

Manoj Parihar  
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Yinglong Chen *Editors*

# Arbuscular Mycorrhizal Fungi in Sustainable Agriculture: Nutrient and Crop Management

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*Editors*

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# Contents

<b>1</b>	<b>Multifaceted Role of Arbuscular Mycorrhizal Fungi in Crop Growth Promotion: An Overview</b> . . . . .	<b>1</b>
	Ravichandran Koshila Ravi, Mayakrishnan Balachandar, and Thangavelu Muthukumar	
<b>2</b>	<b>Agronomic Practices for Optimizing the AMF Abundance and Diversity for Sustainable Food Production</b> . . . . .	<b>55</b>
	Isabela Figueiredo de Oliveira, Mariana Lourenço Campolino, Raquel Gomes de Oliveira, Ubiraci Gomes de Paula Lana, Eliane Aparecida Gomes, and Sylvia Morais de Sousa	
<b>3</b>	<b>Molecular Determinants and Regulatory Mechanisms of Nutrient Exchange Between Plant and AMF</b> . . . . .	<b>77</b>
	Aditi Bisht, Simran Lather, Parveen Goyal, and Neera Garg	
<b>4</b>	<b>Co-inoculation of AMF and Other Microbial Biofertilizers for Better Nutrient Acquisition from the Soil System</b> . . . . .	<b>99</b>
	Ruwanthika Kalamulla and Neelamanie Yapa	
<b>5</b>	<b>Potentials and Prospects of AMF for Soil Carbon Sequestration and Nutrient Cycling in Rice-Based Cropping System</b> . . . . .	<b>113</b>
	Ajay Kumar Mishra, Malay K. Bhowmick, Rajeswari Das, Pavithra Pidikiti, Piyush Kumar Maurya, Sheetal Sharma, Panneerselvam Peramaiyan, and Sudhanshu Singh	
<b>6</b>	<b>Role of AMF in Organic Matter Decomposition, Carbon Sequestration and Climate Change Mitigation</b> . . . . .	<b>131</b>
	Zakaria Solaiman	
<b>7</b>	<b>Role of Arbuscular Mycorrhizal Fungi in Nitrogen and Phosphorus Cycling Within Terrestrial Ecosystems</b> . . . . .	<b>143</b>
	Jan Jansa and Petra Bukovská	

<b>8</b>	<b>The Role of Arbuscular Mycorrhiza Fungi in Zinc and Iron Nutrition of Crops</b> . . . . .	167
	Trupti K. Vyas, Kirti Bardhan, and Susheel Singh	
<b>9</b>	<b>The Abiotic Stress Management in Agroecosystems Through AMF Technology</b> . . . . .	193
	Marc-Antoine Chiasson, Thiago Gumiere, and Silvio J. Gumiere	
<b>10</b>	<b>Plant-Arbuscular Mycorrhizal Fungi Association Under Drought Stress</b> . . . . .	211
	Binod Basyal	
<b>11</b>	<b>Arbuscular Mycorrhizal Fungi: An Eco-Friendly Technology for Alleviation of Salinity Stress and Nutrient Acquisition in Sustainable Agriculture</b> . . . . .	223
	Manisha Phour and Satyavir S. Sindhu	
<b>12</b>	<b>Application of AM Fungi in Phytoremediation of Heavy-Metal Contaminated Soil</b> . . . . .	269
	Xin Zhang, Baodong Chen, Shuping Xing, and Hanwen Chen	
<b>13</b>	<b>The Role of AM Fungi in the Alleviation of Cadmium Stress in Crops</b> . . . . .	295
	Yamin Gao, Runjin Liu, and Yinglong Chen	
<b>14</b>	<b>Success Story of Arbuscular Mycorrhizal Fungi as a Bio Protectant Against Major Plant Pathogens</b> . . . . .	321
	Monika Thakur, Dhriti Sharma, Ankita Thakur, Savita Bhardwaj, Ruby Angurana, Vaidehi Katoch, and Dhriti Kapoor	
<b>15</b>	<b>Deciphering the Role of Arbuscular Mycorrhizal Fungi in Mitigating the Negative Effects of Abiotic Stresses in Legume Crops</b> . . . . .	337
	Aditi Bisht, Vaishali Sharma, and Neera Garg	
<b>16</b>	<b>Role of Arbuscular Mycorrhizal Fungi (AMF) in the Production of Medicinal Crops</b> . . . . .	363
	A. G. Khan and H. Naz	
<b>17</b>	<b>Unveiling the Benefits and Dynamic Regulation of Mycorrhizal Technology in Cereal and Oilseed Production</b> . . . . .	381
	Aiman Slimani, Raja Ben-Laouane, Abderrahim Boutasknit, Mohamed Ait-El-Mokhtar, Mohamed Anli, Khalid Oufdou, Abdelilah Meddich, and Marouane Baslam	
<b>18</b>	<b>Earthworm and Arbuscular Mycorrhiza Interactions: Strategies to Augment Productivity</b> . . . . .	415
	C. S. K. Mishra, Suryasikha Samal, Pratik Acharya, Samrudhi Nayak, Tanushree Moharana, and Stutipragnya Pradhan	
<b>19</b>	<b>Arbuscular Mycorrhizae and Mycorrhizae Helper Organism—A Synergistic Movement Towards Soil and Crop Sustainability</b> . . . . .	429
	Debashis Kuila and Somdatta Ghosh	

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**Manoj Parihar** is currently working at ICAR-VPKAS, Almora, as a Soil Scientist in Crop Production Division. His present research works extend to study the diversity and distribution of AM fungi in North-Western Himalayan region, long-term fertilizer assessment in the rainfed and irrigated soybean–wheat cropping system, soil health management under organic farming, and various agroforestry systems.

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**Alok Adholeya** has over 35 years' significant experience and expertise in the area of translational research and reaching out to millions of common people worldwide through his developed technologies which includes a new biological organisms for soil fertility and crop productivity enhancement known as “mycorrhizal” bioremediation of industrial solid waste aeron chemical and fertilizer industries. He has developed more than 25 IPRs and commercialized most of them through technology transfer to industries. His current involvement in the area of nanointervention in agriculture, microencapsulation technology developed for beneficial yet fragile microorganisms and seed coating technology are few which are making inroads to benefit mankind.

**Yinglong Chen** research interests include the use of recently developed nondestructive imaging, isotope, and metabolism techniques to track rhizosphere interactions (root–soil–microbes, including mycorrhizal fungi), aiming to improve crop nutrient use efficiency and crop production.

# Chapter 1

## Multifaceted Role of Arbuscular Mycorrhizal Fungi in Crop Growth Promotion: An Overview



Ravichandran Koshila Ravi, Mayakrishnan Balachandar, and Thangavelu Muthukumar

### 1.1 Introduction

The crop productivity has enhanced progressively since mid of twentieth century in most of the countries in the world owing to several factors including increased application of chemical fertilizers. Nevertheless, agricultural productivity has declined in the recent times mainly due to unsustainable agricultural practices [1]. Moreover, it is essential to assure food and nutritional safety to the ever-growing human population worldwide by increasing the crop production in a sustainable way. It is estimated that agricultural productivity should be enhanced by the year 2050 by at least 70% [2]. However, enhanced crop yields are often related to increase in input costs, higher application of chemical fertilizers, and financial risk. Also, excessive use of chemical inputs can cause environmental degradation, reduce soil fertility, harden the soil, and decrease soil organic matter thus weakening the cropping systems [3]. Therefore, it is essential to increase the agricultural productivity in a sustainable manner that could reduce the reliance on synthetic fertilizers.

The beneficial interaction between plant and soil microbe could be an efficient sustainable practice to maximize crop yields [4]. The beneficial soil microbial communities including the monophyletic arbuscular mycorrhizal (AM) fungi of the phylum Glomeromycota forming a mutualistic relationship with more than 80% of current terrestrial plant species [5] is a well-known tool for modern sustainable agriculture [6]. The AM fungi imparts several beneficial services to the plants such as improved plant growth, enhanced water acquisition, nutrient uptake, in particular phosphorus (P), and tolerance to abiotic and biotic stresses in both natural and agroecosystems [7–10]. Moreover, AM fungi could be utilized as an effective

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amendment to increase agricultural productivity, soil fertility, and revive the agricultural ecosystem [6]. Owing to its several positive impacts, the application of this fungal group could aid in achieving the goals of sustainable agriculture. In the current chapter, the positive role of AM fungi in plant growth improvement, abiotic and biotic stress tolerance in relation to crop species, importance of AM fungi in soil structure and fertility are discussed. Furthermore, we highlighted the importance of AM fungi in various agricultural practices and factors affecting the AM symbiosis.

## 1.2 Arbuscular Mycorrhizal Fungi

Plants have successfully colonized terrestrial ecosystems through their association with a wide range of microorganisms. Of the diverse microorganisms that interact with plants, those that form a symbiosis with plants are the most influential ones in determining the growth and survival of plants in natural and managed ecosystems. Arbuscular mycorrhiza is one of the most common and widespread types of plant-fungal symbiosis that has greatly helped plants with their diverse functions [5]. It is estimated that the AM symbiosis originated presumably 480 million years ago in the Ordovician era and has persisted over the test of time with great success [11]. Most terrestrial plants either are facultatively or obligately AM (e.g., mycoheterotrophic plants). Contrarily, slightly more than one-quarter of land plants including the model plant *Arabidopsis thaliana* are non-mycorrhizal and are restricted to specific families like Amaranthaceae, Chenopodiaceae, and Brassicaceae [12]. Sometimes non-mycorrhizal nature can also be an exception in mycorrhizal plant families like the genus *Lupinus* in the mycorrhizal plant family Fabaceae. These non-mycorrhizal plants have a wide range of complementary strategies like elaborate root architecture, formation of cluster roots, soil acidification, etc., for nutrient acquisition from resource-poor heterogeneous soil patches [13].

The AM symbiosis is presumed to exist in more than one lakh plant species even though the roots of many extant plant species are yet to be assessed for this association [5]. Although AM symbiosis is common among cultivated cereals and pulses, a sizable number of vegetable crops are non-mycorrhizal. The diversity of AM fungi associating with plants is very small when compared to the diversity of plant species they associate. There are approximately 341 species of AM fungi in 45 genera under 12 families and 4 orders (Fig. 1.1; <http://www.amf-phylogeny.com>). All the fungi that form AM symbiosis are placed under the subphylum Glomeromycotina of the phylum Glomeromycota [14]. AM fungi are obligate symbionts and are presumed to be non-host specific [15]. For instance, several AM fungi belonging to different genera can colonize the root system of a plant [16, 17]. Though functional interdependency occurs among AM fungal species associating with a single root system, a certain level of competition is also a possibility in such mixed AM fungal colonization of plant roots [16].

The dynamic process of a functional symbiosis establishment between the root and AM fungi involves different stages like the (1) exchange of presymbiotic signals, (2) invasion of the roots, (3) endorhizal spread of the fungus, (4) arbuscule

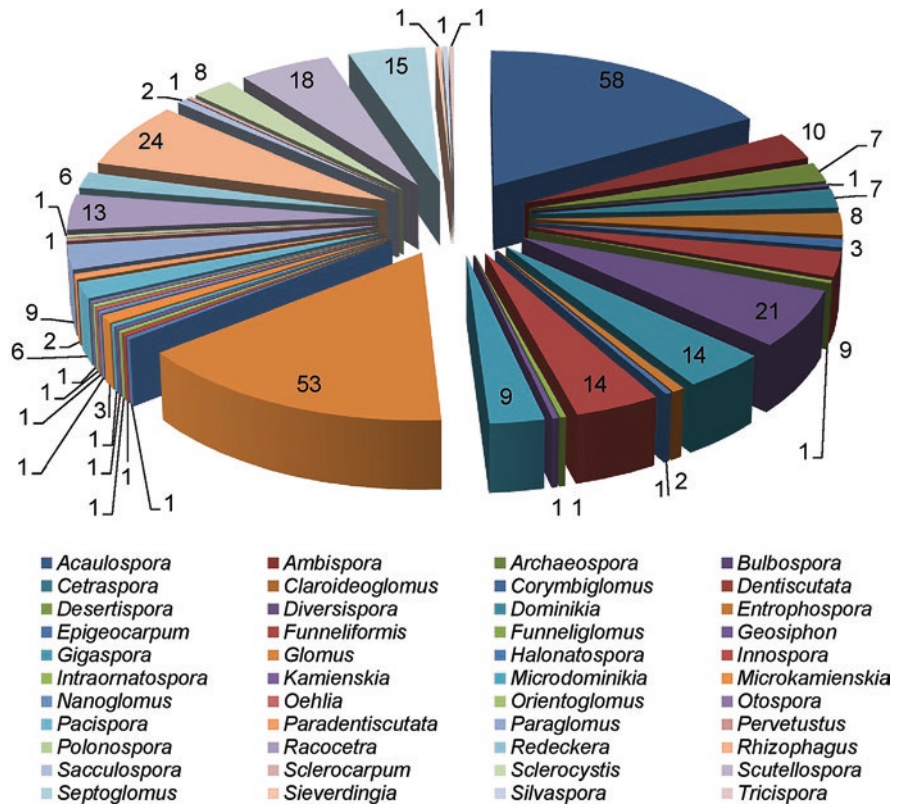


Fig. 1.1 Number of species in different arbuscular mycorrhizal fungal genera

development, and (5) formation of vesicles and spores. The symbiosis is initiated with the exchange of an array of presymbiotic signals between the plant and AM fungus. Different structures formed during the symbiosis like the extraradical and intraradical spores, extraradical hyphae, and mycorrhizal roots can act as propagules in initiating AM fungal colonization in roots. The signal molecules like oligosaccharides and butenolides emanating from the symbiotic partners are perceived by the respective receptors resulting in a cascade of events that result in the launching of the symbiosis [18].

Among the various metabolites released by plants into the rhizosphere strigolactones are considered to be an important stimulant for the development and branching of AM fungal hyphae during the symbiosis establishment. Once the AM fungal hyphae approach a plant root it forms an attachment on the root's surface called hyphopodia or appressoria. This is followed by the formation of peripenetration apparatus in the rhizodermal cells. Once the fungal hyphae enter the rhizodermal cells, the fungal hyphae coil in the first few cells after penetration and then transverse the cortex either inter or intracellularly. The fungal hyphae may also spread intracellularly exclusively by forming coils. In the inner cortex, the fungus penetrates the cells and forms a highly branched tree-like structure called arbuscules.

Various fungus and plant factors play an important role in the development and complexity of arbuscules. Though typical arbuscules occur in roots that form *Arum*-type morphology, arbuscules are rudimentary in roots forming typical *Paris*-type colonization patterns [19]. Arbuscules are considered to be the sites for nutrient transfer from the fungus to the root cells and their development is presumed to be driven by the host nutrient demand [20]. Though arbuscules were once considered the hallmark of functional symbiosis, now it is clear that plants belonging to non-mycorrhizal families can also form these structures [12, 21]. A large number of structural changes happen in an arbusculated plant cell like the reduction of the vacuole size and compaction of the cellular organelles including the nucleus in the cytoplasm.

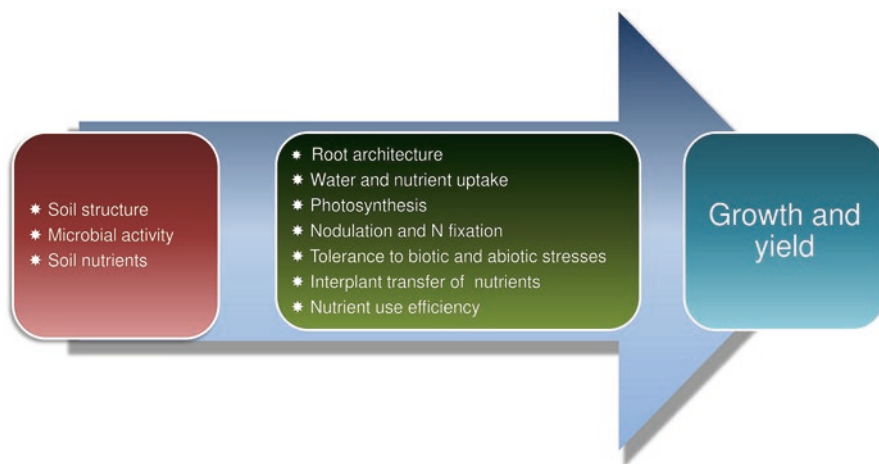
Arbuscules are ephemeral structures with a limited lifespan. The arbuscular collapse is initiated in the fine branches and later proceeds to the larger branches and the arbuscular trunk. A septum formed at the base of the arbuscular trunk separates the living hyphae from the dead hyphae. As the fungal colonization progresses lipid-filled vesicles develop intercellularly or intracellularly by most of the Glomeromycotean fungi except those belonging to the order Gigasporales. Although taxa in Gigasporales fail to form vesicles within the roots, they form extraradical structures known as auxiliary cells. The coenocytic vesicles in addition to acting as storage structures can also act as propagules in initiating mycorrhization [22]. The extraradical fungal hyphae originating from plant roots form an extensive hyphal network in the soil and play an important role in the exploration of soil for nutrients and the exchange of nutrients and signals between plants. At the end of the fungus growth cycle, the fungus forms asexual spores in the soil and/or in the roots depending upon the fungal taxa. In most instances, the sporulation of AM fungi is closely related to root senescence. The fungi perennate chiefly as spores in seasonal vegetations and sporulation is restricted in soils where actively growing roots are present throughout the year. Although the factors that regulate sporulation are not clear, recent evidence does suggest that fatty acids in combination with plant hormones and microbial-derived thiamin may be involved in spore formation [23].

### 1.3 Plant Growth and Yield

The plant growth improvement by AM fungi is a well-known fact as evidenced through a huge array of existing literature. The crops colonized by AM fungi improve the micro- and macronutrient uptake and also the nutritional quality of crop species [24, 25]. In addition, AM fungi also improve crop growth under various biotic and abiotic stresses [26, 27]. In a field experiment, Juntahum et al. [28] determined the influence of AM fungi (*Funneliformis mosseae* and native inoculum: *Acaulospora* and *Glomus* sp.) with or without different doses of P application on the growth and yield of sugarcane (*Saccharum officinarum* L.) and revealed that application of AM fungi along with 50% P fertilization increased the dry weights of stalk and leaves, enhanced P and potassium (K) uptake and boosted the cane and sugar yield when compared to plants grown only in the presence of field inoculum. Apart

from soil inoculation, seed coating with AM fungal inoculum enables AM fungal connection with emerging roots leading to early AM fungal colonization rendering beneficial effects to growing crop species. For example, Rocha et al. [29] reported that seed coating with individual or combined AM fungal inoculum consisting of various isolates of *Rhizophagus irregularis* in chickpea (*Cicer arietinum* L.) significantly increased the shoot dry weight and seed weight by 14% and 21% respectively in greenhouse conditions, while under field conditions the level of root colonization, number of pods and seeds and grain yield of plants originating from seeds coated with AM was enhanced when compared to seeds uncoated with AM fungi.

Zhang et al. [30] conducted a meta-analysis on the influence of AM fungal inoculation on grain yield in cereal crops based on three datasets: a whole dataset that includes laboratory and field studies, field dataset involving only field studies, and field inoculation dataset comprising only AM fungal inoculation under field conditions. The overall results of the meta-analysis indicated that the application of AM fungal inoculation on grain yield in cereal crops was less effective in field conditions than non-inoculation studies despite a 16% increase recorded in grain yield in the field inoculation dataset [30]. For instance, the application of *Rhizophagus clarus* along with different fertilizer dosages in two cultivars of soybean (*Glycine max* L., BRS 133 and BRS 369) increased the grain yield, nutrient uptake, and the effectiveness of fertilizer usage under field conditions [31]. In addition, an increase in crop yield has been reported in several crop species such as garlic (*Allium sativum* L.), tomato (*Solanum lycopersicum* L.), potato (*Solanum tuberosum* L.), cassava (*Manihot esculenta* Crantz), etc. [10, 32–34]. The AM fungi also increases the concentration of photosynthetic pigments, soluble phenolics, and mineral nutrients in crop plants [35]. The mechanisms through which AM fungi promote plant growth include increased water and nutrient uptake, modifications in root architecture, enhanced photosynthesis, and increased nutrient-use efficiency (Fig. 1.2). These are discussed in the upcoming sections.



**Fig. 1.2** Arbuscular mycorrhizal fungi mediated changes in soil and plant growth

## 1.4 Mechanism of Plant Growth Improvement

### 1.4.1 Alterations in Root Architecture

Root architecture has a crucial role in water and nutrient absorption from the soil by plants thereby enhancing crop growth and productivity. The alterations in root architecture have a pivotal role in improving the nutrient uptake efficiency in crop species [36]. The root morphological characteristics can change depending upon the soil conditions in order to reduce the metabolic cost for sustaining the root system and enhance mineral nutrient acquisition [37]. The changes in root characteristics could represent crucial belowground scavenging activities occurring due to soil microbes including AM fungi that in turn may reflect the plant performance [38, 39]. The plants with a coarse root system possess roots with a larger diameter and fewer root hairs resulting in low root density per given volume of soil. These coarse rooted plants largely benefit from AM fungal symbiosis for their growth and development [22]. The extraradical mycelium of the AM fungi helps in the expansion of the root surface area for nutrient acquisition in coarse rooted plant species. However, in a meta-analysis, Maherali [37] showed that possessing coarse roots alone might not exactly determine the growth response of host plants to AM fungal colonization. Nevertheless, modifications in root characteristics such as root length, development of lateral roots, specific root length, and root volume have been reported in many plants in response to mycorrhization [40–42].

The AM fungi can modulate the characteristics of the plant root system depending on the nutritional status of the plants. Toppo et al. [43] determined the effect of AM fungal inoculum containing *Rhizophagus intraradices* on root morphological characteristics in three different varieties of upland rice (*Oryza sativa* L.) with varying AM fungal responsiveness (Sathi 34–36, Jonga, and Vandana). The observations of the study indicated an increased total root length, root volume and diameter, and root surface area in highly AM responsive cultivar Sathi 34–36 and non-AM responsive cultivar Jonga. In addition, rice varieties Sathi 34–36 and Vandana (AM responsive cultivars) were highly dependent on AM fungi for their P uptake and had significantly modified root architecture when compared to the non-responsive variety [43]. Under nutrient-deficient conditions, AM fungal colonization have been shown to increase root growth, lateral root formation, root biomass, and the number of fine roots in different plant species [44–46]. The root volume, root fresh and dry weights, and root branching patterns were also enhanced in maize plants inoculated with *Rhizophagus irregularis* under P-deficient soils [41]. In addition, colonization of AM fungi can modulate changes in the phytohormone levels including auxins, strigolactones, cytokinin, and ethylene in the plant roots [47] which in turn alters the root architecture. Therefore, AM fungi mediated alterations in the root architecture enhance the direct nutrient uptake by plants in addition to AM hyphal networks mediated nutrient acquisition in crop plants.

### 1.4.2 Improved Water and Nutrient Uptake

One of the pronounced strategies through which AM fungi enhance plant growth includes improved water relations. The AM fungi uptake water from the soil via extraradical hyphae and transport it to the plant roots [48]. The dense AM fungal hyphal network expands into the soil away from the roots and increases the roots surface area for water uptake, and consequently increases water uptake in plants by reaching up to some distance where AM fungal hyphae could absorb water from tiny soil pores that are inaccessible to the roots [49]. In addition, AM fungi improve the hydraulic conductivity in plant roots and alter the physiological processes to minimize water stress [50, 51]. For example, in tomato plants inoculation of *F. mosseae* improved the availability and uptake of water and increased transpiration rates, increased hydraulic properties, and improved water retention potential than non-inoculated plants under greenhouse conditions [9]. Similarly, *R. irregularis* inoculated maize plants had enhanced stomatal conductance, photosynthesis, and root hydraulic conductivity under water-limiting conditions [50]. Therefore, AM fungi improve crop growth under normal and water-stressed conditions through osmotic adjustment, increased stomatal conductance, regulation of transpiration and photosynthetic rates, improved water potential, water-use efficiency, increased antioxidant enzyme activities, and modified soil-root hydraulic conductivity [51–53].

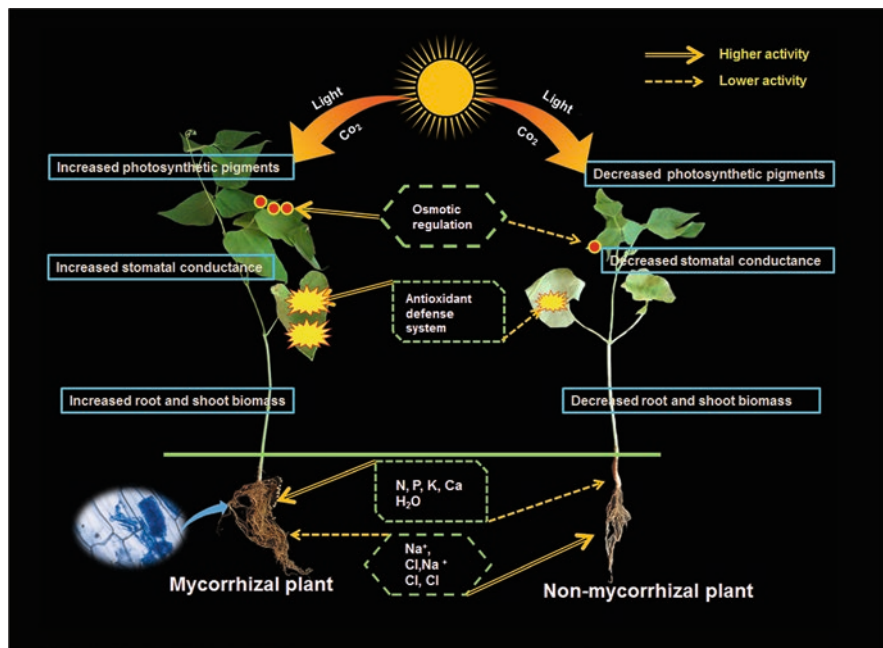
In addition to water uptake, AM fungi are well known to increase both macro- and micronutrients in crop species especially P [54, 55]. Generally, plants obtain the nutrients through two major pathways from soil, which include the plant pathway via root hairs and root epidermis and the mycorrhizal pathway via uptake of soil nutrients, from the surrounding soil by the extraradical hyphae and their transport to the intraradical hyphae and root cells [56]. The AM fungi uptake phosphate from the soil by expanding or enlarging the surface area of the roots through the extraradical hyphae which forage phosphate and transfer it to the root cortex and accumulate P in various forms that allow the AM to transport P from extraradical hyphae to intraradical hyphae [57]. The phosphate transporters for P uptake are upregulated in the extraradical fungal hyphae during phosphate uptake from the soil. The P availability in the soil and its requirement regulates the expression of P transporters in AM fungi [58]. A wide range of studies has reported an increased phosphate uptake in crop plants, but the extent of uptake may differ depending upon the AM fungal species and soil nutrient conditions. For example, Adeyemi et al. [7] conducted a two-year field experiment to determine the influence of individual AM fungal inoculation (*Claroideoglomus etunicatum*, *R. intraradices*, and *F. mosseae*) along with P fertilization on growth and P uptake of two soybean varieties under P-deficient soils. The results of the study demonstrated that *R. intraradices* inoculation increased the shoot (18.60–32.25%) and grain P (8.0–8.66%) content in TGx 1440–1E variety among the different AM fungal inoculations, whereas *F. mosseae* enhanced the shoot P uptake (4.27–10.65%) and grain P content (8.47–17.51%) in TGx 1448–2E variety when compared to *R. intraradices* and *C. etunicatum*. In addition, *R. intraradices* and *F. mosseae* inoculation significantly increased the P acquisition

efficiency and P-use efficiency than non-inoculated controls in both the soybean varieties under low soil P levels [7].

Like P uptake, the AM extraradical mycelium can also uptake inorganic forms of nitrogen (N) from the soil and transfer it to plants through various mechanisms [59]. The extraradical hyphae of AM fungi capture inorganic N and convert it into different amino acids via an enzymatic pathway. These amino acids are then converted into arginine, which is further transported to AM intraradical mycelium where it is further converted into urea and ornithine. The urea then forms ammonia after hydroxylation, which is released into the symbiotic interface to be taken up by plants [60, 61]. It is suggested that the increased P uptake can enhance N uptake in plants [62]. For instance, inoculation of indigenous AM fungi increased the nutrient uptake, shoot and root N (54% and 59%) and P (27% and 48%) concentrations, and P and N use efficiencies by 48% and 19% respectively in pigeon pea cultivars when compared to non-AM plants [63]. Likewise, Nakmee et al. [64] also reported that AM fungi increased the shoot and root K concentrations in sorghum plants. In addition, AM fungi also enhance  $K^+$  ion uptake in mycorrhizal plants when compared to non-mycorrhizal plants thereby maintaining an osmotic balance [65]. In addition to macronutrients, some of the essential micronutrients including copper (Cu), boron (B), iron (Fe), zinc (Zn), and molybdenum (Mo) are required for crop growth. For instance, the wheat and barley (*Hordeum vulgare* L.) plants inoculated with *R. irregularis* under different Zn concentrations increased the Zn uptake by 24.3% and 12.7% in wheat and barley plants through the mycorrhizal pathway [66]. In a meta-analysis, Lehmann and Rillig [67] suggested that AM fungi have a significant contribution to Fe and Cu uptake than Mn in the crop species. These studies indicate the major role of AM fungi in improving the nutritional status of crop plants.

### 1.4.3 Increased Photosynthesis

Photosynthesis is regarded as a key indicator of plant growth owing to its direct connection with crop production. An increased photosynthesis in crop species could help to attain sustainable crop productivity. However, several environmental stresses adversely affect the photosynthetic processes and hamper plant growth. Mycorrhizal plants possess higher photosynthetic rates when compared to non-mycorrhizal plants (Fig. 1.3). This increased photosynthetic rate of AM plants may be attributed to AM-dependent enhancement in P uptake under low soil P level or increased rhizospheric sink strength [68]. In addition, AM symbiosis in plants is known to be carbon sinks indicating that AM fungi can elevate the strength of rhizospheric sink and thereby leading to increased photosynthesis in leaves [69]. Moreover, the proteins and genes involved in the photosynthetic process are upregulated in the leaves of mycorrhizal plants, which is evidenced by data from proteomics, and transcriptomics approaches [70]. Indeed, the



**Fig. 1.3** Plant growth mechanism in mycorrhizal and non-mycorrhizal plants. Arbuscular mycorrhizal fungi improves the nutrient uptake; reduce the reactive oxygen species (ROS) level by up regulating antioxidant defense system, increase photosynthetic pigments, and increase water uptake due to better stomatal conductance which results in higher plant biomass

regulation of genes linked to sucrose synthases, Photosystem II 10 kDa polypeptide, and genes related to sucrose cleavage are stimulated by AM symbiosis in wheat [70]. In addition, the AM fungi could favor plants gas exchange ability by declining stomatal resistance and enhancing transpiration and carbon dioxide assimilation in plant that are essential in delivering photosynthates required by AM fungi [71, 72].

The AM fungi could enhance the photosynthetic efficiency in plants both under normal and stressed conditions. Water-deficit conditions affect photosynthesis by damaging the photosystem and electron transport system and decrease the stability of cell membranes in plants [73]. These negative effects of water stress could be alleviated through AM symbiosis. For instance, inoculation of *R. intraradices* and *F. mosseae* grown under water stressed conditions increased the relative water content in leaf and soil, enhanced chlorophyll content, maximized photochemistry, electron transport, and quantum efficiency of photosystem I and II in wheat plants when compared to uninoculated plants. This indicates the mitigation of damage caused to the structure and function of plant photosynthetic components by AM symbiosis [27]. Besides abiotic stresses, AM fungi (*F. mosseae*) reduce the rate of photosynthetic carbon dioxide assimilation and prevent the down regulation of



photosynthesis-linked genes caused due to cucumber mosaic virus disease in tomato plants [74]. In addition, AM fungal inoculation in maize seedlings under low temperature stress imparted a positive effect by reducing electron transmission and promoting phosphoric acid synthesis in mitochondria and the process of electron flow in chloroplasts [75]. The AM fungi increases the leaf photosynthetic pigment concentrations in maize [76], soybean [77], and rice plants [78, 79].

#### ***1.4.4 Nodulation and Nitrogen Fixation***

The AM fungi and the N-fixing bacteria rhizobia form symbiotic associations simultaneously with plants and have a crucial role in the natural and agricultural ecosystem influencing plant growth and nutrition [80–82]. In agricultural systems, leguminous crops are associated with AM fungi and N-fixing bacteria, *Rhizobium*. The AM fungi colonizing the root cortical cells provide nutritional benefits to rhizobia indirectly whereas fixed atmospheric N is delivered by rhizobia present in the nodules to plants [83]. Phosphorous plays an important in nodulation and N fixation owing to the linear correlation between P supply and N-fixation and nodulation [84]. The AM fungi enhance the major nutrient uptake, which in turn increases the nodulation and N fixation [85]. For instance, dual inoculation of *R. intraradices* and *Rhizobium tropici* CIAT899 in common bean plants under greenhouse conditions significantly increased root nodulation, enhanced shoot N and P accumulation, and improved P-use efficiency under low soil P for N fixation when compared to non-inoculated plants [86]. The AM symbiosis has the capability to increase N-fixation in plants growing in nutrient-stressed conditions. For instance, inoculation of *Glomus macrocarpum* in soybean plant nodulated with *Bradyrhizobium elkanii* enhanced N-fixation by elevating P content in root nodules, leaf N concentrations, nitrogenase activity, and reducing metabolic constraint of photosynthesis in P limitations [87]. Likewise, AM fungi improved root nodulation and N-fixation in various leguminous crops including chickpea, and green gram (*Vigna radiata* L.) under stressed conditions through the synergetic effect of AM-*Rhizobium* symbiosis [88–90].

#### ***1.4.5 Tolerance to Abiotic and Biotic Factors***

It is well known that AM fungi provide tolerance against different stressful conditions to host plants. Being a natural root-associating fungus, AM fungi provide crucial inorganic nutrients that in turn improve the growth of host plants under normal and stressed conditions. The abiotic stress decreases the AM fungal diversity and modifies the composition of AM fungal community leading to a higher amount of phenotypically similar AM fungal species in the community [91]. Moreover, the response of AM fungi varies depending on the various abiotic and biotic stresses

such as salinity, extreme temperature, drought, and heavy metals (Table 1.1) [27, 106, 107] and also protects plants against plant pathogens (Table 1.2) [26, 108]. The AM fungi mitigate or enhance the tolerance in plants against various stresses by enhancing nutrient content, photosynthesis, oxidative scavenging activity, and by regulating water balance in plants [119].

#### 1.4.5.1 Salinity

Soil salinity is an ever-growing environmental issue causing a serious threat to human food security worldwide. Generally, plants residing in saline soils encounter ionic, oxidative, and osmotic stresses. The adverse influence of  $\text{Na}^+$  and  $\text{Cl}^-$  ions prevailing in saline soils interrupts the enzyme and other macromolecule composition, hinders protein synthesis, slows down common metabolic activities, and stimulates ion deficiency in plants [120]. Moreover, salinity hampers plant growth by causing nutrient imbalance due to reduced nutrient uptake and translocation of nutrients to various plant tissues, induces extreme production of reactive oxygen species, and suppresses vegetative development thereby resulting in decreased yield production [121]. Therefore, salinity negatively impacts plant production in both agricultural and natural ecosystems. However, numerous studies have reported the efficiency of AM fungi to mitigate salt stress in plants [122–124].

Many authors have investigated the mechanisms by which AM fungi ameliorate the negative effect of salinity in host plants (e.g., [58, 125]). These include enhanced water uptake, osmolytes accumulation, and antioxidant production to overcome oxidative damage, regulate uptake of ion by plant roots and ion transportation to plant tissues in order to sustain ion homeostasis, manage photosynthetic rate for plant growth, regulate the production of plant hormones and maintain membrane structure and ultrastructure damage [126]. The beneficial aspects of AM symbiosis in salinity tolerance may be attributed to alterations in plant metabolism raised under various salinity levels in crop species [127]. In addition, regulation of the photosynthetic rate through increasing antioxidant production and accumulating osmolytes and protective molecules by AM fungi signifies biotechnological approaches to promote crop productivity [128, 129]. Under salt stress, plants experience decreased growth of primary roots due to the suppression of cell division and elongation of the root epidermis [130]. In such circumstances, AM fungi could induce alterations in the root architecture thereby enhancing plant's tolerance to salt stress [131]. For example, Wu and Zou [132] reported an increased root growth, and root surface area in citrus (*Citrus reticulata* Blanco) seedlings inoculated with *F. mosseae* and *Paraglomus occultum* when compared to uninoculated seedlings under salt stress. The colonization by AM fungi in plants growing in a saline environment has been reported to increase nutrient uptake and sustain ionic homeostasis [93, 133].

The AM fungi are known to naturally persist in saline soils [134]. As already mentioned, AM fungi alleviate the adverse effect of salt stress on plant growth by enhancing the nutrient and water uptake, inducing antioxidant activities that prevent oxidative

**Table 1.1** Effect of arbuscular mycorrhizal (AM) fungi in abiotic stress mitigation in crop species

Crop species	Growth conditions	AM fungal species	Abiotic stress	Inference	Reference
<i>Arachis hypogaea</i> L.	Field	<i>Rhizophagus irregularis</i> , <i>Funneliformis mosseae</i>	Salinity	Increased photosynthetic rate, leaf relative water content, plant height, osmolyte accumulation, enhanced protein concentrations in kernels, increased peanut pod yield, reduced malondialdehyde content, and activated superoxide dismutase, guaiacol peroxidase, catalase, and ascorbate peroxidase enzymes to alleviate salinity	Qin et al. [92]
<i>Cajanus cajan</i> (L.) Huth	Greenhouse	Native AM fungi consortium ( <i>Glomus</i> sp., <i>Acaulospora</i> sp., <i>Gigaspora</i> sp.) Exotic AM fungi ( <i>F. mosseae</i> , <i>R. irregularis</i> )	Salinity	Increased plant biomass, yield, nutrient uptake, improved K <sup>+</sup> /Na <sup>+</sup> and Ca <sup>2+</sup> /Na <sup>+</sup> ratios. Exotic AM fungus <i>R. irregularis</i> was effective than other AM fungi	Garg and Bhandari [93]
<i>Glycine max</i> L.	Greenhouse	<i>F. mosseae</i> , <i>Rhizophagus intraradices</i> , <i>Claroideoglomus etunicatum</i>	Salinity	Promoted nodule formation, increased leghemoglobin content, nitrogenase activity, auxin synthesis, and improved root system and nutrient acquisition under stress	Hashem et al. [94]

(continued)

**Table 1.1** (continued)

Crop species	Growth conditions	AM fungal species	Abiotic stress	Inference	Reference
<i>Lactuca sativa</i> L.	Greenhouse	<i>F. mosseae</i> , <i>Claroideoglossum lamellosum</i> , <i>Claroideoglossum claroideum</i> , <i>Diversispora celata</i>	Salinity	Enhanced proline production, increased superoxide dismutase, catalase and ascorbate peroxidase activities and decreased phenolic compound synthesis, and oxidative damage	Santander et al. [95]
<i>Oryza sativa</i> L.	Greenhouse	<i>F. mosseae</i> , <i>Acaulospora laevis</i> , <i>Gigaspora margarita</i>	Salinity	Enhanced plant growth, biomass, total chlorophyll concentration, shoot $K^+/Na^+$ ratio, and lowered shoot $Na^+$ /root $Na^+$ ratio, increased root biomass, spikelet fertility, and grain yield	Parvin et al. [79]
<i>Phoenix dactylifera</i> L.	Greenhouse	<i>Glomus</i> sp., <i>Sclerocystis</i> sp., <i>Acaulospora</i> sp.	Salinity	Increased photosynthetic efficiency, nutrient uptake (N, P, $K^+$ , and $Ca_2^+$ ), chlorophyll content, relative water content, stomatal conductance, proline synthesis enhanced antioxidant activities (superoxide dismutase, ascorbate peroxidase) and decreased lipid peroxidation and hydrogen peroxide content	Ait-El-Mokhtar et al. [96]

(continued)

**Table 1.1** (continued)

Crop species	Growth conditions	AM fungal species	Abiotic stress	Inference	Reference
<i>Foeniculum vulgare</i> L.	Field	<i>F. mosseae</i> , <i>R. intraradices</i>	Drought	Higher essential oil yield, increased nutrient content in leaf and grains and higher osmotic adjustment parameters	Zardak et al. [97]
<i>G. max</i>	Greenhouse	<i>Septoglomus constrictum</i> , <i>Glomus</i> sp., <i>Rhizophagus aggregatus</i>	Drought	Reduced oxidative damage, increased phosphorous (P) and nitrogen (N) concentrations in leaves and enhanced water content	Gutjahr et al. [40]
<i>Solanum lycopersicum</i> Mill.	Greenhouse	<i>F. mosseae</i> , <i>R. irregularis</i>	Drought	Increased plant vegetative growth, photosynthetic and transpiration rates, increased leaf area and relative water content of leaves, enhanced macro (P) and micronutrients (potassium, calcium, magnesium, zinc, and manganese) concentrations in leaves	Leventis et al. [98]
<i>Solanum tuberosum</i> L.	Field	<i>C. etunicatum</i> , <i>R. intraradices</i>	Drought	Increased leaf area index, leaf water potential, shoot dry weight, tuber dry weight, enhanced tuber P and K content, leaf chlorophyll index and relative water content under water stress	Khosravifar et al. [10]

(continued)

**Table 1.1** (continued)

Crop species	Growth conditions	AM fungal species	Abiotic stress	Inference	Reference
<i>Triticum aestivum</i> L.	Outdoor environmental conditions	<i>R. intraradices</i> , <i>Funneliformis geosporum</i> , <i>F. mosseae</i>	Drought	Increased relative water content in leaf and soil, enhanced chlorophyll content, improved the performance of photosystem I (PSI) and photosystem II (PSII), and increased the quantum yields of photosystems	Mathur et al. [27]
<i>T. aestivum</i>	Outdoor (Semi-field conditions)	<i>R. intraradices</i> , <i>F. mosseae</i> , <i>F. geosporum</i> , <i>C. claroideum</i>	Drought	Enhanced photosynthetic rate, transpiration rate and stomatal conductance, increased, plant height, biomass, grain yield, and N concentrations in roots	Zhou et al. [99]
<i>S. lycopersicum</i>	Plant growth chamber	<i>Septoglomus deserticola</i> , <i>Septoglomus constrictum</i>	Drought, heat	Prevented oxidative stress, decreased lipid peroxidation level, hydrogen peroxide accumulation, increased peroxidase, superoxide dismutase, catalase activities in leaves and roots, enhanced stomatal conductance, water status and plant biomass	Duc et al. [100]

(continued)

**Table 1.1** (continued)

Crop species	Growth conditions	AM fungal species	Abiotic stress	Inference	Reference
<i>T. aestivum</i>	Greenhouse	<i>R. irregularis</i> , <i>F. mosseae</i> , <i>F. geosporum</i> , <i>C. claroideum</i>	Heat	Increased grain number, reduced K/Ca ratio, altered nutrient allocation, and tiller nutrient composition in host under stress	Cabral et al. [101]
<i>Zea mays</i> L.	Greenhouse	<i>R. intraradices</i> , <i>F. mosseae</i> , <i>F. geosporum</i>	Heat	Increased chlorophyll content, photosynthetic rate, improved photochemistry, and prevented PS II from damage under high temperature	Mathur and Jajoo [102]
<i>Solanum melongena</i> L.	Plant growth chamber	<i>F. mosseae</i> , <i>C. etunicatum</i> , <i>R. irregularis</i> , <i>Diversispora versiformis</i>	Cold	Improved photochemical reactions, activated antioxidant defense system, accumulated hydrogen peroxide and reduced membrane damage by low less leakage of electrolytes from the leaf tissues under at 5 °C	Pasbani et al. [103]

(continued)

**Table 1.1** (continued)

Crop species	Growth conditions	AM fungal species	Abiotic stress	Inference	Reference
<i>Medicago sativa</i> L.	Phytotron	<i>R. irregularis</i>	Heavy metal	Improved plant biomass, arsenic (As) decreased AM colonization, enhanced P nutrition, restricted As uptake and reserved more As in roots by upregulating the expression of the AM-induced P transporter and metallothionein genes	Li et al. [104]
<i>Amaranthus hypochondriacus</i> L.	Greenhouse	<i>F. mosseae</i> , <i>R. intraradices</i>	Heavy metal	Increased shoot biomass, root cadmium (Cd) concentration, alleviation of Cd toxic effect, and mitigation of oxidative stress through antioxidant activity regulation.	Li et al. [75]
<i>Z. mays</i>	Plant growth chamber	<i>R. irregularis</i>	Heavy metal	Low accumulation of copper (Cu) in shoot and roots, increased P nutrition, total phytochelatin in shoots, reduced antioxidant activities, and increased tolerance to Cu in AM fungi inoculated plants	Merlos et al. [105]



**Table 1.2** Application of arbuscular mycorrhizal (AM) fungi in tolerance against biotic plant stress

Plant species	AM fungi	Plant pathogen/ disease	Inference	Reference
<i>Arachis hypogaea</i> L.	<i>Glomus</i> , <i>Acaulospora</i> , <i>Gigaspora</i> sp.	Stem rot ( <i>Sclerotium rolfsii</i> )	<i>Acaulospora</i> and <i>Gigaspora</i> sp. suppressed disease incidence and severity, increased root colonization and salicylic acid content	Swandi et al. [108]
<i>Cucumis sativus</i> L.	<i>Funeliformis mosseae</i> , <i>Rhizophagus irregularis</i> , <i>Claroideoglomus claroideum</i>	Root rot ( <i>Pythium ultimum</i> )	<i>F. mosseae</i> completely counteracted plant growth depression caused by pathogen followed by <i>R. irregularis</i>	Ravnskov et al. [109]
<i>C. sativus</i>	<i>F. mosseae</i> , <i>Glomus clarum</i>	Damping-off disease ( <i>Rhizoctonia solani</i> )	Reduced disease severity and enhanced plant biomass	Aljawasim et al. [110]
<i>Cynara scolymus</i> L.	<i>Glomus viscosum</i>	Verticillium wilt ( <i>Verticillium dahliae</i> )	Enhanced defense antioxidant systems, alleviated oxidative stress, increased ascorbate peroxidase, monodehydroascorbate reductase, and superoxide dismutase activities, promoted ascorbate and glutathione and decreased lipid peroxidation and hydrogen peroxide levels	Villani et al. [111]
<i>Medicago sativa</i> L.	<i>Rhizophagus intraradices</i>	<i>Phoma medicaginis</i>	Reduced disease index and leaf spot incidence, induced defense pathways, expressed pathogen resistance-related genes, activated peroxidase, polyphenol oxidase activities and enhanced jasmonic acid and salicylic acid concentrations	Li et al. [112]

(continued)

**Table 1.2** (continued)

Plant species	AM fungi	Plant pathogen/ disease	Inference	Reference
<i>Musa acuminata</i> Colla	<i>Rhizophagus irregularis</i>	<i>Fusarium oxysporum</i> f. sp. <i>Cubense</i>	Improved plant biomass, upregulated genes related to plant resistance and plant growth and suppressed wilt disease	Lin et al. [113]
<i>Oryza sativa</i> L.	<i>Funneliformis mosseae</i> <i>Rhizophagus irregularis</i>	Rice blast ( <i>Magnaporthe oryzae</i> )	Increased root colonization, phosphate concentration, grain yield, growth parameters and induced resistance against blast fungus	Campo et al. [26]
<i>Solanum lycopersicum</i> Mill	<i>Funneliformis mosseae</i>	Early blight disease ( <i>Alternaria solani</i> )	Induced strong defense responses of pathogenesis-related proteins genes and defense-related enzymes in leaves	Song et al. [114]
<i>S. lycopersicum</i>	<i>Rhizophagus irregularis</i>	Root-knot nematode ( <i>Meloidogyne incognita</i> )	Enhanced plant growth, reduced nematode induced parameters, increased phenolics and defensive enzymes and lowered malondialdehyde and hydrogen peroxide contents	Sharma and Sharma [115]
<i>S. lycopersicum</i>	Rhizolive consortorium ( <i>Claroideoglomus</i> , <i>Rhizophagus</i> , <i>Funneliformis</i> , <i>Septoglomus</i> , <i>Diversispora</i> , <i>Glomus</i> , <i>Acaulospora</i> , <i>Entrophospora</i> , <i>Gigaspora</i> , and <i>Scutellospora</i> species)	<i>Verticillium dahliae</i>	Reduced symptoms, increased growth, and yield, decreased malonyldialdehyde accumulation and increased antioxidant enzyme activities	Rahou et al. [116]

(continued)

**Table 1.2** (continued)

Plant species	AM fungi	Plant pathogen/ disease	Inference	Reference
<i>Triticum aestivum</i> L.	<i>Rhizophagus intraradices</i>	<i>Fusarium pseudograminearum</i>	Reduced pathogen population density and disease severity, increased antioxidant enzymes activities and decreased lipid peroxidation levels	Spagnoletti et al. [117]
<i>Zea mays</i> L.	<i>Glomus clarum</i> , <i>Glomus deserticola</i>	<i>Fusarium verticillioides</i>	Decreased the disease severity, improved agronomic characters (husk cover, ear number and quality), enhanced leaf number, stem girth, and plant biomass	Olowe et al. [118]

damage, regulating osmotic balance, and maintaining plant hormonal levels [135, 136]. For instance, Hashem et al. [137] revealed that inoculation of *C. etunicatum*, *R. intraradices*, and *F. mosseae* alleviated the adverse effect of salt stress in cucumber by increasing the plant biomass, chlorophyll content, antioxidant enzyme activities such as catalase, superoxide dismutase, glutathione reductase and concentrations of ascorbic acid and decreasing lipid peroxidation level and electrolyte leakage. Similarly, inoculation of *F. mosseae* and *Acaulospora laevis* decreased the membrane damage and enhanced the growth, nodulation, chlorophyll contents, leaf protein concentration, peroxidase, and phosphatase activity, and nutrient uptake in black gram [*Vigna mungo* (L.) Hepper] exposed to 8 dS m<sup>-1</sup> salinity level through a pot experiment in the greenhouse [115]. Likewise, application of indigenous AM fungal consortia consisting of *Acaulospora*, *Glomus*, and *Sclerocystis* species attenuated the negative effect of salt stress in the woody crop species, date palm (*Phoenix dactylifera* L.). Enhanced growth parameters, P and calcium uptake, increased photosynthetic pigments, antioxidant enzyme production such as catalase and superoxide dismutase, and reduced hydrogen peroxide and lipid peroxidation content evidenced salt stress amelioration in date palm [96]. Therefore, AM fungi can alleviate the deleterious effects of salinity in crop plants through various strategies as discussed above.

#### 1.4.5.2 Drought

Drought represents one of the prime limitations in crop production that could increase with climatic changes. Drought stress negatively influences plant growth as it affects nutrient acquisition, decreases transpiration rate due to shortage of water to roots, enzyme activity, and stimulates oxidative stress [138]. Nevertheless, a huge number of growing strong evidence have suggested amelioration of drought stress by AM fungi in most of the crop species including wheat [27, 139], rice [140], maize [141, 142], and soybean [143]. The AM fungi have been reported to enhance

water and nutrient uptake, rate of photosynthesis, antioxidant enzyme activities, root morphology, soil structure, polyamine homeostasis, aquaporin expression, regulate plant hormones, and maintain osmotic balance under water deficit conditions [141, 144]. Generally, an increased exploration of soil by plant roots and the extraradical AM fungal hyphae may provide resistance to drought in plants [145]. For example, the application of three contrasting commercial AM fungal inoculums consisting of different AM fungal species improved soybean growth characteristics including plant height, shoot and root dry weights, AM fungal colonization when exposed to medium (60% field capacity) and severe (30% field capacity) water stress when compared to uninoculated plants [8]. Further, AM fungal inoculation also improved nutrient [N, P, K, sulphur (S), manganese (Mn), and copper (Cu)] content in leaves of soybean plants exposed to different levels of water stress than uninoculated plants [8].

Polyamines, low-molecular weight aliphatic amines are well known to increase drought tolerance of plants via inhibiting chlorophyll loss, alleviating lipid bilayer surface in plant cells and nucleic acids, balancing cellular pH, altering expression of stress genes, regulating ion homeostasis, and preventing reactive oxygen species [146]. The AM fungi are known to enhance the polyamines that promote plant growth under drought. In a recent study, Zhang et al. [147] revealed that inoculation of *F. mosseae* increased the growth parameters, leaf water potential, chlorophyll content, expression of some aquaporin genes, enhanced concentrations of putrescine and cadaverine with increasing polyamine catabolic enzyme activities, promoted the spermine synthase gene expression (*PtSPMS*) and decreased the polyamine catabolic enzyme genes (*PtPAO1*, *PtPAO2*, *PtCuAO6*, and *PtCuAO8*) and polyamine synthase gene expression (*PtADCI* and *PtADC2*) in trifoliolate orange [*Poncirus trifoliata* (L.) Raf.=*Citrus trifoliata* L.] under drought conditions. In addition, the expression of some of the genes including *PtPAO1*, *PtPAO2*, and *PtPAO3* was higher in AM fungal inoculated plants than uninoculated plants that in turn activating reactive oxidative species-related signals for stress response by upregulation of root superoxide dismutase isozymes and catalase genes under drought stress [147]. This study showed that AM fungi could regulate or modify polyamine metabolism to cope with drought resistance in plants.

Besides, AM fungi can enhance plant tolerance to drought stress by inducing osmotic adjustment through higher solute accumulation, reducing oxidative damage triggered by reactive oxidative species via increased production of antioxidant enzymes during drought [148, 149]. In addition, drought stress is linked with abscisic acid, which controls the response of the plant to water stress [150]. For instance, Ren et al. [142] conducted a pot experiment to determine the effect of AM fungus, *F. mosseae* on root signal alteration, growth, and biochemical changes in maize seedlings exposed to drought stress. The results of the study showed that AM fungus decreased the susceptibility of maize roots to water stress, decreased abscisic acid concentrations in the leaf which serve as a non-hydraulic root signal, and consequently increased the photosynthetic rate. Inoculation of *F. mosseae* also affected the stomatal conductance and enhanced water use efficiency, increased water absorption, antioxidant enzymes such as peroxidase and superoxide dismutase,

decreased malondialdehyde level, and proline content conferring better adaptation in drought-stressed maize seedlings [142]. In addition to abscisic acid, other plant hormones including auxins, jasmonic acid, and strigolactone also have a crucial role in drought stress regulation in plants [151]. Several studies have reported that AM fungi increase the levels of these phytohormones to withstand drought stress [106, 125].

### 1.4.5.3 Heavy Metals

Excessive absorption of essential and non-essential metal ions from the soil leads to heavy metal toxicity in plants. Heavy metal pollution in cultivated soils results from the modifications in agricultural practices, inclusion of modern technologies, and intensified use of farming lands. Increased use of inorganic synthetic fertilizers and chemicals in agriculture has led to heavy metal pollution causing environmental degradation [152]. Indeed, irrigation using wastewater, sewage effluents, and disposal of industrial byproducts constitute the main sources of heavy metal contamination in farmlands. Greater heavy metal accumulation in plants interrupts the permeability of cell membranes, hampers photosynthesis, suppresses the uptake of mineral nutrients, and adversely influences the biological and physiological functions including synthesis of free radicals, inhibition of adenosine triphosphate (ATP) synthesis etc., thereby subsequently inhibiting crop growth [153]. The amelioration of heavy metal contamination via AM fungi-mediated changes is an eco-friendly approach [154].

The AM fungi detoxify the heavy metals via chelation of the heavy metal, immobilization via translocating heavy metals into AM fungal structure and roots within the soil, enhanced nutrient absorption, sequestering heavy metals in vacuoles, and induction of antioxidant mechanisms [155]. In addition, numerous studies have demonstrated that AM fungi could reduce soil contamination by several heavy metals thus aiding crop species to subsist in heavy metal stressed environments [156, 157]. For example, Zhang et al. [158] showed that sunflower (*Helianthus annuus* L.) plants inoculated with two AM fungal species (*F. mosseae* and *Funneliformis caledonium*) in a high and low heavy metal contaminated soils from a electric and electronic waste recycling site in China had an enhanced biomass, P uptake, and tissue P content, AM fungal colonization but had significantly decreased zinc (Zn), nickel (Ni), and chromium (Cr) content in the leaves. Moreover, AM inoculation also increased the uptake and accumulation of copper (Cu), lead (Pb), Zn and Ni in shoots and reduced the total heavy metal concentrations in the soil in sunflower plants in the contaminated soils [158].

The heavy metal remediation by AM symbiosis depends upon the AM fungal species, the characteristic and conditions of the host plant, type, and concentration and form of heavy metal in the contaminated soils [159]. The mitigation of heavy metal toxicity by AM fungi is not only linked with a decrease in heavy metal uptake, but also increases the heavy metal accumulation in plants [160, 161]. The abundance and diversity of AM fungi is usually higher in non-contaminated soils when

compared to heavy metal-polluted soils. Nevertheless, the AM fungal propagules remain in the contaminated soils, and AM fungal species isolated from contaminated soils are resistant to higher levels of heavy metals and are effective in increasing plant tolerance to heavy metals [159]. On contrary, some AM fungi from non-contaminated soils or commercial AM fungal inoculum can also alleviate heavy metal stress in crops. For example, inoculation of soybean with *R. intraradices* isolated from non-contaminated soil and raised under different concentrations of Arsenic (As) increased the plant growth traits such as plant height, leaf numbers, biomass, and root length [162]. The *R. intraradices* colonized plants also had decreased As accumulation in their roots and aerial parts thus ameliorating the negative effects of As toxicity when compared to non-colonized plants [162].

One of the strategies by which AM fungi ameliorates the negative impact of heavy metals in plants include the retention of the metal ions in their hyphae and vesicles, thereby averting their transportation to various plant parts [163]. For example, in a greenhouse experiment AM fungal inoculation (*Gigaspora gigantea* and *R. irregularis*) increased the nutrient uptake (N and P) and translocation of chromium (Cr) to maize tissues when grown in different concentrations of Cr-spiked soils. The alleviation of damage caused by Cr toxicity in maize was through higher retention of Cr in the roots and increased formation of AM structures such as arbuscules and vesicles with increasing Cr concentrations [160]. Another mechanism through which AM fungi mitigate heavy metal stress is by the production of a glycoprotein known as glomalin. In addition to many functions including maintenance of soil structure, increasing soil quality, and preventing soil erosion, the liberation of glomalin by AM fungi into soils helps in heavy metal binding to the fungal cell wall and influences the plants and its fungal partner to cope up metal stress [164, 165]. In a field experiment, glomalin secreted by AM fungi was shown to sequester 0.21–1.78% of Pb and 0.38–0.98% of cadmium (Cd) [166]. In addition, total glomalin content in soil was linearly correlated to Cd and Pb sequestration [167].

#### 1.4.5.4 Temperature

Temperature influences the growth, development, and yield of crop species. Generally, crops require a certain transitional temperature interval for their optimum growth [168]. Extremely high or low temperatures cause physiological, morphological, and biochemical alterations such as reduced growth, water, and nutrient uptake, altered cellular structure, and functioning, reduced transpiration, changes in stomatal conductance, and inhibition of photosynthesis [169]. These temperature-induced modifications can adversely affect the crop growth and yield which could be ameliorated by AM fungal symbiosis [102, 170]. The strategies through which AM fungi protect plants against high-temperature stress includes improved water uptake by the host plant via the extraradical fungal mycelium which subsequently enhances plant or root hydraulic conductivity and regulate the osmotic balance [171]. In addition, AM fungi can improve the net photosynthetic rate in crop plants. For example, maize plants raised in high temperature (44 °C) and inoculated with a