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Review Article

To Understand Arbuscular Mycorrhizal Fungi: A Magical Root Symbiont for Global Sustainable Agriculture

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Microbial populations are key component of soil plant system where they are immense in a network of interactions affecting plant development. Several symbiotic groups, phosphorus solubilizers, plant growth promoters and other such beneficial important micro- organisms are reported from different soils. Balanced microbial system contributes to the sustainability in agriculture, horticulture, forestry and range management. In this regard, an excellent example of microbe- plant mutualism is 'Mycorrhiza'. The mycorrhizal symbiotic association appears to have evolved with plants since the colonization of dry land by plant began as a survival mechanism for fungi and higher plants, thus allowing each to survive in the existing environment of low temperature, low soil fertility, periodic drought, diseases, extreme environments and other stress situations [1].
Among the different types of mycorrhiza, arbuscular mycorrhizae (AM) are the important beneficial micro- organisms of the soil edaphon in most agro-ecosystems. AM, the mother of plant root endosymbiosis, is a wide spread mutualistic symbiosis between land plants and fungi of the phylum Glomeromycota. Kilronomos and Kendrick's [2] statement that, "We may know less that we think about mycorrhizas, since we have consistently based broad hypothesis and conclusions on studies of a small number of taxa", emphasizes the greater diversity of AM. The majority of plants, strictly speaking, don't have roots, they have mycorrhizas. Agricultural sustainability could be viewed as 'maximum plant production with minimum soil loss'. The study of endomycorrhizal biodiversity on some important plants is necessary from efficient utilization and conservation point of view. The management of their population in the soil is an essential tool for overall plant health in the present scenario of sustainable crop productivity. The presence or absence of a host plant has an important role to complete the life cycle of these fungi show host preference to grow. Hence, these fungi are incapable of saprophytic survival and can only be grown with a host plant [3,4,5]. Because of the wide number of hosts all over the world, different soils are involved.

HOST SPECIFICITY OF AM FUNGI

Arbuscular mycorrhizal associations occur in a wide spectrum of agricultural crops, most shrubs, tropical tree species and some temperate tree species. It has been found in some gymnosperms, pteridophytes, bryophytes and in some floating and submerged aquatic plants. A recent analysis of phylogenetic distribution of mycorrhizal occurrence among different species of land plants shows that the AM is the predominant and ancestral type of mycorrhiza. Its occurrence in early divergent lineages of liverworts suggests that the origin of AM probably coincided with origin of land plants [6]. Families, not forming AM include Betulaceae, Orchidaceae, Fumariaceae, Commelinaceae and Ericaceae. Families that rarely form AM include the Brassicaceae, Chenopodiaceae, Polygonaceae and Cyperaceae. Although AM is confined to the roots, they have been reported in diverse structures such as the modified leaves of water fern, *Salvinia cucullata*, fruiting peg of peanut and modified scale like leaves and rhizomes of ginger and canna [7].

MORPHOLOGICAL DIVERSITY OF AM FUNGI

Morphological characters that are stable and discrete are generally used to identify and classify the arbuscular mycorrhizal fungi (AMF). The different morphological characters considered in this microbial interaction are described below:-

Hyphal Characters:

Based on their function, the vegetative hyphae have been differentiated into infective, absorptive and runner hyphae. Fungal hyphae are filamentous network, which tends to form various shapes such as H- shaped parallel connections in *Glomus*, constricted hyphae near branch points as in *Acaulospora* and *Enterophospora* and coiled, swollen and irregularly projections or knobs as in *Gigaspora* and *Scutellospora* [8].

The mycelia also form specialized structures like arbuscules, vesicles and auxillary cells as described below:

Arbuscules:

All the Glomalean fungal species form arbuscules which are small tree like, hyphal filled, invaginations of cortical cells that provide intimate contact between the plasmalemma of two symbiotic partners and are, presumably, the point of material exchange between host and fungus. Abrupt narrowing off of branch hyphae reduction in hyphal width forms arbuscules in *Gigaspora* and *Glomus* respectively [9]. At the later stage, arbuscules are digested by host cells. Firstly, tips are eroded and then entire arbuscules are dissolved and digested.

Vesicles:

Vesicles are spherical to oval, sac like globular to elongated terminal swellings of the hyphae or are intercalary aseptate which develop after the development of arbuscules. They have fat granules that serve as storage organs of the fungus. Vesicles in Glomaceae are sub- globose to elliptical, where as in Acaulosporaceae they are pleomorphic and knobby [10]. Vesicles are produced in enormous number later in the seasons as the plant mature.

Auxillary Cells:

Auxillary cells are cluster of thin walled cells. They differ in shape, size and surface ornamentations. These are only restricted to the sub-order Gigasporaceae [11]. Functionally, they act as a temporary storage structures of carbon compounds.

Subtending Hyphae:

Besides arbuscules and vesicles, an another morphological feature of AM fungi is the stalk of the spore, known as subtending hyphae or sporophore, has importance in identification. Subtending hyphae may be absent as in *Acaulospora*, simple, straight or curved (*Glomus*), swollen and straight, but often appear sessile due to detachment from saccule and two scars present on either side of the spore (*Enterophospora*) and sporophore bulbous as in *Gigaspora* and *Scutellospora* [1].

Spore, Sporocarps and Sub-cellular structures:

AM fungal spores may be azygospores or chlamydospores and formed singly or aggregated in sporocarps. Spores are variable in size and ranging from 10-1000μm. The spores colour also varies from hyaline, yellow, reddish-brown, orange, brown and black. The different shape of the spores may be globose, sub- globose, ovoid, pea shaped, ellipsoid, obovoid, reniform or irregularly elongated. Seven kinds of wall layers have been described in AM spores, namely evanescent, unit, laminated, membranous, coriaceous, amorphous and expanding [1]. The cytoplasm in the spores may be reticulate or vacuolated.

Appresoria- Appresoria are hyphal swellings between two adjacent root epidermal cells. These are the sites where hyphae first penetrate root cells by exerting pressure and/ or by enzymatic activity.

Colony- A colony refers to hyphal colonization of a root resulting from the same external hyphae. These are also called infection units.

ECOLOGICAL DIVERSITY OF AM FUNGI

Arbuscular mycorrhiza (AM) is an ecologically important and more or less uniform distributed symbiotic association. Some of them may be predominant in certain areas with broad ecological range [12]. AM fungi like other soil fungi occur in the top 15-30 cm. of soil and their number decreases with increasing depth [13]. Geographically, AM fungi are ubiquitous and establish mutualistic relationship over 90% of vascular plant species [14]. The distribution of species of AM fungi is affected by climatic and edaphic conditions e.g. *Glomus* is found in acidic soil, *Gigaspora* and *Scutellospora* in tropical soils and *Acaulospora* favours the soil of pH below 5. Regarding the dispersal of AM fungi, it occurs through AM propagules, like mycelia and spores, which can be moved by biotic and abiotic agents. Dispersal of AM spores over greater distances is dependent upon passive dispersal by wind and water, while animal dispersal of AM spores occurs through ingestion and egestion. Reynolds *et al*. [15] reported that this plant microorganism interaction is highly dependent upon the soil environment, pH, moisture availability, nutrient availability and presence or absence of other microbes.

BIOLOGY OF AM FUNGI

AM fungi are obligate biotrophs and in the absence of hosts, they are present as multinucleate spore with thick wall and subtending hyphae. All AM fungi have been described to date reproduce only by asexual mean [16]. These fungi are believed to reproduce clonally via spores, vesicles and hyphae. When the conditions are favorable, the spore of Glomeromycota starts to germinate, form appressoria on host roots and establish a new mycorrhizal symbiosis. Sporewall is the first individual structure to be formed, which originates from the wall of sporogenous hyphae. Within this, phenotypically distinctive layers are synthesized and when the time of dirrentiation completes, each layer acquires its own unique properties. After coming in contact with roots of the host plants, the plants are thought to release some exudates which stimulate the germination of spores. After entering in the roots, AM fungi penetrate into the cortical cells and ultimately form structures like arbuscules and vesicles and then involved in the nutrient and carbohydrate transfer [17]. There is no evidence that the Glomeromycota reproduce sexually [18,19].

TAXONOMIC DIVERSITY OF AM FUNGI

In the present scenario, the major thrust area of research is the scientific classification of AM fungi. Due to the absence of fossil records, it is difficult to develop a non controversial scientific classification system of AM fungi. Taxonomy is entering a new phase and many researchers have attempted to propose a suitable classification for AM fungi on the basis of morphological, biochemical and molecular genetics techniques.

The vesicular arbuscular mycorrhiza forming fungi were classified as the member of Zygomycota and were placed under the order Glomales [20]. But, the gene encoding analysis of the small subunit (18S) ribosomal RNA show the AM fungi are not related to Zygomycota and probably share common ancestry with Ascomycota and Basidiomycota. So, they have been assigned to a new monophyletic group, Glomeromycota [16]. Based on data from molecular, morphological and biochemical investigations, Mortan and Redecker [21] erected two new families in the order Glomales i.e. Archaeosporaceae and Paraglomaceae with two new genera *Archaeospora* and *Paraglomus* respectively. The ordinal name 'Glomales' has now been changed to Glomerales and phylum Glomeromycota has been divided into four orders i.e. Glomerales, Paraglomerales, Diversisporales and Archaeosporales [16]. Several taxonomic and phylogenetic relationships of AM fungi based on molecular characterization have also been reviewed by Reddy *et al.* [22]. As the number of AM species is increasing day by day, it is quite pertinent to revise the classification of these fungi. The genera, which form AM fungal association are *Acaulospora, Ambispora*, *Archaeospora*, *Diversispora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Intraspora*, *Kuklospora*, *Otospora*, *Pacispora*, *Paraglomus*, *Sclerocystis* and *Scutellospora* [16,20,23,24,25,26].

POTENTIAL ROLE OF MYCORRHIZAL FUNGI

The one of the most significant events in the terrestrialization of plant was the evolution of biotrophic root inhabiting symbiosis. The tremendous advances in research on mycorrhizal physiology and ecology over past few years have led to a greater understanding of the multiple roles of mycorrhizal fungi in ecosystem. Some of the benefits of mycorrhizal fungi are described as following:

Rehabilitation and Reclamation of waste land:

The establishment of a plant cover is the most important step in restoration of degraded areas. Transplanting native plants inoculated with AMF is a good system to establish shrubs and trees in eroded semi arid lands [27,28,29]. The soils of disturbed sites are frequently low in available nutrient which results in poor growth of plants. AM fungi is known to enhance fertility of soil [30,31] and inoculation of plants with AMF in wasteland improves absorption of nutrient and significantly increase the growth of plants.

Phytoremediation:

Ecosystems have been contaminated with heavy metals due to various human and natural activities. The use of AM fungi in ecological restoration has been shown to enable host plant establishment on degraded soil and improve soil quality and health [32]. The significance of AM fungi in plant survival in metal contaminated soils have been well documented by several workers [33,34,35].

Production of Plant Growth Hormones:

Roots colonized by AM fungi have often much branched root hairs. Such changes in morphology are expected to be under phytohormonal control [36]. Abscisic acid (ABA) was found to be considerably enhanced in mycorrhizal plants than non- mycorrhizal plant [37]. The production of growth hormones by mycorrhizal fungi such as IAA (Indole Acetic Acid), gibberellin, cytokinin, auxin and growth regulators like Vitamin B have been well documented by many researchers (1,36,38]. The AM fungi are also known to enhance enzyme activities in plants.

Biohardening:

Mycorrhization of micropropagated plantlets is having a positive impact on their post transplanting performance [39]. AM fungi modify root architecture for better nutrient uptake and hence increase the survival rate of plantlets. The significant role of AMF in establishment of micropropagated plant has been studied in *Leucaena leucocephala* and *Scutellaria integrifolia* [40,41].

Soil aggregation and Stability:

Soil aggregation is essential to maintain soil physical properties and facilitate biochemical cycling. AM fungal hyphae and the production of glycoprotein, 'Glomalin' by AM fungi has a cementing capacity to maintain soil particles together, is mainly involved in soil aggregation [42]. Hyphae of AM fungi are considered to be primarily soil aggregators and there is a positively correlation between AM fungal hyphae and aggregate stability in natural systems [43,44].

Alleviation of Environmental Stress:

AM fungi have a pronounced effect to alleviate various environmental stresses. AM fungal symbiosis can protect host plants against detrimental effects such as drought, water stress and soil salinity stress [45,46,47,48,49]. AM inoculation has a high potential as a bio-fertilizer in water stress environment [46].

Increased resistance to root pathogens:

AM fungi are recognized as high potential agents in plant protection and pest management. Mycorrhizal colonization provides a bioprotectional effect against a broad range of soil borne fungi and nematodes [50,51,52]. In several cases direct biocontrol potential has been demonstrated, especially for plant disease caused by *Phytophthora*, *Rhizoctonia*, *Pythium*, *Alternaria* and *Fusarium* pathogens [53,54,55,56]. Several studies have confirmed synergism between AMF and biocontrol agents such as *Burkholderia cepacia* and *Trichoderma viride* [57,58]. AM fungi are known to increase the resistance of plants to pathogens by cell wall modification, production of antimicrobial compounds and altered rhizosphere microflora. The AM fungi might affect plant and soil microbial activity by stimulating the production of root exudates, phytoalexins and phenolic compounds [59,60].

Effect on Plant Diversity:

The community of AMF determines the plant community structure by the response of individual plant species to colonization by single or multiple species of AM fungi. Diversity of AM fungi is a major factor in the maintenance of plant biodiversity and to ecosystem stability and function. AMF can enter the roots of many plant species in the same community resulting in simultaneous colonization by several species of AM fungi which result in interconnection of plants via. extra radical mycelium [61].

Uptake and Transfer of mineral nutrients:

The major role of AM fungi on host plant is to enhance nutrient mobilization. AM fungi colonize plant roots and ramify into the surrounding bulk soil extending the root depletion zone around the root system which transports water and mineral nutrients from the soil to the plant. AM fungi are well known to improve the absorption of all the nutrients required by plants for their growth such as P, K, Zn, Cu, Mg, Mn and Fe. Hyphae of the AM fungi can also take up amino acids and orthophosphate

[62,63]. The enhanced effect of AM fungi on the uptake of water and nitrogen mineralization from organic residue has been well documented [64,65].

Phosphorus Uptake:

AM fungi play a greater role in order to supply infected plant roots with phosphorus because P is an extremely immobile element in soil. As AM fungi increases the surface area of plant roots and resulted in more proliferation of fibrous roots and hence increase uptake of more phosphorus [66]. Alkaline phosphatase activity is related to phosphate metabolism as it is present in the fungal vacuole where polyphosphate granules are present. In the fine branches of arbuscules, these granules are broken down by activity of enzymes and release inorganic phosphorus in the cytoplasm. An increase in phosphorus uptake in mycorrhizal plants than non- mycorrhizal plants has been documented by several workers [67,68,69].

Increased Nitrogen Fixation:

The tripartite interaction between nodulating legumes, AM fungi and nitrogen fixing *Rhizobium* frequently result in increased level of nodulation and nitrogen fixation as the result of improved P nutrition in infertile or P fixing soils [70]. The ease of isolation and use of *Rhizobium* species has masked their crucial interaction with AM fungi. The specific AM fungi and *Rhizobium* can interact on the same plant to produce different growth and development of the legumes [44].

Widespread distribution both in terms of habitats and host species, symbiotic relationships, host growth promotiveness and protection, non specificity for host, positive interaction with other rhizosphere microbes and several other characteristics of AM fungi have obviously forced to find out their practical aspects. Their potential can be best exploited in agricultural crops, which could be grown well under soils of poor fertility and marginal soils. However, more studies is to be emphasized in order to select the suitable indigenous AM fungal strains for establishment and management of natural ecosystem and to make the people conscious about the role of mycorrhiza as a tool to maintain and manage the plant biota by environmental friendly approach.

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