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REVIEW

Arbuscular Mycorrhizal (AM) fungi for sustainable agriculture

K. M. RODRIGUES AND B. F. RODRIGUES*
Department of Botany, Goa University, Goa 403 206, India.

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Arbuscular mycorrhizal (AM) fungi are obligate biotrophic symbionts that form a mutualistic association with plant roots. They are directly involved in plant mineral nutrition and environmental stress tolerance. Most crop plants are symbiotic with AM fungi, and the ability of AM fungal symbiosis to improve crop production is widely recognized. This paper highlights the efficacy of AM fungi as a vital component of sustainable crop production systems, and it's prospective for exploitation as an on-farm agro-input.

Key words : Sustainable agriculture, arbuscular mycorrhizal fungi, ecological processes, AM fungal diversity, biofertilizer

INTRODUCTION

Sustainable agriculture is a method of agricultural production, which chiefly excludes the usage of synthetic agro-inputs (chemical fertilizers and pesticides) and to the maximum extent relies upon the application of environmentally friendly organic agro-inputs (organic wastes and beneficial microbes), thereby promoting and enhancing overall agroecosystem health including biodiversity, biological cycles, and soil biological activity. Some of the latest estimates predict that by 2050, the world's population will reach 9.1 billion, 34 percent higher than today, hence emphasizing the need to increase agricultural productivity (FAO, 2009). The global demand for crops certainly accentuates the necessity to implement eco-friendly agrarian management practices for sustainable agricultural production (Islam and Katoh, 2017).

As a result, the scientific community all over the world is continuously searching for economically viable, socially safe, and environmentally sustainable on-farm resources. Thus the focus shifts increasingly towards the role of soil microbial diversity in general and particularly arbuscular mycorrhizal (AM) fungi in achieving this in a sustainable manner (Bender *et al.,* 2016; Thirkell *et al*., 2017; Sosa-Hernández *et al*., 2019). Soil microbes play an imperative role in most biological transformations, including nutrient recycling, which facilitates the subsequent establishment of plants. Fungi are the most efficient soil microorganisms involved in soil-structure stabilization, and AM fungi often comprise the significant fraction of the soil microbiome.

Arbuscular Mycorrhizal (AM) fungi

Arbuscular mycorrhiza (AM) which constitutes 72% of various types of mycorrhizas (van der Heijden *et al*., 2015; Brundrett, 2017), is ecologically an important type of mycorrhiza which is most widely commercially exploited in agricultural production systems (Owen *et al*., 2015; Rillig *et al*., 2016). AM fungi are ubiquitous soil fungi that form a mutualistic relationship with most land plants. These fungi are a monophyletic lineage of obligate mycobionts belonging to phylum Glomeromycota. As the phylum is evolutionarily an ancient form of symbiosis in plants, about 90% of existing plant species are mycorrhizal, including many crops (Moënne-Loccoz *et al.,* 2015; Brundrett and Tedersoo, 2018), therefore leading to an array of positive effects in both natural ecosystem and agricultural biotas (van der Heijden *et al*., 2015).

***Corresponding author : felinov@gmail.com**

AM fungal-plant root interaction for the establishment of symbiosis

AM fungi are present as chlamydospores (spores) colonizing plant roots in the rhizosphere. In the asymbiotic fungal growth phase, a chlamydospore will germinate by forming aseptate and thick-walled hypha (permanent hypha). Thin-walled short-lived hyphae arise from the permanent hypha and grow along with the roots. The exploratory hyphal growth changes dramatically in the presence of signals derived from plant root exudates (strigolactones) resulting in the development of pre-symbiotic fungal growth phase characterized by profuse hyphal branching, increased physiological activity and continued hyphal growth (López-Ráez *et al*., 2011). It takes one to several weeks for the establishment of host root contact by the fungal hyphae. Once the fungus-plant root contact is established, changes in the fungal morphology and metabolism occur radically, marking the initiation of the symbiotic phase. AM fungi produce mycorrhiza (Myc) factors that can induce calcium oscillations in root epidermal cells and activate plant AM symbiosis-related genes (Bonfante and Genre, 2010). At the point of contact with the plant root, the hyphae bear appressoria and penetrate the root hair or epidermis to reach the cortex, bifurcating intra- and inter-cellularly from the point of entry, leading to the development of intra-radical structures (hyphae, arbuscules, vesicles) in the cortical cells of the root and extra-radical structures (hyphae and spores) in the soil. Arbuscules are repeated dichotomously branched tree-like structures that are formed intra-cellularly within the cortical cells. They act as a site of nutrient exchange and are responsible for transferring carbohydrates from the host plant tissues to the fungus, and supplying mineral nutrients and water from the fungus to the host plant (Rich *et al.,* 2017). Vesicles are thin or thick-walled oval structures that are formed inter- and intra-cellularly within the cortical cells. They act as storage structures, storing materials like lipids, poly-phosphate, and other minerals. Vesicles also function as propagules (chlamydospores) in older roots. AM fungi also produce a mycelial network outside the root in the soil known as the extra-radical mycelium, where spores and sporocarps are produced along with mycelium that serves as propagules to complete the AM fungal life cycle (Barea *et al.,* 2013; Gupta, 2017). The AM fungal inoculum, which includes soil-based propagules (spores, extra-radical hyphae, and colonized root fragments) allows AM fungi to colonize new plant roots through an established extra-radical mycelial network in the soil (Muller *et al.,* 2017).

Agro-ecological functions of AM fungi

AM fungal association is characterized by a bidirectional nutrient flux wherein the mycobiont helps the phytobiont in the acquirement of soil nutrients (mainly P) while the phytobiont provides photosynthates (carbon sources) to the mycobiont (Wipf *et al.,* 2019). The basis of this symbiotic association is the ability of AM fungi to form fine hyphae with a more favourable surface area-to-volume ratio for nutrient uptake and to secrete enzymes or organic acids to mobilize nutrients (Owen *et al*., 2015). AM fungi are primarily known for their capability to increase plant growth and productivity by augmenting macro- and micro-nutrient acquisition (Smith and Smith, 2011; Hart and Forsythe 2012; Pellegrino and Bedini 2014). AM fungal symbiosis allows better plant phosphorus uptake from soils with low levels of available P (van der Heijden *et al.,* 2015); they help in the uptake of nitrogen from the soil and increase the utilization of different forms of N (Jacott *et al.,* 2017); they also contribute in the uptake of calcium, iron, manganese, zinc, copper, sulphur, potassium, magnesium and aluminium in host plants (Hart et al., 2017). AM fungi are most beneficial in improving plant nutrient acquisition, especially in low-fertility soils. It is widely believed that AM fungi can serve as an alternative for inorganic fertilizers because their application can effectively reduce the quantitative use of chemical fertilizer input, especially P (Ortas, 2012).

Besides nutrient acquisition, AM fungi also influence a wide range of other host benefits and ecosystem processes. Such as resistance to several abiotic stress factors (Sun *et al*., 2018); safeguarding the host plants from pathogenic infections (Jung *et al*., 2012), hence AM fungi can be utilized as biocontrol agents. AM fungal symbiosis also stimulates the synthesis of several plant secondary metabolites *viz.,* polyphenols, phytosterols, vitamins, lignins, terpenoids, and carotenoids for increased plant tolerance to abiotic and biotic stresses. The formation of phytotoxins, chitinases, glucanases, peroxidases, PR proteins, phenolics, and hydroxyl proline-rich glycoproteins as defense responses also increases in host plants upon association with AM fungi (Smith *et al.,* 2010). Initiation of AM fungal symbiosis causes the host plants to secrete organic acids, polysaccharides, phenolic compounds, amino acids, and enzymes like phosphatases as exudates from the root system, which favours the growth of AM fungi and host plant. This also has a positive effect on the associated microbiome functioning (Gupta *et al.,* 2018a, b). Improved soil stability, binding, and water retention by the AM fungal hyphae through the ramifying extra-radical mycelial network and secretion of hydrophobic "sticky" proteinaceous substance (glomalin) in the soil, consequently reducing soil erosion. AM fungi, through their extensive extra-radical mycelial network, interconnect several unrelated individual plant species, consequently impacting the function and biodiversity of the entire ecosystem (Bonfante and Genre, 2010). AM fungi also positively influence nutrient cycling, energy flow, and plant establishment in disturbed ecosystems.

Moreover, AM fungi are involved in bioremediation of soil. They help in alleviating heavy metal toxicity to plants by reducing metal translocation from root to shoot. Therefore, they contribute to revegetation and restoration of disturbed or contaminated lands. Thus, AM fungi are imperative endosymbionts playing an efficient role in plant growth and productivity along with the functioning of the ecosystems. They are of immense significance for sustainable crop improvement (Gianinazzi *et al.,* 2010).

Significance of AM fungal diversity and dominance in sustainable agriculture

Ecosystems and plant life are widely influenced by the functionally diverse nature of AM fungi, the symbiosis is considered as a tripartite relationship between plant, fungus, and soil where the fungus creates a close link between the soil and the plant. AM fungi co-exist as assemblages of mixed species in terrestrial ecosystems with certain species being dominant, and a plant may be colonized by several AM species at one time. Most of the AM fungal species are widespread occurring in different terrestrial habitats and are considered 'generalists', however some species appear to be restricted to particular ecosystem types and are considered 'specialists'. According to the latest estimates, approximately 300 species of AM fungi have been reported from all over the world (Öpik *et al.,* 2013). In India, more than 161 species have been reported (Gupta *et al*., 2017). Studies from India showed that *Funneliformis mosseae* is the most widely distributed species, and the genus *Glomus* is represented by the highest number of species (Gupta *et al.,* 2014).

Different soil types showing variation in AM species can be characterized by AM fungal community structure (Oehl *et al*., 2010). AM taxa differ significantly in their life histories and are believed to be nonspecific about their capability to infect and colonize different plant species, although there may be exceptions. There is also variation in response to soil structure, mineral acquisition, plant health, growth rate, biomass allocation, and symbiotic effects. AM species diversity is more distinct in undisturbed ecosystems compared to disturbed ecosystems as in undisturbed ecosystems. There is a greater degree of variability in terms of critical determinants. AM diversity and abundance can be affected by various factors/determinants such as habitat type, edaphic conditions, climatic or seasonal variations, host genotype, and vegetation cover. AM dominance can also be affected by the severity and extent of disturbance in a habitat (Bhatia *et al*., 2013). Plant diversity and productivity are enhanced by AM symbiosis and AM species richness. An increase in AM fungal diversity results in an increase in species richness and hence higher plant productivity. This suggests that changes in below-ground AM fungal diversity can affect changes in above-ground plant diversity and productivity. Assessment of AM fungal diversity is essential if the benefits associated with the symbiosis are to be exploited. Knowledge of AM species diversity in functioning ecosystems is crucial for the development of inocula for agricultural and horticultural crops, and revegetation of degraded ecosystems.

AM fungi as a biofertilizer for sustainable crop production systems

AM fungi form a symbiotic association with most agricultural crops *viz., Triticum* (wheat), *Glycine max* (soybean), *Phaseolus vulgaris* (beans), *Solanum lycopersicum* (tomato), *Sorghum bicolor* (sorghum), *Capsicum annum* (red peppers) and *Daucus carota* (carrot) (Öpik *et al*., 2010). As a result, they have gained growing attention as ecosystem engineers and bio-inoculants (Fitter *et* *al.,* 2011). Currently, AM fungal bio-inoculants are being increasingly considered in agriculture, horticulture, and forestry, as well as for environmental reclamation and remediation, to increase overall crop health and yield, and to limit the usage of agrochemicals. Many fields and greenhouse studies have been limited to the single inoculation of one of the following three species *viz., Rhizoglomus intraradices*, *R. irregulare,* and *Funneliformis mosseae* (Krüger *et al.,* 2012; Pellegrino and Bedini, 2014; Berruti *et al.,* 2015). These AM species are very generalist symbionts that colonize a diversity of host plants. They can be quickly and massively propagated, survive long-term storage, and have a wide geographical distribution all over the world (Öpik *et al*., 2010). Several reports have also highlighted that different isolates within the same species, rather than different species, can cause larger variations in host plant response (Angelard *et al*., 2010). The abovementioned characteristics have made these AM fungal species suitable as premium inoculum components and their application by farmers is increasing (Gianinazzi, 2014; Berruti et al., 2015; Hijri, 2016).

AM fungal inoculum is commercially available in a variety of forms ranging from high concentrations of AM fungal propagules in carrier materials to potting media containing inoculum at low concentrations (Douds et al., 2010). Interest in AM fungi has focused on finding a viable method to optimize the production of high quality AM fungal inoculum to use as a bio-inoculant in cropping systems (Ijdo et al., 2011). *In vitro* culture of AM fungi (monoxenic cultivation) is now a reality offering a several-fold increase in mass production of effective propagules over conventional bulking techniques. This system of AM inoculum production provides potentially high and economically attractive options to chemical fertilization, thus emphasizing its potential importance in sustainable agriculture.

AM fungal symbiosis contributes to sustainable agriculture principally by serving as an advantageous nutrient sink in which AM inoculated or mycorrhizal plants have increased growth and yield as compared to un-inoculated or non-mycorrhizal plants. This is due to better nutrient extraction and uptake capacity and improved soil properties. Thus, AM fungi impart beneficial effects to crops in terms of growth and productivity by increasing favourable microbial interactions and resistance to unfavourable biotic or abiotic conditions (Verbruggen *et al.,* 2010; Lenoir *et al.,* 2016).

CONCLUSION

AM fungi are universal, complex, ancient microorganisms constituting a significant component not only of plant life but also of agro-ecological production. It is clear they significantly impact every terrestrial niche across almost every biome influencing plant functioning. The ecological services provided by AM fungi and the extent of those services at the interface between biotic and abiotic elements suggest that AM fungi are primary ecosystem facilitators “keystone mutualists”.

In sustainable crop production, to obtain maximum beneficial effects from AM fungi emphasis must be on green agricultural practices or organic farming system relying on continuous rotational crops, cover crops, reduced tillage, application of organic fertilizers and manures. This would support the occurrence and functioning of AM fungal diversity as well as nutrient cycling in the long term thereby sustaining higher crop productivity without compromising the soil health.

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