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REVIEW ARTICLE

ROLE OF ARBUSCULAR MYCORRHIZAL FUNGI IN SUSTAINABLE AGRICULTURE

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ABSTRACT

Sustainable agriculture performs a significant part in agroecosystems and decline destructive consequences at the environment through making use of multiple natural processes. Optimum soil fertility is a crucial purpose to be executed in sustainable agriculture system. Arbuscular mycorrhizal fungi (AMF) execute an environmental-friendly way to accomplish the previous objectives. Most of the terrestrial plant species are associated with the AMF and they have a necessary mutualistic link with plants. AMF symbiosis plays a crucial component in the growth and development of plant by increasing the efficiency of root system, root hydraulic conductivity, rate of photosynthesis, improve stomatal conductance, better nutrition absorption (macronutrients and micronutrients) and increased tolerance against various biotic and abiotic stresses and also help in modifying the structure of soil, aggregating soil particle, preventing soil erosion and bioremediation of degraded land. These symbionts also help in increasing the plant yields and productivity and reduce the chemical fertilizer usage and pesticides while maintaining the quality and quantity of plant and thereby promoting the sustainable agriculture. Present review article highlights the various role played by AMF in environmentally friendly agriculture by stimulating plant growth, development, productivity and served for 3E's i.e., eco-friendly, economic and increased yield.

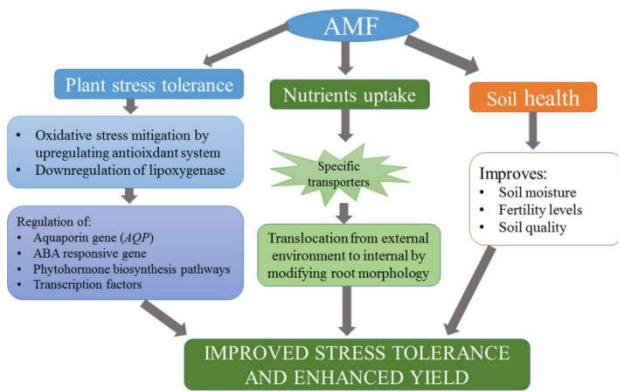
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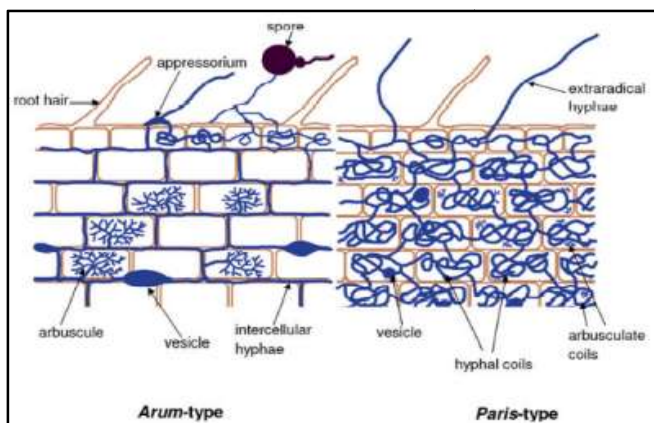
INTRODUCTION

Several stresses of biotic (diseases and pest) and abiotic (unfavourable environment, drought, nutrient deficiency, heavy metal toxicity) determines the productivity and reduction in crop yield (Cardoso et al., 2017; Priyadharsini & Muthukumar 2015). The rapid increase in world's population has been anticipated to reach approximately nine billion by mid of this century that will create an incredible stress on the worldwide agriculture to fulfil the growing population necessitates for food (Srivastava, Saxena & Giri, 2017). Hence increase in the production of crop and land productivity in agriculture is essential. Therefore, by the utilisation of chemical fertilizers and agrochemicals subsequently leads to increase in the crop production. The excessive use of these chemical fertilizers causes various ill effect on agriculture as well as environment ecosystem such as degradation of land, destroy surface and groundwater quality, soil biodiversity and ecosystem functioning (Srivastava, Saxena & Giri, 2017, Priyadharsini & Muthukumar 2015). The major objective for agriculture in future could be the acceptance of new paradigm, sustainable intensification, to fulfil human needs for the production of enough food along with maintaining the quality of environment and decline the risk and input of chemical fertilizers (Giovannini et al, 2020). Soil microorganisms play an important function in obtaining these objectives by improving the soil fertility, reduce the utilisation of chemical fertilizers in agriculture.

The interaction between plant and microorganisms also determines the development and plant growth by promoting production and high nutritional value in food and usually referred as biofertilizers (Giovannini et al, 2020; Bianciotto et al, 2016). Soil microorganisms exhibits a great diversity, among which mycorrhiza are found ubiquitously, present in a required symbiotic interaction with the rhizosphere of plants and plays a significant role in maintaining soil ecosystem (Bianciotto et al, 2016; Srivastava, Saxena & Giri, 2017; Lone et al, 2017). The word mycorrhiza derived from Greek 'muke's' which means fungus and 'rhiza' which means roots. Arbuscular mycorrhizal fungi (AMF) are the most common fungi which is associates with 90% terrestrial plant species in the form of symbiotic relationship (Srivastava, Saxena & Giri, 2017). AMF symbiosis facilitates the mineral nutrition and improves tolerance against biotic and abiotic stresses to the host plant. This symbiosis also helps in carbon sequestration, soil aggregation and increase health promoting phytochemicals, while in return fungus acquires photosynthates of plant. Three-way communication exhibited by this symbiotic associations i.e., between mutualist fungi, host plant and soil ecosystem (Lone et al, 2017; Giovannini et al, 2020). These fungi play a significant role in the growth and development of plants, enhance soil quality (health & fertility) and also declines the utility of chemical fertilizers in agriculture up to 50% and act as a potential tool for sustainable agriculture (Srivastava, Saxena & Giri, 2017). Present article emphasises the potential contribution of AMF to productivity-boosting sustainable agriculture, growth and development of plant by influencing the metabolic activities of plant and reduces the dependence of chemical fertilizers.



Arbuscular Mycorrhizal Fungi: Productivity and development of plant is regulated by the interaction of root microbiome and arbuscular mycorrhizal fungi (AMF) considered as a main member of the root microbiome (Akyol *et al.*, 2018). Arbuscular mycorrhiza fungi are microscopic, obligate symbionts, relates to the Glomeromycotina subphylum which comprises many genera and species and present in the cortical cells of root in a branched manner (Basu, Rabara & Negi, 2018; Anguilar- Paredes *et al.*, 2020; Srivastava, Saxena & Giri, 2017). Arbuscular mycorrhizal fungi colonises the majority of vascular plants except some families such as Betulaceae, Ultracaceae, Commelinaceae, Cyperaceae and Polygonaceae, which significantly increases the uptake of plant nutrition especially phosphorous, iron and zinc, improves soil quality and structure by modifying the biological and physiochemical properties of rhizosphere, enhances plant resistance against biotic and abiotic stresses, reducing the utilisation of chemicals in agriculture and subsequently accelerating plant growth, yield and development. Hence AMF can be used as biofertilizers and plays a vital role for environmentally friendly agriculture and ecosystem stability and development (Srivastava, Saxena & Giri, 2017; Zhao *et al.*, 2017; Basu, Rabara & Negi, 2018; Akyol *et al.*, 2018; Anguilar- Paredes *et al.*, 2020). In the symbiotic relationship with plant, AMF delivers mineral nutrient and water from soil to plant and in return plant supplied carbohydrates and lipids (Srivastava, Saxena & Giri, 2017; Anguilar- Paredes *et al.*, 2020). AMF exhibits speciality in morphology and physiology features. The spore size is also bigger than other fungi that is normally found in soil and its presence in excessive amount on roots is mainly responsible for production of AMF (ud din Khanday *et al.*, 2016). The interaction between host and AMF exhibits microbe associated molecular patterns (MAMPs), exopolysaccharides, volatile organic compounds (VOCs), MYC factors and Nod factors. VOCs involve in the alternation of root structure and regulating symbiotic association and AMF colonisation stimulate by the Nod factor (Basu, Rabara & Negi, 2018). This symbiotic association shows “give and take of nutrient” between plant and AMF. Arbuscular mycorrhizal fungi produce various structures in soil and root during the symbiotic relationship with the host plant (Srivastava, Saxena & Giri, 2017). The fundamental description of Arbuscular fungi is given here. AMF exhibits mainly two types of association on the basis of morphological features that have been detected during colonisation process.



One is Arum type and other type is Paris. Arum type: The arum type is rapidly developed in the root system of host plant. In this type, AM symbiont found intercellularly in between the cortical cells of root and producing arbuscules on intracellular hyphal branches.

Paris type: In the Paris-type, fungus spread directly from cell to cell inside the cortex and produce intracellular hyphal coils along with intercalary arbuscules on the coils (Prasad *et al.*, 2017; Giovannini *et al.*, 2020).

Appressoria: Appressoria is a type of swelling like structure produced by fungal hyphae. This structure introduces fungi in the root by penetrating the epidermal cells of the root. These hyphae also penetrate hypodermis and initiates branching in the cortical region of root and grows in both direction and form a network (Srivastava, Saxena & Giri, 2017).

Arbuscules: Arbuscules are produced by complex dichotomously branching and decreases the width of hyphae inside cortical cell of root. This structure enhances the area of contact between plant root and fungus and act as an interface which facilitates the transfer of nutrient from fungus to host plant root in exchange plant provides photosynthates to fungus (Srivastava, Saxena & Giri, 2017; Priyadharsini & Muthukumar 2015; ud din Khanday *et al.*, 2016; Prasad *et al.*, 2017).

Vesicles: Vesicles are round shaped or balloon like swelling in the cortex of root. This intercellular structure function as storage organ which stores phosphorous, oil droplets and also act as propagules (ud din Khanday *et al.*, 2016; Srivastava, Saxena & Giri, 2017).

Spores: Spores are thick walled, swollen structure and consist of more than one layer formed on the extraradical hyphae in the soil or in roots (ud din Khanday *et al.*, 2016).

Colonisation of AMF with root: During the root colonisation of AMF, fungi hyphae undergo various stages of development. That are described below:

Presymbiotic Stage: This stage mainly involves in the development of hyphae, spore germination and the host recognition (Bhale *et al.*, 2018; Cardoso *et al.*, 2017; Lone *et al.*, 2017).

Symbiotic Stage: This includes in the formation of appressoria and arbuscules (Cardoso *et al.*, 2017; Lone *et al.*, 2017). Through appressoria cell to cell contact between plant and fungus are formed (Basu, Rabara & Negi, 2018).

Root Colonisation: It can be achieved by two ways either Arum type or Paris type. In the Arum type extensively intercellular growth of hyphae takes place till it reaches to the inner cortex and after to cell wall where extensively branching result in the formation of arbuscules is main feature through which transfer of nutrients take place. While in the Paris type, the fungal hyphae's growth takes place intracellular or directly in the cell and the hyphal coil result in the formation of arbuscules (Lone *et al.*, 2017; Basu, Rabara & Negi, 2018).

Sustainable Agriculture and Sustainability: The motto of sustainable development/ agriculture involve in order to achieve the demands of present generation without compromising the demand of future generation (Cardoso *et al.*, 2017). Now days the use of conventional agriculture causes high risk to soil vitality, disturbs the microbial diversity and thus leads to soil degradation, altering food chain and food security in danger, affecting human health and disturb environment (Anguilar- Paredes *et al.*, 2020; Cardoso *et al.*, 2017). The extensive and immoderate application of xenobiotic compound in the form of fertilizers, pesticides and weedicides in agriculture, in term of increasing crop yield. The harmful effect on soil and environment have been consequently recorded by the use of these chemical fertilizers, which degraded the soil quality and soil pH, contaminate water with heavy metals, disturbs carbon-nitrogen (C/N)

ratio, negative impact on microorganism, humans and crop itself and affect ecosystem as well (Anguilar- Paredes *et al.*, 2020; Cardoso *et al.*, 2017; Srivastava, Saxena & Giri, 2017). The increase in crop production is mainly important to meet growing population demand by the chemical fertilizer usage but it is the part of short-term goal. But when we talk about long term sustainability and certainty in crop production, this factor is eliminated (Riling *et al.*, 2019). Currently there is need to practices such agriculture system which are based on environmentally friendly technologies and are not so much dependent on xenobiotic components which declines the risk of harmful effects on environment, enhance overall soil quality and enhances crop quality and quantity (Cardoso *et al.*, 2017). Soil microorganism especially AMF engaged in an important role such as maintaining overall soil structure, soil productivity, increases potential of crop to enhance its quantity and quality with changing environment and maintains environment. All these activities relate to sustainable management and sustainability (Srivastava, Saxena & Giri, 2017; Riling *et al.*, 2019). However, there are many techniques for developing sustainable agriculture and feeding human beings with decreases the risk of environmental affects and has been broadly suggested that promoting agricultural practices that help in enhancing the diversity of soil microbiota, which include organic or agro-ecological agriculture, suggests a crucial opportunity for acquiring better quality crop and improves environment, economics, and social components (Anguilar- Paredes *et al.*, 2020).

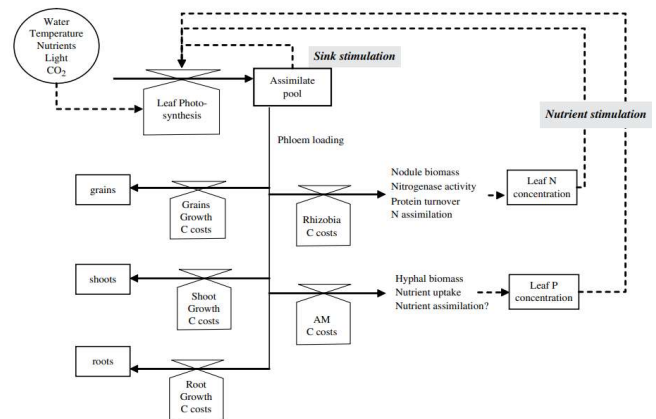
Role of Arbuscular Mycorrhizal Fungi in sustainable agriculture

Changes in morphological and physiological characters of plants

A. Development and growth in plant: Arbuscular mycorrhizal fungi (AMF) represent an interesting opportunity for acquiring the development and growth of plant by using their advantageous consequences (Regvar *et al.*, 2003). The positive effects that shown in the development and growth of plant by the inoculation of AMF are observed during various studies, (i) improves the growth of seedling and their survival rate, (ii) increased the uptake of essential nutrients, (iii) enhance antioxidant properties, (iv) enhance tolerance of plant against biotic and abiotic stresses, (v) improves water uptake, (vi) enhance CO₂ assimilation, (vii) enhance sugar concentration in fruit subsequently increases fruit quality (viii) enhance early flowering and fruiting, (ix) increase quality and quantity of crops (x) increases the production of important phytochemicals in edible plant (Regvar *et al.*, 2003; Srivastava, Saxena & Giri, 2017; Begum *et al.*, 2019; Bhantana *et al.*, 2021). Several studies observed that inoculation of *Glomus mosseae* in *Triticum turgitum* var. *durum* enhances its yield when it cultivated in 10 different soils. Similarly increase in production of chick pea also observed along with increase in protein, Fe and Zn nutrient when incorporated with AMF (Srivastava, Saxena & Giri, 2017). An increase in secondary metabolites enhances in strawberry when inoculated with species of AMF that enhances antioxidant properties. Zeng *et al.* (2014) observed that inoculation of *Glomus versiforme* in citrus crops improve its quality by enhancing sugar content, organic acid, vitamin C and flavonoid (Begum *et al.*, 2019). The inoculation of AMF in tomato enhances its quality by increasing carotenoid content, essential volatile compounds, lycopene content in compare to non-AMF plant. In the *Allium cepa* also remarkably noted the content of proline, sugars and protein enhanced in leaves (Bhantana *et al.*, 2021).

B. Increase in photosynthetic activities: The inoculation of AMF with plant enhances its photosynthetic rate by regulating stomatal opening due to increase in hormonal activities like, cytokinin, gibberellins and auxin and by increasing surface area of leaves (Srivastava, Saxena & Giri, 2017). The rate of photosynthesis also increases by enhancing chlorophyll content, photosynthetic enzymes, sink strength of rhizosphere, regulating genes related to light harvest complex

(LHC) and Photosystems PSI and PSII that help in reduction in the formation and a rise in Reactive Oxidative Species (ROS) and by maintaining N in chlorophyll content, photosystem protein, and in enzymes that related to process of photosynthesis. Increase in the Production of ATP and enhancing Rubisco activity also regulates the photosynthetic activity in a positive manner (Balestrini *et al.*, 2020; Bhantana *et al.*, 2021).

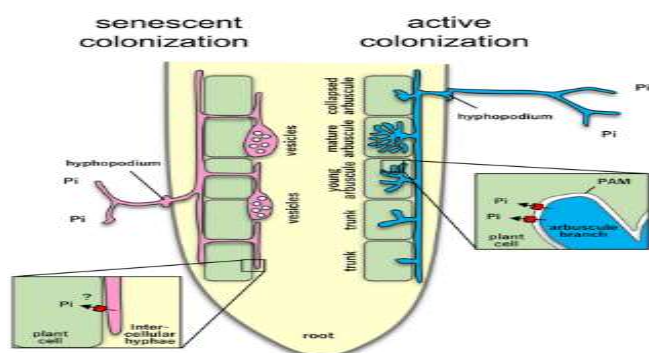


Increase in the activity of gas exchange capacity, content of photosynthetic pigment, photochemistry efficiency of PSII, carbon content, increase surface area are remarkably observed in *Robinia pseudoacacia* (also known as black locust) that significantly increase its photosynthetic activity when incorporated with AMF. Similarly, increase in photosynthetic rate due to improve in stomatal conductance, transpiration rate and osmotic potential of *Citrus tangerine* are also recorded when it is colonised by AMF species, *Glomus versiforme* (Srivastava, Saxena & Giri, 2017). Additionally increase in photosynthetic rate are also noticeable in the leaves of *Lycopersicon esculentum* when colonised by AMF due to accumulation of ferrochelatase-2, regulating genes that are involved in light reaction and calvin cycle and enzyme that involve in repairing of photosystem II i.e., peptidyl -propyl cis-trans isomerase and protease (Balestrini *et al.*, 2020).

Mineral nutrient and nutrient absorption: The mutually beneficial interaction between root and AMF provides mineral nutrition to plants in exchange of photosynthates to fungus (Lone *et al.*, 2017). Plant in symbiotic association with AMF facilitates nutrient absorption through extraradical mycelium by enhancing plant surface area of absorption. The miniature diameter of hyphae facilitates more nutrient uptake from soil solution and also penetrates into small size of soil pore that are not available to root hairs. The mycelium also has capacity to absorb nutrient from the zone where nutrients are restricted that are found close to the root. Fungi that enhance nutrient absorption in plants is phosphorous, zinc, copper, sulphur, aluminium, nitrogen, iron, magnesium and other micro and macronutrients that plays a vital role in growth and productivity of plant (Lone *et al.*, 2017; Srivastava, Saxena & Giri, 2017; Priyadharsini & Muthukumar 2015; ud din Khanday *et al.*, 2016; Jakobsen *et al.*, 2003). Several research papers observed that absorption of mineral nutrients is higher in the plant incorporated with AMF rather than non-AMF plant (Rouphael *et al.*, 2015). When *Allium cepa* colonised with *Glomus versiforme* result in enhancing the absorption of mineral nutrients mainly phosphorous, nitrogen, zinc and magnesium (Bhantana *et al.*, 2021). The inoculation of *Moringa oleifera* with AMF enhances its nutrient absorption especially phosphorous and also increases bioactive compound in plant that are advantageous for human health (Cosme *et al.*, 2014).

Uptake of phosphorous: After nitrogen, phosphorous is an important nutrient for the productivity of plant and fertility of soil (Wahid *et al.*, 2019). Phosphorous is an important mineral nutrient for the development of plant and regulating various metabolic processes in plant (Wahid *et al.*, 2019; Cardoso *et al.*, 2017). Phosphorous present in large quantity in soil either organic or inorganic form but are not available to plant in sufficient

amount because its diffusion rate is low and occur with other soil nutrients in complex way (Wahid *et al.*, 2019; Srivastava, Saxena & Giri, 2017). The negative impact on productivity and plant growth, decrease in photosynthetic and respiration rate and inhibits cell division when the supply of phosphorous is limited (Cardoso *et al.*, 2017; Lone *et al.*, 2017). The inoculation of plant with AMF results in enhancing absorption of phosphorous and improves crop productivity (Bhale *et al.*, 2018). The mutual association with AMF boost soil environment and plays a significant part in the absorption of phosphorous by two ways—through root epidermal cells and hairs, and by AM fungi (Wahid *et al.*, 2019; Cardoso *et al.*, 2017). The AM fungi facilitates phosphorous to plant regulated by the activities of proton ATPases and phosphate transporters (Bhale *et al.*, 2018 Karandashov & Bucher, 2005). The AM fungi are responsible for the development of arbuscules and activates phosphate transporter genes of host plant that regulate the absorption of phosphorous nutrient via arbuscules (Igiehon *et al.*, 2017; Kobae, 2019). The GyPT and GiPT are two genes that involve in the the absorption of phosphorous at fungus and soil interface (Karandashov & Bucher, 2005). *Medicago truncatula* and *Lotus japonicus* shows MtPT4 and LjPT4 Pi transporters when inoculate with AM fungi and involve in phosphorous absorption (Igiehon *et al.*, 2017). When maize plant interacts with *R. irregularis* also activates the phosphate transporter genes and take part in phosphorous absorption (Kobae, 2019). Several studies reported that inoculation of AMF in potato, rice and *Medicago truncatula* give rise to the expression of four different plant phosphate transporters- StPT3, StPT4, ORYsa; Pht1;1 and MtPT4, involve in absorption of phosphorous (Karandashov & Bucher, 2005).



Absorption of nitrogen: Nitrogen is among the essential mineral nutrients for the growth of plant. The colonisation of Plant with AMF regulates the uptake of nitrogen from soil and organic compounds and amino acids through the action of N cycling (Srivastava, Saxena & Giri, 2017). The absorption of nitrogen from soil is achieved by enhancing surface area, through the enlargement of mycelium and stimulating NH_4^+ ammonium transporter that are expressed in arbuscules and regulates its activity under low availability of nitrogen. AMF also controls the absorption of amino acids (Srivastava, Saxena & Giri, 2017; Ibrahim, 2021). The incorporated of *Sorghum bicolor* with AMF enhances the absorption of amino acids are observed (Srivastava, Saxena & Giri, 2017). In the family Papilionaceae incorporated with nitrogen fixing rhizobia and AMF enhances the uptake of nitrogen and also transfer nitrogen to its neighbouring plant (Ibrahim, 2021).

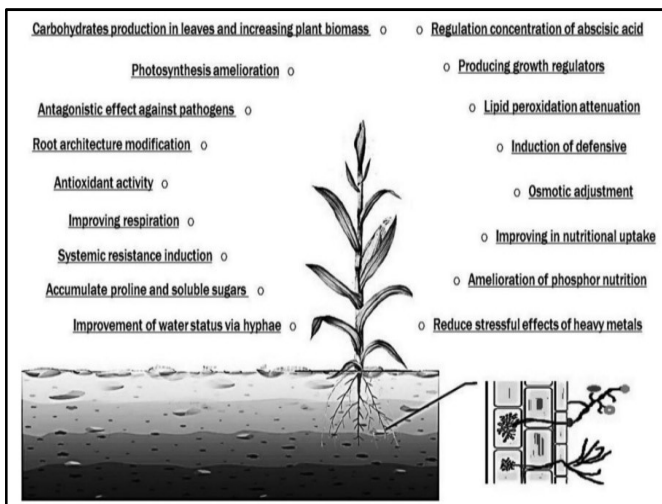
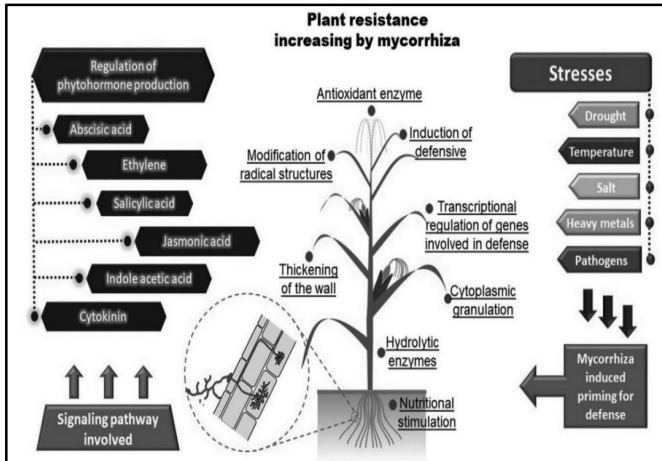
Soil Health: Soil health plays a vital role in sustainability of life of organisms (plant and animal) and maintain environment stability, including agroecosystem (ud din Khanday *et al.*, 2016; Dollinger & Jose, 2018). The concept of soil health refers to soil quality (Dollinger & Jose, 2018). Soil health may be described as the ability of soil to serve as vital function in the ecosystem boundaries that sustain crop productivity, improves environment sustainability, promote plant development and support human and animal health (Dollinger & Jose, 2018; Yang *et al.*, 2020; Wulanningtyas *et al.*, 2021). Soil is an important strategic resource and performs various essential roles that

is; i) supplying of food, fibre and fuel, ii) decaying of organic matter, iii) reprocessing of essential nutrients, iv) reclamation of polluted organic components, v) carbon sequestration; vi) maintaining the water quality and regulate its furnishing vii) maintain habitat for soil biota and, viii) source of organic matters. Unfortunately, due to practices of various anthropic activities in agriculture results in the degradation of soil that shows negative impact on human health (Yang *et al.*, 2020). The disturbance in ecosystem causes the negative impact on soil by altering the physical, chemical and biological properties. Several studies have found that AMF enhances the properties of soil in a positive way and regulates the aggregation of soil particles, subsequently enhances the soil quality and health (Srivastava, Saxena & Giri, 2017). AMF plays a significant part in the secretion of various type of extracellular enzymes that regulates the uptake of nutrients by plant from soil, degradation of organic matter and soil component maintain the balance of carbon and nutrient in the soil, capacity to resist various stresses regulates modification and formation of soil, detoxification of the effect of harmful metal reduce the risk of land degradation (Tahat *et al.*, 2020; Fraç *et al.*, 2018). AMF also secreted glomalin, a glycoprotein which help in maintaining the soil aggregation (Bhale *et al.*, 2018). Hence, AMF plays a significant part in maintaining soil quality and soil health (Srivastava, Saxena & Giri, 2017). The preservation of soil health results in the improvement in crop production, plant development and fruit quality (Tahat *et al.*, 2020).

Secondary Metabolites: The creation of secondary metabolites regulate the resistance activity of plant against abiotic and biotic stress, act as a defence mechanism (systemic acquired resistance & induced systemic resistance) and also gives particular colour, smell and tastes to plants (Srivastava, Saxena & Giri, 2017; Kaur, S., & Suseela, 2020; Silpa *et al.*, 2018). There is no significant role of secondary metabolites are remarkable in regulating the plant development but these is the main source for various biochemicals such as pharmaceuticals, pesticides, and drugs etc. (Silpa *et al.*, 2018). The inoculation of plant with AMF increases the formation of essential oil in medicinal plant, phytoalexins, phytochemicals and phenolic content result in enhancing the plant resistivity against stresses in addition to signal transduction for attracting dispersal of seeds and pollination (Kaur, S., & Suseela, 2020; Silpa *et al.*, 2018; Lone *et al.*, 2017). When *Glycyrrhiza uralensis* colonised with *Glomus mosseae* results in enhancing the production of flavonoids, liquiritin, isoliquiritigenin and glycyrrhizic acid. Similarly, *Stevia rebaudiana* colonised with *Rhizophagus fasciculatus* result in increasing steviol glycosides and improves phosphorous absorption (Srivastava, Saxena & Giri, 2017). The inoculation of onion bulb with AMF enhances the production of sitosterol, stigmaterol and amyrins (Lone *et al.*, 2017). The stimulation of salicylic acid, nitrogen oxide and hydrogen peroxide pathways were recorded against citrus canker disease when AMF inoculated with crop plant. Likewise, in the tomato plant increased flavonoid content along with develop resistance against tomato mosaic virus were also remarkable (Kaur, S., & Suseela, 2020). The production of lignan in *L. album* are also recorded when colonised by AMF. Lignan is utilised in the formation of antitumour agents, etoposide and teniposides. Lignan act as a defence molecule under stress condition (Farkya, 2010). The increase of secondary metabolites in *V. tricolorshoots* result in improves nutrient uptake, enhances phenolic and flavonoid content, and increases tolerance against stresses (Zubek *et al.*, 2015). Therefore, due to the inoculation of AMF in many plants result in increasing the increase of secondary metabolites in plant qualitatively as well as quantitatively (Silpa *et al.*, 2018).

AMF responses to abiotic stresses: In the agricultural productivity, abiotic stresses represent a threatening remark. Poor soil conditions and low water availability leads to abiotic stresses like drought, salinity, extreme temperatures and accumulations of heavy metals (Abo Nouh, 2019; Cardoso *et al.*, 2017). The task of AMF in respond to abiotic stresses are found to be very important by enhancing the plant resistivity towards stresses (Begum *et al.*, 2019; Cardoso *et al.*, 2017). AMF enhances plant growth and productivity under abiotic

stresses through induced systemic response, bioremediation and also act as biofertilizers, bioprotectant and biocontrol agents (Abo Nouh, 2019; Latef *et al.*, 2016; Hashem *et al.*, 2018). The main role that are performed by AMF in respond to abiotic stresses include enhancing water uptake, nutrient uptake, photosynthetic rate, regulation of stomatal opening, improve root to shoot ratio, reduce oxidative damage, change in gene expression – proline synthesis, dehydrin protein and change in antioxidant properties (Latef *et al.*, 2016; Hashem *et al.*, 2018; Srivastava, Saxena & Giri, 2017).

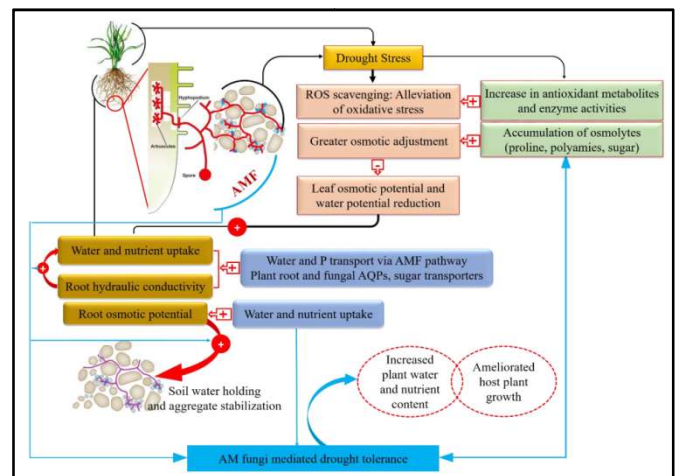


Drought: Drought is the main factor of abiotic stresses which leads to negative impact on plant productivity and growth (Pavithra & Yapa, 2018; Diagne *et al.*, 2020). The symbiotic association with AMF plays a significant role to cope with drought stress (Pavithra & Yapa, 2018; Bahadur *et al.*, 2019; Cheng *et al.*, 2020).

Negative impact on plant: 1. Reduces transpiration and photosynthetic rate, 2. disturbs membrane permeability, 3. Interrupt with phloem activity, 4. Disruption of enzymatic structure, 5. Enhances the formation of ROS, 6. Loss in turgidity, 7. Interfere with metabolic activities. All these leads to damage in cell and therefore interfere with morphological and physiological activity of plant. Hence, subsequently reduces the plant growth and productivity (Pavithra & Yapa, 2018; Bahadur *et al.*, 2019).

Plant inoculates with AMF: The task of AMF in improving plant growth and resist to drought stress includes- 1. Accumulation of proline (act as protectant) 2. Secretion of antioxidant (ascorbate peroxidases, glutathione reductase, glutathione peroxidase, tocopherol etc.) 3. Enhance strigolactones synthesis, 4. Enhances surface area for water uptake, 5. ABA synthesis (positive effect on root conductivity, stomatal conductivity), 6. Aquaporin protein 7. Reducing oxidative stress, 8. Enhance gas exchange, 9. Enhances water potential in leaf, 10. Improves transpiration rate, 11. Enhance

osmotic adjustment (Pavithra & Yapa, 2018; Bahadur *et al.*, 2019; Cheng *et al.*, 2020; Diagne *et al.*, 2020; Begum *et al.*, 2019; Latef *et al.*, 2016). Inoculation of AMF with *Rosmarinus officinalis* and *Poncirus trifoliata* under drought stress results in improving stomatal conductance. Similarly, AMF with *Solanum lycopersicum* help in improving resistivity towards drought stress through ABA signalling pathway and, AMF with lettuce and tomato enhances synthesis of strigolactones that increases the resistivity of plants toward drought stress (Bahadur *et al.*, 2019). Inoculation of citrus plant with AMF result in enhancing gaseous exchange during drought condition (Cheng *et al.*, 2020). AQPs concerns the main intrinsic proteins and plays crucial role in transporting various small molecules across plasma membrane. Homologues of AQPs are based on the sequence of amino acid and subcellular localisation and on this basis AQPs are classified into – plasma intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), NOD26- like intrinsic proteins (NIPs), small intrinsic proteins (SIPs) and Glps-like intrinsic proteins (GIPs). AQPs helps in the movement of water across cell membrane (Cheng *et al.*, 2020; Sánchez-Romera *et al.*, 2015). The inoculation of maize plant with *Glomus intradices* resulted in the expression of aquaporin genes (GintAQP1 and GintAQP2) that increases the resistivity of plant against drought condition by the formation of arbuscules and extra – radical mycelia (Latef *et al.*, 2016). *Funneliformis mosseae* inhibit the PIP gene protein and enhances the resistivity of host plant toward drought but *Rhizophagus irregularis* was known to be more efficient in water absorption and not alters PIP gene expression under drought condition. *R. irregularis* have RiAQP1 gene failed to activate water uptake in *Xenopus laevis* oocytes but in heterogenous system with RiAQP2, resulted improvement in water uptake under drought conditions. So, the AM plant enhances water uptake through AQPs under drought stress was also observed (Sánchez-Romera *et al.*, 2015).

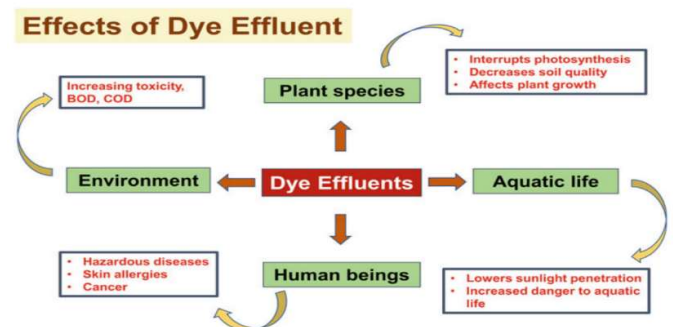


Salt stress: It is widely known that the soil salinization is an increasing environmental problem posing a severe threat to global food security. Salinity stress is known to suppress growth of plants by development by reducing photosynthetic efficiency, mineral assimilation, and antioxidant metabolism. Resulting in reduced yield productivity (Begum *et al.*, 2019; Hashem *et al.*, 2018). It is known that AMF can develop spontaneously in salty settings. They helped to promote the growth of a number of plant species in saline environments. This primarily has to do with a combination of biochemical, physiological, and nutritional effects (Diagne *et al.*, 2020). Several physiological, biochemical, and molecular approaches by which AM plants could alleviate salt stress includes- (i) more osmolytes are accumulating; (ii) maintaining ion homeostasis requires control of ion uptake by roots, ion compartmentation, and ion transport into plant tissues; (iii) increased uptake of water and its distribution to plant tissues with the help of aquaporins; (iv) enhanced production of antioxidants, which control oxidative damage; (v) selective buildup or exclusion of salts; (vi) managing adequate rate of photosynthesis for better plant growth, (vii) maintaining membrane structure and integrity; (viii) regulating phytohormone synthesis and

(ix) controlling ultrastructure damage; (x) stimulate and alter root system morphology; (xi) increase stomatal conductance (Wu, 2017; Latef *et al.*, 2016). Colonization with AMF protects plants against harmful effects of ROS by enhancing antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR). MF-inoculation can also modulate plant status of osmolytes/osmoprotectants (such as proline, glycine betaine and sugars) and that of organic acids. AMF-assisted improved pool of glycine betaine and proline was argued to protect thylakoidal membranes against the ROS damage (Latef *et al.*, 2016; Acosta *et al.*, 2020). Inoculation with arbuscular mycorrhizal fungi (AMF) significantly improved salt tolerance and improved yield in tomato; maize, mungbean, clover and cucumber due to P acquisition, improved osmoregulation by proline accumulation and reduced NaCl concentration (Abo Nouh, 2019). Under both control and medium salinity, P, Cu, Fe, and Zn accumulations were higher in inoculated (*F. mosseae*) tomato plants than in non-inoculated tomato plants, while the amount of Na in the shoot significantly lower in mycorrhized plants, confirming one more time that plant tolerance to salt stress is improved by AMF colonisation (Rouphael *et al.*, 2015). When compared to non-mycorrhizal plants, *Zea mays* plants inoculated independently with three native AMF produced more biomass and had greater shoot potassium and proline levels. AMF structures in the ground and the roots have a filtering action that improves ionic equilibrium by preventing the entry of harmful Na^+ ions (Diagne *et al.*, 2020). To combat the ROS produced by salinity, AMF symbiosis is being reported to strengthen the antioxidative system in *Olea europaea L.*, and tomato. Additionally, it has been hypothesised that AMF improves citrus plant growth and photosynthetic efficiency by reducing the antagonistic impact of Na^+ on Mg^{2+} uptake in citrus plants. Because of the aforementioned methods, AMF improves plant nutrient uptake, which aids in preventing saline stress conditions. (Acosta *et al.*, 2020).

Heavy Metals: Toxic elements in the environment pose a threat to the 'Man and Biosphere' by lowering agricultural output and harming the health of ecosystem. High accumulation of various elevated/toxic metals within plants can bring several consequences such as: (i) inhibition of seed germination, (ii) decrease in root elongation, (iii) inhibition of rapid growth, and (iv) suppression of photosynthesis rate, transpiration, leaf chlorosis and premature leaf senescence (Latef *et al.*, 2016). Due to their potential to boost the defence mechanism of AMF mediated plants, AMF are widely regarded as helping the growth of plants in grounds contaminated with heavy metals (Begum *et al.*, 2019). Different mechanisms are used by mycorrhizal fungi to detoxify the adverse effects of heavy metals on the environment and on the host plant's development including (1) the production of chelating products, (2) the interaction with the plasma membrane, and (3) the effects on the cellular wall components of the fungi and the plant, (4) changes in rhizosphere pH (5) the regulation of gene expression under stress conditions, (6) restriction of metals by compounds secreted by the fungus (7) precipitation in polyphosphate granules in the soil (Wu *et al.*, 2017; Latef *et al.*, 2016). Such mechanisms can be conducted by the following: 1. Plant growth and the subsequent heavy metals' dilution in tissues 2. The production of organic products such as organic acids by plant roots, which prevents the uptake of heavy metals from the rhizosphere by chelating, precipitating, and binding 3. The selective activity of plasma membrane in the absorption or desorption of heavy metals 4. The retention and immobilization of heavy metals by plant roots and the fungal hyphae 5. Metallothioneins in the cytosol of the host plant and fungus chelate heavy metals 6. The function of specific or non-specific carriers and plasma membrane pores (both fungi and host plant) 7. Heavy metal sequestration by plant and fungi cellular vacuoles 8. Transfer of heavy metals by the fungal hyphae 9. The exchange of those metals between the host plant and the fungi 10. Active transfer of those metals by the specific and non-specific pathways in both the host plant and fungi (Wu *et al.*, 2017). AMF identified a few metal transporters that are essential for the control of heavy metals. Multiple Zn transporters were found in AMF in recent

years, such as GintZnT1 from *R. irregularis*. Multiple putative genes coding for Fe, Cu, and Zn transporters have been also identified. These transporters could be involved in plants that can tolerate heavy metals inoculated by AMF (Diagne *et al.*, 2020). This metal resistance in AMF fungi gives defense to both the partners against heavy metals. In the germinating spores of *Gigaspora margarita* BEG34, the cDNA encoding metallothionein like polypeptide (GmarMt1) was able to provide tolerance against Cd and Cu (Latef *et al.*, 2016). In comparison to nonmycorrhizal plants, *Desmostachyabipinnata* colonised with mycorrhizal fungi displayed higher levels of accumulation of Cd and lower root-to-shoot ratio. *Septoglomus deserticola* within roots of *Prosopis*. Higher Cr and Pb deposits were seen in phloem cells and xylem using Xray mapping. Thus, they recommended that communication with *Septoglomusdeserticola* improves metal tolerance/accumulation in *Prosopis* (Kumar and Saxena, 2019).

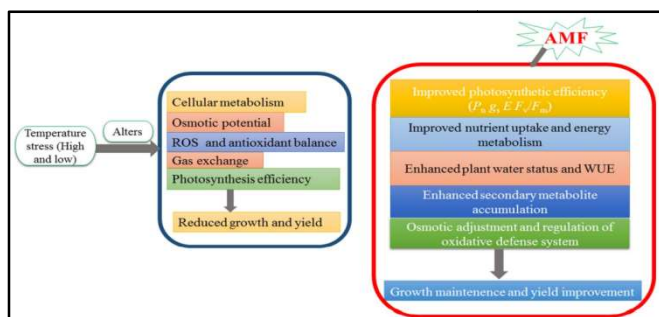


Metallophyte Plant: Metallophytes are plants that are naturally adapted to grow in heavy metal soils. In metallophyte plants, metal hyperaccumulation and hypertolerance capacity are naturally selected (Cardoso *et al.*, 2017). Metallophytes are plant species able to grow in metalliferous soils, as they have evolved a variety of mechanisms dealing with the excessively high internal metal (loid)s concentration via exclusion (preventing the entrance of contaminating elements in the harmful intracellular levels) or uptake and detoxification. Plants possess different avoiding strategies, which include fixation in mycorrhiza, plant cell walls, and root exudates sequestration. PHEs are excluded from the roots by mycorrhiza, which keeps them from reaching the shoots (Rossini-Oliva *et al.*, 2018).

Phytoremediation: The term "phytoremediation" is prefixed with the Greek letter phyto which means 'plant' and using the Latin word remedium which means 'to correct or remove evil' (Mahar *et al.*, 2016; Sumiahadi & Ahar, 2018). Phytoremediation is a technical type of bioremediation using plants, and comprises two biological components, one involving the rhizosphere microbiota and the other involving the intrinsic characteristics of the plant itself (Cardoso *et al.*, 2017). There are numerous plant mechanisms for remediating heavy metal contaminants from the environment. As it functions to remediate contaminant from soils and water, at least there are six mechanisms of plants on phytoremediation process include phytoextraction, phytoremediation, phytostabilization, phytodegradation, phytovolatilation, rhizodegradation (Krishnamoorthy *et al.*, 2019; Mahar *et al.*, 2016; Sumiahadi & Ahar, 2018).

Temperature: Temperature is among the most important environmental factors that determine the growth and productivity of plants across the globe. Many physiological and biochemical processes and functions are affected by low and high temperature stresses. Temperature stress includes both low temperature and high temperature events occurring during the growth season of the crops (Wu *et al.*, 2017). In particular, low temperature stress (cold or chilling;) can affect development and plant growth by impacting cellular metabolism, the activity of macro-molecules and decreased osmotic potential in the cellular milieu, plasma membrane (solidification or rigidification) and antioxidant-ROS balance and destabilization of protein complexes. Reduced leaf expansion and stunted growth), wilting and chlorosis), decreased hydraulic conductance and loss of stomatal control), and decreased

photosynthetic efficiency (Latef *et al.*, 2016). Heat stress significantly affects development and plant growth by imparting - loss of plant vigor and inhibition of seed germination, retarded growth rate, decreased biomass production, wilting and burning of leaves and reproductive organs, abscission and senescence of leaves, damage as well as discoloration of fruit, reduction in yield and cell death and enhanced oxidative stress (Begum *et al.*, 2019). AMF symbiosis was reported to improve plant tolerance against temperature stresses (Latef *et al.*, 2016). The tolerance mechanisms involved in modification of plant cell membrane, accumulation of cytosolic calcium ion, acclimation of photosynthesis, activation of ROS scavenger systems, accumulation of compatible solutes such as proline and sugars (Wu *et al.*, 2017). The ability of the grass *D. lanuginosum* to withstand temperatures in the soil between 38°C and 65 °C in Yellowstone National Park was directly linked to an association with the fungus *C. protuberata* and its mycovirus. *Curvulariasp.* confer thermos tolerance to grasses, and also provided thermos tolerance ability to other plants watermelon, tomato, and wheat (Abo Nouh, 2019). Plants such as maize and tomato inoculated with *G. etunicatum* and *G. mosseae*, respectively were reported to exhibit higher SOD, CAT, POD and APX activities compared to non-inoculated plants under low temperature stress (Latef *et al.*, 2016).



Acidity Stress: Acidic soils are phytotoxic to plant survival, distribution, and interactions with microorganisms. The pH (excessive OH⁻/H⁺ ion concentrations) of the soil solution is influenced by the form of plant ion nutrition because of differences in the cation to anion uptake ratio, ion assimilation, and cellular pH stabilization (Cardoso *et al.*, 2017). Soil acidity mainly due to the associated effects of aluminium and manganese toxicity on plant growth, as the solubility of both ions increases under low soil pH (Alho *et al.*, 2015).

Aluminium Toxicity: Acidity toxicity and Al toxicity cannot be separated, since Al is soluble only in an acid solution. Plants adapted to acid mineral soil may refrain from Al toxicity by a variety of mechanisms, such as avoidance by Al exclusion, high efficiency of nutrient acquisition, favorable soil microbiota and/or tolerance mechanisms (achieved by accumulation) due to the detoxification of Al inside the cells by inductor and excluder plants (Cardoso *et al.*, 2017). AMF can provide a wide array of benefits to the host plant, such as forming a unique mycelial network, connecting plants of different species, regulating their growth, and allowing access to nutrients that would otherwise be unavailable. In both extra- and intraradical fungal structures, AMF can function as a physical barrier that can filter and immobilise poisonous substances, reducing the dangers associated with these phytotoxic substances. Pro is a key amino acid involved in a wide array of plant physiological and developmental processes. By observing the changes in the majority of enzymes and metabolites in the processes of catabolism and Pro biosynthesis, the current study sought to analyse the specific changes in Pro metabolism in AMF-plants influenced by Al⁺³ toxicity. (Alotaibi *et al.*, 2021).

Plant and Manganese Toxicity: Mn in excess quantity act as toxic element. It has been reported that the negative effects of Mn toxicity are alleviated or accentuated by different light levels, depending on the plant variety, tolerance, and improved nutritional status by mycorrhization (Cardoso *et al.*, 2017). When arbuscular mycorrhiza fungi (AMF) colonization is preferentially initiated from an intact

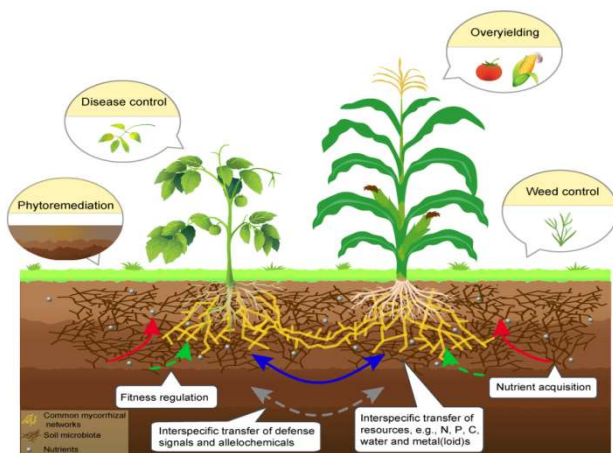
extraradical mycelium (ERM), that is the AM mycelium that grows outside the roots of the host plant, the infection develops faster and P acquisition is greater in earlier stages of plant growth. AMF colonisation decreases the plants' ability to absorb Mn, with changes in Mn concentration more pronounced in the roots than in the shoots (Alho *et al.*, 2015).

AMF and Biotic Stresses: Given that green plants are the ultimate source of energy for most other organisms, it is not surprising that plants evolved a variety of resistance strategies, which can be constitutively induced after damage. By operating alone or in concert with other related microbes residing in areas that are directly influenced by the plant, AMF defends host plants from a variety of biotic stressors (Dowarah, Gill & Agarwala, 2021). In natural ecosystems, species interactions form a complex web of associations. Traditionally, the aboveground component of ecosystems is considered in isolation from belowground. However, there is now increasing recognition that both components interact closely with one another. For example, plants interact simultaneously with aboveground insect herbivores and soil biota, such as arbuscular mycorrhizal fungi (AMF), fungal pathogens and nematodes. These interactions between above- and below-ground components are crucial for regulating ecosystem processes and features (Yang *et al.*, 2014). AMF could directly compete for infection sites or host-derived carbon and thus suppress these pathogens (Yang *et al.*, 2014; Pozo *et al.*, 2010). However, AMF most frequently interacts with diseases indirectly, for example, by promoting root growth or plant tolerance or by upping resistance by generating defensive reactions (Yang *et al.*, 2014). The experiments under controlled conditions confirmed that AMF inoculation leads to a reduction of the impact of Striga, apparently related to a reduction in strigolactones production. All in all, it seems likely that a reduction in strigolactone production underlies the decrease in the incidence of root parasitic plants on mycorrhizal plants (Pozo *et al.*, 2010). Numerous studies have shown that AMF lessens the harm that many plant cause diseases. AMF colonisation has a defence mechanism known as mycorrhiza-induced resistance (MIR), it has traits with and offers systemic defence against a variety of attackers, systemic acquired resistance (SAR) after pathogen infection AMF increases the production of antioxidant enzymes in plants, which can act as a defense against pathogens and other stresses. In addition to the activation of plant defence mechanisms, a number of additional factors, including improved nutrient status of the host plant, changes in root growth and morphology, competition for colonisation sites and host photosynthates, and microbial changes in the mycorrhizosphere, have been linked to reduced pathogen damage by AMF. The improvement of plant growth may have a positive effect because mycorrhizae can facilitate the regrowth of tissues after attacks (Diagne *et al.*, 2020).

Protection Against Pest and Pathogen: Soil borne pathogens are a major limitation for intensive crop production and cause losses as great as 50%. Moreover, the environmental concerns associated with the use of pesticides are limiting other options for their control under field conditions. Only when AMF are inoculated prior to the pathogen infection has the use of AMF to safeguard the crops proved successful (Brito *et al.*, 2019). Through several mechanisms like damage compensation, direct competition for colonization sites or food, changes in root morphology and rhizosphere microbial community composition, biochemical changes associated with plant defense mechanisms and the plant's activation defense. AMF can induce control over various plant diseases (Srivastava, Saxena & Giri, 2017). The noticeable resistance of a plant to a pest or disease may be simply the result of improved nutrition. Colonisation of a root cell by AMF helps the plants to remove the pathogen from the cell, with result plants root is free from the pathogen infection that destroys the root systems in plants (ud din Khanday *et al.*, 2016). Mechanisms by which AM fungi control root pathogens include (i) enhanced host nutritional status, (ii) damage compensation, (iii) competition for host photosynthates, (iv) competition for infection sites, (v) anatomical and morphological changes in the root system, (vi) modifications in the mycorrhizosphere's microbiome and (vii) activation of plant

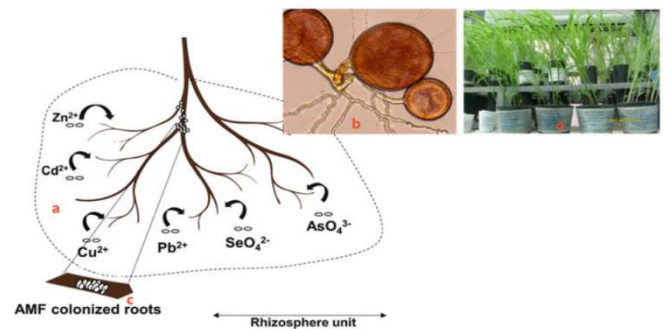
defence mechanisms (Priyadharsini and Muthukumar, 2015). The levels of several phytohormones (mainly salicylic acid (SA), jasmonates (JAs), ethylene (ET) and abscisic acid (ABA)) fine-tune the defence responses in plants through an intricate regulatory network the levels of these hormones seem to be altered in mycorrhizal plants. Probably affecting plant defence mechanisms (Pozo *et al.*, 2010). A small increase in the activity of plant defence genes, especially those involved in the production of chitinases, glucanases, flavonoid biosynthesis and phytoalexins, has been observed during mycorrhizal growth; however, these mycorrhizal defence induction mechanisms remain transitory (Priyadharsini and Muthukumar, 2015). AMF colonization increased resistance in *Poinsettia* against pathogens like *Pythium ultimum*. Mycorrhizal fungus infestation on coffee plants increased resistance to disease *Bidens Pilosa*. Where as Tea plant inoculated with mycorrhizal fungi and other plant growth promoters provided resistance for rot disease. Fusarium induces wilt disease in tomato worldwide, at large its control and management are difficult. Inoculation of tomato with AMF has shown control in the severity of the disease and enhanced overall growth in tomato seedlings (Srivastava, Saxena & Giri, 2017).

Nutrient Transfer in Intercropping System: Intercropping is an ancient technique of growing more than one crop species simultaneously in the same field. It plays a significant part in agriculture rendering advantages to both soil and plant. Intercropping improves soil texture and soil water availability and supplies various organic matters for most efficient proliferation of symbiotic and non-symbiotic microorganisms. The wide and diverse plants in an intercropping favour an increased and viable population of AM fungi (Priyadarshini & Muthukumar, 2015). The three major roles AM fungi play in intercropping systems: 1) mediation of plant interspecific transfer of C, N, P, and water resources and facilitative interactions; 2) control of parasitic weeds and plant pathogens; and 3) remediation of heavy metal(loid)-contaminated soil (Li, Hu & Lin, 2021). AMF are unique because they can establish hyphal connections between multiple plants. These connections can occur between plants of the same or different species and in turn create a common mycorrhizal network (CMN). CMNs can become very extensive as nearly ninety percent of land plants support hyphal connections. It has been proven that these networks are pathways that enable plants to transfer nutrients based on gradients and source-sink relationships (Von Thun, 2013; Priyadarshini & Muthukumar, 2015). In a heavy metal-polluted soil, AM fungal inoculation alleviated the toxicity level and increased the yield of garlic chives (*Allium tuberosum*) intercropped with sunflower (*Helianthus annuus*) via enhancing soil phosphatase activity and plant P acquisition, along with increased availabilities of soil of heavy metals and acquisitions by sunflower (Li, Hu & Lin, 2021). The transfer of nitrogen in non nodulated soyabean from nodulated soyabean was observed under inoculation with AMF (Von Thun, 2013).



Interaction With Other Organisms: Through direct and indirect methods that involve improving plant physiology and supplying resistance to diverse phytopathogens through a variety of modes and

activities, PGPR promotes plant growth. These include nutrient fixation, biotic and abiotic stress neutralisation, the production of volatile organic compounds (VOCs) and enzymes to fight illness, and nutrient fixation. Many PGPRs can increase the antioxidants enzyme, thus preventing the plant cell from the oxidative burst (Gupta *et al.*, 2021). Triple interaction of plant and soil fungus increases plant resistance to diseases, plant resistance to drought, biological nitrogen fixation, photosynthesis rates, and lower concentrations of harmful elements such as cadmium and arsenic in plant tissues as well as improves soil physical properties which ultimately result in better growth (Bhale *et al.*, 2018). Because N_2 fixation involves a high P demand, the interaction between AM fungi and regulating nitrogen fixers has drawn a lot of interest. Under infertile conditions, the two symbionts work in concert to increase the amount of N and P in plants that have been inoculated twice rather than once (Priyadharsini and Muthukumar, 2015). In combination of inoculation Frankia and AMF in Casuarina, there is threshold increase in the number of nodules, levels of N and P, total dry weight of shoots and roots, etc. (Bhale *et al.*, 2018).



Rooting: Arbuscular mycorrhiza (AM) is a mutualistic symbiosis between the roots of terrestrial plants and AM fungi. The extra-matrical mycelium that the fungus produces assists the plant to biotrophically colonise the root cortex and absorb minerals from the soil. It has been recognized that mycorrhizal symbioses play a key role in nutrient cycling in the ecosystem and also protect plants against environmental and cultural stress. The rise in the availability of mineral nutrients to the plant, especially those whose ionic forms have a low mobility rate, is the main result of AM symbiosis, or those which are present in low concentration in the soil solution (Omar *et al.*, 2007). Enhanced root proliferation in response to AM fungal inoculation reportedly occurred in black pepper (*Piper nigrum*). Therefore, it has been speculated that changes in the meristematic activity and plant hormonal balance in response to AM association were responsible for the AM-induced effects on root development (Priyadharsini and Muthukumar, 2015). the inoculation of plants of Avocado with vesicular–arbuscular mycorrhiza fungus improved root growth and increased the top/root ratio. Inoculation of citrus seedling with vesicular–arbuscular mycorrhiza fungus increased growth and dry weight (Omar *et al.*, 2007).

Future Perspective: To conclude the future researches should be aimed at 1) identifying the mechanism of interactions in the natural field conditions 2) explore the beneficial strains of fungus or their combinations that can work in tandem to promote plant growth 3) Study the effect of coinoculation under stressed conditions 4) identification of the genes that help survival under stressful environments, 5) generate transgenic plants overexpressing the target genes and dissect the signalling cascade 6) There will be the need of field-based studies, 7) It will be a strong understanding to the percentage disease incidence controlled by AMF, 8) there is a need to clear understanding of the effects of environmental changes on the AM fungal species. (Basu *et al.*, 2018; Bhale *et al.*, 2018).

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