

Review

# Roles of Arbuscular Mycorrhizal Fungi on Plant Growth and Performance: Importance in Biotic and Abiotic Stressed Regulation

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**Abstract:** Arbuscular mycorrhizal fungi (AMF) establish symbiotic associations with most terrestrial plants. These soil microorganisms enhance the plant's nutrient uptake by extending the root absorbing area. In return, the symbiont receives plant carbohydrates for the completion of its life cycle. AMF also helps plants to cope with biotic and abiotic stresses such as salinity, drought, extreme temperature, heavy metal, diseases, and pathogens. For abiotic stresses, the mechanisms of adaptation of AMF to these stresses are generally linked to increased hydromineral nutrition, ion selectivity, gene regulation, production of osmolytes, and the synthesis of phytohormones and antioxidants. Regarding the biotic stresses, AMF are involved in pathogen resistance including competition for colonization sites and improvement of the plant's defense system. Furthermore, AMF have a positive impact on ecosystems. They improve the quality of soil aggregation, drive the structure of plant and bacteria communities, and enhance ecosystem stability. Thus, a plant colonized by AMF will use more of these adaptation mechanisms compared to a plant without mycorrhizae. In this review, we present the contribution of AMF on plant growth and performance in stressed environments.

**Keywords:** AM fungi; plant; abiotic stress; biotic stress

## 1. Introduction

Arbuscular mycorrhizal fungi (AMF) are soil microorganisms that form a symbiotic relationship with 80–90% of vascular plant species and 90% of agricultural plants [1], including most agricultural crops, particularly cereals, vegetables, and horticultural plants. They have a ubiquitous distribution in global ecosystems that are primarily defined by the global distribution of known plant hosts [2,3]. AMF are classified as a member of subkingdom *Mucoromycota* and the phylum *Glomeromycota* including three classes (*Glomeromycetes*, *Archaeosporomycetes*, and *Paraglomeromycetes* [4]). AMF belong to 11 families, 25 genera, and nearly 250 species [5,6]. *Glomeromycota* are obligate symbionts that rely on the carbon substrates provided by their host plants (up to 20% of plant-fixed carbon) to survive [7,8]. In return, the fungi improve the supply of water and nutrients, such as phosphate and nitrogen to the

host plant through extraradical and intraradical hyphae, arbuscules, and the root apoplast interface [9]. Based on fossil records and molecular data, this symbiosis dates back to the first appearance of land plants, about 400 to 450 million years ago [1]. The Arbuscular mycorrhizal (AM) symbiosis is probably the most widespread beneficial interaction between plants and microorganisms [9]. Several studies have reported that they play a crucial role in plant nutrition and growth in stressed conditions and enhance a number of essential ecosystem processes [7,10].

The purpose of this review is to summarize knowledge about AM associations, in particular the beneficial effects on host plants and soil. First, the role of AMF in plant nutrition, growth, and resistance to biotic and abiotic stress is considered. The indirect contribution of AMF in soil aggregation and stability is discussed. Finally, the diversity of interactions between AMF and other soil microorganisms are examined (Figure S1).

## 2. Contribution of Arbuscular Mycorrhizal Fungi to Plant Nutrition and Growth

Among beneficial microbes, AMF are one of the most widespread symbiotic fungi colonizing the majority of agricultural plants [11]. The effects of AMF on plant growth and physiological elements contents have been widely studied in many species including relevant crops such as *Solanum lycopersicum* L. [12,13], *Sorghum bicolor* (L.) Moench [10,14], *Withania somnifera* (L.) Dunal [15], *Cucurbita maxima* Duchesne [16], *Piper longum* L. [17], *Phaseolus vulgaris* L. [18], *Panicum hemitomom* Schult [19], and some free fruits such as *Citrullus lanatus* (Thunb.) Matsum. & Nakai [20], *Musa acuminata* Colla [21], and *Prunus cerasifera* L. [22]. In all these species, AMF improved plant growth parameters [10,12–15,17] and the uptake of several major nutrients such as nitrogen and phosphorus in stressed conditions [23,24]. This growth stimulation is linked to the fact that AMF extends the absorbing network beyond the nutrient depletion zones of the rhizosphere, which allows access to a larger volume of soil [25]. Furthermore, fungal hyphae are much thinner than roots and are able to penetrate smaller pores and uptake more nutrients [26].

By extending the root absorbing area, AMF increases the total absorption surface of inoculated plants and thus improves plant access to nutrients, particularly those whose ionic forms have a poor mobility rate or those which are present in low concentration in the soil solution [1]. It is calculated that the rate of water transport from external hyphae to the root ranges from 0.1 [27] to 0.76  $\mu\text{L H}_2\text{O h}^{-1}$  per hyphal infection point [28]. Furthermore, AMF contributes approximately 20% to total plant water uptake [29], highlighting the role of the symbiosis in the water status of host plants. AMF significantly improved *Cucurbita maxima* growth and metabolism, such as the concentrations of fat, crude protein, crude fiber, and carbohydrates in shoot and root systems of inoculated plants compared to control treatment [16]. Inoculation with this fungus significantly increased plant growth as well as phytochemical constituents such as sugar, protein, phenol, tannin, and flavonoid content [15]. In watermelon (*Citrullus lunatus* Thunb.), mycorrhizal colonization was found to improve not only the plant yield and water use efficiency but also the quality of the fruits [30]. Similar results were obtained in mycorrhizal tomato plants with an increase in the concentrations of sugars, organic acids, and vitamin C in fruits [12]. It has been demonstrated by [31] that AMF improved peach seedlings' performance under the potted conditions, and also significantly elevated K, Mg, Fe, and Zn concentrations in leaves and roots, Ca concentration in leaves, Cu and Mn concentrations in roots, which were obviously dependent on the AMF species. Compared to three AMF (*Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler 2010, *Glomus versiforme* (P. Karst.) S.M. Berch 1983, and *Paraglomus occultum* (C. Walker) J.B. Morton & D. Redecker 2001), *F. mosseae* exhibited the best mycorrhizal efficiency on growth and nutrient acquisition of peach seedlings [31]. Compared to uninoculated plants, AMF inoculation had positive effects on the growth of carrot and sorghum [14]. In carrot, *Scutellospora heterogama* (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders 1986, *Acaulospora longula* Spain & N.C. Schenck 1984, and *F. mosseae* had a positive effect on the growth of the host, whereas AMF had only weak effects on the growth of red pepper and leek [14].

Therefore, it is important to mention that the extent to which a host plant benefits vary with the AMF species used [14]; and macro and micro-nutrients uptake could depend partly not only on the fungal partner but also on the host plant [32]. A study carried out by [33] indicates that the contribution of the mycorrhizal pathway to nutrient acquisition also depends on fungal effects on the activity of the plant pathway and on the efficiency with which both partners interact and exchange nutrients across the mycorrhizal interface [34]. For various crops such as sweet potato [35] or pepper plant [17], the beneficial effect on plant nutrient content has also been shown to be dependent on fungal diversity.

A similar positive effect was reported in sorghum with an enhancement of plant height, the number of leaves, biomass, total nitrogen, phosphorus and potassium uptake [10]. Although, among some species of native AMF tested (*Glomus aggregatum* N.C. Schenck & G.S. Sm 1982, *F. mosseae*, *Acaulospora longula*, and *Acaulospora scrobiculata* Trappe 1977) some species like *Acaulospora scrobiculata* are more efficient for improvement of all these parameters in sorghum [10]. The effect of an AMF, *F. mosseae* was examined regarding the morphological and biochemical properties of different genotypes of the medicinal plant *W. somnifera*, commonly called Ashwagandha [15]. In addition, several studies reported that the responses of plants to colonization by AMF vary depending on inoculum composition, and a combination of mycorrhizal fungi is more effective than a monospecific inoculum [10,14,17,18].

AMF colonization by *F. mosseae* or *R. intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler 2010) increased both the survival and growth (by over 100%) of micropropagated transplants of *Prunus cerasifera* L., compared with either uninoculated controls or transplants inoculated with the ericoid mycorrhizal species *Hymenoscyphus ericae* (D.J. Read) Korf & Kernan 1983 [22]. Thus, inoculation of woody species' seedlings under nursery conditions is a valuable strategy to produce seedlings with good vigor, which would translate into high survival and growth at the field [36–38].

AMF play an important role in biofortification [39,40]. AMF inoculation may affect selenium uptake from soil and the level of antioxidant compounds in vegetable crops such as the green asparagus *Asparagus officinalis* L. Research carried out by [41,42] showed increasing selenium (Se) content in wheat grain through inoculation. It has been found by [43] that AMF modifies the concentration and distribution of nutrients within wheat and barley grain. Inoculation with AMF improves the grain nutritional content in protein, Fe, and Zn [44]. Under distinct environmental conditions, [45] concluded that AMF symbiosis positively affected the Zn concentration in various crop plant tissues. AMF can contribute substantially to the Zn nutrition of cereal crops such as bread wheat and barley but the role played by AMF on Zn uptake depends on the functional compatibility between AMF isolate and inoculated cereal species [40].

It is well-known that AMF symbiosis specifically induces the expression of transporters such as the plant aquaporin (AQ) genes, Pi transporters (PT), ammonium transporter (AMT), nitrate transporter (NT), sulfur (S) transporter, Zn transporter, carbon transporter, protein transporter etc. [46–50]. In wheat plants treated with *F. mosseae* and *R. intraradices* Zn concentration is 1.13–2.76 times higher than non-inoculated plants observed [51]. Further, it has been demonstrated that fungal form a network called mycorrhizal networks (MNs) that improve nutrients transfer between plants through the extension of fungal mycelium [52,53]. Also called common mycorrhizal networks, these MNs can integrate multiple plant species and multiple fungal species that interact, provide feedback, and adapt, which comprise a complex adaptive social network [52]. Results obtained by [54] confirm the role of AMF in driving biological interactions among neighboring plants.

### 3. Role of Arbuscular Mycorrhizal Fungi in Alleviation of Abiotic Stresses in Plants

AMF respond differently to abiotic stresses such as drought, flooding, extreme temperatures, salinity, and heavy metals [55–58]. Studies carried out by [59] showed that AMF communities would change in composition in response to abiotic stress [59]. These stresses reduce AMF diversity and alter AMF community composition resulting in an AMF community with a higher proportion of species that are phenotypically similar, because they are more tolerant of that specific abiotic stress. Changes in the diversity of AMF will feed back into the plant community and cause corresponding changes in

the diversity of plant species and productivity [60]. The feedback will become stronger with climate change [61]. AMF will adapt to abiotic stress independently of its host plant. However, despite the negative effects of stresses on AMF, several studies have demonstrated that AMF symbiosis improves plant growth, hydration, and physiology under various environmental stress conditions like salinity, drought, and the presence of heavy metals [62,63]. Depending on the stress, the benefits of AMF to plant partners can vary [64], and mycorrhizal fungal types vary in their responses to climate change.

### 3.1. AMF and Plant Drought Tolerance

Drought is one of the major stresses that can reduce plant productivity considerably [11]. Water constraints provoke stomatal closure with a subsequent reduction of CO<sub>2</sub> influx resulting in a decrease in photosynthetic activity and carbon partitioning [65] and a decrease in plant productivity and agricultural yield. It has been demonstrated that AMF improves plant performance in drought stress [66]. Table 1 shows the different effects of AMF on plants' drought tolerance. Mycorrhizal plants deal with water deficit through drought mitigation and drought tolerance [67]. A drought mitigation strategy is mediated by indirect AMF benefits and enhanced water uptake, whereas drought tolerance includes a combination of direct AMF benefits that improve the plant's innate ability to cope with the stress [11].

Through drought mitigation, the improvement of plant fitness by AMF is possibly due to the increased surface area for water absorption provided by AMF hyphae [68], increased access to small soil pores, or improved apoplastic water flow. Numerous studies have related the mechanisms of drought mitigation [69–72]. It has been shown by [73] that in field-grown tomato plants, root colonization by the AMF *R. intraradices* enabled plants to grow well under water stress conditions through an improvement of nutrient contents and water use efficiency. These beneficial effects of AMF on tomato tolerance to water stress have also been reported in several other plant species such as *Lactuca sativa* L. [74], *Triticum aestivum* L. [75], *Lavandula spica* L. [76], *Allium cepa* L. [77], *Trifolium repens* L. [78], *Pistacia vera* L. [79], *Acacia auriculiformis* A.Cunn. ex Benth, *Albizia lebbek* (L.) Benth., *Gliricidia sepium* (Jacq.) Kunth ex Walp. And *Leucaena leucocephala* (Lam.) de Wit [80].

Other mechanisms are involved in plant response to drought stress, among them, the production of phytohormones. Hormone homeostasis regulates plant tolerance against abiotic stresses. Abscisic acid (ABA) is the most fundamental stress hormonal signal, modulating transpiration rate, root hydraulic conductivity, and aquaporin expression. ABA responses regulate stomatal conductance and other related physiological processes [81]. ABA induces stomatal closure and reduces cell water loss. Inoculation with AMF influences the control of stomata functioning by the regulation of abscisic acid [81,82]. A lower ABA concentration was found in roots and leaves of mycorrhizal plants versus nonmycorrhizal plants under drought stress [10,71,72]. It has been also demonstrated that Jasmonic acid (JA) interacts with abscisic acid to regulate plant responses to water stress conditions [82]. JA can mitigate water stress in plants [83]. This hormone is involved in the regulation of the expression and the abundance of aquaporins and plays an important role in water uptake and transport, on stomate and root hydraulic conductance.

Other mechanisms are involved in plant tolerance to drought. Among these mechanisms, the osmotic adjustment that allows plants to maintain their turgor and physiological activity [11] by accumulating compatible solute compounds such as sugars, proline, glycine betaine, polyamines, and organic acids such as oxalate and malate. As described in saline conditions, drought stress induces the production of reactive oxygen species (ROS) [84].

Other phytohormones, such as strigolactone and auxin, are involved in plant water stress regulation [85]. It has been demonstrated that the inoculation with AMF strengthens strigolactone and auxin responses to drought stress [74].

**Table 1.** Contribution of AMF in helping plants to cope with drought stress.

| Host Plants   | AMF Strains  | Responses Related to AMF Inoculation  | References |
|---|--|---|------------|
| <i>Zea mays</i> L.<br><i>Solanum lycopersicum</i> L.  | <i>Rhizophagus irregularis</i><br>(Błaszk., Wubet, Renker<br>& Buscot) C. Walker & A.<br>Schüßler 2010         | Enhanced apoplastic water flow  | [69]       |
| <i>S. lycopersicum</i> L.                             | <i>F. mosseae</i><br><i>R. irregularis</i>   | Increased plant height and biomass, intrinsic water use efficiency (iWUE) index, stomatal density, capacity to absorb CO <sub>2</sub> and proline concentrations, and reduced hydrogen peroxide, leaf and root ABA contents   | [71]       |
| <i>Lycopersicon. esculentum</i><br>L.                 | <i>Glomus clarum</i> T.H.<br>Nicolson & N.C. Schenck<br>1979   | Improved leaf area, dry mass, stomatal conductance, photosynthetic activity, and root hydraulic conductivity  | [72]       |
| <i>L. esculatum</i> L.                                | <i>R. irregularis</i>  | Increased plant height, number of primary branches, flowers, and fruits, shoot and root dry matter, N and P contents, fruit yields, leaf relative water content (RWC), water use efficiency (WUE) and quality of fruits (less acidity and quantities of ascorbic acid and total soluble solids) | [73]       |
| <i>S. lycopersicum</i><br><i>Lactuca sativa</i> Linn. | <i>R. irregularis</i>  | Improved shoot dry weight, stomatal conductance, photosystem II efficiency, ABA and strigolactone contents  | [74]       |
| <i>Triticum aestivum</i> L.                           | <i>R. fasciculatus</i><br><i>F. mosseae</i>  | Enhanced stomatal conductance and leaf osmotic adjustment   | [75]       |
| <i>Lavandula spica</i> L.                             | <i>R. irregularis</i><br><i>F. mossea</i>  | Increased biomass, N, K and water contents, and reduced antioxidant compounds (glutathione, ascorbate and H <sub>2</sub> O <sub>2</sub> )   | [76]       |
| <i>Allium cepa</i> L.                                 | <i>Glomus etunicatus</i> W.N.<br>Becker & Gerd. 1977   | Improved fresh and dry weights and phosphorus nutrition   | [77]       |
| <i>Trifolium repens</i> L.                            | <i>R. irregularis</i>  | Enhanced dry weight, nutrients content (P, K, Ca, Mg, Zn and B), relative water content, proline concentrations, and glutathione reductase activity   | [78]       |
| <i>Pistacia vera</i> L.                               | <i>G. etunicatum</i>   | Increased shoot and root weights, leaf area, total chlorophyll, and flavonoids contents, nutrient concentrations (P, N, K, Ca, Fe, Zn, and Cu), soluble sugar, proline, and soluble proteins contents, CAT and POD activities   | [79]       |
| <i>L. esculatum</i> L.<br><i>Capsicum annuum</i> L.   | <i>Rhizophagus irregularis</i><br><i>Rhizophagus fasciculatus</i><br>(Thaxt.) C. Walker & A.<br>Schüßler, 2010 | Improved biomass, root length, shoot length, and chlorophyll contents, and reduced proline concentration  | [86]       |

### 3.2. AMF and Plant Flooding Tolerance

Some AMF can also face other constraints, such as flooding [87]. In wetland ecosystems, [88] found a higher diversity of the communities of AMF. In these conditions, AMF could greatly improve the growth of plants through enhanced absorption of nutrient elements [89] (Table 2). These authors found that a considerable amount of P was transported to rice plants via the mycorrhizal pathway under wetland conditions. Results obtained by [90] indicate that AMF may assist *Phragmites australis* (Cav.) Trin. ex Steud. in coping with a medium frequency of drying-rewetting cycles. Similar results were found by [91], who showed the contributions to the flood tolerance of *Pterocarpus officinalis* Jacq. seedlings by improving plant growth and P acquisition in leaves. It has been demonstrated by [92], that the better growth of plants with mycorrhiza on flooding condition is linked to the improvement of osmotic adjustment. Since AMF needs oxygen to thrive, flooding may inhibit AMF colonization, and accordingly previous studies have found a decrease in the degree of AMF colonization with flooding along wetland gradients [92]. Furthermore, results obtained by [93] have indicated that

the distribution of AMF in tropical low flooding forest is related to the characteristics of vegetation, chemical parameters of the soil and identity of the AMF.

**Table 2.** Contribution of AMF in helping plants to cope with flooding stress.

| Host Plants   | AMF Strains   | Responses Related to AMF Inoculation                                | References |
|---|---|---|------------|
| <i>Panicum hemitomon</i> Schult. Schultes<br><i>Leersia hexandra</i> Schwartz | <i>Acaulospora trappei</i> R.N. Ames & Linderman 1976, <i>Scutellospora heterogama</i> , <i>Acaulospora laevis</i> Gerd. & Trappe 1974, <i>Glomus leptotichum</i> N.C. Schenck & G.S. Sm 1982, <i>G. etunicatum</i> and <i>Glomus gerdemannii</i> S.L. Rose, B.A. Daniels & Trappe 1979 | Improve phosphorus (P) nutrition<br>Greater tissue P concentrations | [19]       |
| <i>Pterocarpus officinalis</i> (Jacq.)  | <i>Glomus intraradices</i>  | Improve plant growth and P acquisition in leaves                    | [91]       |
| <i>Aster tripolium</i> L.   | <i>Glomus geosporum</i> T.H. Nicolson & Gerd.) C. Walker 1982   | Higher concentrations of soluble sugars and proline                 | [93]       |

### 3.3. AMF and Plant Tolerance to Extreme Temperatures

Temperature is one of the most important environmental stresses that can negatively affect the growth and productivity of plants [94]. It is well known that AMF improves plant performance to tolerate temperature (heat and cold) [95] stress by enhancing water and nutrient uptake, improving photosynthetic capacity and efficiency, protecting plants against oxidative damage, and increasing the accumulation of osmolytes [96] (Table 3). At low or high temperatures, it was reported that shoot and dry root weights of mycorrhizal plants were higher than non-mycorrhized plants [97]. At high temperature, AMF help plants to develop their root system for absorption of water to ensure high photosynthetic capacity and to prevent the photosynthetic apparatus from being damaged [98]. Regarding cold stress, [99] showed that *G. versiforme* was often more effective than *R. irregularis* for the alleviation of low-temperature stress in the winter and the spring cultivars, whereas *R. irregularis* was more effective in increasing the survival rate. For these authors, the response to cold stress depends on the AMF strains. At low-temperature conditions, the inoculation of Barley (*Hordeum vulgare* L.) with AMF resulted in improved growth, photosynthesis, osmotic homeostasis and potassium uptake [99]. However, extremely low and high temperatures reduced AMF fungal growth inhibited the formation of the extra radical hyphal network and AMF fungal activity. AMF may, therefore, play a key role in the mitigation of climate change [100], such as tolerance to a wider range of temperatures. AMF also improves the reduction of N<sub>2</sub>O emissions by enhancing N uptake and assimilation by plants. Consequently, as a result, the soluble N in the soil decreases and it can negatively affect the denitrification process [100,101]. However, seasonal and climate changes, including temperature fluctuations, can affect the temporal structuring of AMF communities [102].

**Table 3.** Contribution of AMF in helping plants to cope with extreme temperatures stress.

| Host Plants                    | AMF Strains  | Responses Related to AMF Inoculation  | References |
|--------------------------------|--|---|------------|
| <i>Cucumis sativus</i> L.      | <i>R. irregularis</i>                                  | Increases the photosynthetic efficiency of cold-stressed cucumber seedlings by protecting their photosynthetic apparatus against light-induced damage and increasing their carbon sink. | [51]       |
| <i>Zea mays</i> L.             | <i>Funneliformis</i> ( <i>Glomus</i> ) <i>species.</i> | Regulated photosystem (PS) II heterogeneity   | [98]       |
| <i>Hordeum vulgare</i> L.      | <i>G. versiforme</i><br><i>R. irregularis</i>          | Increasing the survival rate, alleviation of low-temperature stress   | [99]       |
| <i>Cyclamen persicum</i> Mill. | <i>R. fasciculatum</i>                                 | Enhanced biomass production and heat stress response<br>Increase activity of antioxidative enzymes such as superoxide dismutase and ascorbate peroxidase                                | [103]      |
| <i>Elymus nutans</i> Griseb.   | <i>F. mosseae</i>                                      | Less oxidative damage<br>Promoted plant growth and enhanced the level of chlorophyll and antioxidant compounds such as glutathione and soluble sugars                                   | [104]      |

### 3.4. AMF and Plant Tolerance to Salinity

AMF have been known to occur naturally in saline environments [105,106]. Their contribution to the improvement of the growth of several plant species under saline conditions is well known [107,108] (Table 4). This is mainly related to a combination of biochemical, physiological, and nutritional effects [97,109–116]. Among the mechanisms involved in salinity tolerance in AMF inoculated plants, we have the enhancement of water absorption capacity and nutrient uptake, the accumulation of osmoregulators like proline and sugars [105], the ionic homeostasis [87,117], and the reduction in  $\text{Na}^+$  and  $\text{Cl}^-$  uptake [118]. In addition, it has been demonstrated that AMF colonization improves stomatal conductance and reduces the oxidative damage in plants exposed to salinity [112,119,120]. For example, inoculation with *F. mosseae* of tomato plants irrigated with saline water significantly increased plant biomass, fruit fresh yield, and shoot contents of P, K, Cu, Fe, and Zn [121]. In another study, plant root colonization with this same AMF decreased Na concentration and enhanced the activity of various enzymes related to the mitigation of salt stress [97]. Similar results were reported for cereals such as wheat [112] and maize [119]. Under salt-stressed conditions, [116] showed that AMF inoculation significantly reduced the oxidative damage in wheat plants. They also reported higher gas exchange capacity, stomatal conductance, and concentrations of sugars, free amino acids, proline, and glycinebetaine in plants colonized by AMF [116]. *Zea mays* plants inoculated separately with three native AMF showed better biomass production and higher shoot potassium and proline contents, as compared to non-mycorrhizal plants [119]. It has also been demonstrated that AMF alleviates the deleterious effects of salt on plants growth in *Acacia* species [109,122,123]. This is mainly related to greater nutrient acquisition, total chlorophylls, carbohydrates, and proline contents elevated K/Na ratios in root and shoot tissues, and changes in root morphology [109,124] in mycorrhizal plants as compared nonmycorrhizal plants. These results were more significant when salt-stressed plants were co-inoculated with selected rhizobium strains, ectomycorrhizal fungi and/or endophytic bacteria, in addition to AMF [86,123,125]. Nevertheless, it should be mentioned that in studies where different strains were tested, the extent of AMF response on plant growth as well as root colonization varied with fungal species, and with the level of salinity [126]. These authors found that AMF differ in their

effects on *Chrysanthemum morifolium* Ramat. plants under saline conditions and *Diversispora versiformis* (P. Karst.) was the most active than *F. mosseae*. Regarding ions homeostasis, AMF improve ionic balance by filtering effect of AMF structures both in the soil and in the root that prevents the entry of toxic Na<sup>+</sup> ions [107,124].

**Table 4.** Contribution of AMF in helping plants to cope with salinity stress.

| Host Plants   | AMF Strains   | Responses Related to AMF Inoculation   | References |
|---|---|--|------------|
| <i>Lycopersicon esculentum</i> L.                     | <i>F. mosseae</i>   | Increased plant growth, fruit weight, and yield, chlorophyll content, concentrations of P and K, antioxidant enzymes activities (SOD, CAT, POD, and APX), and reduced Na concentration in leaves   | [97]       |
| <i>Capsicum annuum</i> L.                             | <i>R. irregularis</i>   | Increased leaf area, mineral content, proline, sugars, and cell membrane integrity, and reduced shoot content of Na  | [106]      |
| <i>Acacia auriculiformis</i> A. Cunn. ex Benth.       | <i>R. fasciculatus</i><br><i>Glomus macrocarpum</i> Tul. & C. Tul. 1845   | Increased root and shoot weights, and greater nutrient acquisition, changes in root morphology, and electrical conductivity of the soil  | [109]      |
| <i>Solanum lycopersicum</i> L.                        | <i>R. irregularis</i>   | Enhanced shoot and root dry weights, chlorophyll and proline concentrations, nutrient uptake (P, Ca, and K), stomatal conductance, the activity of ROS scavenging enzymes (APX, CAT, POD, and SOD) and protecting photochemical processes of PSII  | [111]      |
| <i>Triticum aestivum</i> L.                           | <i>G. etunicatum</i><br><i>F. mosseae</i> <i>R. irregularis</i>   | Increased plant growth, nutrient uptake and grain yield, and reduced concentrations of Na <sup>+</sup> and Cl <sup>-</sup>   | [112]      |
| <i>Zea mays</i> L.                                    | <i>R. irregularis</i> (isolate EEZ 58)<br><i>R. irregularis</i> (Ri CdG)<br><i>S. constrictum</i> (Trappe) Sieverd., G.A. Silva & Oehl 2011 (Sc CdG)<br><i>Claroideoglomus etunicatum</i> (W.N. Becker & Gerd.) C. Walker & A. Schüßler, 2010 (Ce CdG) (Ce CdG) | Improved K <sup>+</sup> and Na <sup>+</sup> homeostasis, shoot and root dry weights, K concentration in shoots, and reduced Cl and Na contents in shoots   | [119]      |
| <i>Digitaria eriantha</i> Steud.                      | <i>R. irregularis</i>   | Increased stomatal conductance, antioxidant enzymes activities (CAT et APX), jasmonate content, and reduced root and shoot hydrogen peroxide accumulation  | [120]      |
| <i>Lycopersicon esculentum</i> Mill. Cv. Marriha      | <i>F. mosseae</i>   | Improved plant biomass, fruit fresh yield and shoot contents of P, K, Cu, Fe and Zn, and reduced shoot Na concentrations   | [121]      |
| <i>Acacia nilotica</i> Willd.                         | <i>R. fasciculatum</i>  | Improved root and shoot biomass, and nutrient concentrations (P, Zn, K, and Cu), and Na concentration  | [122]      |
| <i>Acacia saligna</i> (Labill.) H.L. Wendl.           | AMF   | Improved plant growth and dry weight, nodulation parameters, chlorophylls, carbohydrates, proline and nutrient contents (N, P, K and Ca) and reduced Na concentrations   | [123]      |
| <i>Acacia auriculiformis</i><br><i>Acacia mangium</i> | <i>R. irregularis</i>   | Enhanced plant growth and nodulation, and nutrient contents (P, N)   | [125]      |
| <i>Gossypium arboreum</i> L.                          | <i>F. mosseae</i> (isolate GM1)<br><i>F. mosseae</i> (isolate GM2)  | Increased biomass and phosphorus concentrations  | [127]      |
| <i>Cucumis sativus</i> L.                             | <i>C. etunicatum</i><br><i>R. irregularis</i><br><i>F. mosseae</i>  | Enhancing the biomass, synthesis of pigments, activity of antioxidant enzymes, including superoxide dismutase, catalase, ascorbate peroxidase, and glutathione reductase, and the content of ascorbic acid<br>Enhancing jasmonic acid, salicylic acid and several important mineral elements (K, Ca, Mg, Zn, Fe, Mn, and Cu)<br>Reducing the uptake of deleterious ions like Na <sup>+</sup> | [128]      |



Table 4. Cont.

| Host Plants                   | AMF Strains  | Responses Related to AMF Inoculation   | References |
|-------------------------------|--|--|------------|
| <i>Glycine max</i> L. Merrill | <i>C. etunicatum</i><br><i>R. irregularis</i><br><i>F. mosseae</i> | Protected soybean genotypes from salt-induced membrane damage<br>Reduced the production of hydrogen peroxide and lipid peroxidation<br>Improved plant growth and symbiotic performance by stimulating the endogenous level of auxins that contribute to improved root systems and nutrient acquisition under salt stress | [129]      |

### 3.5. AMF and Plant Tolerance to Heavy Metals

Mining sites and polluted sites with heavy metal contain AMF that are specifically adapted to soil pollution by heavy metals [130,131].

Numerous studies showed that more than 80% of surveyed plants growing on mining sites are colonized by AMF, and a great number of AMF species and a large AMF diversity exist in various mining-impacted sites [131]. These authors summarized studies that showed that AMF exhibit significant positive effects, such as increased plant survival, enhanced growth and nutrition, improved soil structure and quality, and greater plant re-establishment.

Several studies revealed that mycorrhiza could be used as a stress-reducing agent in soils contaminated by heavy metals helping plants to survive in such stressed conditions [24,41,86,132–135] (Table 5). Heavy metal remediation by AMF can happen through hyphal “metal binding”, which reduces the bioavailability of elements, such as Cu, Pb, Co, Cd, and Zn [136]. The alleviation of heavy metal toxicity by AMF depends on the fungal partner, plant growth conditions, the type of heavy metal, and its concentration [130]. Inoculation with AMF showed the best results in terms of percentage of seed germination, the sustainability of seedlings, fresh weight, and dry weight of plants. In two different heavy metal-polluted soils, root colonization of maize plants with *Glomus* isolates reduced heavy metal concentrations in shoots and roots, and increased the contents of essential elements like K, P, and Mg in roots [133]. This result was more significant in maize plants colonized with the *Glomus* isolate Br1 from *Viola calaminaria* (DC.) Lej. (zinc violet) compared with plants grown with a common *Glomus* strain or to non-colonized controls. These authors also reported distinct differences in the cellular distribution of heavy metals and essential elements in mycorrhiza compared with the non-colonized control roots, suggesting that AMF might cope with heavy metal toxicity for each metal individually [133]. When maize was grown in soil contaminated with Cd, AMF inoculation significantly increased growth and reduced Cd uptake, suggesting that AMF can be used in association with plants for the mitigation of heavy metal such as Cd in soils [137]. AMF expressed some metal transporters that play a crucial role in heavy metal regulation. In recent years, several Zn transporters were identified in AMF, such as *GintZnT1* from *R. irregularis* [138]. Several putative genes coding for Cu, Fe, and Zn transporters have been also identified [139]. These transporters could be involved in heavy metal tolerance in plants inoculated by AMF.

Table 5. Contribution of AMF in helping plants to cope with heavy metals stress.

| Host Plants                         | AMF Strains                                    | Responses Related to AMF Inoculation  | References |
|-------------------------------------|--|---|------------|
| <i>Trigonella foenum-graceum</i> L. | <i>F. mosseae</i>                              | Better plant performance  | [132]      |
| <i>Zea mays</i> L.                  | <i>Glomus</i> isolates                         | Improved dry weight and contents of essential elements (K, P, and Mg), and distinct differences in the cellular distribution of heavy metals and essential elements | [133]      |
| <i>Lonicera japonica</i> Thunb.     | <i>G. versiforme</i> R.<br><i>intraradices</i> | Decreased Cd concentrations in shoots and roots,<br>Reduced Cd concentrations in shoots but increased Cd concentrations in roots                                    | [140]      |

Table 5. Cont.

| Host Plants  | AMF Strains  | Responses Related to AMF Inoculation   | References |
|--|--|--|------------|
| <i>Solanum lycopersicum</i> L.                                       | <i>F. mosseae</i> (syn. <i>Glomus mosseae</i> ),<br><i>R. intraradices</i> (syn. <i>Glomus intraradices</i> )<br><i>C. etunicatum</i> (syn. <i>Glomus etunicatum</i> ) | AMF reduced the production of malonaldehyde and hydrogen peroxide by mitigating oxidative stress. AMF strengthened the plant's defense system and provide efficient protection against Cd stress | [141]      |
| <i>Populus alba</i> Villafranca<br><i>Populus nigra</i> Jean Pourtet | <i>F. mosseae</i> or <i>R. irregularis</i>   | Alleviation of Cu and Zn phytotoxicity   | [142]      |
| <i>Trifolium pratense</i> L.   | <i>Glomus mosseae</i>  | Decreases in Zn uptake and in root and shoot concentrations  | [143]      |

#### 4. Role of AM Fungi in Alleviation of Biotic Stresses in Plants

The role of microsymbionts in the management of biotic stresses is gaining importance. Numerous studies have proven that AMF reduces the damage caused by various plant pathogens [144–146] (Table 6). For example, studies carried out by [147] demonstrate that the severity of charcoal root-rot disease in soybean can be reduced by AMF inoculation. In the presence of *Fusarium*, arbuscular colonization increased shoot dry weight [144]. Colonization by AMF has a protective effect termed mycorrhiza-induced resistance (MIR) [146,148,149], which provides systemic protection against a wide range of attackers and shares characteristics with systemic acquired resistance (SAR) after pathogen infection and induced systemic resistance (ISR) following root colonization by non-pathogenic rhizobacteria [150]. This mycorrhiza-induced resistance to diseases was described by [150]. These authors showed that AMF increases the production of antioxidant enzymes in plants, which can act as a defense against pathogens and other stresses. In addition to the activation of plant defense mechanisms, several other reasons for reduced damage of pathogens by AMF have been reported such as improved nutrient status of the host plant, change in root growth and morphology, competition for colonization sites and host photosynthates, and microbial changes in the mycorrhizosphere [144,151,152]. The improvement of plant growth may have a positive effect because mycorrhizae can facilitate the regrowth of tissues after attacks. However, it may have negative effects because as plant nutrition improves, it becomes more nutritive or attractive to herbivore insects [153]. The contribution of AMF in the protection of plants against pathogenic fungi and nematodes is well documented. Although, it should be mentioned that the effectiveness of the interactions varies depending on the host plant and the cultural system [5]. The colonization of tomato roots by *F. mosseae* induced systemic resistance against both the sedentary nematode *Meloidogyne incognita* (Kofoid & White, 1919) and the migratory nematode *Pratylenchus penetrans* (Cobb, 1917) Filipjev & Schuurmans Stekhoven, 1941 [144]. The presence of this AMF reduced nematode infection by 45% and 87% for *M. incognita* and *P. penetrans*, respectively, in AMF-colonized plants as compared to controls. Further studies carried out on root exudates have shown that the reduction of nematode infection in mycorrhizal plants is probably related to an alteration of their root exudates by AMF [154]. Indeed, the application of mycorrhizal root exudates further reduced nematode penetration in mycorrhizal plants and temporarily paralyzed nematodes, in comparison with the application of water or non-mycorrhizal root exudates. Root colonization by *F. mosseae* caused also a reduction in galling, nematode reproduction and morphometric parameters of females in tomato plants inoculated with *Meloidogyne javanica* (Treub, 1885) [151]. Regarding pathogenic fungi, mycorrhizal inoculation with *F. mosseae* significantly alleviated tomato diseases caused by *Alternaria solani* (Ellis & G. Martin) L.R. Jones & Grout 1896 and *Fusarium oxysporum* *Fusarium oxysporum* Schltdl. 1824, respectively [155–157]. This beneficial effect was more pronounced when plants were inoculated with AMF and sprayed with hormonal inducers (Jasmonic acid and Salicylic acid), suggesting a synergistic and cooperative effect between them leading to an enhanced induction and regulation of disease resistance [156]. These beneficial effects of AMF have also been reported in potato [158] and chickpea [152] infected with pathogens.

In contrast to the well-known effect on pathogenic nematodes and fungi, there are relatively few studies on the impact of AMF on herbivore insects [159,160]. The meta-analysis conducted by [159] on the published and unpublished studies on this topic revealed that the effects of mycorrhizal fungi on herbivore insects varied depending on the parameter measured and the degree of herbivore feeding specialization. Some AMF like *R. intraradices* tended to have a negative effect on chewer performance, as opposite to other fungal species studied [159]. For example, in *Plantago lanceolata* L., mycorrhizal infection increased the resistance of leaves to the chewing insect *Arctia caja* (Linnaeus, 1758), while the performance of the sucking insect *Mysus persicae* (Sulzer) was greater on mycorrhizal plants [161]. It has been shown by [160] that parasitism of *Chromatomyia syngenesiae* by *Diglyphus isaea* (Walker, 1838) was lower on mycorrhizal plants, while in the laboratory the effects of three species of AMF on parasitism rates were dependent on the species of AMF [160].

Among biotic constraints that mostly affect productivity in developing countries is the African witchweed *Striga* (hereafter, referred to as “*Striga*”), mainly in sub-Saharan Africa. This parasitic plant is a socioeconomic problem that has forced many poor farmers to abandon their farms due to high infestation rates [162]. Soil microorganisms including AMF can inhibit or suppress *Striga* germination [163]. AMF can affect the interaction between *Striga* and cereals [164]. These authors showed that AMF negatively impacted *Striga* seed germination, reduced the number of *Striga* seedlings attaching and emerging, and delayed the emergence time of *Striga*. Studies carried out by [165] confirmed the effectiveness of AMF in protecting sugarcane against *Striga* infestation as well as promoting crop growth and reducing the soil *Striga* seed bank. By doing so, AMF enhanced the performance of the plant host, allowing it to better withstand *Striga* damage [164].

**Table 6.** Contribution of AMF in helping plants to cope with several biotic stresses.

| Host Plants                                   | Disease or Pathogen  | AMF Strains  | Responses Related to AMF Inoculation   | References |
|---|--|--|--|------------|
| <i>Solanum lycopersicum</i> L.                | <i>M. incognita</i>  | <i>F. mosseae</i>  | Induced systemic resistance against both the sedentary nematode <i>Meloidogyne incognita</i> and the migratory nematode <i>Pratylenchus penetrans</i>  | [144]      |
| <i>L. esculentum</i>                          | <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>                | <i>Glomus</i> sp.  | Production of antimicrobial compounds from the mycorrhizal root that arrested the mycelial growth of the fungal pathogen<br>Reduced the disease incidence<br>Increased the plant growth, dry weight, N, P, K content, chlorophyll content and yield of the plant | [145]      |
| <i>Glycine max</i> (L.) Merr.                 | <i>Macrophomina phaseolina</i> (Tassi) Goid 1947                   | <i>R. irregularis</i>  | Improve plant height and the number of functional leaves   | [147]      |
| <i>Solanum lycopersicum</i> L.                | <i>M. javanica</i>   | <i>F. mosseae</i>  | Caused also a reduction in galling, nematode reproduction and morphometric parameters of females in tomato plants inoculated with  | [151]      |
|   | <i>Alternaria solani</i> Sorauer 1896<br><i>Fusarium oxysporum</i> | <i>F. mosseae</i>  | Alleviated tomato diseases   | [155,156]  |
| <i>Saccharum officinarum</i> L.               | <i>Striga hermonthica</i> Del Benth 1836                           | <i>G. etunicatum</i> ,<br><i>Scutellospora fulgida</i> Koske & C. Walker 1986, <i>G. margarita</i> | Stimulated plant growth, plant biomass and physiological parameters of plants in the presence of <i>Striga</i>   | [165]      |
| <i>Solanum lycopersicum</i> L.                | <i>Cladosporium fulvum</i> Cooke 1883                              | <i>F. mosseae</i>  | Higher resistance against subsequent pathogen infection<br>higher fresh and dry weight<br>increases in total chlorophyll contents and net photosynthesis rate  | [166]      |
| <i>Astragalus adsurgens</i> var. Shanxi Yulin | <i>Erysiphe pisi</i> DC 1805                                       | <i>C. etunicatum</i> , <i>G. versiforme</i> ,<br><i>F. mosseae</i>                                 | Increased the shoot and root growth of standing milkvetch even though their presence in the roots increased susceptibility to powdery mildew.  | [167]      |

Table 6. Cont.

| Host Plants   | Disease or Pathogen  | AMF Strains   | Responses Related to AMF Inoculation   | References |
|---|--|---|--|------------|
| <i>Capsicum annum</i>                                 | <i>Pythium aphanidermatum</i> (Edson) Fitzp 1923   | <i>Glomus sp.</i>   | Mycelial growth of the fungal pathogen reduced the disease incidence and increased the growth and yield of crop plants | [168]      |
| <i>Cicer arietinum</i> L.                             | <i>Fusarium wilt</i>   | <i>Glomus hoi</i> S.M. Berch & Trappe 1985, <i>R. fasciculatum</i>  | Increased total contents of P and N in treated plants  | [169]      |
| <i>Cucumis melo</i> L.                                | <i>Fusarium wilt</i>   | <i>F. mosseae</i>   | Greatest capacity for reduction of disease incidence   | [170]      |
| <i>Arachis hypogaea</i> L.                            | <i>Sclerotium rolfsii</i> Sacc 1911  | <i>R. fasciculatum</i> , <i>Gigaspora margarita</i> , <i>Cucumis melo</i> L., <i>A. laevis</i> , and <i>Sclerocystis dussii</i> (Pat.) Höhn. 1910 | Eliminated the damaging effects of <i>S. rolfsii</i>   | [171]      |
| <i>Solanum melongena</i> L. <i>Cucumis sativus</i> L. | <i>Verticillium dahliae</i> Kleb 1913<br><i>Pseudomonas lacrymans</i> (Smith and Bryan) Carsner 1970 | <i>G. versiforme</i>  | Alleviated wilt symptoms caused by <i>V. dahliae</i>   | [172]      |
| <i>S. tuberosum</i>                                   | Potato virus Y (PVY)   | <i>R. irregularis</i>   | Milder symptoms and significant stimulation of shoot growth were observed in PVY-infected plants inoculated            | [173]      |
| <i>Nicotiana tabacum</i> L.                           | Tobacco mosaic virus (TMV) <i>Cucumber green mottle mosaic virus</i> (CGMMV)                         | <i>R. irregularis</i>   | Showed reduced disease symptoms and virus titer if compared to non-mycorrhizal plants                                  | [174]      |
| <i>Zea mays</i> L.                                    | <i>Striga hermonthica</i> Del Benth 1836   | <i>G. etunicatum</i> , <i>Scutellospora fulgida</i> Koske & C. Walker 1986, <i>G. margarita</i>   | Reduced <i>Striga</i> plant incidence, plant biomass, and phosphate content  | [175]      |
| <i>Sorghum bicolor</i> (L.) Moench                    | <i>S. hermonthica</i>  | <i>F. mosseae</i>   | Improved the performance of sorghum  | [176]      |

## 5. Interaction between AMF and Other Beneficial Soil Microorganisms

AMF interacts with a wide assortment of soil microorganisms [177–179]. Interactions can be either positive, neutral, or negative on the mycorrhizal association or on other microorganisms in the rhizosphere [180–183]. They may be involved in nutrient acquisition, biological control of root pathogens, improvement of plant tolerance to abiotic stress and soil quality [184].

### 5.1. Interaction between AMF and Nitrogen Fixing Bacteria

#### 5.1.1. Interaction between AMF and Rhizobia

AMF and nitrogen-fixing bacteria provide plants with essential soil nutrients, and the expectation is that co-inoculation will result in the strongest synergistic effects. Several experiments have demonstrated a positive effect of the interactions between AMF and nodulating rhizobial bacteria [185]. Numerous studies showed a beneficial effect of the interaction between AMF and Rhizobia in legumes such as *Amorpha canescens* Nutt., *Lens culinaris* Medik. [186,187], *Glycine max* [188,189], *Pisum sativum* L. [190], *Vicia faba* L. [191] and *Lathyrus sativus* L. [192]. These interactions can induce changes in the microbial environment through their secretions [193]. It has been demonstrated by [193] that the dual inoculation with Rhizobium and AMF is more effective for promoting the growth of Faba bean in alkaline soils than the individual treatment. The dual inoculation of AMF and nitrogen-fixing bacteria increased nodulation, nitrogen fixation, plant growth and yield. Co-inoculation with selected AMF and rhizobia also improved outplanting performance, plant survival, and biomass development of woody

legumes in desertified ecosystems [194]. This is in accordance with the strong synergistic effects of AMF and rhizobia inoculation found on the biomass production of *Atriplex canescens* (Pursh) Nutt. [186]. However, these interactions were contingent on several factors, like the amounts of phosphorus and nitrogen available [186]. Similar results were obtained by [188], which showed a synergistic relationship dependent on N and P status between rhizobia and AM fungi on soybean growth.

### 5.1.2. Interaction between AMF and Frankia

As was observed in legumes, the synergistic effects of AMF and the nitrogen fixing actinobacteria Frankia improve actinorhizal plants performance in various environments [195–201]. In *Casuarina cunninghamiana* Miq. and *C. equisetifolia* L., dual inoculation with a mycorrhizal fungus and a Frankia isolate significantly increased the height of seedlings and trees, depending on the levels of available phosphorus [199]. Regarding the impact on nitrogen levels, [200] studies on the natural abundance of  $^{15}\text{N}$  in four species of *Casuarina* revealed that the interactions between Frankia and AMF were species-dependent and is also influenced by the availability of P and N. This is in accordance with [198] studies which showed that AMF plus Frankia had no effect in wood volume growth of *C. cunninghamiana*, while this parameter was favored by fertilization with N. Interactions between AMF and Frankia have been well studied in the pioneer species, *Alnus glutinosa* L. Gaertn. [195–197]. In a highly alkaline anthropogenic sediment, dual inoculation of Black alder plants with *R. intraradices* and Frankia spp significantly increased leaf area, shoot height, total biomass, and N and P leaf contents when compared with the uninoculated control, the Frankia spp. and the *R. intraradices* treatments alone [197]. In addition, the numbers and dry weight of root nodules, as well as the development of the AM symbiosis were greater when dual inoculation was performed, suggesting a synergistic effect of these microsymbionts, which allowed *A. glutinosa* plants to grow under these hostile conditions. Although, it has been reported in this species that interactions between AMF and Frankia are not always positive [195]. Indeed, in a glasshouse experiments, early interactions between different AM species (*Glomus hoi*, *F. mosseae*, *Gigaspora rosea* T.H. Nicolson & N.C. Schenck 1979, *A. scrobiculata* and *Scutellospora castanea* C. Walker 1993) and Frankia lead to a depressive effect on plant biomass [195]. This effect resulting possibly from the competition with microsymbionts for resources such as photosynthates may only be temporary.

### 5.2. Interaction between AMF and Plant Growth Promoting Rhizobacteria

AMF also interact with the plant growth-promoting Rhizobacteria (PGPR) [202–205]. PGPR are soil and rhizosphere bacteria that can be of benefit to plant growth by several different mechanisms such as a symbiotic  $\text{N}_2$  fixation, ammonia production, solubilization of mineral phosphate, and other essential nutrients, production of plant hormones, and control of phytopathogenic microorganisms [206]. Under field conditions, dual inoculation of *Schizolobium parahyba* (Vell.) S.F. Blake, 1919 with AMF and PGPR increased wood yield by about 20% compared to the application of chemical fertilizers alone [199]. Inoculation of *Acacia gerrardii* Benth. with AMF and *Bacillus subtilis* Ehrenberg, 1835 Cohn, 1872 induced a significantly greater shoot and root dry weight, nodule number and leghemoglobin content than those inoculated with AMF or *B. subtilis* alone under salt stress [207]. These authors found a positive synergistic interaction between AMF and *B. subtilis* regarding nitrate and nitrite reductase and nitrogenase activities and the contents in total lipids, phenols, fiber, and osmoprotectants such as glycine, betaine, and proline [207]. AMF and phosphate solubilizing bacteria (PSB) could interact synergistically because PSB solubilizes sparingly available phosphorous compounds into orthophosphate that AMF can absorb and transport to the host plant [179].

Under drought stress, dual inoculation with AMF and PGPR allowed to alleviate water deficit damage and improve water stress tolerance in *Cupressus arizonica* Greene through a better accumulation of ascorbate peroxidase and glutathione peroxidase, in comparison to plants inoculated with a single microorganism [203]. Inoculation with AMF and PGPR also has a positive effect on plant

metabolism. [203] showed that co-inoculation of *Stevia rebaudiana* Bertoni) Bertoni, with AMF and PGPR enhanced significantly plant growth parameters, NPK, total chlorophyll, and stevioside contents.

### 5.3. Benefits of the Tripartite Symbiosis (AMF, Nitrogen Fixing Bacteria, PGPR, or Ectomycorrhizal Fungi)

The benefits of the tripartite symbiosis (AMF, nitrogen-fixing bacteria, PGPR, or ectomycorrhizal fungi) are also known [208–210]. As shown by [209], inoculation with a combination of AMF, Frankia, Azospirillum, and Phosphobacterium significantly increased the total height and total biomass of *C. equisetifolia* plants. The same authors measured an enhanced nutrient uptake for N, P, K, Ca, and Mg in triple inoculated plants. AMF can also co-exist with ectomycorrhizal fungi (EMF) and improves plant growth [208,211]. EMF and AMF plant colonization do not occur simultaneously. Generally, AMF is established first, followed by EMF, but less often, EMF establishes first then reduces AMF colonization by forming a mantle that acts as a barrier to AMF infection. However, when AMF is established first, it has no negative effects on EMF infection [211]. In different *Acacia crassicarpa* A. Cunn. ex Benth. provenances, combined EMF and AMF symbioses improved plant growth and the rhizobial nodulation process [208]. Similar results were obtained in *Robinia pseudoacacia* L. plants inoculated with a combination of EMF, AMF, and Rhizobium [212]. In *C. equisetifolia* plants, [213] observed that inoculation with both AMF and EMF significantly increased biomass and P content compared to plants inoculated with either AMF or EMF alone. Inoculation of *C. equisetifolia* with Frankia increased nitrogen fixation, ectomycorrhizal, and endomycorrhizal colonization [214]. However, an antagonistic effect was observed when both symbionts were inoculated and were generally the result of high ectomycorrhizal colonization [211].

### 5.4. Interaction between AMF and Mycorrhization Helper Bacteria

AMF interacts positively with Mycorrhization Helper Bacteria (MHB) [215–217]. Because of the beneficial effect of bacteria on mycorrhizae, the concept of Mycorrhization Helper Bacteria (MHB) was created. Five possible ways of action of MHB on mycorrhiza were proposed by [217]: in the receptivity of the root to the mycobiont, in root-fungus recognition, in fungal growth, in the modification of the rhizospheric soil, and in the germination of fungal propagules. These authors showed that MHB is fungus-specific but not plant-specific.

## 6. Conclusions

AMF play an important role in improving the adaptation to biotic and abiotic plant stresses and to alleviate the effects of these stress on plants. Their role in increasing plant growth and yield, disease resistance, biotic and abiotic tolerance provides an environmentally friendly solution to reduce the use of hazardous pesticides and industrial fertilizers. However, more research is needed to test in the field the results obtained in the laboratory and in the greenhouse. The application of this knowledge in real environments and according to biogeographical zones becomes essential in order to promote their industrial production for a large scale used and increase their impact to ensure enough food for every human being on the planet now and in the future. As an ecofriendly method, some work must be done by researchers, private and public sectors, to promote the use of AMF by increasing their production, particularly in developing countries where AMF inocula are not accessible and not affordable.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/12/10/370/s1>, Figure S1: The role of AMF on plant growth in stressed environment.

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