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Arbuscular Mycorrhizal fungi: an evolutionary-developmental perspective

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INTRODUCTION

Arbuscular Mycorrhiza is mutuality associations formed between the roots of 80 % of terrestrial plant species and fungi from the small phylum Glomeromycota. The term "mycorrhiza" was coined by A. B. Frank, a scientist in Germany, more than 100 years ago. It literally means fungus-root, and describes the mutualistic association existing between a group of soil fungi and higher plants. The association is based on the plant component providing carbohydrates and other essential organic compounds to the fungi. In return, the fungal component, which colonizes both the root and the adjacent soil, helps the plant take up nutrients by extending the reach of its root system. There are many types of mycorrhizal association two are of major economic and ecological importance: ectomycorrhizal associations, and the endomycorrhizal association of the arbuscular- vesicular (AV) associations, the fungi invades the cortical region of the host root without penetrating cortical cells. The main diagnostic features of this type of mycorrhiza are (i) the formation within the root of a hyphal network known as the Hartig net around cortipecal cells and (ii) a thick layer of hyphal mat on the root surface known as sheath or mantle, which covers feeder roots. Infection of host plants by ectomycorrhizal fungi often leads to changes in feeder roots that are visible by the naked eye. Feeder roots colonized by the fungi are thicker and more branched than uncolonized roots; ectomycorrhizal feeder roots also tend to be colored differently in endomycorrhizal associations of the VA type, the fungi penetrate the cortical cells and form clusters of finely divided hyphae known as arbuscules in the cortex. They also form vesicles, which are membrane-bound organelles of varying shapes, inside or outside the cortical cells Arbuscules are believed to be the sites where materials are exchanged between the host plant and the fungi. Vesicles generally serve as storage structures, and can serve as reproductive structures. Vesicles and arbuscules, together with large spores, constitute the diagnostic features of the VA mycorrhizas. Roots have to be cleared and stained in specific ways and examined under a microscope to see that they are colonized by VA mycorrhizal fungi. Because vesicles are not always found in these types of mycorrhizal associations, some researchers now prefer the designation arbuscular mycorrhiza (AM) over the term vesicular-arbuscular (VA) Mycorrhiza. Both AM fungi and ectomycorrhizal fungi extend hyphae from the root into the soil, and these external (or extraradical) hyphae are responsible for translocation nutrients from the soil to the root. Most ectomycorrhizal fungi belong to several genera within the class basidiomycetes, while some belong to the zygosporic zygomycetes and ascomycetes. On the other hand, AM fungi belong to six genera within the azygosporous zygomycetes.

Host specificity

Arbuscular mycorrhiza associations occur in a wide spectrum of tropical and temperate tree species. They are known to occur in a few plants, namely members of the famlies Amaranthaceae, Pinaceae, Betulaceae, Cruciferae, Chenopodiaceae, Cyperaceae, Juncaceae, Proteaceae, and Polygonaceae. The ectomycorrhizas, on the other hand, occur primarily in temperate forest species, although they have been reported to colonize a limited number of tropical tree species.

Taxonomy of AM fungi

AM fungi show the peculiar characteristics in morphology and physiology. Spores of AM fungi are generally formed in soil and their sizes (50-500 μm in diameter) are much larger than those of other fungi. Colonization on plant roots is essential for proliferation of AM fungi. AM fungi are thus recognized as obligate symbiotic fungi. The interaction between AM fungi and plants is generally mutualism based upon nutrient exchange. Because of morphological characteristics such as no hyphal septum, AM fungi had long been recognized as a member of Zygomycota. Recent molecular phylogenetic studies showed that Zygomycota is poly-phyletic and that AM fungi should be separated from other Zygomycota. A new Phylum Glomeromycota has been proposed for AM fungi. Current classification system is summarized in Fig 1. This classification is mainly based upon the sequence data of rRNA gene. However, some new genera have been raised with relatively small numbers of isolates, so further study may revise the present classification system. In this, the morphological characteristics of representative genera are shown in the following sections. Although there is a recent trend that the sequence data of AM fungi is over-emphasized for the identification, the conventional morphological observation is still important and should not be neglected for identification.

Structural features of Arbuscular Mycorrhiza fungi:

Mainly four types arbuscules, vesicles, spore, external hyphae. Arbuscules:- Arbuscules are formed by repeated dichotomous branching and reductions in hyphal width. Arbuscules start to form approximately 2 days after root penetration. Arbuscules are considered the major site of nutrient exchange between the fungus and host. Vesicles: - Vesicles are rounded intercellular structures which act as storage organs of P and oil droplets and also function as propagules. Spores:- Spores usually develop thick walls, which often have more than one layer. Swollen structures with one or more subtending hyphae that form in the soil or in roots. They function as propagules. Spores of VAM fungi are called chlamydospores. External hyphae:- They are thick and runner type. There are different distributive hyphae as well as thin absorptive hyphae and responsible for nutrient acquisition and spore formation.

The world is on the brink of a new agriculture, one that involves the marriage of plant biology and agroecology under the umbrella of biotechnology and germplasm improvement (Vance *et al.,* 2003). One in six people in developing countries suffer from chronic hunger, so, food security at local, regional and global levels will need to be realized in the face of emerging challenges. First, we assist to the rapidly changes socio-economic environment. It is estimated that the world population will increase from about 7 to 9 billion people by 2050. The proportion living in urban areas will increase from about 50% to 70% by 2050. People's diets will change, shifting to increased proportions of vegetables, fruits and livestock products. To maintain or increase agricultural productivity and more efficient investigation and management of soil resources in agroecosystems should be practicing a sustainable agriculture, both economically and environmental protection view point. Moreover, the importance of the mycorrrhizal arbuscular fungi in organic farming and farmers' potential to increase the benefits of arbuscular mycorrhizae (AM) associations in such systems represented interesting subjects as it was synthesized by Gosling *et al*. (2006)

Rhizosphere: Concept and molecular signaling in the context of promoting mycorrhizal simbiosis

Plants growth and development is under the control of internal signals that depend on assuring adequate amounts of mineral elements from soil, to roots. Below-ground biological systems need the same care as above ground systems, as is the case of AM which are essential in sustainable management practices. Extremes changes of the chemical composition within minutes and spaces of millimeters, and the density and diversity of soil organisms play a major role. Anthropogenic action on it, namely the introduction of fertilizers and pesticides, including adding organic amendments should be also considered in terms of its influence on microbial activity, on the agricultural soils biological indicators, considering that the soil biodiversity determine economic benefits for society, as part of a broader strategy of conservation and use of the agro biodiversity. Roots are plants organs which very easily adapt their growth to the most profitable areas, thanks to a chemical communication between plant roots and between these and other rhizosphere organisms (Hause & Schaarschmidt 2009). Products of the living roots into soil (rhizodeposits) are not only a source of carbon substrate for microorganisms growth, but also signal molecules that promote chemotaxis of microorganisms in the soil, to rhizosphere (Dennis *et al*., 2010). Rhizodeposition is a carbon and energy flow which gives to the rhizosphere the characteristics of a rich habitat, as regard as nutrients supply to the heterotrophic micro-organisms.

General aspects as regard as arbuscular mycorrhizae symbiosis

Mycorrhizae are classic examples of mutualistic symbiosis, primarily characterised by carbon gain by the fungus from the plant, also a reciprocal nutrient transfer from fungus to plant, next to other effects relating to improving water relation and pathogens tolerance. Depending on their morphology and the involved plants and fungus species, it can be distinguish several types of mycorrhizae associations. The first *mycorrhizae classification* was made by Frank (1887) and subsequently there have been various classifications. For instance, based on hyphal structures, mycorrhizal interactions have been classified into ectomycorrhiza and endomycorrhiza recommended to define and classify mycorrhizal association by anatomical criteria, regulated by the host plant. He also provided a new classification scheme for categories, subcategories and morphotypes.

Plants compatibility with mycorrhizal fungus

is a widespread and an ancient phenomenon. Fossil samples suggest that this kind of symbiosis have been with more than 400 million years ago, in the tissues of the first terrestrial plants (Remy *et al*. 1994). Plant capacity to form AM must be under the control mechanisms that were preserved in the new plant species that occurred during evolution, involving selective recognition processes and certain specific plants to discriminate between beneficial microorganisms and harmful ones. The molecular basis of this process started to be understood and point to common signaling pathways shared with other microbe plant associations and to AM specific signaling pathways.

Symbiotic relationships involve the development of specific adaptations for both partners and coordination of their development, with specific signals (Hause & Schaarschmidt, 2009). Plants produce an early signal, to initiate interaction, and fungus produces at least three signals: one diffusible, the second locally, allowing the plant to detect the appresorium position and last one, an autonomously cell signal, in the colonized cells which induces gene expression. As regard as the molecular bases of this interaction, there are already published a number of research results and of course researches continue. The fungus invades the root, both intercellular and intracellular, determines extensive cytological changes, as well as in terms of pathogenesis related proteins (PR proteins) (Gianinazzi-Pearson *et al*. 1996). Plastids appear to be key cell organites to establishing symbiotic interface in the case of arbuscular mycorrhiza (Fester *et al*. 2007).

Arbuscular mycorrhizae benefits in the context of agroecosystems sustainability

Mycorrhizae have a particularly importance for plants and ecosystem. From the biological view point, mycorrhizal fungus affects two aspects of sustainable agriculture: plant production and soil quality. The beneficial effects of mycorrhizae fungus on plants performances and soil health are essential for sustainable management of agricultural ecosystems (Celik *et al*. 2004) Arbuscular mycorrhizae have multiple functions in the effective exploitation of soil mineral resources and because of their bioprotective role against many soil pathogens are suitable tools for survival of many species of plants in different ecosystems, including many species of cultivated plants.

Inoculation of AMF to the roots micropropagated plantlets play a beneficial role on their post-transplanting performance: development of a superior root system; increased photosynthetic efficiency; enhanced nutrient uptake; alleviate environmental stress; averts attack by harmful soil borne pathogens. The cooperation between micropropagation and mycorrhizal inoculation is an important tool in more sustainable horticultural production in vitro raised plantlets of *Terminalia bellerica* were biotized using an endosymbiotic root fungus *Piriformospora indica* during their hardening and acclimatization. Improved overall growth and higher rate of survival were observed with colonized plantlets. The fungus colonized in more than 80% of inoculated plantlets and about 90% of such plantlets showed survival in the greenhouse and subsequent under nursery shed. Colonization of fungus also promoted root growth, increased biomass and total chlorophyll content in inoculated plantlets. In the early phase of colonization strigolactone (SL) production is still high. Initially the AMF is perceived as an alien organism and as a consequence salicylic acid (SA) levels increased. In a well-established mycorrhiza both SL and SA production are repressed while biosynthesis of jasmonates (JA).

Factors Contributing to Utilization of VAM by Plants

Climatic and edaphic factors such as temperature, rainfall, light, atmospheric CO_2, soil pH, moisture content, fertility level and density of inoculums have significant influence on VAM and root colonization. The influence of climatic and soil factors vary with plant species and can be positive or negative.

Climatic Factors

The effects of climatic factors on VAM root colonization and diversity are complex. In the relationship between light, temperature, rainfall, atmospheric CO_2 and VAM colonization, positive (Li and Zhao, 2005) as well as negative correlation have been observed. It is generally considered that of light were positively correlated with mycorrhizal colonization (Koide and Mosse, 2004), and higher light levels can enhance the efficiency of photosynthesis, which can contribute more carbon compounds to VAM growth. Light duration and intensity increased VAM colonization and spore density of most plant species Although VAM colonization has been found in plant at temperature as low as 5^oC, a temperature range of 18-40^oC with the optimum for most fungal-host species near 30^oC are usually observed (Entry et al., 2002; Smith and Read, 1997). The influence of temperature on arbuscular mycorrhizal plants appears related to the exact fungal-host species combination, the development stage of the plant, temperature controlling fungal germination, photosynthesis and carbon flow to roots.

Soil Factors

Soil condition is also an important factor in the extent of VAM root colonization and diversity. Soil pH, moisture, nutrient status and texture have shown correlation with VAM root colonization and diversity (Klinomoros et al., 2001; Miller and Jackson, 1998). Soil pH influences VAM fungal species composition, colonization and effectiveness (Van Aarle *et al*., 2002). It has been reported that spore germination, hyphal elongation and infection with VAM fungi are suppressed on acidic or alkaline agar or soil (Van Aarle et al., 2002). On the contrary, Ulhamm (2006) and Siquiera *et al.* (1984) reported no significant correlation between colonization, spore density and spore pH. In China, Glomus sp. appears to dominate in alkaline and neutral soils while Acaulospora sporulate more abundantly in acid soils

Agriculture, Tillage and Phosphorus Fertilizer

Many modern agronomic practices are disruptive to mycorrhizal symbiosis. There is great potential for low input agriculture to manage the system in a way that promotes mycorrhizal symbiosis. Conventional agriculture practices, such as tillage, heavy fertilizers and fungicides, poor crop rotations and selection for plants which survive these conditions, hinder the ability of plants to form symbiosis with arbuscular mycorrhizal fungi. Most agricultural crops can perform better and are more productive when well colonized by VAM fungi. VAM symbiosis increases the phosphorus and micronutrient uptake and growth of their plant host (George et al., 1992). Management of VAM fungi is very important for organic and low agriculture systems where soil phosphorus is generally low, although all agroecosystems can benefit by promoting arbuscular mycorrhizae establishment. Some crops that are poor at seeking out nutrients in the soil are very dependent on VAM fungi for phosphorus uptake. Heavy usage of phosphorus fertilizer can inhibit mycorrhizal colonization and growth. As the soil's phosphorus levels available to the plants increases, the amount of phosphorus also increases in the plant's tissues and carbon drain on the plant by the VAM fungi symbiosis become non-beneficial to the plant (Grant *et al.*, 2005). A decrease in mycorrhizal colonization due to high soil phosphorus levels can lead to plant deficiencies in other micronutrients that have mycorrhizal mediated uptake such as copper (Timmer and Leyden, 1980)

Tillage reduces the incoculation potential of the soil and the efficacy of mycorrhizaes by distrupting the extraradical hyphal network (Miller *et al*. 1995; Mozafar *et al*. 2000). By breaking apart the soil macro structure the hyphal network is rendered non-infective (Miller *et al.*, 1995; McGonigle and Miller, 1999). The distruption of the hyphal network decreases the absorptive abilities of the mycorrhizae because the surface area spanned by the hyhae is greatly reduced. This in turn lowers the phosphorus input to the plants which are connected to the hyphal network (McGonigle and Miller, 1999). In reduced tillage system heavy phosphorus fertilizer input may not be required as compared to heavy tillage systems. This is due to the increase in mycorrhizal network which allows mycorrhizae to provide the plant with sufficient phosphorus

Perennialized Cropping Systems

Cover crops are grown in the fall, winter and spring, covering the soil during periods when it would commonly be left without a cover of growing plants. Mycorrhizal cover crops can be used to improve the mycorrhizal inoculums potential and hyphal network (Kabir and Koide, 2000; Boswell *et al.*, 1998; Sorensen *et al.*, 2005). Since VAM fungi are biotrophic, they are dependent on plants for their hyphal networks. Growing a cover crop extends the time for VAM growth into the autum, winter and spring. Promotion of hyphal growth creates a more extensive hyphal network. The mycorrhizal colonization increase found in cover crops systems may be largely attributed to an increase in the extraradical hyphal network which can be colonize the roots of the new crop

Soil Quality

Restoration of native VAM fungi increases the success of ecological restoration project and the rapidity of soil recovery (Jeffries *et al*., 2003). There is evidence that this enhancement of soil aggregate stability is due to the production of a soil protein known as glomalin. Glomalin related soil proteins (GRSP) have been identified using a monoclonal antibody (Mab32B11) raised against crushed VAM fungi spores. It is defined by its extraction conditions and reaction with the antibody Mab32B11. There is other circumstancial evidence that glomalin is of VAM fungal origin. When VAM fungi are eliminated from soil through incubation of soil without host plants the concentration of GRSP declines. A similar decline in GRSP has also been observed in incubated soils from forested, afforested and agricultural land and grasslands treated with fungicide (Rilling *et al*., 2003). Glomalin is hypothesized to improve soil aggregate water stability and decrease soil erosion. A strong correlation has been found between GRSP and soil aggregate water stability in a wide variety of soils where organic material is the main binding agent, although the mechanism is not known

Arbuscular Mycorrhizal Fungi and Sustainable Soil health

Soil structure exerts important influences on the functioning of soil, its ability to support plant and animal life, controlling environmental quality with special emphasis on soil C sequestration, nutrient and gas fluxes and water quality. Soil structure is often expressed as the degree of stability of aggregates being a major factor which moderates physical, chemical, and biological processes leading the soil dynamics (Bronick and Lal, 2005). Soil aggregates results from a combination of primary mineral particles with organic and inorganic materials. This process, dynamic and complex, is influenced in turn by the interaction of several factors including environmental components, soil management, plant effects but largely by soil properties. Among these the most significant are moisture availability, mineral composition, soil texture, the quantity and quality of SOM, microbial and enzyme activities, mineral nutrients and others such as polycations, etc. Soil aggregation, begins with the consolidation of soil particles into microaggregates (< 250 µm) and further formation of macroaggregates (>250 µm). The mechanism involved in soil aggregation is complex but in general is viewed as microaggregates being formed from organic molecules tied to clay and polycations, which in turn are linked with other microaggregates to form macroaggregates. Briefly, aggregation is the result of rearrangement, flocculation and cementation of soil particles where soil organic carbon, polycations, clay, minerals and, especially biota are playing a key role. The wide variety on chemical nature of soil organic compounds determines its formation and decomposition rates which induce transient or prolonged effects. However, all factors for soil aggregates formation are directly or indirectly related in this process (Chenu *et al*., 2000). Therefore, the effect on aggregation of labile sources of organic C is transient whereas carbon sources with higher stability increase the permanence of such effect (Schulten and Leinweber, 2000). Chorover *et al*. (2004) studying a weathering chronosequence of volcanic soils in Hawaii found that aliphatic and aromatic components of organic matter dominate humic acids in later stages of soil development. Particulate organic matter may be an important factor in the formation of macroaggregates throughout direct binding action over microaggregates or indirectly through the polysaccharides produced by microorganisms when metabolizing POM (Jastrow, 1996).

Polycations

Polyvalent cations such as Aluminum and iron habitually found in acidic soils improve soil aggregation through bridges formation between inorganic minerals or clay and soil organic carbon. Aggregates containing clays and Al and Fe oxides or hydroxides promote soil organic C incorporation conferring aggregate stability, especially in volcanic soils. Recently, consequently, the use of soil amendments such as lime, gypsum or dolomite can have significant effects on soil aggregates formation.

Clay minerals

Clay minerals influence properties affecting soil aggregation. As clay interacts with soil organic carbon and both are intimately related with aggregates. All soil properties affecting one also affect to the other and soil aggregation as a whole. Thus, pH, CEC, ions and the nature of mineralogy influence soil aggregation. In general, aggregation is high in high-activity clays and soil organic carbon is associated to high CEC. Non-crystalline clay minerals such as allophane and imogolite, both typic from Chilean volcanic derived soils, with high variable charge tend to produce high aggregation. Clay type also affect decomposition rate of soil organic carbon.

Biota

There is consensus that among soil biota, fungi are the most important agents involved in soil aggregation through fungal mycelia network, although roots and bacteria have a significant role as well The role of fungi in soil aggregation can be passive) due to a physical network of hyphae maintaining soil particles together active by cementing capacity of the extracellular compounds released. Among this, arbuscular mycorrhizal fungi (AMF) appear to play a predominant effect on aggregates formation because the symbiosis significantly changes the root functioning. They also have vast and more extensive hyphal mycelia in comparison with saprobic fungi. It is also known that plant species may differ in their effects on soil aggregation, in agricultural soils as well as in natural ecosystems (Eviner and Chapin, 2002; Pietrowski *et al*., 2004) and, consequently, changes in plant community are also affecting soil structure. However, as AMF diversity affects plant community composition soil aggregated in turn will be influenced (van der Heijden *et al*., 1998).

CONCLUSION

Arbuscular mycorrhizae (AM) are widespread symbiotic associations where both partners benefit from the reciprocal nutrient exchange. AM symbiosis improve the absorption of the nutrient elements those are of low mobility in soil, particularly N, P as well as the different micronutrients like Cu, Zn hence improves the plant growth and yield of many crops. Among the different Arbuscular mycorrhizal fungi, *Glomus mosseae* exihibits the best mycorrhizal efficiency on growth and nutrient acquisition of plants. It also acts as a Bio-control agent for control of plant diseases and root-knot nematode which in turn results in better health of the plant. So, emphasis should be given for efficient utilisation of AM fungi in plant nutrition and bio-control of pests for better crop yield. Soil structure stability is strongly influenced by the nature and content of soil organic matter. Land use and management practices influencing SOM will be determinant in soil aggregation. That gives the most importance of soil aggregation to the functioning in the ecosystems.

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