



Review

Unraveling the Interaction between Arbuscular Mycorrhizal Fungi and *Camellia* Plants

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Abstract: *Camellia* is a genus of evergreen shrubs or trees, such as *C. japonica*, *C. sinensis*, *C. oleifera*, etc. A group of beneficial soil microorganisms, arbuscular mycorrhizal fungi (AMF), inhabit the rhizosphere of these *Camellia* spp. A total of eight genera of *Acaulospora*, *Entrophospora*, *Funneliformis*, *Gigaspora*, *Glomus*, *Pacispora*, *Scutellospora*, and *Sclerocystis* were found to be associated with *Camellia* plants with *Glomus* and/or *Acaulospora* being most abundant. These mycorrhizal fungi can colonize the roots of *Camellia* spp. and thus form arbuscular mycorrhizal symbionts. AMF is an important partner of *Camellia* spp. in the field of physiological activities. Studies indicated that AMF inoculation has been shown to promote plant growth, improve nutrient acquisition and nutritional quality, and increase resistance to drought, salinity and heavy metal contamination in potted *Camellia*. This review thus provides a comprehensive overview of AMF species occurring in the rhizosphere of *Camellia* spp. and summarizes the variation in root AMF colonization rate as well as the environmental factors and soil nutrients affecting root colonization. The paper also reviews the effects of AMF on plant growth response, nutrient acquisition, food quality, and stress tolerance of *Camellia* spp.

Keywords: diversity; mycorrhizas; symbiosis; tea



Citation: Liu, R.-C.; Xiao, Z.-Y.; Hashem, A.; Abd_Allah, E.F.; Xu, Y.-J.; Wu, Q.-S. Unraveling the Interaction between Arbuscular Mycorrhizal Fungi and *Camellia* Plants. *Horticulturae* **2021**, *7*, 322. <https://doi.org/10.3390/horticulturae7090322>

Academic Editor: Stefano Ghignone

Received: 28 August 2021

Accepted: 14 September 2021

Published: 17 September 2021

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1. Introduction

Arbuscular mycorrhizal fungi (AMF) are widely found in various soils [1]. AMF colonize roots of about 80% of vascular plants and thus form arbuscular mycorrhizas in host roots [2]. AMF promote plant growth, increase mineral element absorption, and improve plant stress tolerance [3–5]. AMF absorb more water for the host through the extraradical hyphae [6,7], and also secrete glomalin into the soil (defined as glomalin-related soil protein) to cement soil aggregates and improve soil moisture-holding capacity and permeability [8]. In addition, AMF can mitigate the toxicity of heavy metals by competitive uptake of heavy metal ions from the soil [9,10], as well as improve the soil environment [3,4,11,12].

Camellia is a genus of evergreen shrubs or trees in the Camelliaceae family, which is mainly concentrated in eastern and southeastern Asia [13]. *Camellia* is mainly composed of *Camellia sinensis* (one of the three major beverages in the world), *C. oleifera* (an oil seed crop), and *C. japonica* with ornamental value. *C. sinensis* grows in acidic soil [14,15], where a certain amount of AMF communities are inhabited in their rhizosphere [16]. In natural fields, AMF colonization frequency and colonization rate of tea trees are 7.3–86.7% and 0.8–32.7%, respectively, with large variation among varieties [17]. AMF have an impact on

tea growth and nutrient absorption [18]. *C. oleifera* is a small evergreen tree and its seeds contain high-quality edible oils [19,20], along with abundant AMF communities in the rhizosphere [21]. *C. japonica* is an excellent tree species for urban and rural greening [22,23]. In this paper, we review the diversity AMF of *Camellia* plants and their impacts on plants, with a view to provide the reference for the screening of dominant AMF strains for their production and application.

2. AMF Diversity in Rhizosphere of *Camellia* spp.

2.1. Morphological Identification

AMF diversity of *Camellia* spp. has been reported, based on morphological identification (Table 1). Tunstall [24] first identified arbuscular mycorrhizas from the roots of *C. sinensis*. In India, Singh et al. [25] conducted morphological identification of AMF diversity in “natural” and “cultivated” tea trees in Uttarakhand Himalaya and found 51 AMF species belonging to four genera, including *Glomus*, *Gigaspora*, *Acaulospora* and *Scutellospora*, of which 21 species were identified, with *Glomus* as the dominant genus. Gupta and Sharma [26] isolated six AMF species from four tea districts of Dehradun based on their morphology, and three identified AMF species belonged to *Glomus*. Sharma et al. [27] identified *Acaulospora*, *Glomus*, and *Gigaspora* in four tea plantations in Dehradun Himalaya (India), with the dominant genera being *Glomus* and *Acaulospora*. In China, Lu and Wu [28] identified 12 AMF species in tea plantations in the southern region of Henan province, belonging to *Acaulospora*, *Glomus*, *Gigaspora*, and *Scutellospora*, of which the dominant genera are *Acaulospora* and *Glomus*. Wu et al. [29] isolated 22 AMF species of three genera in the tea of Qingdao, including 13 species of *Acaulospora*, 8 species of *Glomus* and 1 species of *Gigaspora*, and the relative abundance of *Glomus* and *Acaulospora* was higher than that of other genera. In ten regions of Guizhou with five tree varieties, Xing et al. [30] identified 31 species of AMF belonging to four genera, including 18 species of *Glomus*, 9 species of *Acaulospora*, 3 species of *Gigaspora* and 1 species of *Entrophospora*, with the dominant genera *Glomus* and *Acaulospora*. Due to the large geographical difference between China and India, the growth environment of tea is quite different, but the dominant genera of AMF in tea in the two countries are similar, both of which are *Glomus* and *Acaulospora*. AMF community in *C. oleifera* was studied by Chinese scholars only. In Hunan province, Deng et al. [31] identified eight AMF species, belonging to *Glomus*, *Acaulospora*, and *Scutellospora*, with *Glomus* as the dominant genus.

Table 1. AMF diversity of *Camellia* plants.

<i>Camellia</i> Plants	Sampling Regions	Identification Method	Identified Genena of AMF	Dominant Genus of AMF	Reference
<i>C. sinensis</i>	Uttaranchal Himalaya (India)	Morphology	<i>Acaulospora</i> ; <i>Gigaspora</i> ; <i>Glomus</i> ; <i>Scutellospora</i>	<i>Glomus</i>	[25]
	Dehradun District (India)	Morphology	<i>Glomus</i>	<i>Glomus</i>	[26]
	Dehradun Himalaya (India)	Morphology	<i>Acaulospora</i> ; <i>Glomus</i> ; <i>Gigaspora</i>	<i>Acaulospora</i> and <i>Glomus</i>	[27]
	Henan (China)	Morphology	<i>Acaulospora</i> ; <i>Gigaspora</i> ; <i>Glomus</i> ; <i>Scutellospora</i>	<i>Acaulospora</i> and <i>Glomus</i>	[28]
	Qingdao (China)	Morphology	<i>Acaulospra</i> ; <i>Gigaspora</i> ; <i>Glomus</i>	<i>Acaulospra</i> and <i>Glomus</i>	[29]
	Guizhou (China)	Morphology	<i>Acaulospora</i> ; <i>Entrophospora</i> ; <i>Gigaspora</i> ; <i>Glomus</i>	<i>Acaulospra</i> and <i>Glomus</i>	[30]
<i>C. oleifera</i>	Hunan (China)	Morphology	<i>Acaulospora</i> ; <i>Glomus</i> ; <i>Scutellospora</i>	<i>Glomus</i>	[31]
	Wuhan (China)	High-throughput sequencing of 18S rRNA gene	<i>Acaulospora</i> ; <i>Ambispora</i> ; <i>Archaeospora</i> ; <i>Claroideoglomus</i> ; <i>Diversispora</i> ; <i>Gigaspora</i> ; <i>Glomus</i> ; <i>Paraglomus</i> ; <i>Redeckera</i> ; <i>Scutellospora</i>	<i>Glomus</i>	[21]
	Jiangxi (China)	High-throughput sequencing of 18S rRNA gene	<i>Acaulospora</i> ; <i>Ambispora</i> ; <i>Archaeospora</i> ; <i>Claroideoglomus</i> ; <i>Diversispora</i> ; <i>Geosiphon</i> ; <i>Gigaspora</i> ; <i>Glomus</i> ; <i>Pacispora</i> ; <i>Paraglomus</i> ; <i>Scutellospora</i> ; <i>Septoglomus</i>	<i>Glomus</i>	[32]
	Guiyang (China)	High-throughput sequencing of 18S rRNA gene	<i>Acaulospora</i> ; <i>Archaeospora</i> ; <i>Claroideoglomus</i> ; <i>Diversispora</i> ; <i>Glomus</i> ; <i>Paraglomus</i>	<i>Glomus</i>	[33]
<i>C. japonica</i>	Fanjing Mountain (China)	Morphology	<i>Acaulospora</i> ; <i>Funneliformis</i> ; <i>Glomus</i> ; <i>Pacispora</i> ; <i>Scutellospora</i> ;	<i>Glomus</i>	[34]
	Chongqing (China)	Morphology	<i>Acaulospora</i> ; <i>Gigaspora</i> ; <i>Glomus</i> ; <i>Scutellospora</i>	<i>Acaulospora</i> and <i>Glomus</i>	[35]
	Shimane prefecture (Japan)	High-throughput sequencing of 18S rRNA gene	<i>Acaulospora</i> ; <i>Ambispora</i> ; <i>Archaeospora</i> ; <i>Claroideoglomus</i> ; <i>Diversispora</i> ; <i>Funneliformis</i> ; <i>Geosiphon</i> ; <i>Gigaspora</i> ; <i>Glomus</i> ; <i>Paraglomus</i> ; <i>Redeckera</i> ; <i>Rhizophagus</i> ; <i>Scutellospora</i>	<i>Glomus</i> and <i>Rhizophagus</i>	[23]
	Diankwan Island (Korea)	High-throughput sequencing of 18S rRNA gene	<i>Acaulospora</i> ; <i>Ambispora</i> ; <i>Claroideoglomus</i> ; <i>Glomus</i> ; <i>Rhizophagus</i> ; <i>Scutellospora</i>	<i>Acaulospora</i> and <i>Rhizophagus</i>	[36]

AMF population diversity of *C. japonica* was rarely reported, relative to *C. sinensis* and *C. oleifera*. A total of five genera and nine species of AMF were isolated from the rhizosphere of *C. japonica* forests in the Fanjing Mountains [34], including *Acaulospora*, *Glomus*, *Scutellospora*, *Pacispora* and *Funneliformis*, with the dominant genus being *Glomus*. He [35] conducted an AMF diversity study on the rhizosphere of *C. japonica* in Nanshan Botanical Garden, Chongqing, and found five species of *Acaulospora*, two species of *Gigaspora*, ten species of *Glomus* and one species of *Scutellospora*, with a total of four genera and 18 species, of which the dominant genera were *Glomus* and *Acaulospora*.

In short, a total of eight genera of *Glomus*, *Gigaspora*, *Acaulospora*, *Scutellospora*, *Entrophospora*, *Sclerocystis*, *Pacispora* and *Funneliformis* were found in the genus *Camellia* by morphological identification, with the dominant genera being *Glomus* and/or *Acaulospora*. The AMF resources of *Camellia* spp. are relatively abundant, but few genera of AMF were detected in these studies because the spore isolation of AMF is accidental. However, some studies have shown that AMF diversity in roots is relatively higher than in rhizosphere soil [21,37]. Morphological identification is inconsistent, limited, and contingent [38], which completely depends on the identifier's own knowledge and discrimination of AMF genera species [39].

2.2. Molecular Identification

Relative to morphological identification, molecular identification of AMF displayed different numbers of AMF species in the root and rhizosphere of *C. oleifera*. Liu et al. [21] analyzed the AMF community in roots and rhizosphere of *C. oleifera* grown in Wuhan (China) through high-throughput sequencing of 18S rRNA, and detected 411 and 351 OTUs of AMF, respectively, a total of 467 OTUs, belonging to 10 genera and 138 species, of which *Glomus* was dominant (>86%), and the rest *Paraglomus*, *Claroidoglomus*, *Diversispora*, *Ambispora*, *Acaulospora*, *Archaeospora*, *Gigaspora*, *Redeckera* and *Scutellospora* were lower. In the rhizosphere of five cultivated varieties of *C. oleifera* in Jiangxi, Lin et al. [32] identified 2538 OTUs, based on high-throughput Illumina sequencing of 18S rRNA, belonging to 1 phylum, 1 class, 4 orders, 10 families and 12 genera, with *Glomus* as the dominant genus. Zhou et al. [33] found 58 OTUs of AMF in the rhizosphere of *C. oleifera* in Guiyang (China) through high-throughput Illumina sequencing of 18S rRNA, belonging to 42 species in 6 genera (*Glomus*, *Archaeospora*, *Claroidoglomus*, *Acaulospora*, *Paraglomus*, and *Diversispora*) with *Glomus* as the dominant genus (87.63%). In conclusion, the dominant genus of *C. oleifera* is still *Glomus*.

South Korean and Japanese researchers also sequenced the AMF community of *C. japonica*, and found more than 10 genera and more than 100 kinds of AMF. Berruti et al. [23] observed a total of 254 OTUs in *C. japonica* in Shimane (Japan), and the AMF diversity of the root (216 OTUs) was greater than that of the soil (125 OTUs), which was similar to the result of Liu et al. [21] in *C. oleifera*. Through the comparison of OTU sequences, the 254 OTUs were classified into 1 phyla, 1 class, 4 orders, 9 families, 13 genera (*Rhizophagus*, *Glomus*, *Paraglomus*, *Scutellospora*, *Gigaspora*, *Claroidoglomus*, *Funneliformis*, *Diversispora*, *Acaulospora*, *Redeckera*, *Ambispora*, *Archaeospora*, and *Geosiphon*), and the dominant genera were *Rhizophagus* and *Glomus*. Lee et al. [36] sampled the rhizosphere of *C. japonica* in Dian Guan Island, South Korea, isolated 248 spores of AMF, and conducted high-throughput sequencing of 18S rRNA to obtain 11 species of AMF belonging to 6 genera, of which *Acaulospora* (49.60%) and *Rhizophagus* (31.29%) were the dominant genera, followed by *Glomus* (12.03%), *Scutellospora* (4.09%), *Claroidoglomus* (2.39%) and *Ambispora* (0.58%). The dominant AMF genera of *C. japonica* in Japan and South Korea are different, which may be caused by environmental factors, implying that AMF diversity shows regional distribution characteristics.

Based on molecular identification, *Glomus*, *Paraglomus*, *Gigaspora*, *Archaeospora*, *Acaulospora*, *Ambispora*, *Scutellospora*, *Diversispora*, *Pacispora*, *Geosiphon*, *Septoglomus*, *Claroidoglomus*, *Rhizophagus*, *Funneliformis*, and *Redeckera* were found in *Camellia*, and the detected AMF resources were more abundant than the morphological identification.

The dominant genus, *Glomus*, was detected from the root and rhizosphere soil of *C. oleifera*, which was consistent with morphological identification. The dominant genera detected from *C. japonica* were *Rhizophagus*, *Glomus* and *Acaulospora*, which were higher than the dominant genera (*Glomus* and *Acaulospora*) previously identified by morphology, because molecular identification was more comprehensive [40,41].

3. AMF Colonization of *Camellia* Plants and Its Influencing Factors

3.1. Root AMF Colonization of *Camellia* Plants

AMF can colonize the roots of plants to form intraradical hyphae, which are denser and finer than the root [42]. Thus, mycorrhizal hyphae help host plants absorb more nutrients than non-mycorrhizal plants. Singh et al. [25] observed that AMF colonization in natural and planted tea plantations in India could be as high as 97.33% and 98.13% during the dormant stage. However, Morita and Konishi [43] observed an AMF colonization rate of only 17% in tea trees, and Gao et al. [17] revealed 7.01% of root mycorrhizal colonization rate in tea trees under open field, indicating relatively low root colonization. In Himalayas of India, AMF colonization (Figure 1a) was 62.29%, 55.68%, 33.10% and 63.36% in tea trees in four different areas [27]. In southern Henan (China), tea trees recorded 66.07% of root mycorrhizal colonization [28]. These results suggest that the root of the tea tree could be colonized by indigenous AMF. In tea, arbuscules are arum-type, and mycelium in roots is rare [17]. Interestingly, arbuscules are digested by the host cells and then changed into spongy structures [17]. Vesicles are sac-like structures formed by the apical expansion of the intraradical mycelium, mostly oval ($64\text{--}80 \times 112\text{--}128 \mu\text{m}$), but also spherical in the shape [44]. When the cortex of the root is shed, the vesicles may also enter the soil with the root tissue and become a new infester and dormant spores.

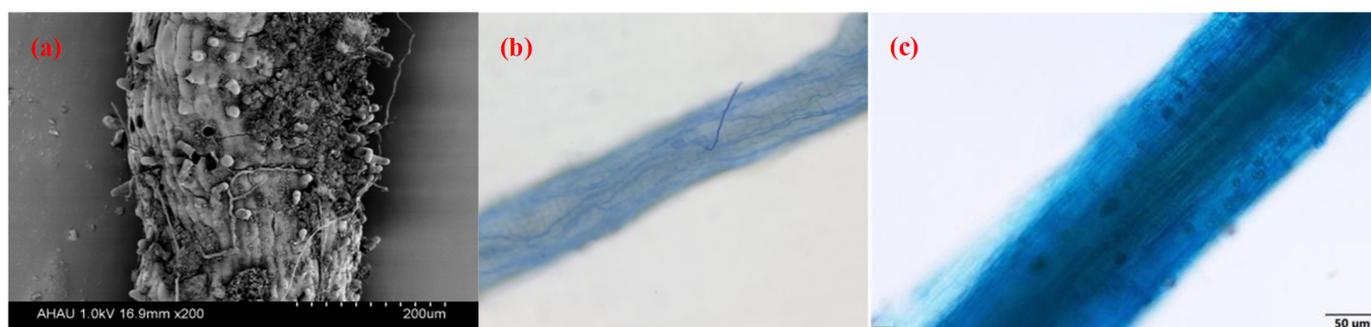


Figure 1. Root mycorrhizal colonization of *Camellia* spp. (a) mycorrhizal colonization in roots of *Camellia sinensis*; (b) mycorrhizal colonization in roots of *C. oleifera*; (c) mycorrhizal colonization in roots of *C. japonica*. These figures were derived from unpublished data by the authors.

However, AMF colonization (Figure 1b) in *C. oleifera* is relatively low, with 30.73–41.68% of AMF colonization in Wuhan (China) [21], which was close to the 20–42% of root colonization observed by Lin et al. [32] in Jiangxi (China). Mejsirik [45] found root mycorrhizal colonization of *C. japonica* in New Zealand, coupled with typical vesicles and arbuscules (Figure 1c). Later Borriello et al. [46] in Piedmont (Italy) observed 14.12%, 32.55%, and 9.92% of root AMF colonization in three regions. In short, *Camellia* spp. is colonized by indigenous AMF thus forming a symbiosis, but the degree of AMF colonization varies.

3.2. Factors Affecting AMF Colonization

3.2.1. Seasonal Variations

AMF diversity of plants varies with seasonal climate [47,48]. Sharma et al. [27] studied AMF colonization of tea plants in annual dynamic change and found that AMF colonization rates of tea trees varied drastically with seasonal changes, with the highest AMF infestation rates occurring in summer (rainy season). Their results were consistent with those of Chandra et al. [49], who observed that AMF activity in the soil was highest in summer,

along with the highest spore numbers and colonization rates [50]. Similarly, Singh et al. [25] also pointed out seasonal changes in root AMF colonization of tea plants, followed by the highest colonization in summer.

3.2.2. Soil Factors

Root AMF colonization can be affected by levels of mineral elements in the soil [51]. The colonization rate of AMF on tea trees decreased significantly with the increase of soluble P application [52]. Soil pH value significantly affected the AMF community of tea trees, because most AMF species prefer to inhabit slightly acidic soils [53]. Among five soil factors (pH, hydrolytic N, Olsen-P, available K and organic matter), the root AMF rate of tea trees was significantly more influenced by soil organic matter content than by available K and Olsen-P [17]. In *C. oleifera*, root AMF colonization was significantly and positively correlated with soil ammonium nitrogen and available potassium, but negatively correlated with soil pH value [21]. In *C. japonica*, soil mineral elements like N, P, K, and Mg are associated with root mycorrhizal development [23,47]. The excess of soil mineral elements such as N and P negatively affects the growth of mycorrhizal mycelium [54], and soil pH value is even more directly affecting AMF diversity [40]. Thus, soil physico-chemical properties strongly affect AMF colonization in *Camellia* plants [34].

4. AMF Diversity in Rhizosphere of *Camellia* spp.

AMF in the soil colonize the roots of *Camellia* spp. and confer many benefits to the host plants, such as improved food quality, increased resistance, accelerated nutrient acquisition, and improved plant growth, as detailed in Table 2.

Table 2. Roles of AMF fungi in *Camellia* plants.

<i>Camellia</i> Plants	Mycorrhizal Fungi	Mycorrhizal Effects on <i>Camellia</i> Plants	Reference
<i>Camellia sinensis</i>	<i>Acaulospora scrobiculata</i> , <i>Glomus aggregatum</i> , <i>G. fasciculatum</i> , <i>G. geosporum</i> , <i>G. intraradices</i> , and <i>Scutellospora calospora</i>	biomass ↑	[6]
	<i>Ac. spinosa</i> , <i>Ac. sp. 1</i> , <i>G. aggregatum</i> , <i>G. ambisporum</i> , <i>G. clavisporum</i> , <i>G. geosporum</i> , <i>G. mosseae</i> , <i>G. pustulatum</i> , and <i>Glomus</i> sp.	leaf sugar ↑; amino acids ↑; proteins ↑	[15]
	<i>Claroideoglossum etunicatum</i> , <i>Diversispora spurca</i> , <i>D. versiformis</i> , and mixed-AMF	stem diameter ↑; plant height ↑; leaf area ↑; bud number ↑; root morphogenesis ↑; root-hair growth ↑	[18]
	<i>G. epigaeum</i>	biomass ↑; mineral elements ↑; leaf P, Mg, Fe, Zn, and Cu ↑; chlorophyll ↑; soil phosphatase activity ↑	[55]
	<i>C. etunicatum</i> under P stress	root system architecture ↑; root P ↑; root acid phosphatase in P ₅₀ ↑; soil neutral and total phosphatase ↑; <i>CsPT1</i> ↑; <i>CsPT4</i> ↓	[56]
	<i>G. intraradices</i> under Pb stress	Biomass ↑; glomalin ↑; Pb in glomalin ↑	[57]
	<i>G. versiforme</i> under salt stress	growth ↑; leaf and root N, P, K, Mg, Fe, and Zn ↑; water saturation deficit ↓	[58]
	<i>Clariodeoglossum etunicatum</i> under drought stress	leaf water content ↑; antioxidant enzyme activity ↑	[59]
	<i>G. intraradices</i> , <i>G. mosseae</i> , and <i>G. versiforme</i> under drought stress	plant growth performance ↑; soluble protein ↑; proline ↑; malondialdehyde ↓; superoxidase ↑; peroxidase ↑; catalase ↑; glutathione ↑	[60]
	<i>Camellia oleifera</i>	<i>Funneliformis mosseae</i>	total leaf area ↑; root length ↑; root average diameter ↑
<i>G. versiforme</i> and <i>G. mosseae</i>		root biomass ↑; root P ↑; leaf N ↓	[62]
<i>G. intraradices</i> , <i>G. mosseae</i> , and <i>G. versiforme</i>		leaf water content ↑; stability of cell membrane ↑; soluble sugar ↑	[63]
<i>Camellia japonica</i>	<i>F. mosseae</i>	number of flowers ↑; flower depth ↑; leaf size ↑; chlorophyll ↑; root Ca, Mg, K, Cu, Mn, Fe, and Zn ↑; leaf Cu and Mn ↑	[64]

4.1. Plant Growth and Development

AMF plays an important role in plant growth [65]. AMF inoculation in *Camellia* spp. affects its growth parameters, depending on the AMF strain (Figure 2). In tea, inoculation with *Claroideoglossum etunicatum*, *Diversispora spurca*, *D. versiformis* and mixed-AMF increased stem diameter, plant height, leaf area, and bud number, of which *C. etunicatum* displayed the highest effect [18]. In addition, AMF inoculation also significantly improved root morphogenesis of tea and promoted root-hair growth [18]. Karthikeyan et al. [6] studied the effects of six AMF species on the growth and development of tea and found that each species promoted the growth of tea, with *Scutellospora calipers* being the more efficient species than the other five AMF species. *Funneliformis mosseae* stimulated the increase in plant height, total leaf area, root length and root average diameter of *C. oleifera* [61]. Further, *F. mosseae* also increased the number of flowers, leaf size, and chlorophyll content of *C. japonica*, along with the increase in plant growth [64].



Figure 2. Plant growth performance of *Camellia oleifera* seedlings after two months of the inoculation with *Funneliformis mosseae* and *Glomus intraradices* (unpublished data by the authors).

4.2. Nutrient Uptake

AMF form extraradical mycelium in the soil, thus promoting nutrient uptake of the host plant [66]. In tea, AMF inoculation had significant and positive effects on leaf sugar, amino acids, and protein contents [15]. Shao et al. [67] found similar effects in tea treated with four AMF species. In addition to nutritional quality, AMF enhanced the uptake of mineral elements such as N, P, Mg and Fe in tea [55] and promoted photosynthesis in tea trees, thereby, increasing the production of photosynthates [68]. The P increase of tea under mycorrhization is due to the fact that AMF stimulated soil neutral and total phosphatase activity and up-regulated *CsPT1* expression levels, independent on soil P levels [56]. However, in *C. oleifera*, two AMF species, *Glomus versiforme* and *G. mosseae*, greatly increased the root biomass and the P content of the whole plant, along with the decrease of N content [62]. Wu et al. [69] further observed that inoculation with *Funneliformis mosseae* increased soil acid phosphatase, alkaline phosphatase, and phytase activity, thus decomposing the organic P in the soil into inorganic P, which is uptaken by plants. As a result, AMF enhance the mineralization of soil organic P. In addition, AMF also increased the content of mineral elements like Ca, Mg, K, Cu, Mn, Fe, and Zn in roots of *C. japonica*, as well as increased chlorophyll content and photosynthetic rate [64]. In conclusion, AMF significantly increased the mineral element content and nutrient quality of *Camellia* spp.

4.3. Stress Resistance

AMF improve plant stress resistance by a series of mechanisms including water absorption of mycorrhizal extraradical hyphae [70], improved root-hairs and root microenvironment, enhanced antioxidant defense systems, improved osmotic adjustment, and up-regulated stress gene expression [4,7,71–74]. In tea, AMF inoculation improved the uptake of mineral elements under salt stress and reduced the damage caused by Pb stress in tea [75]. Under Pb stress, AMF (e.g., *G. intraradices*) inoculation induced the accumulation of total glomalin-related soil protein in tea, whose cysteine-containing peptide chains bound Pb, and could substantially increase the accumulation of Pb into the protein by 89.98%, thus preventing the transport of heavy metals to plants [57]. Liu et al. [58] also found that inoculation of AMF alleviated the inhibition of tea plants under salt stress. Additionally, *Clariodeoglossum etunicatum* accelerated leaf water content of drought-stressed tea plants, along with higher antioxidant enzyme activity like catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) [59]. AMF also dramatically increased SOD, POD, and CAT activities of tea under soil moisture deficit conditions, coupled with the increase in soluble protein, proline, and glutathione and the decrease in superoxide anion radicals, hydrogen peroxide and malondialdehyde [60]. Inoculation with *G. mosseae*, *G. versiforme*, and *G. intraradices* increased leaf water content and the stability of cell membrane, and accelerated soluble sugar accumulation in *C. oleifera* subjected to soil moisture deficit conditions [63]. In addition to these physiological responses, little research has begun on the molecular level to uncover the response on the molecular level. Liu et al. [59] revealed higher expression levels of *CsSOD* and *CsCAT* in AMF-colonized tea seedlings versus non-AMF seedlings, irrespective of water status. Nevertheless, little research has been reported on the resistance of AMF to *C. japonica*.

4.4. Food Quality

Among *Camellia* plants, the tea plant is famous for its tea drinks and therefore the food quality of tea is important. AMF colonization can cause significant changes in the food quality of tea leaves. Soluble sugars, proteins, tea polyphenols, caffeine, free amino acids, flavonoids, and water leachate content were increased after inoculation with *G. mosseae* [63]. The increase in total amino acids under mycorrhization was associated with up-regulation of glutamine synthetase (*CsGS*), glutamine oxoglutarate aminotransferase (*CsGOGAT*), and glutamate dehydrogenase (*CsGDH*), and the increase in caffeine was related to upregulation of tea caffeine synthase 1 gene (*CsTCS1*) [67]. The positive effect of AMF on food quality of tea was also observed under drought stress and P stress [76–78]. Inoculation with *Clariodeoglossum etunicatum* distinctly increased leaf sucrose, glucose, fructose, catechins, amino acids and tea polyphenols contents under soil adequate moisture and soil moisture deficit conditions [78]. This change is also associated with the expression of related genes under AMF regulation. For example, *C. etunicatum*-inoculated tea plants recorded higher expression levels of *CsGDH*, *CsGOGAT*, and 3-hydroxy-3-methylglutaryl coenzyme (*CsHMGR*) genes under soil drought than non-inoculated plants [77]. AMF colonization could promote the accumulation of amino acids in tea leaves by up-regulating the expression of *CsGOGAT* and thus activating the activity of GOGAT under soil drought, which further explains higher total amino acid content after AMF inoculation [77]. Overexpression of *CsHMGR* would improve crop quality by increasing terpene content. Under P stress condition, *C. etunicatum* accelerated total amino acids accumulation, coupled with higher expression of *CsGDH*; total flavonoid content was higher in mycorrhizal than non-mycorrhizal plants, together with induced expression of phenylalanine ammonia-lyase (*CsPAL*) and cinnamic acid 4-hydroxylase (*CsC4H*) [78]. However, the improvement of food quality by mycorrhization was different between different substrate P levels, suggesting differential regulated mechanisms. In short, AMF have positive effects on leaf food quality partly by means of up-regulation of relevant gene expression in tea plants. In addition, AMF inoculation could also increase the number and depth of flowers, and improve the quality of flowers [64].

5. Conclusions

There are many AMF populations in the rhizosphere of *Camellia* plants (Figure 3), which can colonize the root system and establish a symbiosis. These AMF species have shown positive benefits for *Camellia* spp. such as promoting plant growth and development, accelerating nutrient uptake, and enhancing stress resistance (Figure 3). Season and soil nutrient levels affect the root AMF colonization, spore number, and AMF diversity in the rhizosphere of *Camellia* spp. Compared with other mycorrhizal plants (e.g., citrus and maize), the study of AMF in *Camellia* spp. is still in the initial stage, and future studies on mycorrhizas of *Camellia* spp. need to focus on the following aspects:

- (1) The rhizosphere of *Camellia* plants in open-field under non-AMF inoculation conditions has an AMF community based on morphological identification. Indigenous AMF colonizes roots of *Camellia* plants to form a symbiotic association. Due to the limitation of morphological identification, more work around high-throughput sequencing should be performed as much as possible to accurately identify the AMF community and provide a basis for screening of the suitable dominant strains for its application. In addition, future work needs to screen effective AMF strains in promoting plant growth of *Camellia* under non-sterilized soil conditions and in different soil types.
- (2) Among *Camellia* plants, tea plants are rich in natural tea polyphenols, caffeine and other active ingredients; seeds of *C. oleifera* can be extracted as oil (tea oil) for consumption; the flower size, number and brightness of *C. japonica* (an ornamental plant) are important indicators for ornamental purposes. Earlier studies on AMF and *Camellia* plants focused on plant growth, nutrients and stress resistance. However, few studies have addressed the effects of AMF on functional constituents of tea and the oil yield and composition in the seeds of *C. oleifera*. The effects of AMF on the ornamental properties of *C. japonica* are also unknown. Future experiments should focus on the above aspects.
- (3) AMF promote the absorption of nutrients (especially P) from the soil of *Camellia* plants, while the underlying mechanism is unknown. In addition, tea plants are typically grown in extremely acidic soil conditions where aluminum is relatively rich, resulting in aluminum stress in tea plants. Future work needs to revolve around whether and how AMF affects the aluminum tolerance of tea plants.
- (4) In-depth study on the mechanism of AMF on enhancing stress tolerance of *Camellia* plants at physiological and molecular levels.

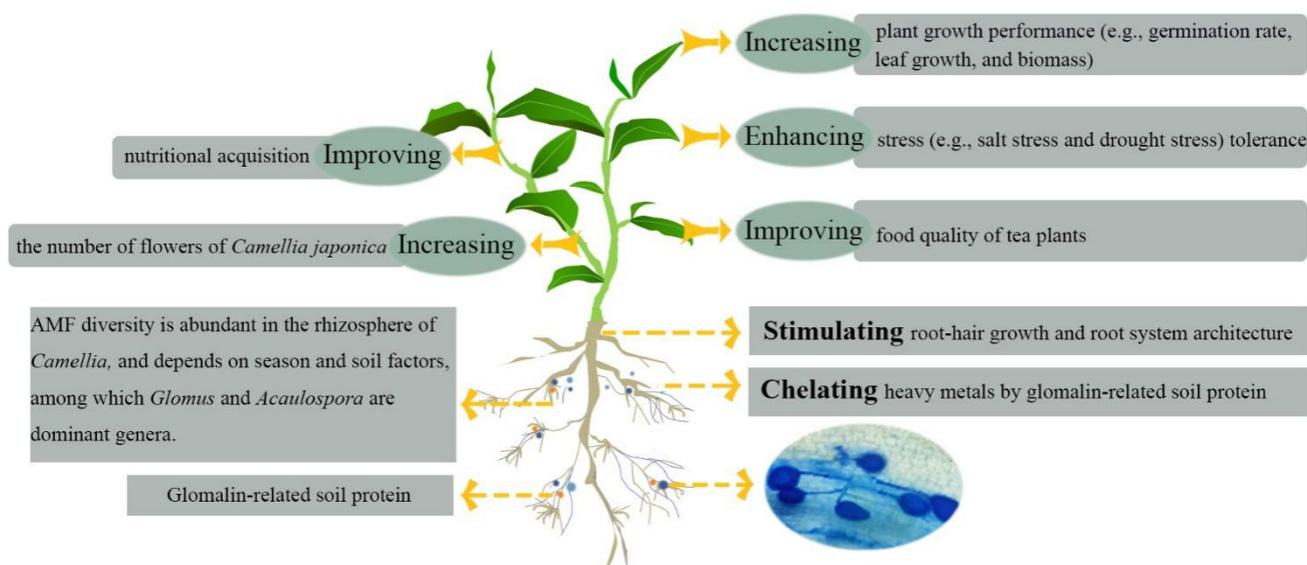


Figure 3. A diagram regarding mycorrhizal fungal roles in physiological activities of *Camellia* plants.

Author Contributions: Conceptualization, R.-C.L. and Q.-S.W.; writing—original draft preparation, R.-C.L. and Q.-S.W.; writing—review and editing, A.H., E.F.A. and Q.-S.W.; supervision, A.H., Y.-J.X., Z.-Y.X., E.F.A. and Q.-S.W. All authors have read and agreed to the published version of the manuscript.

Funding: The authors thank Wuhan Forestry Workstation providing the funding to support the study. The authors would like to extend their sincere appreciation to the Deanship of Scientific Research at King Saud University for funding this research group NO (RGP-271).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All the data supporting the findings of this study are included in this article.

Conflicts of Interest: The authors declare no conflict of interest.

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