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Arbuscular mycorrhizae fungi a potential eco-friendly tool for sustainable agriculture under changing climatic conditions/ in biotic and abiotic stress conditions

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Resumen

Los hongos micorrízicos arbusculares (HMA) son biotrofos obligados que viven en asociación simbiótica con las raíces de las plantas. Se encuentran entre los microorganismos del suelo más extendidos que proporcionan a la planta huésped nutrientes y protección contra patógenos. Las prácticas agrícolas modernas, como la labranza frecuente, el alto empleo de fertilización inorgánica pesticidas junto con condiciones climáticas cambiantes debido al calentamiento global, tienen enormes impactos en la colonización de los HMA, la interacción con las plantas y la productividad de los cultivos. Los HMA afectan positivamente la tolerancia de las plantas al estrés biótico y abiótico, a los ecosistemas severos y sus patógenos al alterar la estructura de las raíces, la exudación, la microflora de la rizosfera, la producción de antifúngicos y antibacterianos, y al competir con los patógenos por la absorción de nutrientes. Por lo tanto, juegan un papel importante en el crecimiento, la productividad y la calidad de las plantas. Además, el efecto de un fungicida varía según su modo de acción y las especies de HMA asociadas, lo que sugiere que estos hongos tienen un gran potencial como herramienta para la agricultura sostenible ecológica en el actual escenario de calentamiento global.

Palabras clave: Hongos micorrízicos arbusculares (HMA), Agricultura, Calentamiento global.

Abstract

Arbuscular Mycorrhizal Fungi (AMF) are obligate biotrophs living in symbiotic association with roots of plants. They are among the most widespread soil microorganisms that provide the host plant with nutrients and pathogen protection. Modern farming practices like frequent tillage, high input inorganic fertilization and pesticide along changing climatic conditions due to global warming, have huge impacts on AMF colonization, interaction with plants and on crop productivity. AMF positively affect the plant tolerance to biotic and abiotic stresses, harsh ecosystems and plant pathogens by altering root structure, exudation, rhizosphere microflora, production of anti-fungals, antibacterials, and competing with pathogens for nutrient uptake. Thus, it plays a significant role in plant growth, productivity and quality. Further, the effect of a fungicide is varied depending on its mode of action and the associated AMF species, suggesting that these fungi have a strong potential as a tool for eco-friendly sustainable farming in the present scenario of global warming.

Keywords: Arbuscular Mycorrhizal Fungi(AM Fungi or AMF), Agriculture, Global warming

Introduction

Mycorrhizal association is one of the pre-eminent examples of symbiotic association, which refers to the association of fungi with plant roots. Mycorrhiza are usually specialized in serving the plant with increased water and nutrient uptake (Cu, Fe, P, K, and N) and in return, the plant nourishes the fungus with carbohydrate formed by photosynthesis. The fungus uses this carbohydrate for its extensions and to synthesize glomalin molecules which is an N-linked glycoprotein that is composed of N, C, H, O, P, and Fe. It is glue-like and hydrophobic which helps in stabilization of soil aggregates and also protect soil from desiccation by improving the water holding capacity of soil. (1-5). They play a major role in the growth of the plant and its productivity while also affecting growth-related functions, such as, stomatal conductance, relative water content and leaf area (6,7). Arbuscular mycorrhizal fungi belong to the phylum Glomeromycota which is marked by the formation of specialized structures called arbuscules (8). These fungi are capable of invading the cortical cells of the plant roots forming an extensive network of hyphae to suck nutrients, they also confer resistance to plants against harsh conditions like drought, salinity, stresses, pathogens, etc (9). Agriculture, a major sector of the Indian society is the primary source of livelihood for a majority of India's population. Varying climatic conditions and excessive application of agricultural practices are having a drastic effect on the different forms of agriculture thus hampering a wide range of ecosystem services. To establish a method of sustainable agriculture, it has become critical to identify and evaluate eco-friendly options for adapting to climate change and harsh agricultural practices. In this review we discuss AM fungi symbiosis, their mechanisms and benefits in sustainable crop productivity, especially in the present scenario of global warming, under high stress conditions of drought, changing temperature and elevated levels of CO_2.

TYPES OF MYCORRHIZAE

Based on the location of fungal hyphae in relation to the root tissues of the plant, Mycorrhizae are classified in two types, Ectomycorrhiza and Endomycorrhiza. Endomycorrhiza comprises 3 major groups i. e, Orchid, Ericoid and Arbuscular mycorrhizae.

Arbuscular mycorrhiza

AM fungi are the most important member of the group Endomycorrhiza, earlier known as Vesicular Arbuscular Mycorrhizae (VAM) now termed as Arbuscular mycorrhiza (AM) (1). AM fungi form thick-walled resting spores called extramatricular chlamydospores that can survive and germinate in unpropitious conditions. They form appressoria on the root surface, the hyphae invade the root and form branches in the cortex. From the branches, the intercellular hyphae run longitudinally to enter the cortical cells and develop short branched hyphal structures called arbuscules which help absorb nutrients for plants (10-11). The germ tube disintegrates if they do not successfully penetrate the roots of the host. Further, thin-walled structures are also formed in the root cortex which are of different shape and size, they function as storage organs, known as vesicles.

SIGNIFICANCE OF AMF IN CROP PRODUCTIVITY

The symbiosis of AM has raised the standards of commercial application, improved agricultural practices and crop productivity. Studies have reported that AMF colonization of the plant roots improves plant nutrition by various mechanisms. They form a hyphal network with the plant root which significantly enhances access to larger soil surface areas and increases the surface absorbing capability of the host root. Colonization with AMF increases the availability, translocation and uptake of various nutrients like P, K, Fe, Zn, and Cu and trace elements like boron and molybdenum to the plant (12-14). They increase the capability of the plant to absorb phosphorus, an element mostly inaccessible to plants and mobilized organically bound to nitrogen. (15). AMF help the plant in better nutrient absorption from nutrient deficit soils, they facilitate selective uptake of ions under stressed conditions in phosphorus and water-deficient soils, thus providing protection from extremes in the environment. In many cases AMF have themselves conferred resistance to stress conditions like high salinity and metals (16-19). AMF can help transfer about 20–75% of the total N uptake to its host plants. Assimilation and absorption of inorganic phosphate is assisted by the extra-radicle hyphae.

It has also been reported that inoculation with AMF increases the photo-availability of micronutrients like Cu and Zn and increase the biomass accumulation in plants by enhancing significantly the concentration of macro and micronutrients, leading to increased photosynthate production. Improved levels of protein, Fe, and Zn were observed in mycorrhizal chickpea (20).

The water-stable aggregates formed by the production of glomalin on AMF colonization improves the soil structure, promoting better provisions for the survival of a plant, especially in adverse or low-nutrient environments. Studies suggest that the fungi may also protect plant roots from invasion by plant parasitic pathogens (PPN) by altering the root morphology (21), competing for space and nutrition (22-23), by systemic suppression of nematode infection (24), and by altering root exudation composition and level which can have an effect on the hatching, motility and chemotaxis of PPN in the surrounding rhizosphere (25), thus conferring resistance to plant pathogens and diseases (26-28). Colonization with AMF influences plant exudation patterns that alter the microflora of the rhizosphere which could influence plant growth, stability, survival, and yield (29-31). AMF are known to associate synergistically with other beneficial micro-organism and improve plant growth. AMF act as biofertilizers, bioprotectants, or biodegraders and hence can alter plant productivity under unstressed and stressed regimes by providing essential inorganic nutrients to host plant (32-33). Figure 1 shows the impact of AMF on crop productivity.

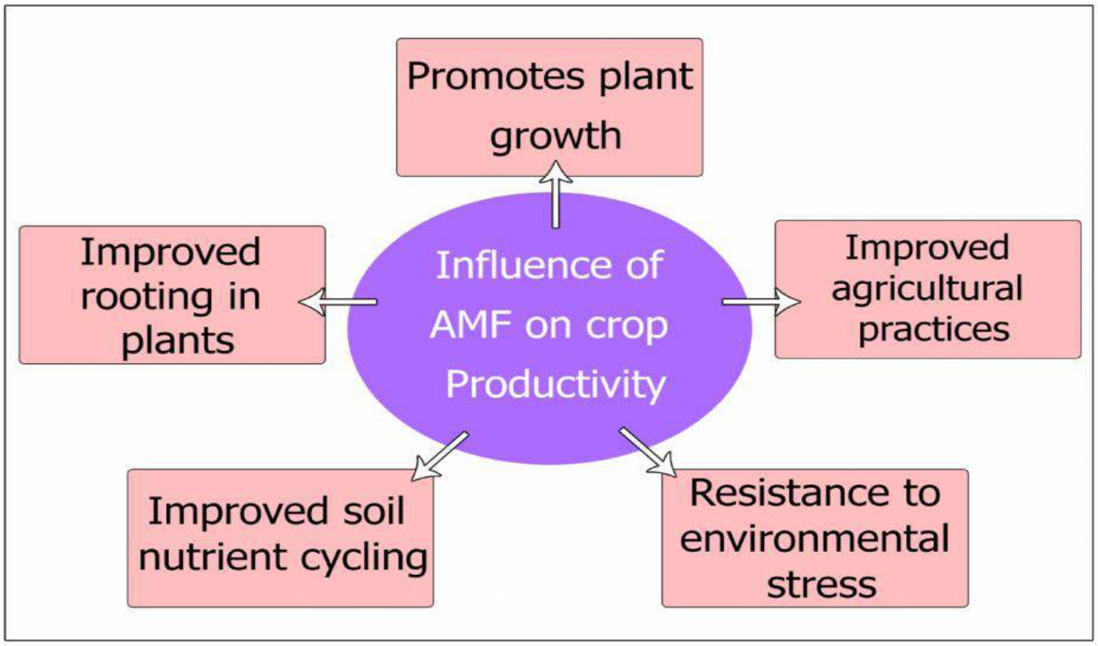

Figure 1. The impact of AMF on crop productivity

MECHANISMS OF ARBUSCULAR MYCORRHIZAL FUNGI IN PROMOTING PLANT GROWTH AND PRODUCTIVITY

Mechanism for the biocontrol of pathogens

The soil-borne pathogens usually controlled by agricultural practices such as chemical, fungicides, soil fumigation, resistant cultivars, crop rotation, etc., are not effective in the long-term due to various reasons. Consequently, researchers tried to use alternative approaches based on manipulation and addition of microbes to inflate the plant protection against pathogens (34). The biocontrol of pathogens was facilitated by utilization of beneficial microorganisms (*Pseudomonas fluorescens*) and fungi (AMF and *Trichoderma*) that compete for nutrient uptake and space with plant pathogens, they parasitize the pathogen and produce antibiotics thus impelling resistance in the host plant (35). AM fungi symbiosis compensates for the loss of root biomass or function caused by pathogens thus boosting the tolerance level of the host to attack by pathogen (36), nematodes (37) and fungi (38). A reduction in the soil-borne pathogenic diseases, caused by fungal pathogens such as *Phytophthora, Gaeumannomyces*, *Fusarium, Chalara* (*Thielaviopsis)*, *Pythium*, etc was observed when AM fungi interacted with plant pathogenic fungi (38). Some of the mechanisms that can explain bio-control by AMF include biochemical changes in plant exudates, e.g. peroxidases, phytoalexins, phenolics, etc., changes in the rhizosphere microbial flora, change in nutrient status of the host, anatomical changes in root cells, changes in the root system morphology of the host plant that facilitates damage compensation, tolerance to heavy metals and stress alleviation (39).

Mechanism of phytoremediation

The effect of AMF on metal uptakes is influenced by various factors, such as fungal genotype, the type and concentration of metal, interaction between P and the metal to name a few (40). Studies have suggested that AMF *R. Pseudoacacia*, due to its fast growth, high biomass, its capacity of accumulating large amounts of heavy metal (HM), and atmospheric nitrogen fixation, have the potential for extracting metal contaminants from soil (41). Higher root to shoot Pb ratio in mycorrhizal plants enhances Pb uptake and accumulation in the root system. *R. intraradices* plays a sequestering role in Pb detoxification (42). Fungal vacuoles play an important role in retention, binding, and immobilization of heavy metals. They facilitate the regulation of cytosolic metal ion concentrations and detoxification of toxic metal ions. The long extramatrical fungal hyphae help in the uptake of large amounts of nutrients, including heavy metals (43-44). Some of these fungi have also evolved a heavy metals tolerance (45-46).

Mechanism for enhanced Nutrient Uptake

AM fungi facilitate the uptake of primary soil nutrients (N, P, K) as well as Mg, Ca, Cu, Zn, Fe, Ni, Cd through plant roots. The hyphal network is optimally stationed to efficiently absorb nutrients and water from the soil but only a few of these transporters are involved, especially those who are responsible for the uptake of phosphate, ammonium, and zinc. Since diffusion is quite slow, the nutrients are made to move in a packaged form amongst extra-radicle and intra-radicle mycelium. Some AMF synthesize phosphatases which enhance mineralization of organic phosphate and increase phosphate availability, whilst few AMF produces organic acids which optimizes the pH and in turn increases its emulsification and availability of phosphate (47-48). Under conditions of reduced phosphorus availability, the AMF interfered transfer of nutrients has been observed from the host plant to another plant through AM hyphal colonies. For example, C^{14} photosynthate from one plant to another was transported primarily through AM hyphae instead of leaking out through roots of the donor plant. While in ^{32}P experiment, the hyphal linkage between plants was the dominant factor for the transfer (49).

Further Nutrient uptake is easier under mycorrhizal inoculation; even in saline conditions (50-52). N uptake was increased in the presence of *Glomus sp*. in saline conditions by *Cajanus cajan* and *Sesbania sp*. respectively (53-54). AMF symbiosis increased biomass accumulation and photosynthate production by increasing the mobilization of various macro-nutrients (N, P, K, Ca, S) and micro-nutrients (Fe, Cu, Zn) into plants (55). Under different irrigation regimes it has been observed that, AMF symbiosis promote development in plant at higher and lower P levels by maintaining N and P uptake (56).

Alteration of root structure and space

AM colonization changes the root architecture of the host plant (57). The plants show an increase in root growth and branching, (21) meristematic, nuclear activity of the root cells and root morphology. This may increase the nutrient uptake and change the rhizosphere interaction exceptionally in pathogen-infection development (58). The root morphology emerging from AM colonization seems to be contingent with the specificity of the plant. It mostly appears to be more accounting for the tap root system than the fibrous root system. Positive collegial effects can be seen by enhancement in the root endurance because the higher ability of nutrient uptake outweighs the suppressed root growth caused by infection due to root pathogens.

The negative influence of migratory endoparasitic nematodes like *Radopholus similis* and *P. coffeae* on the root branching in the banana plant was compensated by the increase in branching of roots due to colonization by AMF *Funneliformis mosseae* (59). AMF alters the root space and, geometry, and enhances the root surface area for improvised absorption (47) AMF symbioses enhances biomass, root length, root density and increases the uptake of P, Fe and Zn in wheat and Sweet Sorghum (18,60).

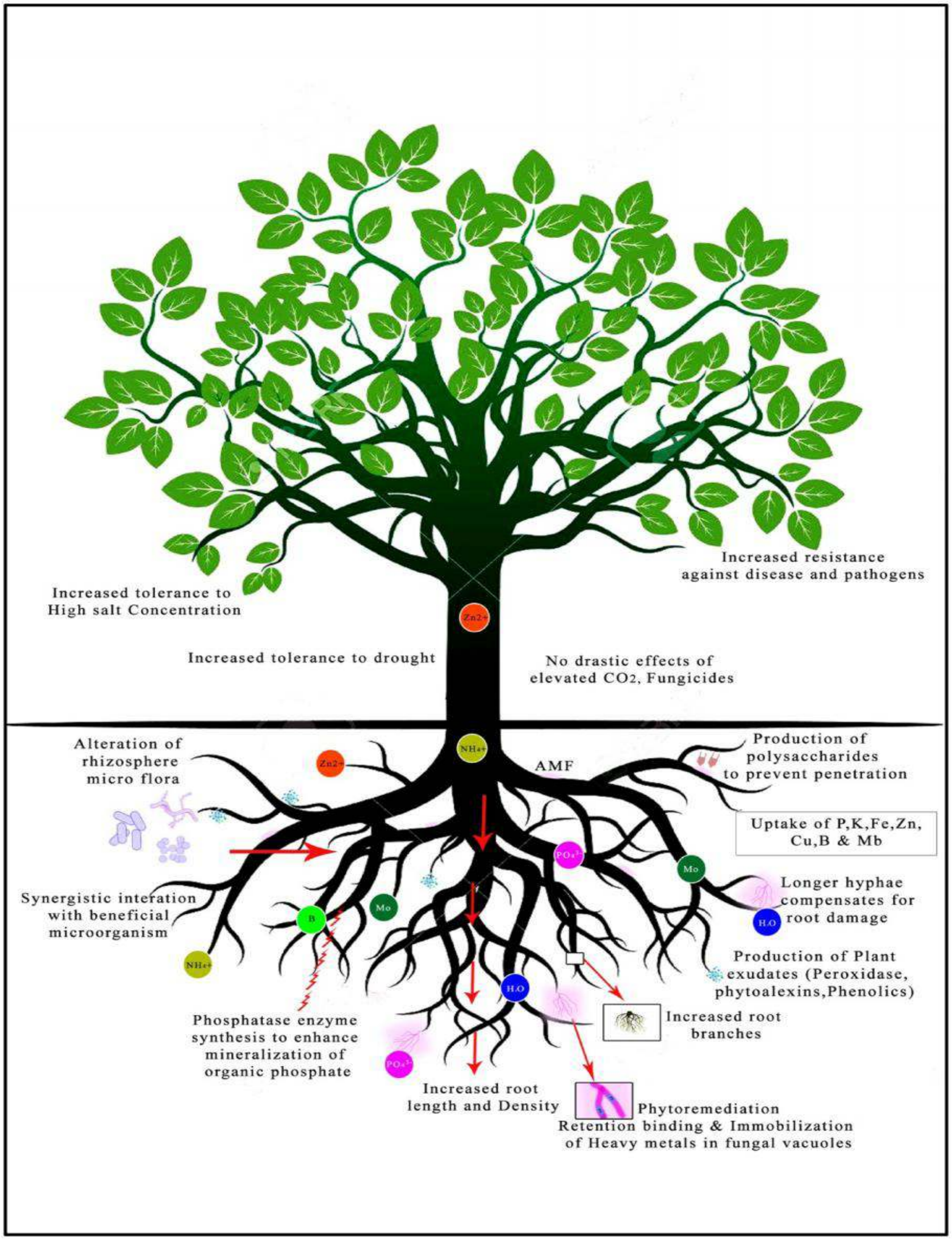

Figure 2 An Overview of the Role of AMF

BENEFICIAL INTERACTION AMONGST AM FUNGI AND OTHER ESSENTIAL MICROORGANISMS

Interaction of AM Fungi with Symbiotic Nitrogen Fixers

The interaction between AM fungi and Leguminous plants is reported to be synergistic; with improvement in nodulation and AMF colonization (61) The colonization of AM fungi increases the amount of flavones (phytoelexins) in some leguminous plants, which increase the expression of nodulation gene (62). Further *Rhizobium* produces extracellular polysaccharides which increases the number of entry points per unit length of root. (63-64). AM fungi and legumes-Rhizobium enhance plant growth with improvement in mineral nutrient and their ability to tolerate biotic and abiotic stress (environmental stresses), which increase the rate of re-vegetation in the semiarid ecosystem (65). Synergic interaction with AM fungi and Rhizobia works as biofertilizers and helps in reducing the root diseases by biological processes (66-67).Nodulation in Soyabean plant by AM fungi association helps maintain symbiotic N_2 fixation (SNF) under P scarcity (68).

Interaction of AM Fungi with Asymbiotic Nitrogen Fixers

Many of the free-living bacterial species of *Azotobacter, Azospirillium,Berijinckia, Clostridium*, and *Derxia* are known to fix atmospheric nitrogen (69). Studies reveal that infection with mycorrhiza enhanced and maintained the levels of *A. Chroococcum* populations in the rhizosphere and in return the spore production and colonization by the mycorrhizal fungus were increased by *A. Chroococcum*. Similar results were observed in paspalum and tall fescue on the interaction of *A. Paspali* with AM fungi and *A. chroococcum* with *G. fasciculatum* respectively (70). The interaction between *Beijerinckia mobiles, Aspergillus niger* and *G. Fasciculatum* enhanced the growth of onion due to synergistic effects of hormones produced on their mycorrhizal efficiency (71).

Interaction of AM Fungi with Phosphate solubilizers

There exist certain environmentally friendly phosphate solubilizing microorganisms (PSM) which can be used as an alternative to chemical fertilizers (72). They are termed as phosphobacteria, they solubilize the unavailable forms of phosphorus and provide it to the plant (73). An experiment showed that the combination of arbuscular mycorrhizal fungi (AMF), phosphate-solubilising bacteria (PSB) and phospho-compost (PC) increased seedling, shoot height, root dry weight, growth and phosphorus solubilization in tomato (*Solanum lycopersicum L.*) plant (74). AM fungi interact with phosphate solubilizing microbes and enhance plant growth and improved plant biomass (75). Inoculation of seedlings with phosphate solubilizing bacteria such as *Agrobacterium sp*. and *Pseudomonas sp*. or dual inoculations maintained higher populations for longer durations in the mycorrhizal rhizosphere compared to non-mycorrhizal roots, increased phosphorus uptake, increased production of plant growth hormone and plant dry matter (76-77). Synergic interaction with AM fungi and bacterial communities of mycorrhizosphere works as biostimulants and helps in enhancing plant growth, plant health and plant nutrition by encompassing nitrogen fixation and P solubilization (78).

Interactions of AM Fungi with helper mycorrhiza

Some microorganisms known as MHO (Mycorrhiza Helper Organism) residing in the soil, can improve the initiation of mycorrhizal symbiosis. These bacteria that are linked to the rhizosphere of the mycorrhiza, encourages the growth of the fungus and aids mycorrhizal colonization. Actinomycetes like *Streptomyces coelicolor* (79) and fungus like *Trichoderma harzianum* also facilitate colonization of AMF. Several workers have shown that inoculation of AM fungi in combination with MHO improves the colonization of mycorrhiza, growth of plant and yield. Bacteria that were isolated from mycorrhizosphere (mycorrhizal roots or AMF's hyphae or spores) enhance the germination of AMF spore and root colonization of AMF (80-82). This is due to the capability of certain bacteria to degrade insoluble biopolymers like chitin and chitosan, which are major constituents of the AMF spore wall. The bacteria living in the mycorrhizosphere and sporosphere enhance the extension of extraradical mycelium (ERM), hence acting as mycorrhiza helpers (83-84).

Interactions of AM fungi with Neighbouring Plants

AMF play a role in inducing biological interactions among neighbouring plants. AMF grow an extensive hyphal network below the soil in and around the roots of the plants on which they grow. This network provides a physical link between the soil and the roots of multiple host plants. The interaction by AMF with the neighbouring plants mediates plant-plant interactions by facilitating the transfer of nutrients, carbon and water from one plant to another (9). Several studies demonstrate that AMF play a major role in nitrogen transfer to nearby plants or host plants (85). Interaction of cereals with Faba bean inoculated with AMF increase the percentage of N transfer to the cereal and the percentage of N in the cereal derived from the Faba Bean. (60).

Interactions of AM Fungi and Plant Pathogens

AMF are known to affect rhizosphere interactions by altering root morphology and activity (39). Suppression of the pathogenic activities is due to morphological, biological, and physiological changes that take place in host plant. Lignification that is induced by AMF increases the thickness of the cell walls and the production of polysaccharides which prevent the penetration and growth of pathogens like *Fusarium oxysporum, Meloidgyne incognita*, etc., thus decreasing the rate and severity of diseases caused due to the pathogens penetrating the soil (86). The arbuscules formed on the interaction of AM-Phytophthora prevent the penetration of cortical cells. Mycorrhizal plants in symbiosis with AMF have a stronger vascular system that imparts greater mechanical strength, increases the nutrient supply and decreases the effect of vascular pathogens, thus increasing the tolerance to pathogen infection (9, 27, 54, 87).

AMF reduce the number of pathogenic fungi in roots by interference competition and exploitation competition (28, 88, 89). Phosphorus plays an important role in root exudation that reduces the germination of pathogenic spores. (27, 90, 91).

CLIMATIC FACTORS

Temperature

The effect of temperature or global warming is plant species and AMF strain dependent (92-95).The variation in climatic factors affects the AMF present in the soil as well as their symbiotic activity. This may alter the C allocation to the root zone, root exudation, nutrient availability (C/N ratio), etc. The optimum temperature for the function of AMF is similar to the range required for plant vegetation. AMF promotion was observed at temperatures below 27 degrees C (96). Extremely low or high temperature lessens the population of AMF in the soil.(97). Mohan et al summarized that mycorrhizal abundance increased in 63% of works with no effect on 20% at elevated temperatures, thus concluding that elevated temperatures have a positive impact on the growth of external hyphae and diversity of mycorrhizae.(98) The AMF adapt to higher temperatures by altering the structure of their hyphal network, to a more extensive extra-mycorrhizal type to facilitate higher respiration and quicker C allocation (99,100).

Light

Light is known to influence mycorrhizal colonization significantly. Plants exposed to sunlight show higher hyphal colonization rate, higher number of arbuscules and the higher number of vesicles per field of microscope, thus enhancing mycorrhizal symbiosis in plant roots exposed to sunlight compared to those in the shade (101). High intensity of light enhances the root colonization as well as AMF spore production. These characteristics make mycorrhizal fungi a strong tool to be used in the sustainable management of the environment. (102-103).

Elevated CO_2

Global warming majorly alters the atmospheric CO_2 concentrations, soil temperature, and drought stress, which have indirect effects on symbiotic associations between plant and microorganisms and ultimately influence crop productivity.

The response of plant species and its functional groups to elevated levels of CO_2 is highly variable (104), it to some extent dependent on the patterns of C allocation within the plant (105-106). Under increased C allocation AM fungi strains are positively influenced by increased growth in the rhizosphere, and enhanced colonization, thus promoting plant growth by increasing nutrient uptake (107-108). Experiments showed that the forage quality in alfalfa leaves and nutritional quality in strawberry onion bulbs were enhanced by the interaction between humic substances, the mycorrhiza, and elevated CO_2 (109-110).

Drought

Water deficit is an important factor that affects crop growth, survival, and yield. The effect of drought on AMF is strain dependent (111). Drought conditions influence and alter the type of mycorrhizae colonization and, in many cases different crops such as strawberry, wheat, barley and sweet potato, the beneficial effect of AMF is evident under low water conditions (112-114). Studies by Auge et al. suggest that drought resistance in plants can be enhanced in the presence of AMF. Thus, emphasizing the capability of AMF to adapt to climatically stressed conditions and facilitate the survival of plants, increasing their root shoot ratio and biomass. AMF symbiosis aids seedling establishment in the harsh desert environment by improving nutrient uptake and regulating phytohormone concentration (115-116). Further, studies by Mena-Violante et al, 2006 showed that compared to non-mycorrhizae plants, in conditions of drought the fruits of chile ancho peppers in the presence of AMF showed higher amount of carotenoids with similar intensity in color and chlorophyll content, thus also improving the crop quality (117). Amiri et al., 2017 reported that, in *Pelargonium graveolens L.*, the concentration of N, P and Fe is increased by mycorrhizal symbiosis under drought stress condition (118). Under pulsed or low water conditions, Bowles et al., 2018 reported that plant P uptake and the shoot N concentration is increased in the presence of AMF, which results in enhanced plant nutrient acquisition under water scarcity (119).

Fungicides

Seeds of muskmelon (*Cucumis melo*), squash (*Cucurbita pepo* and *C. moschata*), bean (*Phaseolus vulgaris*), tomato (*Lycopersicon esculentum*) and corn (*Zea mays*) treated with fungicides mefenoxam, thiram, tebuconazole+metalaxyl, and captan showed minor effects on colonization by the AMF *Glomus intraradices* on their roots, suggesting that the effect of fungicides on AMF inoculation and colonization is compatible (120). On the other hand, a study by Channabasava et al., 2015 show that there is significantly higher AM colonization, spore density, plant growth, and grain yield in mycorrhizal Proso millet plants treated with fungicide captan compared to other fungicides, while treatment with benomyl had an adverse effect in all the above measured parameters. This suggests that the type of fungicide applied in soil and its effect on plant performance is varied depending on the mode of action of the fungicide and the AMF species (121-122).

CONCLUSION

In the present day scenario of high industrialization and global warming, heavy metal pollution and drastic changes in climatic conditions like elevated CO2, high temperatures and water deficiency are negatively influencing the growth and productivity of plants. On the other hand agricultural practices like tillage, excessive use of chemical fertilizers, pesticides, etc., are decreasing soil fertility, the nutritive value of food and crop yield, thus posing a threat to humanity presently and to the future generations.

Studies reveal that AMF symbiosis increases the uptake of nutrients. They act as biofertilizers, bioprotectants, or biodegraders benefitting plant growth and productivity. They adapt and help the plant cope with stressed conditions like high salinity, heavy metal contamination, drought, and protect them against plant diseases and pathogens. Further application of fungicides had minor or no effect on the AMF. AMF play a role in phytoremediation which will aid in decreasing the heavy metals contamination of soils. They are ubiquitous in distribution and interact with more than 80% of plant species. Hence, we conclude that AMF can be used as a potential eco-friendly tool for sustainable agriculture to raise the standards of commercial application, to facilitate better agricultural practices, to maintain soil fertility, crop productivity, nutritive value of food, to reduce metal contaminations, and finally, to support healthy human life.

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