrhizal fungi by Gerdemann (Gerdemann and Nicolson 1963).

## 2. AMF Reproduction and its Morphological Traits

All AMF that have been described to date reproduce only by asexual means (Schubler *et al.* 2001). There is no evidence that the Glomeromycota reproduce sexually. AMF reproduce clonally via spores, vesicles and hyphae. Furthermore, Kuhn *et al.* (2001); Pawlowska and Taylor (2004); Hijri and Sanders (2005) argued on the question, whether the nuclei in the mycelium and spores of one organism are genetically identical or not. Under favorable conditions glomeromycotan spores germinate, form appressoria on host roots and establish a new mycorrhizal symbiosis.

Mycorrhizal fungal hyphae are aseptate to sparsely septate viz. they are generally not divided by cell walls as described by Isaac (1992) and Schubler *et al.* 2001). This is unusual feature of the AMF, as most fungi, including members of the most phyla have septae (Isaac 1992) and a lack of septae is a good first sign in identifying an AM fungus. To identify AM fungus at the lower taxonomic levels, certain hyphal traits have been used which include the number of hyphae per spore, and hyphal colour, shape and size, among others (Morton 1988; Merryweather and Fitter 1998; Prasad and Rajak 1999). Different infection patterns viz. the

arrangement of hyphae, vesicles and arbuscules are characteristic of different groups of species as described by Abbott (1982). Hence, the fine morphological details of AMF may help in species diagnosis. On the other hand this can be difficult as vesicles, hyphae and particularly arbuscules often are visible as darker, blurry areas of stained root cortex cells. In addition to this, a single fungal species can have a different morphological appearance, which depend on the species of its host plant (Merryweather and Fitter 1998).

### **3. Species Concept in Relation to AMF**

The biological species concept (Coyne 1994) is irrelevant for asexual groups such as the AMF (Freeman and Herron 1998). A typological species is usually delineated as a group of organisms that appear similar to one another and different to other groups of organisms. This species concept can be applied when the interbreeding criterion cannot be tested viz. in fossil organisms or in asexual lines such as the AMF (Futuyma 1998) or when accurate phylogenies are not available. It is said that the typological species (morphospecies; Freeman and Herron 1998) are convenient for describing particular syndromes of traits, but they do not inevitably bear a strong resemblance to consider being 'species'.

Furthermore, researchers have imposed a taxonomic system on AMF but it is not yet a 'natural systematics' (Schubler *et al.* 2001). Since the AMF are asexual, we cannot describe AMF in terms of biological species. However, we could define them in terms of phylogenetic species if accurate phylogenies were available at the fine scale, but until now this is not the case. We can define AMF in terms of typological species, but many biologists are disagreed with typological definitions because they do not generally reflect the evolutionary history of the organisms that are being classified. As per Wiley (1978) asexuality has been called "the bane of all proposed (species) definitions that are not obviously typological".

### **4. Biological Network of Mycorrhiza**

Beneficial microbial interactions involving arbuscular mycorrhiza is the omnipresent fungus–plant beneficial symbiosis (Barea *et al.* 2005). The great majority of land plants are host for some type of mycorrhiza and members of most plant families form AM (Smith and Read 1997). Other types of mycorrhiza are formed with fungi from the phyla Ascomycota or Basidiomycota viz. ectomycorrhiza of trees and shrubs, ericoid mycorrhiza of Ericales, orchid mycorrhiza and some others.

Only a few plant families are regarded as non-mycorrhizal, among them the Brassicaceae viz. cabbage, Caryophyllaceae viz. carnation and Chenopodiaceae viz. spinach. AMF are best known for their obligatory symbiotic relationship with plants. This exclusive association is found in virtually all terrestrial ecosystems and environments (Morton 2001) and associated with the species in a majority of plant families (Rillig 2004).

Different AMF species are better/worse mutualists than others. Other fungi form symbiotic mutualisms viz. ‘mycobionts’ in lichens, including mutualisms with plants viz. endophytes, but the mycorrhizal mutualism formed by AMF and their host plants have a distinct biological network. The mycorrhizal mutualism is based primarily on the exchange of nutrients. Mycorrhizal fungi are better than roots at acquiring poorly mobile phosphate from the soil, which they exchange with their host plant for their sole source of carbon (Bolan 1991; Chandrashekara *et al.* 1995). In addition to their role in phosphate acquisition, AMF have other potential benefits to plants as described by Morton (1988), Prasad (2000), Prasad and Prasad and Rajak (2002) and Rillig (2004), viz. the uptake of other important nutrients such nitrogen, protection against root pathogens and water acquisition.

According to Smith and Read (1997), host specificity of AM appears to be very low as many species were observed by them to colonize a wide range of host plants in the greenhouse study. Furthermore, plants are generally colonized by a mixture of AM fungal species, often within the same root (Helgason *et al.* 1999). Field studies using molecular identification methods have demonstrated that distinct fungal communities are associated with different hosts (Vandenkoornhuyse *et al.* 2002). While according to Bidartondo *et al.* (2002) certain non-photosynthetic plants may cheat the fungus by obtaining all their nutrients from them, including carbohydrates.

## **5. Effects of AMF on Host Plant**

Generally most researchers consider fungi, infecting plant tissues as pathogens or parasites and names as “Rhizophagus” (Dangeard 1900), which means “root eater”. Rayner (1926–1927) accepted that ectomycorrhizal fungi might be beneficial to their hosts but she did not state the same for AM fungi. Using non-sterile soil as an inoculum, it was Asai (1943) who demonstrated that mycorrhizal plants grew faster than non-mycorrhizal plants. Nicolson (1967) and Gerdemann (1971) produced large volumes of AMF inoculum in pot cultures, which they produced from single isolates of fungal species. However, disagreement in the

nature of mycorrhizal effects on the host has been also reported (Lohman 1927; Janos 1980; Johnson *et al.* 1997).

Thus there are prominent cases of growth depression apparently caused by AMF in “non-host” species (Francis and Read 1984) or in host species when phosphate availability in soil is high (Mosse 1973; Peng *et al.* 1993). Gerdemann (1964) confirmed that nonmycorrhizal plants exhibited “severe phosphorus deficiency symptoms” and had significantly lower P concentrations and higher K and Mg concentrations than mycorrhizal plants.

Bowen and Rovira (1968) reported first that transfer of nutrients from fungus to host occurred across functional, intact arbuscules (Woolhouse 1975). Marx *et al.* (1982) described the first biochemical evidence that made clear the role of the intact arbuscule in P transfer. They showed that the host plasma lemma, which invaginates around the arbuscular hyphae, had a very high ATP-ase activity, which later shown to be H<sup>+</sup>-ATP-ase (Gianinazzi-Pearson *et al.* 1991; 2000), suggesting the presence of active transport mechanisms. Smith and Smith (1997) questioned whether arbuscules (alive or dying) are needed for P transfer, as intercellular hyphae may also be a site of P transfer.

AM fungi also absorb K, Ca, S, Fe, Mn, Cu, and Zn from the soil and then translocate these nutrients to the host plants (Gerdemann 1975; Hayman 1982; Tinker and Gildon 1983; Newsham *et al.* 1994). Moreover, they are also very useful to plant species that inherently lack morphological or physiological mechanisms for efficient P uptake (Manjunath and Habte 1991). The early emphasis, placed on the role of mycorrhizal fungi in encouraging plant growth may have distracted us from an added, very significant role they play as stabilizers of soil structure (Clough and Sutton 1976; Nicolson and Johnston 1979; Tisdall and Oades 1979; Miller and Jastrow 2000) and as integral components of a very diverse soil biota (Bethlenfalvay and Schuepp 1994; Franke-Snyder *et al.* 2001).

Nevertheless non-nutritional effects of AMF viz. root branching (Berta *et al.* 1990), ethylene production (McArthur and Knowles 1992) or protection from pathogens (Prasad and Rajak 2002), the suppression of plant diseases (Hooker *et al.* 1994; Newsham *et al.* 1994; Trotta *et al.* 1996) including nematode infection (Cooper and Grandison 1986; Habte 1999), stimulate hormone production in plants which aid in improving soils structure (Wright and Upadhyaya 1996; Bethlenfalvay 1998; Wright and Upadhyaya 1998), enhance leaf chlorophyll levels, (Tsang and Maun 1999) and improve plant tolerance to water stress, salinity, soil acidity, and heavy metal toxicity (Bethlenfalvay 1992) are very important as

well. Some of these functions may be the indirect effects of improved P nutrition (O'Keefe and Sylvia 1991; Sieverding 1991).

Several mechanisms have been proposed to explain the protection of AMF symbiosis, such as changes in plant hormones (Allen *et al.*1982; Barea and Azcon-Aguilar 1983; Danneberg *et al.*1992; Goicoechea *et al.*1995), increased leaf gas exchange and photosynthetic rate (Ruiz-Lozano *et al.*1996a), acidification of the rhizosphere (Bago and Azcon-Aguilar 1997), increases in root phosphatase activity (Fries *et al.*1998), direct hyphal water uptake from the soil and transfer to the host plant (Hardie 1985; Faber *et al.*1991; Ruiz-Lozano and Azcon 1996), enhanced activity of enzymes involved in anti-oxidant defense (Ruiz-Lozano *et al.*1996), nitrate assimilation (Ruiz-Lozano and Azcon 1996), enhanced water uptake through improved hydraulic conductivity and increasing leaf conductance and photosynthetic activity (Koide 1985), osmotic adjustment (Auge *et al.*1986) and changes in cell-wall elasticity (Sanchez-Diaz and Honrubia 1994).

## Future Prospects

AMF have some important ecological effects at the ecosystem scale. They are known to have profound effects on plant species composition, diversity and productivity. Rillig called AMF fungi as 'keystone mutualists' due to their vital importance for plant species composition and ecosystem properties and all the indirect effects associated with it. It is clear that the reciprocal influences between plants and their fungal symbionts can promote and maintain both above and below ground diversities. Our understanding of this system is still incomplete, due to our lack of data on individual plant fungal species interactions. This is mainly due to a complex fungal genetic structure, which makes species identification difficult and inability to grow the mycobionts in pure culture. Recent efforts embrace promise for advancing our understanding of the role of AMF in the functioning of natural eco-systems.

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