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Review

Role of Arbuscular Mycorrhizal Fungi in Maintaining Sustainable Agroecosystems

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Abstract: Arbuscular mycorrhizal (AM) fungi play a crucial role in maintaining sustainable agroecosystems by forming mutualistic relationships with plant roots, improving soil health, facilitating nutrient uptake, and enhancing resilience to abiotic stresses. The mutualistic relationship between AM fungi and plants promotes a balanced microbial community and improves soil structure by forming stable soil aggregates. Additionally, AM fungi can lower the adverse effects of high soil phosphorus (P) while also enhancing plant tolerance to drought, salinity, and heavy metal toxicity through osmotic regulation and antioxidant production. Arbuscular mycorrhizal fungi also support beneficial microorganisms, such as potassium (K)-solubilizing microbes and nitrogen (N)-transforming bacteria, which enhance the nutrient dynamics in soil. However, intensive agricultural practices, including heavy tillage and continuous monoculture, disrupt AM fungal networks and reduce microbial diversity, impairing their effectiveness. Adopting conservation practices such as reduced tillage, crop rotation, and organic amendments supports AM fungal growth. Incorporating mycorrhizal crops and utilizing native fungal inoculants can enhance AM fungal colonization and plant growth. These strategies collectively bolster soil health, crop productivity, and resilience, offering a promising solution to the environmental and agricultural challenges posed by intensive farming. By promoting AM fungi growth and colonization, agroecosystems can achieve long-term productivity and increased sustainability.

Keywords: mycorrhiza; AM symbiosis; microbial community; plant–microbe interactions

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1. Introduction

A plant microbiome comprises a diverse community of microorganisms, including bacteria, fungi, viruses, and archaea associated with various plant species. These microorganisms have distinct habitats in and around the plant, such as the rhizosphere (the soil near the roots), the phyllosphere (leaf surfaces), the endosphere (within plant tissues), and the spermosphere (around seeds) [1]. The plant microbiome significantly impacts plant health, growth, and development, contributing to various processes, including soil health, nutrient management, abiotic/biotic stress tolerance, and disease resistance, while supporting a more balanced and sustainable agroecosystem [2–8].

A sustainable agroecosystem is a complex and dynamic system that integrates ecological processes with an agricultural landscape to optimize resource utilization, enhance biodiversity, and maintain long-term productivity while ensuring economic viability and environmental stewardship [9–12]. Mycorrhizal fungi are particularly significant among various microorganisms due to their symbiotic associations with host plants [13]. Mycorrhizal fungi have been demonstrated to confer protection to host plants against various environmental stressors, including metal toxicity [14], root pathogens [15], salinity, drought [16], acidity [17], and temperature fluctuations [14]. Furthermore, AM fungi enhance plant nutrient uptake, especially nitrogen (N), phosphorus (P), and potassium (K), and promote overall plant growth and development [18–21]. The multifaceted benefits provided by AM fungi to their host plants contribute significantly to the resilience and sustainability of agroecosystems [22].

The most common and well-known type of mycorrhizal association is a symbiotic relationship, where host plants provide food (sugar), particularly glucose, to the fungi, and the fungi provide the mineral nutrients to the plants [22,23]. Fungi have colonized the roots of about 240,000 plant species so far, and the association between them is identified as an important phenomenon in the biology and ecology of many terrestrial plants, as they affect the growth of plants and water and nutrient uptake and interact with the root diseases [24]. There are two types of mycorrhizas, 'endomycorrhiza' and 'ectomycorrhiza', which are differentiated according to the plant's taxonomic status and fungal characteristics. The hyphae of ectomycorrhiza are extracellular and grow between root cells, causing little changes to the epidermis. In contrast, endomycorrhizal fungi, which include arbuscular mycorrhizal (AM) fungi, ericoid mycorrhizas, and orchid mycorrhizas, develop an intracellular relationship where their hyphae penetrate and grow within the root cells of their host plants [25].

In this review, we have focused mostly on AM fungi. Arbuscular mycorrhizal fungi are formed by members of the Glomeromycota and form symbioses with a diverse range of plant taxa, including angiosperms, gymnosperms, pteridophytes, and some lower plants. These fungi colonize plant root cortical cells and develop highly branched structures called arbuscules, which provide an extensive surface area for efficient nutrient exchange, thus maintaining sustainable ecosystems [26–28]. This review aims to elucidate the mechanisms how AM fungi associations contribute to soil fertility and the development of sustainable agroecosystems. Before discussing the role of AM fungi in sustainable agroecosystems, this paper will briefly describe AM development and sensitivity to abiotic and biotic factors.

2. Formation of AM Symbiosis

The AM fungi form endosymbiosis with most flowering plants, where the branched hyphae called arbuscules are formed within the cortical cells and colonize the root cortex. The symbiotic interface between the symbionts, fungus, and host plants is the pathway for nutrient exchange [29]. The lifecycle of a mycorrhizal association begins with the dispersal of fungal propagules in the soil. A molecular dialogue occurs between the plant and fungus through chemical signals—plants release strigolactones, while fungi release oligosaccharides. When the plants detect fungal oligosaccharides, they trigger calcium spikings in the root's outer layer (rhizodermis). It activates the common symbiosis signaling pathway (CSP), a molecular mechanism that facilitates plant–fungal interactions and controls the expression of genes necessary for fungal entry into the root tissue [30]. Active soil hyphae proliferate on the root surface, aided by appressoria in AM and mantle in ectomycorrhiza (ECM). They penetrate into or between root cells, forming an exchange site with branched structures like arbuscules in AM and Hartig net in ECM. The exchange of nutrients between host and fungus is a complex process, heavily influenced by the interaction between host, fungus, and environment. This interaction dictates the duration of the exchange processes, leading to the eventual senescence of hyphal structures and the formation of the resting spores by the fungal propagule in soil or root [31].

Arbuscular mycorrhizal fungi are the most common type of mycorrhiza and are named after the arbuscules and vesicles. Arbuscules are penetrating hyphae that branch to form a complex, branched structure, giving a bush-like structure. Arbuscules act as a passage to pass the materials between the symbionts along with other simpler hyphae [32]. The hyphae within the roots are connected to the external mycelium, which acts as an infection source and probably helps exchange materials between symbionts. The fungus receives carbon compounds from its host, absorbs nutrients from the soil (especially phosphate), and passes a certain amount of that nutrient to the host plants. Also, plant roots produce a hormone called strigolactones that helps in fungal metabolism and branching [33,34]. Strigolactones are a class of sesquiterpene lactones derived from carotenoids [35]. Arbuscular mycorrhizal fungi can detect these molecules easily [36] and respond by increasing their metabolic activity, growing towards them, and branching extensively [37]. Different plant species' affinity to attract AM fungi varies depending on the types and amount of strigolactones they release [38]. Crops like rice and sorghum [39,40] were found to be more attractive to AM fungi than tomato and lettuce [41,42], which correlated with their higher strigolactone exudation. Also, the amount of N and P around the rhizosphere affects the production of strigolactones. Strigolactone production was higher in rice under mineral deficiency conditions, while an increase in the N and P decreased the amount of strigolactones in the exudates (Table 1) [43]. Table 1 summarizes the root exudate compounds and AM fungi species attracted by them.

Table 1. Root exudate compounds secreted by various plant species and arbuscular mycorrhizal fungi species attracted by those root exudates to form a symbiotic relationship.

Compound	Plant Species	AM Fungi Species	References
Strigolactones	*Lotus japonicus*	*Gigaspora margarita*	Akiyama et al. [33]
Strigolactones	*Sorghum bicolor*	*G. rosea*	Besserer et al. [36]
Flavonoids	White clover (*Trifolium repens*)	*Glomus intraradix*	Siqueira et al. [44]
Orobanchol	Rice (*Oryza sativa*)	*G. rosea*	Cardoso et al. [45]
5-dexoystrigol, Sorgonol	Maize (*Zea mays* L.)	Glomeraceae, Gigasporaceae	Yoneyama et al. [46]
Strigolactone (GR24)	Wheat (*Triticum aestivum* L.)	*G. mossae*, *G. intraradices*, *G. etunicatum*	Moosavi et al. [47]
Flavonoids	Alfalfa (*Medicago sativa* L.)	*G. etunicatum*, *G. macrocarpum*	Tsai et al. [48]
1-hydroxy fatty acid, 2-hydroxytetradecanoic acid	Carrot (*Daucus carota*)	*G. gigantea*	Nagahasi et al. [49]

At the cellular level, the exchange of nutrients between the plant host and the mycorrhizal fungi is mediated by transport proteins present in the cell membranes of both organisms. The AM fungi were found to induce the expression of phosphate transporters that help in the phosphate acquisition from the soil and transfer it to the plant [50]. The host plants, in turn, induce the expression of sugar transporters that facilitate carbohydrate/sucrose flux from the host plants to the fungus [51]. The plants maintain fungal colonization by regulating the expression of genes responsible for defense mechanisms [50], while the AM fungi regulate the nutrient uptake and transfer based on the nutrient status of the host plants [52]. This regulation at the cellular level makes the plant–fungal symbiosis efficient and adapts dynamically to meet the requirements of each organism.

Brundrett et al. [53] experimented with leek roots to study the early stages of AM formation. They transplanted the leek seedlings into a pot culture containing the inoculum, and data on the different stages of the AM formation were collected in two-day intervals after exposure of the leek seedlings with inoculum. They found infection initiation in the roots by external hyphae in about 1 day, penetration of hyphae in 2 days, arbuscule formation in 3–4 days, and vesicle formation in 4–5 days. The following figure shows the penetration of the root cell by the AM fungi and the formation of arbuscules and vesicles (Figure 1).

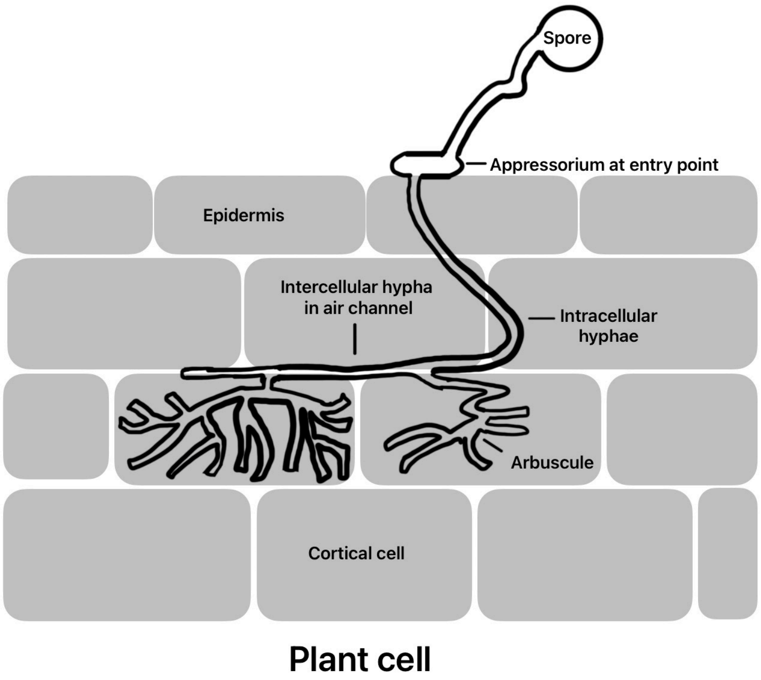

Figure 1. Development of the arbuscular mycorrhizal symbiosis is initiated when a fungal hypha contacts the root of a host plant, where it forms an appressorium. The development of a penetration hypha and penetration of the root follows appressorium formation. On reaching the inner cortex, branches arising from the intercellular hyphae penetrate the cortical cell walls and form branched structures known as arbuscules.

3. Factors Affecting AM Fungi Association

Plant genotype, microbe, and environment are significant in any plant–microbe interaction. If plants and microbes are present but the environment is not conducive, then interaction will not happen. Arbuscular mycorrhizal fungi and plant interaction are also affected by these three parameters: (i) AM fungi, (ii) host plant, and (iii) environment (abiotic and biotic). The effectiveness of AM associations is affected by climate, root properties, organisms present in the soil, soil condition, host–fungus relationship, nutrient competition between mycorrhizal and non-mycorrhizal plants, mycorrhizal interaction with rhizosphere, allelopathy, and pollution and other stresses [31]. In general, this relation is shown in Figure 2.

Biotic factors, such as competing organisms or pathogens, can disrupt or enhance this symbiosis, whereas abiotic factors, such as drought and salinity, determine its effectiveness and ecological significance. Arbuscular mycorrhizal fungi are non-specific and infect various host plants, and some hosts are also found to be related to more than one species of fungus [32]. Different research studies have found a significant positive correlation between AM root colonization and plant responsiveness, particularly regarding root hair length and incidence. In contrast, a negative correlation was observed with root diameter in early successional species. This relationship suggests an increase in AM fungi hyphae in soil is likely with an increase in the root area for nutrient uptake. Conversely, late successional species were found to have larger root tissue densities that were more resistant to AM hyphae penetration, hence causing the decrement in AM root colonization [54].

Arbuscular mycorrhizal fungi establish complex relationships within the ecosystem, interacting with both living organisms (biotic factors) and environmental conditions (abiotic factors) [26]. These fungi also interact synergistically with beneficial soil bacteria, including mycorrhiza helper bacteria and N-fixing organisms, which can enhance mycorrhizal development and improve plant nutrition [55]. Additionally, AM fungi protect against soil-borne pathogens through mechanisms like competition and induced systemic resistance in host plants [56]. Arbuscular mycorrhizal fungal community structures are influenced by various factors, including farming practices, N addition, and elevated environmental carbon dioxide levels. Gigasporaceae have been found to thrive in conditions where host plants can efficiently trade carbon for P, especially when a sufficient amount enables optimal photosynthesis [57].

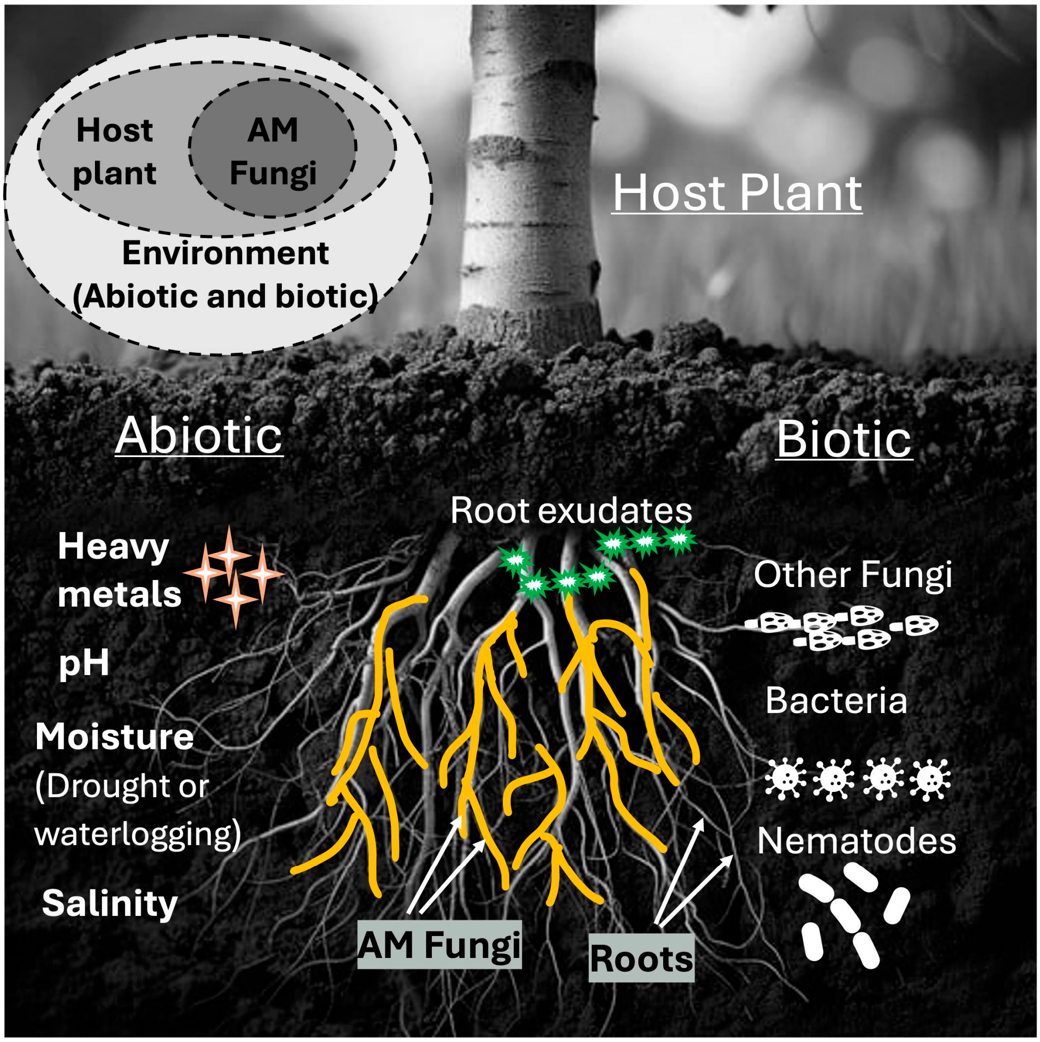

Figure 2. The figure shows the relationship between arbuscular mycorrhizal (AM) fungi and host plants and what abiotic and biotic factors affect this relationship between AM fungi and host plants.

4. Contribution of AM Fungi in Agroecosystem Sustainability

An agroecosystem is a complex, interconnected network of biotic and abiotic components within a defined agricultural area [9]. A sustainable agroecosystem maintains long-term productivity by balancing resource conservation, economic feasibility, social acceptance, and environmental integrity [10–12]. The symbiotic association between the host plants and AM fungi is nature's gift for maintaining a sustainable agroecosystem in today's dynamic environment [58]. Munyanziza et al. [59] explored the intricate relationship between AM fungi and their host plants, revealing several key benefits of this symbiosis. One of the primary advantages of mycorrhizal associations is the increased absorptive surface area provided by the fungal hyphae. This extensive network of fungal filaments allows host plants to access a larger volume of soil and, consequently, a greater pool of nutrients. As a result, plants colonized by AM fungi exhibit improved nutrient uptake compared to their non-mycorrhizal counterparts. In addition to enhancing nutrient acquisition, AM fungi confer a higher tolerance to various environmental stressors. These fungi have been found to protect host plants from the detrimental effects of toxic metals, root pathogens, drought, salinity, elevated soil temperatures, unfavorable pH conditions, and transplantation shock [59–61]. By buffering the host plants against these adversities, AM fungi are crucial in promoting plant survival and resilience in challenging environments, increasing and maintaining agroecosystem sustainability. The multidimensional nature of these benefits underscores the pivotal importance of AM fungi in shaping plant performance and adaptability across diverse environments to promote sustainability. Below are some of the components of a sustainable agroecosystem, and the AM fungi ameliorate those components.

4.1. Contribution of AM Fungi in Maintaining Soil Health and Nutrient Cycling and Reducing Chemical Fertilizer

The capacity of the soil to optimize crop production, along with balanced soil functional activities like carbon transformations, nutrient cycles, soil structure maintenance, and insect and disease regulation, determines soil health [62]. Arbuscular mycorrhizal fungi can take up a wide range of nutrients, including macronutrients and micronutrients. They are particularly efficient at absorbing P compared to other nutrients, which is attributed to their ability to produce enzymes like phosphatase, which enhance the solubility of P, making it more accessible for plant uptake [26]. The potential of AM fungi to provide host plants with essential nutrients while maintaining soil health has increased interest in the commercial production of AM fungal inoculants. Arbuscular mycorrhizal fungi are naturally present in the roots of most plants and have unique abilities to assist plants in nutrient uptake and maintaining plant stress [63].

Arbuscular mycorrhizal fungi, being a natural root symbiont, provide host plants easy access to various inorganic nutrients like N and P and have been found to increase the phyto-availability of micronutrients like Zn and Cu, allowing for efficient nutrient cycling between plants and microbes [64]. Mycorrhizal associations have been found to enable better use of sparingly soluble P pools, increasing the efficiency of added P fertilizer and immobile P pools [65]. Milleret et al. [66] found that AM fungi increase the P acquisition by leek plants from the soil and increase the plant biomass. They also found that the interaction of leek roots and AM fungi improves the water-stable macroaggregates, which is supposed to be the combined effect of root exudates and glomalin secretion from AM fungi. Astiko et al. [67] found that inoculation of AM fungi into soil and a combination of cattle manure had significantly higher concentrations of N, P, K, and organic-C and higher yield than other treatments like AM fungi alone, AM fungi combined with rock phosphate, AM fungi combined with inorganic fertilizers, and control (soil without any inoculation). These results showed that using AM fungi with cattle manure could be a suitable soil amendment option for sustainable soil health and productivity in the soybean growing system.

Arbuscular mycorrhizal fungi also improve the soil structure by forming stable soil aggregates [68]. The formation of stable soil aggregates includes the production of glycoprotein and glomalin deposited on the hyphal walls and adjacent soils. Glomalin acts as a hydrophobic glue that prevents macroaggregate disruption during the drying and wetting events by decreasing the movement of water into the pores within the aggregate structure. This way, AM fungi form stable soil aggregates, which are the building blocks of soil structure [69]. Research has also shown that AM fungi can reduce the negative effects of soil compaction on plant growth. Miransari et al. [15] found AM fungi to reduce the impact of soil compaction on wheat growth and increase the root, shoot, and grain dry weight. Similarly, mycorrhizal fungi (*Melanogaster variegatus* s.l.)-inoculated White Alder (*Alnus incana*) had significantly more roots and higher soil aggregate stability than non-mycorrhizal White Alder [70].

Arbuscular mycorrhizal fungi also help to mitigate nutrient toxicity in soil. An experiment by Mosse [17] found that the plant growth response of P applied to soil depends on the soil type. Toxic P concentration was found to be lower in light or sandy soil where added phosphate quickly becomes unavailable to plants. Plant P was found to increase slowly with an increase in the amount of phosphate in mycorrhizal plants in clayey soil and was found to perform better in mycorrhizal plants than non-mycorrhizal plants. On the other hand, there was a rapid increase in plant P in mycorrhizal plants in sandy soils, which were only better with small amounts of added phosphate, which would cause toxic P concentration too quickly. It shows that mycorrhizal plants' roots absorb more phosphate to reach the optimum level of P, even with a small addition of phosphate.

Liu et al. [71] found that high fertilizer application in an alpine meadow ecosystem caused a dramatic loss of *Glomus* species but a significant increase in genus richness. It was attributed to the competition between the AM fungal communities for photosynthate from host plants. Plant growth response to AM fungal inoculation varies within an ecosystem, ranging from parasitism to mutualism. The sensitivity of mycorrhizal species is more pronounced in native AM fungi than in exotic AM fungi, underscoring the crucial role of mycorrhizal fungi in the ecosystem [72].

4.2. Contribution of AM Fungi in Transferring Resources Within Agroecosystems

In intercropping systems, mycelial networks of AM fungi can facilitate the nutrient distribution between crop species, alleviating nutrient deficiencies in one crop while improving nutrient use efficiency across the intercropping system [73,74]. Arbuscular mycorrhizal fungal inoculation has been found to enhance soybean plants' N fixation efficiency and facilitate the transfer of fixed N from soybean to maize in intercropping systems, ultimately leading to increased yields. This finding highlights the potential of AM fungi to optimize nutrient sharing and productivity in mixed cropping scenarios [73].

Similarly, Wahbi et al. [74] demonstrated that inoculation with the AM fungus *Rhizophagus irregularis* promoted the transfer of fixed N from faba bean to wheat in a faba bean–wheat intercropping system. It suggests that AM fungi can play a crucial role in facilitating nutrient exchange between legumes and non-legumes in intercropping arrangements.

Furthermore, Saharan et al. [75] discovered that AM fungi can aid in redistributing water from well-watered plants to water-stressed plants in intercropping systems. In a greenhouse experiment simulating intercropping between finger millet and pigeon pea, they observed that AM fungi enabled water transfer from plants with access to water to those experiencing drought stress. Additionally, they found that AM fungi enhanced the uptake of both N and P in finger millet and pigeon pea plants, regardless of water availability. These diversified benefits demonstrate the vital role of AM fungi in enhancing the productivity, resilience, and sustainability of intercropping systems. Arbuscular mycorrhizal fungi can contribute to diversifying cropping systems' overall productivity and resilience by optimizing resource sharing and mitigating stress.

4.3. Contribution of AM Fungi to Mitigate Enviornmental Stresses

The symbiotic relationship between AM fungi and crop plants plays a crucial role in enhancing crops' resilience to various environmental stresses, abiotic and biotic [60,76]. These factors can impact the abundance and diversity of mycorrhizal populations in the soil, affecting soil health and crop productivity [14]. The increasing prevalence of climate change and the widespread use of conventional agricultural practices, including synthetic fertilizers and pesticides, have exacerbated the effects of abiotic stresses on crop plants. These stresses can negatively impact crop quality and yield.

Lenoir et al. [60] explored the potential of AM fungi to enhance plant tolerance against a range of abiotic stresses, such as pollutants, salinity, drought, extreme temperatures, elevated CO2 levels, and soil acidity. They found that AM fungi contribute to increased tolerance to salt and drought stress and better adaptability to both heat and cold stress, allowing plants to thrive under challenging environmental conditions by regulating various biochemical processes like osmotic and stomatal regulation along with the production of proline, glutathione, and soluble sugars [14,61]. The detrimental consequences of climate change on crop yields can be mitigated by harnessing the beneficial effects of AM fungi interactions, thereby promoting food security and sustainable agriculture in the face of a changing environment [77].

4.3.1. Plant and AM Fungi Interaction and Abiotic Stress

Abiotic factors such as climate, drought, pollution, pH, and organic matter content can affect AM fungi populations, soil health, and crop production [78]. Climate change and conventional agricultural practices like synthetic fertilizers and pesticides have increased the effects of abiotic stresses on crop plants and hampered the quality and productivity of the crop [14]. Lenoir et al. [60] discussed the role of AM fungi in tolerance against various abiotic stresses (pollutants, salinity, drought, extreme temperatures, CO_2, acidity) through multiple mechanisms like morphological adaptation, production of antioxidants, chaperone proteins, and trehalose to protect cells against damage. A comprehensive evaluation of the population of AM fungi in the semi-arid agroecosystem of North Jordan revealed that abiotic factors and cropping patterns significantly influenced the population of AM fungal species. They discovered a noteworthy positive correlation between spore density, organic matter (OM), and $CaCO_3$ percentages. Additionally, they observed a weak correlation between spore density with decreasing soil pH and increasing electrical conductivity (EC). Conversely, they found a negative correlation between spore density and soil P [79].

Arbuscular mycorrhizal fungi protect host plants against salt stress through multiple mechanisms that enhance their resilience. These include the accumulation of osmolytes, which reduce the osmotic potential of the cell sap, and increased nutrient and water uptake, ensuring better overall plant health. Additionally, AM fungi help maintain a high Na^+/K ratio, supporting ionic balance within the plant. They also stimulate the production of antioxidants in the host plant, which mitigates oxidative damage caused by salt stress [16]. Porcel et al. [61] discussed the mechanisms like improved host plant nutrition, K^+/Na^+ ratios, osmotic adjustment, and accumulation of solutes like proline and soluble sugars exhibited by mycorrhizal plants that help host plants from salinity stress. They also discussed the regulation of plant genes involved in the biosynthesis of proline and aquaporins by AM symbiosis that helps maintain water status in the tissues of mycorrhizal plants. Hajiboland et al. [80] found that AM fungi-inoculated tomato plants have higher Ca^{2+}/Na^+ and K^+/Na^+ ratios and elevated stomatal conductance that protects host plants against salt tolerance. Mycorrhization increased the uptake of P, Ca, and K and reduced salt stress in tomato plants.

Drought stress induces the generation of reactive oxygen species (ROS), which cause significant damage to plant cellular membranes [81]. Arbuscular mycorrhizal fungi have been found to enhance antioxidant activity within plants, like increased activity of peroxidase, catalase, and ascorbate peroxidase under drought stress, thereby stabilizing cellular structures and alleviating the detrimental effects of ROS associated with drought conditions. Moreover, AM fungi inoculation also reduced malondialdehyde levels, improving plasma membrane stability in drought-stressed plants [82]. A report on the differences in proline accumulation in lettuce leaves inoculated with different fungal species belonging to the genus *Glomus* suggests that the AM fungi induced different degrees of osmotic adjustment and helped the host plant tolerate drought stress [83]. Furthermore, AM fungi inoculation has increased fungal diversity and richness, promoted beneficial bacteria accumulation in the rhizosphere, and helped plants cope with drought stress [82]. Research by Neto et al. [84] found that *Aster tripolium* L. plants inoculated with AM fungi had improved performance under conditions of tidal flooding. The AM fungi helped the plants adjust to the osmotic stress caused by the flooding, as evidenced by higher concentrations of the osmolytes proline and soluble sugars in the plant tissues.

Additionally, the AM fungi enhanced the plants' uptake of N, which likely contributed to their increased tolerance of the flooded conditions. According to Xiang et al. [85], the AM fungal treatment increased the glucose, sucrose, betaine, and proline content of the cucumber plants under waterlogging stress, thereby maintaining the osmoregulation and better managing the waterlogging stress. Furthermore, AM fungi inoculation upregulated 13 of the 14 *CsPIP* genes in cucumber plants, showing higher tolerance against waterlogging stress.

Arbuscular mycorrhizal fungi inoculation has been shown to mitigate heat stress damage in plants by enhancing the activity of antioxidant enzymes such as superoxide dismutase and ascorbate peroxidase. Additionally, it increases the levels of ascorbic acid and polyphenols, thereby minimizing the harmful effects of ROS under heat-stress conditions [86]. Arbuscular mycorrhizal fungi-inoculated maize was found to have higher water content and water use efficiency under cold stress conditions, further improving gas exchange capacity, osmotic adjustment, and the efficiency of the quantum yield of PSII [87]. Inoculation with the AM fungus *Funneliformis mosseae* has increased secondary metabolites, including phenols, flavonoids, lignin, and other phenolic compounds, in cucumber seedlings under cold stress. Additionally, it increases the activity of antioxidant enzymes such as polyphenol oxidase (PPO), glucose-6-phosphate dehydrogenase (G6PDH), and guaiacol peroxidase (G-POD). The expression of stress-related marker genes is also upregulated in AM fungi-inoculated cucumber seedlings, demonstrating the role of AM fungi in improving cold-stress tolerance [88]. The role of various AM fungi is listed in Table 2 below. Figure 3 depicts the role of AM fungi in maintaining soil and plant health during abiotic stress.

Table 2. Types of arbuscular mycorrhizal fungi that are adapted to stress-related soil or environmental conditions.

Abiotic Stresses	AM Fungi	References
Salinity/salt stress	*Glomus intraradices*, *G. versiform*, *G. Etunicatum*	Evelin et al. [16]; Hajiboland et al. [80]; Porcel et al. [61]
Drought	*G. deserticola*, *G. fasciculatum*, *G. mosseae*, *G. etunicatum*, *G. intraradices*	Evelin et al. [16]; Ruiz-Lozano et al. [83]
High or low soil P levels	*G. intraradices*, *Gigaspora rosea* Nicol. & Schenck	Mosse [17]; Cardosso and Kuyper [65]
Acidity	*G. mosseae*	Mosse [17]; Mohammed et al. [79]
Metal toxicity	*Gigaspora margarita*, *Rhizophagus irregularis*, *G. mosseae*, *G. monosporum*	Begum et al. [14]; Lenoir et al. [60]
Extreme temperatures	*G. fasciculatum*, *R. irregularis*, *R. intraradices*	Begum et al. [14]

Table 2. *Cont.*

Abiotic Stresses	AM Fungi	References
Cold stress	*G. etunicatum*, *F. mosseae*	Zhu et al. [87]; Chen et al. [88]
Low light stress	*G. mosseae*	Zhang et al. [89]
Waterlogging/flooding stress	*G. intraradices*, *G. geosporum*	Fougnies et al. [90]; Neto et al. [84]; Xiang et al. [85]

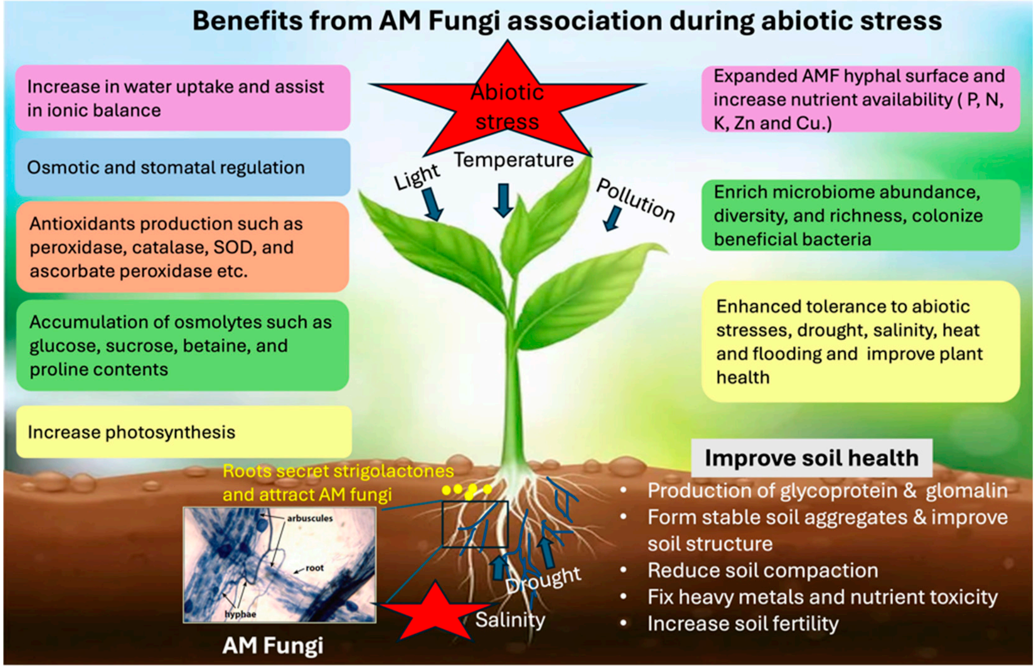

Figure 3. Figure depicting the plant–AM fungi association and its impact on soil and plant health during abiotic stress. Plant roots secrete root exudates containing chemical compounds like strigolactones, which attract AM fungi towards the roots to form a symbiotic association with host roots. Arbuscular mycorrhizal fungi enhance plant tolerance to abiotic stresses by improving nutrient and water uptake through their extensive hyphal networks. They boost antioxidant enzyme activity, reducing oxidative damage from stresses like drought or salinity. They also regulate osmolyte production, stabilize soil aggregates, and minimize soil compaction.

4.3.2. Plant and AM Fungi Interaction and Biotic Stress

Arbuscular mycorrhizal fungi interact with various soil organisms found in roots, the rhizosphere, and bulk soil. These interactions can be inhibitive, stimulative, competitive, or mutualistic [91]. Microbial interaction is an important factor in soil fertility, and various arbuscular mycorrhizal fungi are found to interact with the host plant species in symbiotic relationships, exchanging nutrients. Arbuscular mycorrhizal fungi affect the soil's microbial community both qualitatively and quantitatively, resulting from the changes in the root and fungal exudates. Arbuscular mycorrhizal fungi benefit from other microorganisms present in the rhizosphere, like K-solubilizing microorganisms (KSMs), as they increase the bioavailability of K in the soil, increasing the K absorption capacity by AM fungi hyphae [92]. It was found that the root nematode *Meloidogyne incognita*'s penetration was significantly decreased in the mycorrhizal roots than the control roots, and the application of mycorrhizal root exudates further decreased nematode penetration and paralyzed the nematodes temporarily [93].

A study on the response of N-transforming microorganisms to AM fungi in pot cultures of mycorrhizal and non-mycorrhizal maize found that the number of autotrophic ammonium oxidizers in pot cultures of AM fungi was significantly higher than in non-mycorrhizal cultures. They also found that these bacteria were seen only after 15 days in non-mycorrhizal cultures compared to AM cultures. Compared to the control, the number of ammonifying and denitrifying bacteria was significantly reduced in the AM pot cultures. It shows the variable effects of AM fungi in different microbial groups [94]. Another study reported the growth of *Pseudomonas chlororaphis* and the conidial germination of *Trichoderma harzianum* in the presence of the *G. intraradices* AM fungal extract. In contrast, the conidial germination of *Fusarium oxysporum* f. sp. *Chrysanthemi* was reduced, and growth of *Clavibacter michiganensis* subsp. *michiganensis* was unaffected. These results suggest the possible interactions between AM fungi and soil microorganisms [95].

The relationship between the different biotic organisms and the AM fungi and their interaction with the host plant has been shown in Table 3.

Table 3. Common mycorrhizal fungi and how they interact with other micro-organisms.

Biotic Stresses/Organisms	Mycorrhizal Fungi	Type of Association	References
Bacteria			
Rhizobacteria	AM fungi	AM fungi enrich the bacterial flora	Andrade et al. [96]
Paenibacillus validus	*G. intraradices*	Forms new spores, supports growth of fungus	Hildebrandt et al. [97]
Bacillus subtilis	*G. intraradices*	Increases root colonization, P solubilization	Toro et al. [98]
Enterobacter species	*G. intraradices*	Increases root colonization, P solubilization	Toro et al. [98]
Pseudonomas species	*G. versiforme*	Spore formation	Mayo et al. [99]
Corynebacterium species	*G. versiforme*	Spore formation	Mayo et al. [99]
Ammonifying and denitrifying bacteria	AM fungi	Presence of mycorrhizal hyphae reduces the number of ammonifying and denitrifying bacteria	Amora-Lazcano et al. [94]
P. chlororaphis	*G. intraradices*	Growth of bacteria stimulated	Filion et al. [95]
Fungi			
T. harzianum	*G. intraradices*	Conidial germination stimulation in presence of AM fungal extract	Filion et al. [95]
F. oxysporum f. sp. *Chrysanthemi*	*G. intraradices*	Conidial germination reduced by AM fungal extract	Filion et al. [95]
Nematode			
M. incognita	AM fungi	Mycorrhizal hyphae decrease nematode penetration	Vos et al. [93]

4.4. Contribution of AM Fungi in Maintaining Biodiversity

Biodiversity plays an important role in the functioning of agroecosystems. Arbuscular mycorrhizal fungi interact with various soil organisms found in roots, the rhizosphere, and bulk soil. The presence of AM fungi significantly influences the composition and abundance of the soil microbial community. This impact is attributed to the alterations in the exudates released by the plant roots and the fungi. The changes in these exudates' chemical composition and quantity create a unique environment that favors the growth and activity of specific microbial populations while potentially suppressing others [92]. Arbuscular mycorrhizal fungi promoted the development of the beneficial bacterium *P. chlororaphis*. They enhanced the germination of conidia of the fungus *T. harzianum*, which is known for its plant growth-promoting and disease-suppressing properties. On the other hand, AM fungi inhibited the conidial germination of the plant pathogenic fungus *F. oxysporum* f. sp. *Chrysanthemi* while having no significant impact on the growth of the bacterial plant pathogen *Clavibacter michiganensis* subsp. michiganensis. These findings highlight the potential for complex interactions between AM fungi and other soil microbes, with some interactions being beneficial and others being antagonistic [95]. Vos et al. [93] found that the presence of AM fungal mycelium reduced the penetration of root-knot nematode (*M. incognita*) through altered root exudation of their host.

4.5. Contribution of AM Fungi in Soil Bioremediation

Arbuscular mycorrhizal fungi could be a valuable tool for effectively rehabilitating deteriorated ecosystems. Medina and Azcon [100] explored AM fungi's potential to restore degraded soils. They highlighted the enhanced tolerance of plants to adverse conditions such as heavy metal contamination and drought stress. In a related study, Janouskova et al. [101] investigated AM fungi's influence on plants' cadmium toxicity. They conducted experiments comparing the effects of cadmium on mycorrhizal and non-mycorrhizal plants. The results revealed that plants associated with AM fungi exhibited lower cadmium toxicity levels than those without symbiosis. The researchers attributed this protective effect to the ability of AM fungi to immobilize cadmium in the soil, thereby reducing its availability and uptake by the plants. These findings emphasize the significant role of AM fungi in mitigating the harmful impacts of cadmium on plant health and suggest their potential application in the remediation of cadmium-contaminated soils.

Furthermore, Chibuike [102] discussed using AM fungi to treat polluted soils, known as mycorrhiza-assisted remediation (MAR). He concluded that MAR is a suitable method for detoxifying organic and inorganic soil pollutants intended for crop production. However, the efficiency of the MAR method depends on carefully selecting the species and origin of fungi used, the type of plant colonized, and the type and concentration of pollutants.

4.6. Contribution of AM Fungi in Pathogen and Weed Suppression

Mycorrhizal fungi, particularly AM fungi, have been shown to play a crucial role in promoting plant health and resilience through various mechanisms. These beneficial fungi form symbiotic relationships with the roots of host plants, providing protection against soil-borne pathogens and helping to regulate populations of soil insects [64]. Experiments conducted on wheat plants have demonstrated the effectiveness of AM fungi in mitigating the stress caused by soil pathogens. The presence of these fungi in the plant roots helps to enhance the plant's defense mechanisms and reduce the severity of pathogen attacks. Furthermore, AM fungi have been found to improve nutrient uptake in host plants, even under challenging conditions. They can contribute to better plant growth and overall health, making the plants more resilient to various environmental stresses [15,103].

Arbuscular mycorrhizal fungi can act as a tool to suppress weed species and be a potential agroecosystem engineer that can replace herbicides in controlling weed species [18]. Rinaudo et al. [104] found 47% reduced total weed biomass with AM fungi in microcosms where weeds and sunflowers were grown together, whereas only 25% reduced total weed biomass where weeds were grown alone. Also, the presence of AM fungi significantly reduced the biomass of two among six weed species, and the biomass of the remaining weeds was only slightly reduced.

5. Challenges of AM Fungi in Maintaining Soil Health and Sustainable Agroecosystem

Arbuscular mycorrhizal fungi are crucial players in maintaining soil health and a sustainable agroecosystem through the formation of symbiotic associations with plant roots, enhancing plant nutrient uptake, and improving soil structure. However, maintaining the health and functionality of AM fungi faces several challenges. Intensive agricultural practices such as heavy tillage, continuous monoculture, and overuse of chemical fertilizers can significantly impact mycorrhizal populations and diversity [105,106].

Heavy tillage fragments the vital hyphal networks that AM fungi depend on to support plant health and nutrient uptake, thus diminishing the symbiotic advantages they offer to crops that follow. The breaking apart of these networks by tillage impedes the mycorrhizae's functionality and impacts the broader soil ecosystem, reducing soil organic matter and disrupting essential nutrient cycling processes. These changes are detrimental to soil health and development, impairing the soil's ability to support robust plant growth and maintain ecological balance [107]. Jansa et al. [108] found a reduced number of non-*Glomus* AM fungi species in tilled soil compared to non-tilled soil and decreased mycorrhizal diversity of certain AM fungi species.

The widespread application of chemical fertilizers and pesticides in traditional farming practices has detrimental impacts on the populations and functions of AM fungi. Additionally, the use of pesticides and herbicides can disrupt the composition of soil microbial communities, posing a risk to the advantageous AM fungi [63,109]. Helander et al. [110] found that using herbicides containing glyphosate diminished the colonization of AM fungi in perennial grass species, leading to changes in the composition and productivity of plant communities. Munyanziza et al. [59] also discussed the effects of converting natural systems into agricultural systems on AM fungi. They concluded that high-input agricultural methods are harmful to AM fungi. Hence, low-input sustainable agriculture practices should be encouraged among growers to enhance the population of AM fungi in soil and to maintain a sustainable agroecosystem.

The dominance of crop monocultures presents significant obstacles to the diversity and efficacy of AM fungi. A rich array of plant species typically fosters a diverse AM fungi community. Conversely, the homogeneity of monocultures can result in a diminished variety of mycorrhizal fungi, adversely impacting the symbiotic relationships that sustain soil vitality and plant health. This reduction in mycorrhizal diversity can undermine soil structure, nutrient availability, and the overall sustainability of agricultural systems [4]. The study by Fu et al. [111] revealed that with the increase in continuous monoculture cycles of tomatoes, soil quality indicators such as microbial diversity and enzyme activities initially improved but then deteriorated. This pattern was linked to decreased tomato yields, emphasizing that long-term monoculture, significantly beyond 11 cycles, negatively impacts soil health and agricultural productivity.

6. Ways to Increase the Efficiency of AM Fungi in Maintaining Sustainable Agroecosystems

The extensive use of chemical fertilizers and pesticides in conventional farming practices has adversely affected the populations and functioning of AM fungi. Jiang et al. [112] conducted a meta-analysis of 162 field experiments from 54 published studies and found organic fertilizers to increase AM fungi biomass and have a less harmful impact on AM fungi diversity than mineral-only fertilization. The decline in AM fungi populations is primarily attributed to nutrient enrichment from chemical fertilization. In a field and pot study with okra (*Abelmoschus esculentus*), organic pesticides (neem oil and D-Limonene) showed minimal impact on AM fungi colonization. In contrast, synthetic chemicals, particularly glyphosate in potted studies and carbaryl in field studies, significantly reduced colonization. These findings suggest that organic sprays are less disruptive to AM fungal associations compared to synthetic pesticides [113].

Cropping sequence also plays a critical role in influencing AM colonization. A field study conducted from 1990 to 1992 evaluated the effects of fallow periods and the cultivation of various crops in AM colonization in maize and found that growing mycorrhizal crops, such as sunflower, maize, soybean, and potato, enhances AM colonization in maize roots, improving P absorption and plant growth and ultimately increasing grain yield compared to maize following non-mycorrhizal crops like rape, sugar beet, or fallow [114]. A deeper understanding of the relationship between cropping systems and AM fungi is essential to effectively incorporate AM fungi into crop models [115].

The effectiveness of AM fungal colonization is significantly influenced by the type of inoculum used, the diversity of inoculum, and application methods. Native or indigenous AM fungi derived from local soils have been found to contain a higher diversity of species compared to commercial inoculants and have been shown to perform equally or even better than commercial isolates. However, the effectiveness of native AM fungal inoculants can vary depending on the source of the soil and the specific method used to produce the inoculum [116–118]. Hussain et al. evaluated the effects of four AM fungal species applied via seed coating, soil application, or both on maize growth. *Funneliformis mosseae* applied through seed coating, and soil application was most effective, enhancing root architecture, colonization, and nutrient uptake. Seed coating alone showed comparable benefits, highlighting it as a cost-effective method for large-scale AM fungi application [119].

Thus, AM fungi's efficiency can be improved by reducing chemical inputs, adopting organic fertilization, and incorporating mycorrhizal crops into cropping systems. Utilizing native fungal inoculants, optimizing application methods like seed coating, and deepening research on cropping system interactions are pivotal for promoting sustainable agricultural practices with AM fungi.

7. Conclusions

A sustainable plant ecosystem occurs when the soil's productive capacity is conserved with minimum use of energy and resources without the degradation of the ecosystem. It can be gained by the efficient utilization of nutrients by the plants, which the symbiotic association of the AM fungi facilitates. These fungi also help to form soil structures that improve water retention and reduce erosion. They produce a substance called glomalin, which binds soil particles together to form aggregates. These aggregates can hold water and nutrients and support robust plant growth. Arbuscular mycorrhizal fungi are also important in helping plants cope with stress, such as drought, salinity, and heavy metals. They assist plants by enhancing their water uptake and helping them with internal water management and protection mechanisms. Furthermore, AM fungi contribute to the natural control of pests, diseases, and weeds. They can outcompete harmful pathogens and suppress weed growth by making conditions less favorable for weeds and more favorable for crops. It helps reduce chemical pesticides and herbicides, which can harm the environment and human health.

However, the effectiveness of these AM fungi can be diminished by intensive farming practices such as excessive tillage, increased fertilizer and pesticide use, and monoculture. These practices can harm the fungi's surroundings and reduce their ability to work effectively with plant roots. Growers can adopt sustainable practices like reduced tillage, organic farming, crop rotation, and cover crops to support AM fungal colonization and maintain a diverse microbial life.

In conclusion, AM fungi are crucial in agriculture and environmental sustainability. They help improve soil health, increase plant nutrient uptake, and reduce chemical inputs. Thus, it is essential to understand the interactions of soil biotic and abiotic factors with AM fungi and their impacts on soil health, crop production, and the agroecosystem. Future research can be conducted to optimize the conditions beneficial to mycorrhizal associations with plants, potentially leading to more resilient agricultural systems.

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