Potential of Arbuscular Mycorrhizal Fungi for Sustainable Agriculture

Mythili Veshala

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Global climate change has rendered a substantial amount of Earth's landmass unconducive to crop growth. In accordance with extreme temperatures and rising chemical fertilizer and pesticide usage, detrimental conditions of drought and salinity are projected to worsen overtime. This paper evaluates arbuscular mycorrhizal fungi (AMF) as a viable solution to the need for sustainable agricultural practices. We consider how the relationship between host plants and the mycorrhizal species results in improved root and shoot biomass, stronger plant defenses to biotic and abiotic stresses, and improved crop yield. AMF directly increases the rate of nutrient uptake through root modifications and the common mycorrhizal network. Emerging research has identified molecular pathways through which AMF operates. Finally, the enhancement of these pathways is considered in this paper, as it has the potential to improve AMF performance in agricultural fields, providing an important insight into the untapped potential that symbiotic AMF has as a biofertilizer.

Introduction

Current agricultural practices are proving to be unsustainable for the growing human population. The global demand for chemical fertilizers has been steadily rising, with the total fertilizer usage reaching around 195 million tons in 2020[1], while in 2010 the usage was just over 170 million tons[2]. Its importance, however, is accompanied by various adverse long-term effects, which ultimately results in the need to look for alternatives that will reduce our dependency on fertilizer.

For example, the introduction of heavy metals and toxic compounds in excess into our ecosystems is caused by the overuse of chemical fertilizers and pesticides.[3] Even with overapplication, only around half of the amount of nitrogenous fertilizer is utilized by the plant, while the rest evaporates, reacts with organic soil compounds, or dissolves into water[4]. The usage of nitrogen fertilizer, for example, has been associated with fluxes of nitrous oxide in the atmosphere. The process of nitrification, as well as microbial activity in the soil, is perpetuated by added fertilizers, which subsequently increases the atmospheric nitrous oxide concentration. Nitrous oxide traps heat at a different frequency than carbon dioxide does, providing stronger insulation of heat within the Earth[5]. Currently, 5% of emissions are due to the use of nitrogen fertilizers. This figure is likely to increase without sustainable alternatives[6].

Pesticides and herbicides, additionally, when taken into the human body through long-term exposure, are potential mutagens. Studies have shown that greater exposure to chemical pesticides coincides with a greater likelihood of genetic mutation[7], which can potentially lead to illnesses such as cancer. It is vital, therefore, to seek alternative methods of maximizing crop yield in order to reduce chemical fertilizer and pesticide consumption.

Over the past few decades, researchers have begun to examine how soil microbiota form complex, beneficial relationships with plants to help promote plant growth. A greater focus on bioprospecting[8], which is the identification of natural molecules that can potentially be implemented on a large scale for commercial purposes, has helped researchers explore sustainable solutions to maintaining agricultural efficiency in the face of a changing environment.

A promising group of soil microorganisms that researchers have been examining more closely in recent years are arbuscular mycorrhizal fungi (AMF). Forming symbiotic relationships with over 80% of terrestrial plants[9,10] AMF colonize the root cortex cells of a host plant, forming arbuscules, or centers for nutrient exchange between the fungus and the plant, shown in Figure 1.

The symbiotic relationship can range from being mutually beneficial to having a neutral effect, with the majority of these relationships being beneficial. AMF are obligate biotrophs, meaning that the fungal species cannot exist outside of a living plant host, which is its primary and only source of nutrition. In exchange for carbon, the photosynthetic product of plants, the AMF develops a widespread network of extraradical mycorrhiza[11,12]. The subsequent increase in the surface area for nutrient absorption directly accelerates plant growth. In this way, the AMF and plant host perform a trade of sorts, wherein the AMF receives the carbohydrates it needs for growth, while the plant receives nutrients from the AMF.

AMF are observed to have a mutualistic relationship with host plant species in conditions of abiotic stress such as nutrient deficiency, drought, salinity, heavy metal stress, and temperature stress[10], and can help the plant in defending against these stressors. The projected net positive effect of this symbiotic relationship has opened up the possibility of AMF being used as a biofertilizer, as well as a mechanism to improve crop yield in unfertile soil. This paper evaluates the nature of AMF symbiosis as well as its benefits. Additionally, it explores the challenges of implementing AMF in global agriculture and several strategies to improve this relationship in the future.

How do AMF Establish Symbiosis?

AMF (blue) locates and invades the tomato root cortex cells following the secretion of Myc factors and strigolactones. The symbiosis between plant and AMF is facilitated by structures such as the hyphopodium and arbuscules, which serve as centers of nutrient exchange between the two species

The soil ecosystem consists of a vast number of diverse microorganisms, which requires AMF and the plant host to have a specific mechanism of identifying each other. Before the establishment of symbiosis, AMF survive limitedly in the soil. Among the abundance of signaling molecules present in the rhizosphere of a plant, it is crucial that the AMF species perceives and responds to the right signaling molecule to ensure its continued survival under a plant host.

The molecular communication prior to symbiosis is an intricate process that aims to increase the likelihood of physical contact between the two organisms. Research has shown that plant metabolites released into the rhizosphere can stimulate hyphal growth. Plants exude a signaling compound called strigolactone, which is produced by the root cells and perceived by the AMF when it is in the immediate surroundings of the root. Strigolactones induce mitotic division in mycorrhizal fungi, as well as the development of dense, highly branched hyphal growth. While these signaling molecules are a factor in a larger surface area of colonized root cells, colonization does occur to a lesser extent in their absence[13,14].

Upon mycelial contact with the root cell membrane, hyphopodium formation occurs, physically attaching the fungal species to the plant host. Hyphae continue to penetrate through the root, growing intercellularly until they reach the root cortex. The invasion of a root cortex cell and the subsequent development of arbuscules leads to several previously unexpressed genes in the plant nucleus being switched on, as the cell modifies its operation to accommodate symbiosis[9].

Strigolactones additionally stimulate the fungal secretion of Myc factors, which are responsible for the initiation of symbiosis. Myc factors initiate a signaling cascade within the plant cell, involving conserved receptor-like kinase signaling, calcium signaling, and the activation of genes that facilitate the formation of symbiosis. This signaling pathway is referred to as the common signaling (SYM) pathway, and is shared between mycorrhizal fungi and rhizobia[15].

In summary, AMF and host plants are able to identify each other in a complex soil ecosystem through the secretion of strigolactones from the plant that act as a homing beacon for the AMF, and the subsequent secretion of Myc factors from the AMF which serve to strengthen the symbiosis. These metabolites lead to changes in gene expression and the establishment of a physical interface called an arbuscule for the exchange of nutrients between the symbionts.

How Effective are AMF?

0.1 Altering Root Structure

This figure shows the growth of a tomato plant that has not been inoculated compared to plats that have been inoculated. The inoculated plants show a more complex lateral root system stimulated by colonization, along with a dense common mycorrhizal network allowing for the exchange of nutrients.

As previously mentioned, one predominantly observed effects of AMF colonization is an increase in root and shoot biomass of the host plant. An overview of these features is shown in Figure 2. AMF have the capability to change the morphology of host plants in response to nutrient requirements[13,14,16]. The root system of colonized plants is highly complex and sensitive to environmental changes. The improvement of plant root systems by mycorrhization not only leads to a greater surface area for water and nutrient absorption, but is also incredibly useful in making the soil more stable, protecting it from erosion and weathering[9].

Complex root structures are developed according to molecular signaling, which is carefully modulated by both the fungus and host plant[17]. Between lateral and non-lateral roots, the latter is not conducive to AMF growth due to the presence of lignin, leaving an unsurpassable membrane. Lateral roots are more responsive to pre-symbiotic signaling molecules released by the AMF, which supports to idea that these roots more readily allow for the onset of symbiosis. Experimental data has shown that the allocation of carbohydrates to the plants is predominantly to lateral roots in order to meet energy requirements of the AMF that have colonized cortex cells[14].

Alternatively, fine lateral roots are rarely colonized, or often not colonized at all, most likely due to the absence of cortex tissue, as well as the fungi being possibly unable to recognize fine lateral roots as viable areas for hyphal growth, suggesting that the appropriate signaling molecules are not produced or exuded.

As noted by Cruz et al, 2004, root structure alteration after colonization was observed to affect the adventitious roots in Allium porrum. The roots were more abundant after the formation of arbuscules, but were much shorter in length. As time progressed, however, lateral root growth was prioritized over adventitious root growth. Regardless of root type, all colonized roots were highly branched in nature. They contained a higher number of necrotic or inactive root apices, which is a marker for new root growth in comparison to non-colonized

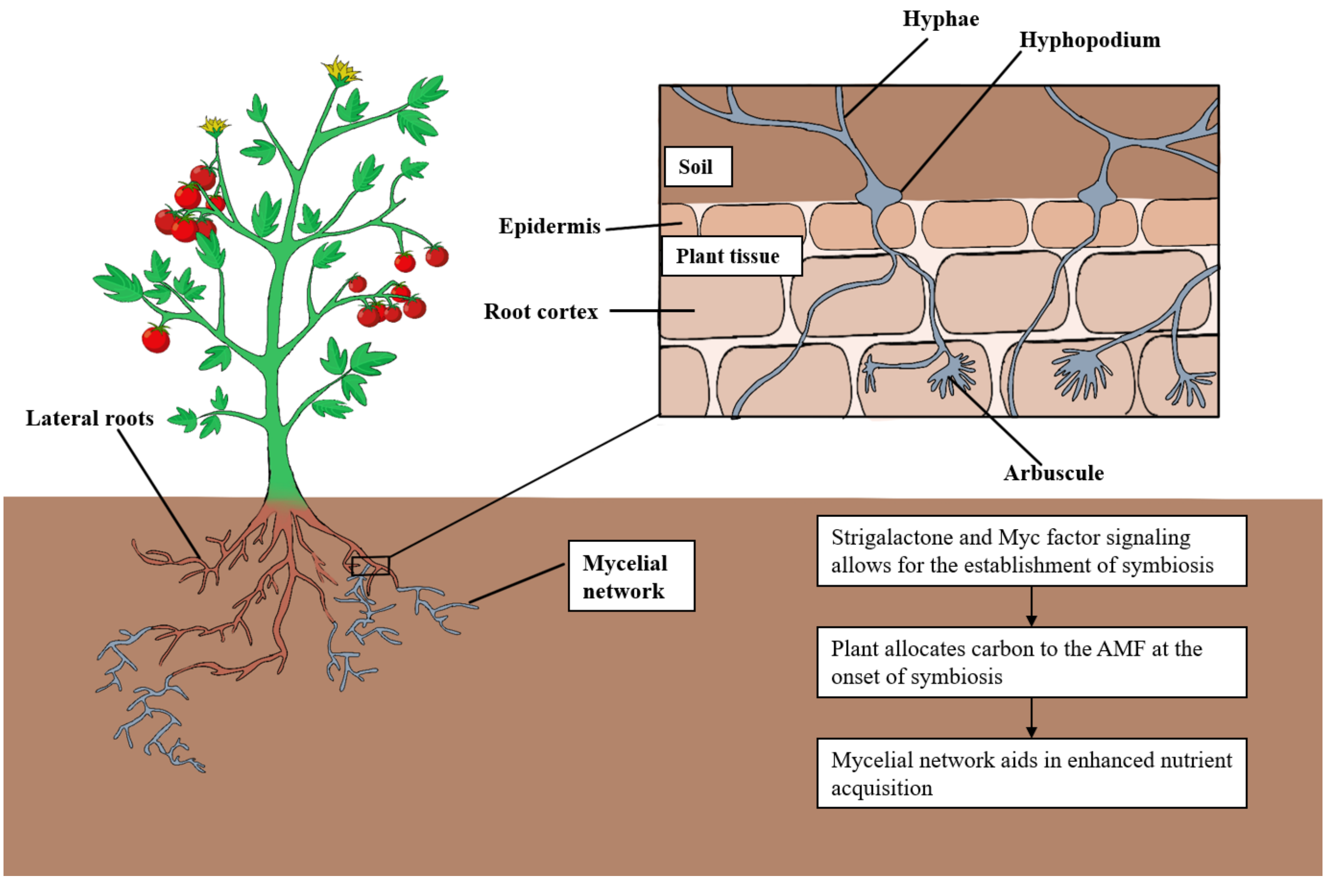

Fig. 1 Illustration of a tomato plant colonized by AMF

roots. The detection of localized differences in nutrient concentration by the plant subsequently leads to accelerated lateral root formation.

Most notably,[16] conducted an analysis of a transcription factor that was found to be expressed more in Lotus japonicus roots that were colonized. The factor, referred to as a putative MYB-like (LjMAMI) transcription factor, was found to be involved in phosphate starvation responses. The expression of this transcription factor was increased in lateral root primordia and root meristems that had arbuscules within their cortex tissue. The factor enhanced the expression of a marker gene for mycorrhizal function, confirming the hypothesis that the transcription factor responded to colonization. Silencing of the gene for the transcription factor reduced the rate of root elongation.

This strongly implies a relationship between AMF colonization and the stimulation of root growth, as the plant that was used had been modified to have stunted lateral root growth. This pathway is one example of how AMF can directly control plant responses by altering the expression of genes, resulting in enhanced root growth and a strengthening of the symbiosis.

In Medicago truncatula, Myc factors were linked to lateral root induction. Furthermore, it is possible that AMF produce plant growth hormones, explaining changes in root architecture outside of the SYM-pathway. Enhanced root growth due to AMF colonization has the potential to catalyze the replacement of shallow rooted annual species with deep rooted species[14].

The positive relation that AMF colonization has with root growth is promising in potential efforts to strengthen current crop root systems[14,15,18]. The decades long process of selectively breeding plant species to conform to the requirements of maintaining monocultures has led to the phasing out of perennial root systems. The integrity of topsoil is more susceptible to degradation with shallow root systems.

Keeping in mind the greater utility of leached nitrogen to deep-rooted species compared to shallow-rooted ones, AMF can make the process of crop rotation much more efficient. Crop rotations are generally advised for nutrient-deficient soils, which also happens to be a condition in which the net benefit of AMF is at its greatest. AMF can also mitigate the risk of crop rotation in terms of the potential failure of the growth of a species[19]. The hiked costs of the practice can also be compensated due to the increase in yield that inoculation results in. The incorporation of inoculation and crop rotation

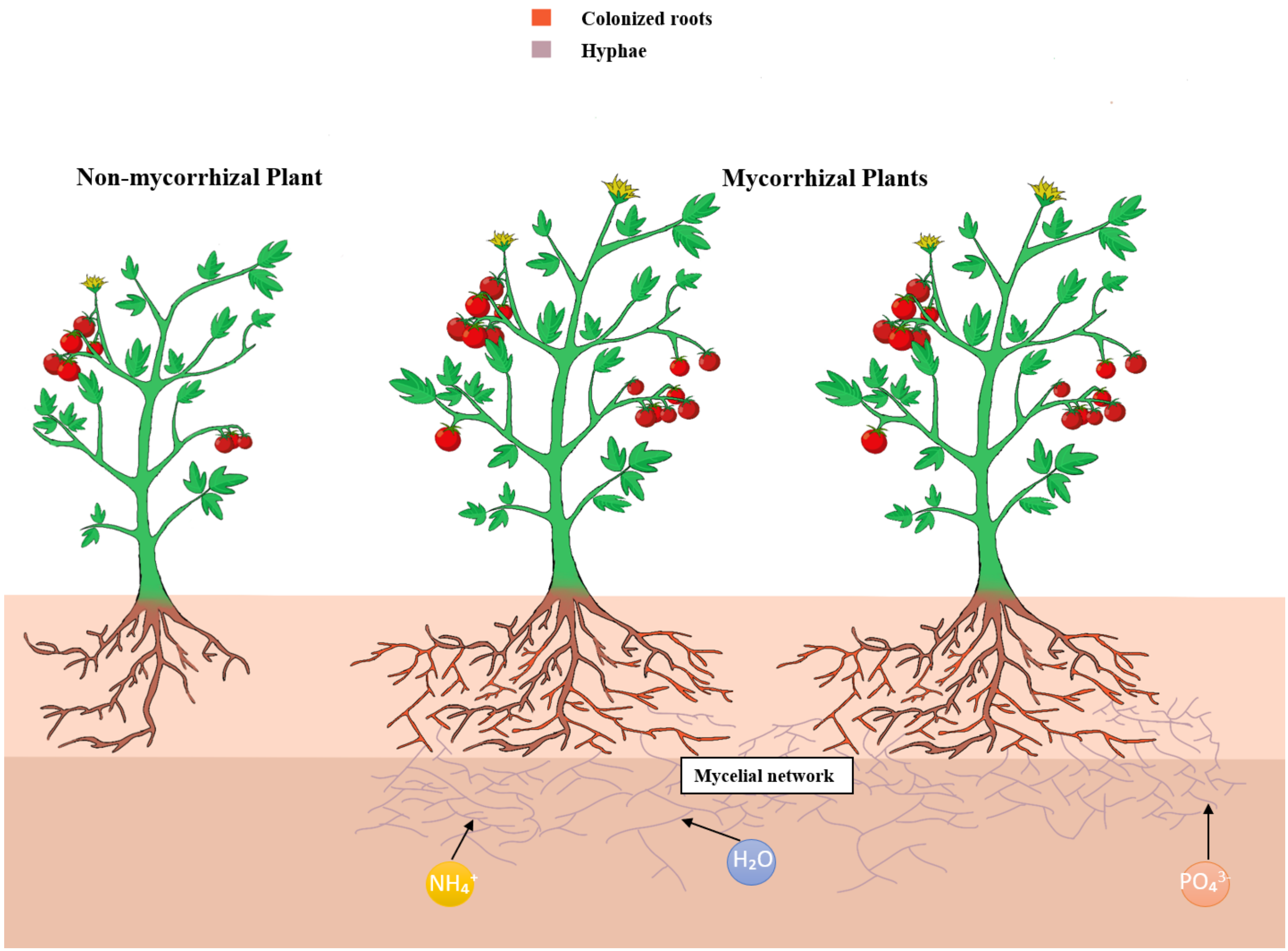

Fig. 2 Mycorrhization leads to improved plant yield by allowing access to nutrients in the subsoil

strengthens the likelihood of the success of both.

AMF colonization ultimately results in a more developed, efficient root system that guarantees the host plant's grasp over the soil's nutrient and water supply, as shown in Figure 2. Lateral roots are the most responsive to colonization due to their structure, and grow in areas where the concentration of nutrients is greater. The stimulation of root growth by mycorrhization was so strong that Lotus japonicus, modified to lack lateral roots, was seen to have a flourishing lateral root system proceeding inoculation. The increased root density associated with AMF has promising implications with sustainable agricultural practices such as crop rotation.

The Common Mycorrhizal Network and Mineral Uptake

Numerous studies have repeatedly demonstrated that AMF provides a net benefit in terms of nutrient uptake[8–11,20]. AMF are found most abundantly in the subsoil, which is unsuitable for root growth due to factors such as a lower oxygen concentration and compaction. A mutualistic relationship, therefore, presents itself as a practical solution to the plant host's barrier for growth and the AMF's need for carbon[20]. In combination with the eventual formation of highly branched lateral roots, the expansion of the plant's overall surface area is favorable to soil health.

Over time, AMF forms a sprawling mycelium network that acts as a broad, effective site of nutrient exchange with the host plant[20]. Connected plants can be of the same or different species, which allows for the AMF to be seen much like an appendage to existing root systems. Mycorrhizal species secure a large carbon supply for themselves through the network, and ensure their chance of survival by having several sources of carbon should a plant host be rendered unable to meet the requirements of the AMF. The AMF carefully keeps a balance in assessing the costs and benefits of symbiosis with each plant, which then begin to compete to reap the greatest benefit from the AMF. Plants connected through a CMN benefit from the vastly increased surface area for nutrient absorption and water uptake as a result of the extensive AMF hyphae network[21].

When nutrients are in abundance in the soil, the carbon consumption of AMF is suppressed by the plant host[12,22]. In this instance, the cost of symbiosis to the plant is not particularly appealing when it can acquire sufficient nutrients with its own root systems. A meta-analysis done by Hoeksema et al, 2010 illustrates clearly the conditions wherein AMF are the most beneficial. Nutrient deficient soils, namely soils deficient in phosphorous, and contaminated soils containing heavy metals results in AMF being nearly vital to plant and soil prosperity. Regardless of soil conditions, inoculated plants will exhibit a higher growth rate than uninoculated plants.

The inoculation of soybean plants with AMF, for example, led to an increased rate of phosphate uptake[8]. Phosphorous is essential in the formation of phospholipid membranes, protein phosphorylation, energy production, and metabolic processes. The biomass and height of inoculated plants was greater in comparison to uninoculated plants, and the soil of the former showed greater phosphatase activity. Trichoderma released organic acids, which converted phosphates in the soil into a form that was readily absorbed by the plant.

During the process of phosphorous solubilization, soil pH drops, further increasing the solubility of phosphorous. Overly alkaline soils, therefore, are detrimental to the functioning of ability of AMF to contribute to phosphorous uptake. The inadequate phosphorous concentration in agricultural soils propagates our current overuse of chemical fertilizer and the imminent depletion of phosphorous resources. The application of deep-reaching hyphae to use phosphorous and nitrogen resources before they become inaccessible has the possibility to reduce the problem of fertilizer wastage.

It is widely known that AMF improve nitrogen uptake substantially. In wheat plants, AMF improves nitrogen concentration in plant tissue, directly impacting the growth of plants as well as photosynthetic rate[11,23]. Apart from being the defining component of amino acids and nitrogenous bases, nitrogen is required in the structure of chlorophyll, the light-trapping organelle present in plant cells. Up to 80% of nitrogen uptake can be accredited to AMF colonization under favorable circumstances. More nitrogen direcftly leads to increased chlorophyll contents, which inevitably results in a greater photosynthetic rate.

Photosynthetic rate is regulated and enhanced by various factors caused by colonization, such as the upregulation of the antioxidant system and tuber growth[24]. This increase in plant metabolism has positive morphological effects that extend into insect ecosystems. Pollinating insects are attracted more frequently to inoculated plants as the number of flowering buds is comparatively larger. This undoubtedly will lead to a greater yield as well[25].

The nutrient uptake of a plant is a key variable that determines the practicality of implementing AMF in agricultural soils. The positive results of mycorrhization have been replicated throughout several different studies. Conclusively, nutrient acquisition is carried out through the roots of the plant and the hyphal network. The surface area for absorption following colonization increases along with the metabolic rate of the plant, which ultimately leads to greater yield. The mycorrhizal network is a conduit for communication between different plants as well, regulating behavioral changes in plants. The integral nature of the hyphal network in soil ecosystems is a positive indicator that its role in agriculture may increase with future research.

Response to Abiotic Stresses

This section explores the role that AMF plays in mediating plant responses to abiotic stresses such as drought and salinity. A summary of how AMF can protect against various stresses is provided in Table 1. Plant Responses to Abiotic Stresses Following AMF Colonization. For each study, species of AMF and plant are listed, as well as the specific abiotic stress plants were challenged with. The Results column describes changes in plant responses observed when comparing groups inoculated versus not inoculated with AMF.

Drought and High Temperatures

Drought is one of the most detrimental abiotic stresses that can affect a plant. Enhanced by climbing global temperatures, drought can cause a significant reduction in yield. As temperature extremities intensify, the surface area of land suitable for cultivation will decrease. To combat this, crops with robust soil microbiota may be vital in securing higher yields.

Under drought conditions, (Lafitte et al, 2006) reported between a 53-92% reduction in the yield of Oryza sativa L, while (Kamara et al, 2003) reported between a 63-87% percent reduction in the yield of Zea mays L. Physiologically harmful to plants, drought can cause reduce the dry weight and leaf size of plants, along with recued transpiration and stomal conductance. This can be accredited to a lower photosynthetic rate, which harms plant growth processes such as cell elongation and mitotic division. Damage to the photosynthetic apparatus can also be caused by higher temperatures, and in combination with drought, can halt plant growth altogether[36]. Plants adapted to temperatures above 30°C have been shown to store a greater amount of carbohydrates while maintaining a low photosynthetic rate to prevent water loss, however this means that the yield of these plants will be considerably low[37].

Drought can lead to soluble compounds being irregularly distributed to prevent mineral nutrients from moving to various parts of the plant. Hypertonic cells damage chlorophyll in some plants while drought stress triggers an increase in chlorophyll in others. It can also lead to protein denaturation due to an increased viscosity of the cell contents, ultimately leading to decreased photosynthetic rates[38].

The aforementioned extraradical mycorrhizal network has the ability to increase root surface area for water absorption. As shown by Table 1, it enhances plant responses to drought in

Table 1: Summary of the Findings[26–35]

AMF species	Plant host species	Stress	Results	References
R. irregularis	*Malus hupehensis*	Drought	Increased photosynthetic rate, reduced relative electrolyte leakage, upregulation of the antioxidant regulatory system, increased root and shoot biomass	(Huang et al, 2020)
Funneliformis mossae	Triticum aestivum L. (Common wheat)	Drought	Increases root and shoot biomass and length with Funneliformis mossae, greater up-regulated genes with inoculation, improved water and mineral uptake	(Moradi Tarnabi et al, 2020)
Funneliformis mossae *Rhizophagus intraradices*	San Marzano nano	Drought	Increased root and shoot biomass with *R. intraracides*, improved water use efficiency, improved photosynthetic rate	(Chitarra et al, 2016)
	Capsicum annuum L.	Drought	Increased root and shoot biomass, decreased rate of flower wilting, increased number of flowers, increased rate of colonization	(Pischl and Barber, 2016)
Glomus fasciculatum Mixed *Glomus* species	*Capsicum annuum* L.	Drought	Improved leaf water potential, reduced wilting, increased shoot to root ratio, decreased rate of colonization	(Davies et al, 2002)
Glomus intraradices	*Lotus glaber*	Salinity	Improved plant growth, improved protein concentration, improved root and shoot biomass, increased K+ concentration, reduced Na+ accumulation	(Sannazzaro et al, 2006)

Glomus mosseae *Rhizophagus intraradices* *Glomus etunicatum*	*Panicum turgidum*	Salinity	Increased antioxidant enzyme activity, upregulation of antioxidant system, improved protein concentration	(Hashem et al, 2016)
Glomus etunicatum *Glomus intraradices* *Glomus mosseae*	*Cucumis sativus* L.	Salinity	Reduced electrolyte leakage, improved photosynthetic rate and chlorophyll synthesis, upregulation of antioxidant system	(Hashem et al, 2018)
Glomus clarum *Gigaspora margarita* *Acaulospora* sp.	*Coffea arabica* L.	Heavy metal (Cu and Zn)	Reduced Cu accumulation in leaves, greater Cu concentration in the stem, only very high Zn concentrations reduced biomass	(S.A.L. Andrade et al, 2010)
Glomus intraradices	*Helianthus annuus* L.	Heavy metal (Cd)	No symptoms of Cd toxicity could be seen, Cd was accumulated in the shoots, increased photosynthetic rate and chlorophyll synthesis, increased phosphorous concentration	(Sara Adrián López de Andrade et al, 2008)

several different plant species. A key response pathway is the mitogen-activated protein kinase (MAPK) cascade reaction, which activates kinases and leads to the activation of stress response genes. This pathway regulates hormone signaling and plant stress responses. Proline accumulation is also known to be a drought response in plants as it aids in cell wall formation and plant growth. Proline insolubilizes in the cell wall which is followed by defenses in the plant activating. In Phaseolus vulgaris, glycoproteins containing proline were abundant in areas under drought stress, mainly where cell elongation was occurring. Proline therefore is involved in maintaining cell wall integrity as a response to abiotic stresses[27,28,38].

Under conditions of drought stress, the apple species, Malus hupehensis, which was inoculated with AMF showed a higher average expression of these kinases and proline than uninoculated plants. Enzymes involved in the synthesis of proline were also more abundant in inoculated plants. Table 1 also shows that the removal of reactive oxidative species was higher in inoculated plants due to the increase in the synthesis of scavenging enzymes. This was a direct result of higher rates of nutrient absorption as the required metals were taken up by the mycorrhizal network. Lipid peroxidation of polyunsaturated fats produces malondialdehyde, which indicates membrane damage and is increased by drought. Inoculation reduces MDA levels, indicating reduced damage from oxidative stresses. Levels of MDA were also seen to be comparatively lower in inoculated Zea mays L. crops than in non-inoculated crops under conditions of high temperature[36]. Hydrogen peroxide is an indicator of environmental stress, but its levels in drought-stressed inoculated plants was similar to well-watered non-inoculated plants, indicating an alleviation of the symptoms of stress[27].

The extent to which thermophilic and non-thermophilic plant roots can grow in soils above 35°C is quite limited. This in turn results in the reduced uptake of nutrients and water, negatively effecting crop yield. Inoculated plants, however, have greater access to these resources as mycorrhizal hyphae are more resistance to the heat in comparison to plant roots. Inoculated D. lanuginosum was better adapted to high temperature soil, as shown by the increase in biomass and flowering35. While inoculation causes much of the plant's carbon resources to be allocated to the fungi, which tend to respire more under higher temperatures, the photosynthetic rate does increase[36].

Generally, the photosynthetic rate drastically decreases under drought and heat stress. However, the reduction was much less extreme in inoculated plants because of the climbing chlorophyll concentration[36]. The expression of the genes coding for aquaporins was amplified additionally after inoculation, increasing the amount of water transported to the plant by the AMF, leading to decreased relative electrolyte leakage[27].

The exact mechanism through which AMF alleviates the negative effects of drought stress are unknown, however it is likely that it involves the MAPK signaling pathway. Further understanding the way that AMF regulates plant responses to drought has positive implications for how crops may be able to cope with more extreme drought in the future. Currently, the amount of water available for agricultural uses has been decreasing due to changing global climates and water pollution, among other factors. The need to conserve water while simultaneously maintaining yields high enough to feed the rising population comes across as unrealistic, but can be potentially achieved through efforts to improve soil ecosystems.

Salinity

Compounded with drought, salinity can completely halt plant growth and render the yield of a crop to be halved at most. This is detrimental not only to large scale, commercial agriculture, but most harshly to smaller agricultural fields and rural communities. Inherent chemical properties of the soil can be difficult to remedy, as salinity is most commonly caused by the presence of chlorides, metal sulphates, and occasionally nitrates. Plants are extremely sensitive to changes to pH levels and ion concentrations in the soil. Without sufficient water content to dissolve ions and aid in their migration deeper into the earth, topsoil becomes excessively saline. Increased chemical fertilizer usage increases ion concentration in the soil, decreasing agricultural productivity and the area of arable land found on Earth. Around seven percent of Earth's land is infertile due to salinity[39].

Chlorine, sodium, and boron are toxic to plants in larger amounts, causing exosmosis in plant cells. Salinity additionally tampers with the growth of sexual organs, namely filaments as well as initiating apoptosis in cells. Chloride ions can change the conformation of proteins, effectively denaturing them, and sodium ions have the tendency to replace potassium ions in biochemical reactions. Key metabolic processes such as enzyme functioning and cyclin expression decreases due to ionic imbalance, ultimately resulting in cell death.

AMF occurs to varying extents in saline areas. It has been suggested that AMF can tolerate an average of 50 mg of dissolved salt per milliliter of soil water[40]. Though the Glomus species primarily are observed in saline soils, they are not unconditionally nor inconsequentially present in those conditions. Salinity affects every microorganism in the soil's ecosystems. For example, the rate of AMF colonization, spore germination, and hyphal growth all have the potential to be reduced by dissolved salts. The effects of salinity vary between each fungal species, and can occur at different stages of fungal growth. Several external factors, including the physical distribution of the host plant within the soil and the specific localization of biochemical signals on the surface of root cells can impact fungal growth. The plant's dependency on AMF increases with increasing salinity.

As seen in Table 1, AMF inoculation increases water absorption as well as the production of antioxidants, prevents cell dehydration through exosmosis, and reduces the rate of chloride absorption by the plant[15]. (Giri et al, 2007) reported improved root and shoot dry weight in Acacia nilotica, as well as nutrient uptake and retention after inoculation with AMF. The rate of inoculation was reported to be greater in saline conditions than in regular conditions, supporting the idea that AMF have the most beneficial effects under conditions of abiotic stress. (Hajiboland et al, 2015) reported improved dry mass, stomatal conductance, soluble sugars and K+ uptake in Aeluropus littoralis. However, in contradiction, the colonization of the plant host was decreased in saline soils. Corroborating the findings of (Giri et al,. 2007), (Hashem et al, 2018) reported improved antioxidant enzyme production, growth and photosynthetic rate in Cucumis sativus L after inoculation. Molecules involved in plant defense, such as jasmonic acid and salicylic acid were produced at a greater rate in inoculated plants. Both (Hajiboland et al, 2015) and (Hashem et al, 2018) found evidence that water use efficiency is improved in inoculated plants.

Interactions between various microorganisms in the rhizosphere strengthen plant defense responses against abiotic stresses. Salt tolerant rhizobium are nitrogen fixing bacteria found in the nodes of legumes. The mechanism of salt tolerance by the rhizobium involves the accumulation of osmotic regulatory substances in the bacterial cells. In coordination with one another, the AMF and rhizobia share a common symbiosis pathway with host plants. The discovery of this shared pathway begs the further exploration of links between microorganisms existing in the rhizosphere and the host plant, especially with regard to defense responses. Given the increase in soil salinity across the globe, AMF may be a possible solution to help plants resist high salinity conditions and allow large- and small-scale agriculture to proceed in these soils.

Heavy Metals

One of the most concerning effects of our current practices of breeding livestock, agriculture, and waste management is the accumulation of heavy metals in the environment. While heavy metals are naturally and unintentionally deposited into soil and water bodies through incidents such as flooding, volcanic activity, or corrosion, industrial processes are the most notable contributor to pollution2. Over time, repeatedly dumping sewage sludge rich in heavy metals into local water bodies will lead to a toxic concentration of heavy metals in nearby aquatic ecosystems. The improper handling of wastage in landfills and animal manure may lead to heavy metals leaching into the soil, and furthermore into groundwater sources. The overuse of chemical pesticides and fertilizer, often composed of heavy metals, leads to heavy metal buildup in the environment as well.

Ultimately, a polluted environment will lead to the bioaccumulation of heavy metals in a food chain as metals cannot be further broken down. Upon human consumption, the heavy metals in meat and plant products in these food chains will be absorbed by the body[41].

Heavy metals bond with the nonmetallic elements in macromolecules found within cells, changing their properties and resulting in a toxic effect. This disrupts cell processes and can damage the nervous system, nuclear DNA, protein synthesis and modification, and metabolic processes[3].

In humans, depending on the metal consumed and factors such as region, an excess of heavy metals causes various forms of cancer, kidney or liver damage, nausea, birth defects, and an increased infant mortality rate.

Similarly, heavy metals are also quite damaging to plants. In plants, absorbing an excessive concentration of heavy metals from the soil interferes with the photosynthetic apparatus. Moreover, the rate of chlorophyll synthesis decreases as enzyme activity is interrupted by the presence of toxic heavy metals. Morphological changes can be induced as well, impacting the rate of transpiration. As a result of this, metabolic activity is thus reduced, leading to a lower supply of energy available to the plant. Lead, for example, is able to oxidize proteins, altering their function. The concentration and interactions between certain proteins change, more or less hindering the plant from performing metabolic functions[21,42].

In the presence of AMF, however, plant defense responses to heavy metal stress are enhanced. One of the greatest advantages of the widespread hyphal network of AMF, as discussed before, is the drastic increase in the surface area for absorption. AMF are much more efficient at absorbing heavy metal ions than plant root systems, and are subsequently equipped with defense mechanisms to isolate heavy metal ions from reaching the xylem or phloem. Furthermore, plant tolerance to heavy metals increases with the biomass of the AMF the plant is inoculated by[21,42]. This could be a product of increased phosphorous uptake providing more energy for the plant defend against the imbalance in heavy metal concentration.

Since heavy metals exist as reactive ions, they are bonded with chelating agents in the soil, which are produced by both the plant and AMF. Chelating agents are produced when the concentration of heavy metals outside of the cell exceeds a certain threshold. Chelation renders heavy metals ions to be less soluble and reactive. Once absorbed into the AMF or plant cells, the heavy metal and chelating agent complex are isolated in the vacuole of the fungal or plant cell, effectively halting the heavy metal from entering the cell cytoplasm. The chitin and polysaccharides present in fungal cell walls promote the adsorption of heavy metal ions. The aim of isolating heavy metals by rendering them unreactive and accumulated in fungal and plant vacuoles is to prevent them from travelling further through the plant tissue and damaging the photosynthetic apparatus[41,42].

An important indicator of heavy metal stress in plants is the increase in reactive oxygen species (ROS). AMF upregulate the transcription of genes involved in synthesizing proteins responsible for metal transportation, as well as proteins produced in response to environmental stresses. The concentration of ROS is less in inoculated plants than in non-inoculated plants, showing better plant growth in inoculated conditions[41].

Certain plants named metallophytes are able to tolerate high concentrations of heavy metals in the soil, and are often used in phytoremediation, which is the reduction of environmental pollutants through plant systems[42]. Plants such as Thlaspi calaminare or Viola tricolor are considered to be metallophytes. The compatibility of a metallophyte plant host and an AMF species depends heavily on species specificity and environmental factors, including the type and concentration of heavy metal, and growth conditions[41]. However, finding compatible species of both symbionts would benefit soil ecosystems greatly: both the efficiency and degree of heavy metal absorption and sequestration would improve. While not only contributing to the goal of phytoremediation, the use of AMF at present could accelerate the process of recovering agricultural land rendered infertile and subsequent loses in yield due to pollution.

Response to Biotic Stress

The microbiome of the rhizosphere is so deeply associated with the regulation of plant defense responses that it can be viewed as its own system that operates in conjunction with the plant. Mycorrhization ignites several changes in the rhizosphere which could potentially impact plant interactions with soil microorganisms. It can also impact the relationship the host plant has with the modulation of its own defense system. The organisms in the rhizosphere can separately identify foreign pathogens, which initiates the secretion of compounds. These compounds result in a decreased rate of survival of foreign pathogens. For example, experimentation has suggested that AMF increases the susceptibility of larvae in experiencing the lethal effects of plant and entomopathogen toxins[43].

When engaged in symbiosis, the immune response of plants is heightened and is referred to as induced systemic resistance, more specifically mycorrhiza-induced resistance (MIR)[44,45]. MIR increases the intensity of plant defense responses during times of biotic stress. The similarities AMF shares with pathogenic fungi leads to the ability to survive plant defenses, and subsequently control plant defenses in a process called priming. This process prepares plant defenses by bracing plant tissue for attack.

The factors affecting the efficiency of MIR are based mainly on the species of herbivorous organism attacking the plant. Plant defenses function through the identification of molecular structures that are inherently associated with microbes or pathogens. Different defense molecules in plants are associated with different defense pathways. To be specific, jasmonic acid and its derivatives are responsible for defense against herbivorous organisms[25]. AMF colonization can change the type of compound as well as the amount of compound released by roots, which generally has an effect on organisms in the rhizosphere. This can be anything from affecting the metabolism of microbes to reducing their reproductive capacity. Defense responses can therefore vary drastically based on the species of the attacker.

Research on the effects of AMF on the survival of herbivorous organisms has shown a broad spectrum of results, ranging from negative to beneficial impacts. For example, instances of Violet root rot are reported by (Matsubara et al, 2000), of which the negative effects have been alleviated by mycorrhizal colonization. (Kasiamdari et al, 2002) reported similar results with root and stem rot in Vigna radiata inoculated with Glomus coronatum. A reduction in herbivory by nematodes, necrotrophic organisms, and herbivorous insects was observed. Priming, together with enhanced plant growth due to amplified nutrient uptake overall increases the immune capacity of the plant. Opposingly, (Bødker et al, 2002) reported no correlation between disease severity and inoculation. Mycorrhization can have a beneficial effect on certain parasites and herbivores, which is a restriction posed by the AMF's ability to enhance the jasmonic acid signaling pathway. Insects that are immune to this pathway can consume leaves that have comparatively more nutritional value due to mycorrhization. Insects that feed upon phloem and certain chewing insects that have high adaptability show improved growth in inoculated plants as well. A potentially adverse side effect of mycorrhiza securing their colonization is the suppression of salicylic acid related responses by the plant. Consequently, the plant may be weak to insects that are targeted with salicylic acid related responses.

The requirements of each field with regard to the herbivorous communities present must be assessed so that the most appropriate AMF species can be utilized. Minimizing the negative outcomes of mycorrhization and herbivory is a goal of future research as well. The widespread enhancement of plant defenses in agricultural fields using AMF can reduce the application of chemical pesticides and fungicides without impeding the cultivation of adequate crop yield. However, the variance of defense responses calls for further research into identifying the specific signaling pathways that AMF affects.

Discussion

Arbuscular mycorrhizal fungi can result in neutral to positive outcomes in plant growth. Their effects are most effectively in deprived soils due to the increased dependence of the plant host on the mycorrhiza for survival, and thus a greater importance is placed upon the allocation of carbon to the AMF. The relationship between the plant host and AMF is never truly parasitic, as there will always be a benefit that the AMF provides to the plant[46]. The uptake of phosphorous and nitrogen are significantly enhanced in colonized plants. Resultantly, shoot and root biomass increase along with the photosynthetic and metabolic capabilities of the plant. This enhanced plant

Table 2: Summary of the Findings[29,43,45]

AMF species	Plant host species	Stress	Results	References
Funneiliformis mosseae	*Solanum lycopersicum*	Herbivory by *Spodoptera exigua* caterpillars	Increased susceptibility of insects to toxins, decreased rate of survival of insects	(Frattini et al, 2022)
	Capsicum annuum L.	Elevated temperatures and Herbivory by *Manduca sexta* caterpillars	Improved protein content, decreased caterpillar mass, improved phosphorous uptake	(Pischl and Barber, 2016)
Glomus intraradices	*Cucumis sativus* L.	Herbivory by *Spodoptera exigua* caterpillars	Mycorrhizal plants experienced greater consumption only if already damaged, increased rate of colonization, reduced leaf area consumed, reduced caterpillar growth	(Barber, 2013)

growth helps improve crop survival rates in the presence of both biotic and abiotic stresses, possibly resulting in improved crop yields in agricultural fields.

Abiotic stress is an inescapable consequence of exponentially increasing food requirements being fulfilled using unsustainable practices. The disastrous side effects of chemical fertilizers and pesticides paired with extreme climates due to global warming will ultimately increase the likelihood of soil becoming infertile. Despite AMF existing naturally and forming mutualistic relationships with a majority of terrestrial plants, modern agricultural practices have disrupted ancient soil ecosystems and interfered with soil integrity.

In addition to the preestablished damage that machinery has done to the soil, there is a lot of variability in the potential results that AMF can have on a plant due to the specificity of each plant species to AMF. While it has been shown through experimentation involving growing plants in various different levels of soil biodiversity that AMF on the whole are beneficial, there are outliers in almost every instance and the range of results is vast. An example of this is shown by the results of (Thirkell et al, 2020) as each wheat cultivar has a different response to the AMF species. To commercialize a product that is a result of bioprospecting, the possibility of a net negative symbiotic relationship due to incompatibility of each symbiont must be minimized. The economic viability of such a variable relationship must be most thoroughly assessed.

The growth and cultivation of AMF will also prove to be a challenge, as the growth medium in accordance with current knowledge must be a three-dimensional soil environment with a suitable plant host. Although (Hildebrandt et al, 2002) were able to grow Glomus intraradices in modified agar plates, the abundant growth of the fungi was not able to be sustained with newer spores. Plants of the same species can additionally have varying genomes that lead to variation in genetic expression, and an individual species of plant can support many genotypes. Wellbeing of the ecosystem is extremely important if the aim of future agricultural practices is to move away from the monoculture and cultivate relationships between many organisms in order to improve the fitness of crops[47].

Due to this, even after the identification of a suitable species of AMF for the species of host plant, the AMF genome may need to be further modified to reduce the potential negative effects of specificity. Perhaps enhancing the rate at which receptor-like kinases are expressed by the plant cell or enhancing the rate at which Myc factors are produced within the AMF may allow for quicker, more successful colonization. In terms of defense against biotic stresses, perhaps strengthening compounds related to the salicylic acid signaling pathway may widen the insect species that AMF can defend against. Plant defense compounds used to curb excessive fungal colonization can additionally be isolated and studied as a potential of controlling invasive fungal species[25]. The degree of control and integration that AMF have with their host is still unknown. Despite this, the identification of various signaling pathways opens up the prospect of increasing the success rate of colonization through genetic modification.

Further research into the specific mechanisms of symbiosis is essential in developing a sustainable method of agricultural production. Though AMF have established symbiosis with over 80% of terrestrial plants, modifying their vast genome to accommodate the challenges faced by climate change could be a feasible solution to maintaining crop yields. Previous research has shown that AMF can improve plant responses to abiotic stresses, and with genetic engineering, these benefits could be enhanced with the goal of sustainably meeting global food requirements.

Conclusion

The acceleration of environmental change, while alarming, can potentially be combatted by the diversity of AMF-plant symbiosis. Under several conditions of abiotic and biotic stress, the symbiotic relationship between mycorrhizal fungi and the plant host has consistently shown positive responses to adverse growth conditions. This makes AMF, and further, the microbiome of the rhizosphere, viable options in pursuing sustainable agricultural practices due to their robust defenses. Increased inoculation with AMF, especially in fields experiencing abiotic stresses, has been proven to enhance plant defenses, diversify the soil ecosystem, and refine growth conditions for future crops by supporting soil fertility. Most importantly, the extent of the mycorrhizal network allows plants to acquire nutrients that would otherwise be unattainable, directly resulting in greater yield as compared to a non-inoculated field. Furthermore, AMF's ability to contribute to phytoremediation initiatives additionally makes it an advantageous tool in reversing and enduring the effects of pollution. Further research will continue to explore the advantages of AMF on modern agriculture, and it is very likely that symbiotic fungi will play a key role in sustainable agricultural practices in the face of our changing global climate.

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