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Role of Arbuscular Mycorrhizal (AM) Fungi in Crops Plants – A review

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ABSTRACT

Humans depend on many different plants as food sources, and since ancient times, cereals have been the most important. Cereals are a nutritionally important source of dietary proteins, iron, vitamin B complex, vitamin E, carbohydrates, niacin, riboflavin, thiamine, fiber, and traces of minerals essential for both humans and animals. Arbuscular mycorrhizal (AM) fungi are soil fungi that form a mutualistic symbiosis with the roots of plants. The review summarizes recent research on AM fungal symbiosis in crop plants. It also provides a comprehensive knowledge of AM fungi, their influence on crop plants at various stages of growth, their role in improving yield and productivity, increased tolerance to various environmental stresses, and their effect on agricultural management practices.

Keywords: AM fungi, Growth stages, Yield, Productivity, Agricultural management

INTRODUCTION

Crop plants are grown by humans for food and other resources. Based on their usage, crops are divided into four major divisions, *i.e*., food (wheat, maize, rice, millets, and pulses), cash (sugarcane, tobacco, cotton, jute, and oilseeds), plantation (coffee, coconut, tea, and rubber) and horticulture (fruits and vegetables).

Chemical fertilizers have become a significant input in crop production worldwide (Tilman *et al*., 2002). However, further increases in N and P application are unlikely to be as effective at increasing yields (Wang *et al.*, 2011) as crops uptake only 30-50% of applied N fertilizer and 10-45% of P fertilizer (Adesemoye and Kloepper, 2009; Garnett *et al*., 2009). In addition, the abundant use of chemical fertilizers in agriculture has had some deleterious environmental consequences and is a global concern (Tilman *et al.*, 2002). There is an urgent need to improve food security and protect and promote soil biodiversity and functionality by implementing sustainable management practices.

The soil is a life-supporting system rich in microorganisms with many interactions that determine plant growth. Microorganisms in the soil provide nutrients to plants, protect them from biotic and abiotic stresses, and boost their growth and yield (Bagyaraj and Jamaluddin, 2019; Enebe and Babalola, 2018). The narrow zone of soil around plant roots is the rhizosphere, which is very rich in microbial activity due to root exudates with nutrients, sloughed-off root cells, and mucilage released by the plant root. The rhizosphere harbours 10-50 times more bacteria and 5-10 times more fungi than soil away from the roots (Richards, 1976). Interaction between microorganisms in the rhizosphere profoundly affects the growth, nutrition, and health of plants in agro- and natural ecosystems (Philippot *et al*., 2013).

Arbuscular mycorrhizal (AM) fungi are a promising option for sustainable agriculture and food security (Thirkell *et al*., 2017). These fungi are integral to soil and plant roots, forming a symbiosis with many food crops (Smith and Smith, 2011). The interactive effect of AM fungi in the soil and their potential to improve the growth of food crops is discussed in this review.

AM FUNGI IN AGRICULTURE

AM fungal symbiosis is the most common type of association involved in agricultural systems. They are associated with improved growth of many plant species due to increased nutrient uptake, production of growth-promoting substances, induced tolerance to drought, salinity and transplant shock, and synergistic interaction with other beneficial soil microorganisms such as N-fixers and P-solubilizers (Sreenivasa and Bagyaraj, 1989). Symbiotic association of plant roots with AM fungi can enhance growth because of the increased acquisition of P and nutrients with low mobility in soil. Effective nutrient acquisition by AM fungi is generally attributed to the extensive hyphal growth beyond the nutrient depletion zone surrounding the root (Tisdale *et al.*, 1995). Thus, the AM fungi enable their host plants to gather mineral nutrients from a much larger soil volume than the roots could reach (Jansa *et al*., 2009).

Nearly 90% of plant species, including flowering plants, bryophytes, and ferns, can develop interdependent connections with AM fungi (Ahanger *et al*., 2014). They form hyphae, arbuscules, vesicles in the roots, and spores and hyphae in the rhizosphere. Formation of the hyphal network by the AM fungi with plant roots significantly enhances the access of roots to a large soil surface area, causing improvement in plant growth (Bowles *et al*., 2016). AM fungi improve plant nutrition by increasing the availability and translocation of various nutrients (Rouphael *et al*., 2015). They are also very effective in helping plants take up nutrients from nutrient-deficient soils (Kayama and Yamanaka, 2014). Apart from the macro-nutrients, the AM fungal association is known to increase the availability of micro-nutrients like zinc and copper (Smith and Read, 1997). Besides, they improve the surface-absorbing capability of host roots (Bisleski, 1973).

AM FUNGAL RESPONSE UNDER GLASS HOUSE/NURSERY AND FIELD CONDITIONS

Due to the functional attributes of AM fungi, they may be used as bioinoculants to improve crop production. However, several factors influence the success rate of AM fungal inoculation. These include AM fungal species compatibility with the host, interaction with other soil organisms, environment in the target niche, *etc*. They mutually interact with other beneficial soil microorganisms, enhancing plant growth (Hashem *et al*., 2018). The best way to utilize AM fungi for crop production would be to concentrate on crops commonly grown on nursery beds, root trainers, or polybags, where they could easily be inoculated with desired AM species and then transplanted to the field (Nikhil *et al*., 2019).

Wheat plants inoculated with AM fungi generally have higher grain yield, improved nutrient uptake (especially P), and increased nutrient content in the plant itself when compared to non-inoculated plants. Studies performed under greenhouse and field conditions support these findings (Al-Karaki *et al*., 2004; Saed-Moucheshi *et al*., 2012). AM fungal contribution of more than 50% of the P uptake was reported in spring wheat (*Triticum aestivum*) inoculated with *Rhizophagus irregularis* (Li *et al*., 2006). Inoculation with *Funneliformis mosseae* in durum wheat (*Triticum durum*, cv. Petra) showed a plant dependency on mycorrhizae for P uptake (Al-Karaki, 2002). Higher differences in P plant acquisition in *Triticum aestivum*, cv. Otto inoculated with *Claroideoglomus etunicatum* reflects the beneficial mineralizing phosphatase effect of the AM-fungus-colonized roots. In field conditions, a synergistic effect of plant-growth-promoting rhizobacteria and AM fungus on P uptake in wheat was reported with the co-inoculation of *Azotobacter chroococcum* with *Bacillus* sp. and *Rhizophagus fasciculatus* (Khan and Zaidi, 2007).

Maize is highly mycorrhizal, and there is evidence from different studies that AM fungi play an essential role in increasing maize productivity (Gomes *et al*., 2015; Cozzolino *et al*., 2013; Symanczik *et al*., 2018). Subramanian *et al*. (1995) conducted greenhouse experiments with a drought-tolerant maize genotype obtained through recurrent selection and compared it to the original drought-susceptible cultivar. Upon AM inoculation, both variants responded to drought treatment with higher leaf water potential and stomatal conductance values and recovered quicker from water stress than their non-mycorrhizal counterparts. Arihara and Karasawa (2000) reported that the preceding crop affected the growth of succeeding maize mainly by influencing AM colonization and development. Concerning crop rotation, when maize was rotated with a mycorrhizal crop, it showed enhanced AM fungal colonization compared to non-mycorrhizal or fallow fields (Dias *et al*., 2018). AM fungal species with features similar to *Rhizophagus irregularis* were suitable as components for large-scale inoculum production programs as the inoculums showed good colonization potential (Cely Martha *et al*., 2016). Hence, AM fungi were introduced as a biofertilizer for farming technology, including maize monocropping (Dias *et al*., 2018).

Rice plants are grown mainly in anoxic paddy fields, in which AM fungi are debated (Lumini *et al*., 2011; Wang *et al*., 2015). However, AM fungal species belonging to four genera, *viz*., *Acaulospora*, *Glomus*, *Funneliform*, and *Entrophospora* were recorded from the rhizosphere soil of rice cultivated in the wetlands (Xavier Martins and Rodrigues, 2018). In a laboratory experiment, the colonization of AM fungi decreased under flooding conditions (Vallino *et al*., 2009). In contrast, rice seedlings were colonized well under drained upland conditions (Vallino *et al*., 2009; Xavier Martins and Rodrigues, 2020). In rice, associations with AM fungi result in changes in plant competitive ability (Roger *et al*., 2013), ecotype-specificity (Diedhiou *et al*., 2016), functional diversity (Li *et al*., 2011), nutrient acquisition (Hoseinzade *et al*., 2016), and growth and gene expression (Colard *et al*., 2011). The AM fungus *Rhizophagus irregularis* is one of the world's most widespread AM fungal species (Cornell *et al*., 2022). Evidence also supports that *R. irregularis* can grow and colonize rice plants in flooded soil while maintaining functional capacities (Vallino *et al*., 2014). In other studies, the application of AM fungi at the nursery stage increased the yield by 14-21% in the wetland rice cultivar Nipponbare (Solaiman and

Hirata, 1997b). In wetland rice var. Prakash, grain yield increased by 35-62% upon inoculation with *Acaulospora* sp., *Glomus fasciculatum,* or *G. mosseae* (Secilia and Bagyaraj, 1994).

Millet develops an extensive root system with high root length densities. The relative impact of AM fungi on millet nutrient uptake is less than for leguminous crops or other semi-arid cereals (Bagayoko *et al*., 2000). However, millet and corn seem able to induce the multiplication of AM spores in the soil (Muok *et al*., 2009). AM fungi provide drought tolerance to finger millet seedlings through a stronger root system, greater photosynthetic efficiency, a more efficient antioxidant system, and improved osmoregulation (Tyagi *et al*., 2021).

The importance of AM fungal associations in crops, especially legumes, and their significance in nodulating N-fixing plants have been well documented (Barea and Azcon-Aguilar, 1983). Khalil *et al*. (1994) studied mycorrhizal dependence and nutrient uptake by corn and soybean cultivars. They showed that soybeans had a higher mycorrhizal dependence than corn because the legume roots are less extensive due to nodule formation than non-legumes. Differences in the relative mycorrhizal dependence between crop species or even cultivars are also related to other plant factors, such as root structure, plant growth rates (Sieverding, 1986), and microorganisms in the rhizosphere, which could affect the demand for P (Xie *et al*., 1995). Practical application of *Glomus intraradices,* on the production of different bean genotypes has indicated that AM fungi significantly increased plant growth and production (Hacisalihoglu *et al*., 2005).

Table 1: Role of AM fungi in nutrient uptake at different stages of plant growth.

Plant	AM Fungi Spore	Plant Stage	Nutrient Uptake	Environmental Condition	Reference
Wheat	*Glomus* sp.	Tillering	N	Ozone stress	Cui *et al.,*2013
Wheat	*Rhizophagus tenuis*	Vegetative, fruiting	P	Semi-arid field	Smith *et al*., 2015
Wheat	*Rhizophagus fasciculatus,* *Funneliformis mosseae*	Fruiting	Zn	Drought stress	Pellegrino *et al*., 2015
Wheat	*Rhizophagus intraradices*	Tillering	Zn	Under P application	Ma *et al*., 2019
Maize	*F. mosseae,* *Claroideoglomus etunicatum*	Tillering	N	Under Zn-deficient soil	Watts-Williams *et al*., 2017
Maize	*F. mosseae*	Vegetative	N	Field	Meng *et al.,* 2015
Maize	*Rhizophagus irregularis*	Fruiting	P	Compartmented pots with radioactive P tracer	Battini *et al*., 2017
Maize	*Glomus clarum*	Fruiting	P	P deficient	Amerian *et al.,* 2001
Rice	*R. intraradices*	Tillering, Maturity	N, P, C	Greenhouse	Zhang *et al.,* 2017
Rice	*Glomus* sp.	Early tillering	N, P	Wetland	Solaiman and Hirata, 1997
Rice	*Funneliformis geosporum,* *F. mosseae*	Fruiting	P	Under As soil conditions	Chan *et al.,* 2013
Barley	*F. mosseae*	Seedling, Flowering, Fruiting	Zn	Under Cd conditions	Garg and Kaur, 2013
Barley	*R. intraradices*	Fruiting	Zn	Drought stress	Bhantana *et al.,* 2021
Sorghum	*G. clarum*	Harvesting	N	Greenhouse	Nakmee *et al.,* 2016
Sorghum	*Glomus* sp.	Harvesting	P	Greenhouse	Nakmee *et al.,* 2016

AM FUNGAL RESPONSES IN STRESSED ENVIRONMENTS

AM fungi respond differently to abiotic stresses such as drought, flooding, extreme temperatures, salinity, and heavy metals (Diagne *et al*., 2020). Drought is a major stress that can considerably reduce plant productivity (Posta and Duc, 2020). Water constraints provoke stomatal closure with a subsequent reduction of CO_2 influx, resulting in decreased photosynthetic activity, carbon partitioning (Osakabe et al., 2014), and reduced plant productivity and yield. It has been demonstrated that AM fungi improve plant performance in drought stress (Balestrini and Lumini, 2018). Improvement of plant fitness by AM fungi is possibly due to the increased surface area for water absorption provided by AM fungal hyphae (Augé, 2001).

Phytohormones play an important role in plant response to drought stress. Hormone homeostasis regulates plant tolerance against abiotic stresses. Abscisic acid (ABA) is the most fundamental stress hormonal signal, modulating transpiration rate, root hydraulic conductivity, and aquaporin expression. ABA responses regulate stomatal conductance and other physiological processes (Ouledali *et al*., 2019). ABA induces stomatal closure and reduces cell water loss. Inoculation with AM fungi influences the control of stomata functioning by regulating abscisic acid (Ouledali *et al*., 2019). A lower ABA concentration was found in the roots and leaves of mycorrhizal plants versus non-mycorrhizal plants under drought stress (Nakmee *et al*., 2016; Chitarra *et al*., 2016). It has also been demonstrated that Jasmonic acid (JA) interacts with abscisic acid to regulate plant responses to water stress conditions (De Ollas and Dodd, 2016). JA is known to mitigate plant water stress (Yosefi *et al*., 2018). Phytohormones, such as strigolactone and auxin, regulate plant water stress (Mostofa *et al*., 2018). It has been demonstrated that inoculation with AM fungi strengthens strigolactone and auxin responses to drought stress (Ruiz-Lozano *et al*., 2015).

Several studies revealed that mycorrhiza could be used as a stress-reducing agent in soils contaminated by heavy metals helping plants to survive in such stressed conditions (Song *et al*., 2020; Conversa *et al*., 2019; Padmavathi *et al*., 2016). Heavy metal remediation by AM fungi can happen through hyphal "metal binding," reducing the bioavailability of elements such as Cu, Pb, Co, Cd, and Zn (Audet and Charest, 2007). The alleviation of heavy metal toxicity by AM fungi depends on the fungal partner, plant growth conditions, the type of heavy metal, and its concentration (Hildebrandt *et al*., 2007).

AM fungi occur naturally in saline environments (Yamato *et al*., 2008). Their contribution to improving the growth of several plant species under saline conditions is well known (Evelin *et al*., 2009; Amanifar *et al*., 2019). Enhancement of water absorption capacity, nutrient uptake, accumulation of osmoregulators like proline and sugars (Yamato *et al*., 2008), ionic homeostasis (Munns and Tester, 2008), and the reduction in Na^+ and Cl^- uptake (Li *et al*., 2020) has been observed in plants inoculated with AM fungi. In addition, AM fungal colonization improves stomatal conductance and reduces oxidative damage in plants exposed to salinity (Estrada *et al*., 2013; Pedranzani *et al*., 2015).

Inoculation with AM fungi has been well-reported to stimulate wheat growth under drought-stress conditions. A metabolomic analysis by Bernardo *et al*. (2019) in a water deficit regime on *Triticum durum* and *T. aestivum* wheat cultivars supported the hypothesis that AM fungi enhance the plant response to water stress. Inoculation with *Funneliformis mosseae* significantly improved the plant biomass, resulted in a positive trend in Water Use Efficiency (WUE), and reduced oxidative damage. Inoculation of *Triticum aestivum* var. Buck Pronto with *Glomus claroideum* alleviated the deleterious effects of drought stress, revealing a significant increase in total dry weight, Relative Water Content (RWC), and leaf chlorophyll content (Beltrano and Ronco, 2008). Field inoculation with *Funneliformis mosseae* or *Claroideoglomus etunicatum* on Steardy (drought-sensitive) and TAM-105 (drought-tolerant) winter wheat cultivars resulted in enhanced yield in both the cultivars (Al-Karaki *et al*., 2004). *Triticum aestivum* plants, exposed to water stress and grown in soil inoculated with a mixed starter culture of AM fungi (*Rhizophagus intraradices*, *Funneliformis mosseae*, and *F. geosporum*), recorded less damage to the structure and function of PSII and PSI systems and exhibited an increase in RWC for both leaf and soil, indicating the ability of AM fungal hyphae to penetrate deep into the soil and provide moisture to the plants (Al-Karaki and Al-Omoush, 2002).

Maize plants inoculated with *Rhizophagus irregularis* had longer roots and higher P absorption under alkaline conditions because AM fungi facilitate N and P uptake (Merlos *et al*., 2016). *R. intraradices* enhanced P concentration in rice and increased grain yield and straw biomass by reducing the negative effect of heavy metals under arsenic (As) conditions (Li *et al.*, 2011). This may be because the 'dilution effect' lowers the As concentrations in the grains due to the higher growth in AM-inoculated plants.

Compared to non-inoculated plants, sorghum plants inoculated with *F. mosseae* showed a higher Fe content in shoots under low-nutritional soil conditions due to C_4 crops being considered more responsive toward AM colonization than C_3 plants (Caris *et al*., 1998). *Claroideoglomus etunicatum* considerably enhanced P, N, sulfur (S), and molybdenum (Mo) concentrations in both roots and shoots of Sorghum (Shi *et al*., 2020).

In barley (*Hordeum vulgare*), inoculation with *F. mosseae* decreased cadmium (Cd) and cobalt (Co) uptake under conditions of heavy metal (Cd, Co, and Pb) polluted soil, demonstrating that AM colonization has an alleviating effect on barley under heavy metal conditions (Beltrano and Ronco, 2008). Watts-Williams *et al*. (2020) reported that *R. irregularis* boosted Zn uptake in barley plants compared to non-inoculated plants since AM fungi are known to explore the soil volume beyond the nutrient depletion zone.

Begum *et al.* (2019) opined that under salinity conditions, AM fungi improve the uptake of most essential nutrients and decrease the uptake of sodium (Na) and chloride (Cl), resulting in better growth. The increase in the uptake of nutrients like phosphorus (P), nitrogen (N), potassium (K), Copper (Cu), and zinc (Zn) helps to maintain ionic homeostasis (Evelin and Kapoor, 2014). Mycorrhizal colonization boosts the production of antioxidant molecules. It increases the activities of enzymes such as catalase, peroxidase, superoxide dismutase, and ascorbate peroxidase (Hashem *et al.*, 2018), thus providing an improved oxidation scavenging system (Evelin and Kapoor, 2014). Besides, they help the plants maintain water status, increase stomatal conductance, and enhance photosynthetic pigments to combat the effects of salts and increase photosynthesis for growth and development (Chaves *et al.*, 2009). *Rhizophagus intraradices* promoted P, Fe, and Zn uptake and inhabited the uptake of Na in barley plants (Mohammad *et al.*, 2003).

In buckwheat (*Fagopyrum esculentum*), the total N and P absorptions were positively affected by the mixed AM fungi under inorganic and organic P applications (Boglaienko *et al*., 2014). It has been stated that mixed AM fungi might have a more positive impact on plants. Bagayoko *et al*. (2000) reported higher levels of P, K, Ca, Mg, and Zn in roots compared to control in millet (*Pennisetum glaucum*) plants treated with mixed AM fungi. Similarly, the application of three AM fungi, *viz.*, *Funneliformis mosseae, Rhizophagus fasciculatum*, and *Gigaspora decipiens*, enhanced plant growth and glomalin-related soil protein (GRSP) under barren soil conditions in millet (Pal and Pandey, 2017), suggesting that AM fungi contribute to heavy metal sequestration in polluted soils and sediments in semi-arid environments.

AGRICULTURAL MANAGEMENT PRACTICES INFLUENCING AM FUNGAL RESPONSE

The persistence of AM fungi in the field depends on the formation and survival of fungal structures inside and outside the plant roots. AM fungal spores and colonized root pieces are considered the most relevant survival structures, even without a viable host plant. Under natural conditions, spore and hyphal densities are subject to seasonal variations (McGonigle and Murray, 1999). Moreover, AM fungal species and their colonization strategies determine which fungal structures (spores, colonized root pieces, or hyphal fragments) are relevant for survival and establishing a new symbiotic relationship after the absence of a host plant (Hart and Reader, 2002).

In agroecosystems, the land use type, the farming system, the tillage system, and the fertilization strategy are major factors influencing AM fungal persistence and development. Local AM fungal communities are periodically challenged by host plant turnover, crop rotations, and soil management, especially in annual crops. Evidence shows that tillage systems, which turn the soil, can negatively affect AM fungi by destroying the extraradical hyphal network. By contrast, no-tillage systems can foster AM fungi and increase benefits for the host plant due to better plant P uptake and soil aggregate stability (Säle *et al.*, 2015).

Previous studies have shown that fertilizer input has varying effects on AM fungal growth by altering the soil micro-environment. Chen *et al*. (2014) reported that N application mainly changed the species composition of AM fungi, whereas P application affected the abundance of AM fungi. However, Xiao *et al.* (2019) revealed that adding N affected the AM fungal abundance. In contrast, adding P affected the diversity of AM fungi, and adding N and P had no significant effect on the community composition of AM fungi in the ecosystem.

Qin *et al*. (2015) reported that high soil nutrient content such as N and P promotes AM fungal sporulation. They stated that the input of organic fertilizer is beneficial to the growth of soil flora and that the soil pH and K significantly affect the community composition of AM fungi.

Table 2: Role of AM fungi in a stressed environment.

Plant	AM Fungi Spore	Plant Stage	Changes after AM colonization	Stressed environment	Reference
Wheat	*R. irregularis*	Vegetative	Enhanced macro- and micro-nutrient concentration	Low- or high-temperature stress	Zhu *et al*., 2017
Wheat	*F. mosseae*	Vegetative	Increased concentrations of P, N, K, and Mg	Saline soil condition	Abdel-Fattah and Asrar, 2012
Wheat	*F. geosporum*	Seeding and vegetative	Upregulation of water and nutrient uptake	Salt, drought, and heavy metal conditions	Ibrahim *et al*., 2011
Wheat	*G. claroideum*	Tillering	Enhanced total dry weight and leaf chlorophyll concentration	Drought stress condition	Beltrano and Ronco, 2008
Maize	*F. mosseae*	Pre-flowering	Increased N and P concentration	Under water deficit conditions	Ghorchiani *et al.*, 2018
Maize	*G. etunicatum*	Tillering	Increased plant Biomass	Under P-deficient conditions	Almagrabi and Abdelmoneim, 2012
Maize	*C. intraradices*	Vegetative stage	Increased water uptake and leaf water potential	Under sandy loam soil	Amerian *et al.*, 2001
Maize	*R. irregularis*	Seedling, tillering, and fruiting	Increased Cu tolerance	Under heavy metal condition	Merlos *et al.*, 2016
Rice	*C. etunicatum*	Heading and flowering	Improving nutrition status and plant growth	Under salt stress conditions	Porcel *et al*., 2015
Sorghum	*R. irregularis*	Fruiting	Improved their transpiration efficiency and drought tolerance	Under drought conditions	Symanczik *et al*., 2018
Barley	*F. mosseae*	Flowering	Increased resistance against heavy metal conditions	Increased resistance against heavy metal conditions	Mohammad *et al.,* 2015

CONCLUSION

Mycorrhizae and their use in crop plants have been experimented worldwide. Most of the research is focused on the benefits the host plants enjoy from the viewpoint of nutrient availability, growth, productivity, and increased tolerance against environmental stress. AM fungi are used as an inoculum in greenhouses but can also be used on a larger scale in fields. Therefore, future research should identify efficient AM fungi that can be used as biofertilizers to overcome soil fertility problems, improve plant health, and increase crop yield.

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