

Exploring mycorrhizal fungi in walnut with a focus on physiological roles

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Abstract

Walnuts are an economically important forest tree used for timber and nut production, and the nut of fruits is rich in various nutrients, becoming one of the four important nuts in the world. Walnuts have deep roots, which can be colonized by either ectomycorrhizal fungi or arbuscular mycorrhizal fungi in the soil. These mycorrhizal fungi form beneficial symbioses in roots of walnut. A large number of ectomycorrhizal fungi have been identified, whilst *Boletus edulis*, *Calvatia uiacina*, and *Cantharellus cibarius* isolated from walnut orchards stimulated plant growth and gave the capacity of stress tolerance in walnut. Moreover, *Carya illinoensis* is a very good host plant for commercial production of truffles, especially *Tuber indicum*. In addition, ectomycorrhizal fungi accelerate plant growth and enhance potential stress tolerance of walnuts. Inoculation with arbuscular mycorrhizal fungi also showed the improvement of plant growth and nutrient acquisition of walnut, the enhancement of drought tolerance in walnut, nutrient redistribution under walnut interplanting patterns, and the delivery of juglone by mycorrhizal hyphae. A culturable *in vitro* arbuscular mycorrhizal like fungus *Piriformospora indica* also enhanced salt tolerance of walnut plants. In this mini-review, the physiological roles of mycorrhizal fungi, including arbuscular mycorrhizal fungi, ectomycorrhizal fungi and arbuscular mycorrhizal like fungus (*P. indica*) on walnut plants are summarized, and future outlooks in the field are proposed.

Keywords: endophytic fungi; mycorrhiza; nut trees; symbiosis; truffle

Introduction

Walnut (*Juglans regia* L.) is a deciduous fruit tree, originating in northwest China. Walnut is one of the world's famous "four nut fruits" along with lentil, cashew and hazelnut (Shi *et al.*, 2018). Walnuts bloom in spring and bear fruit in autumn, and their kernels are rich in nutritional value, including unsaturated fatty acids, proteins, vitamins B1 and E, iron, and selenium (Bender and Bender, 2005). Walnuts have a long history of

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cultivation in both the north and south of China, and fossilized walnut pollen has been found by Chinese archaeologists at the Hanpo clan site in Shaanxi Province, which is more than 6000 years old.

Mycorrhiza is a prevalent symbiosis in nature, which is a combination of mycorrhizal fungi in the soil and plant roots (Brundrett *et al.*, 2009; Pohjanen *et al.*, 2014). Mycorrhiza can improve the absorption of mineral elements in the soil, and also enhance the ability of host plants to resist drought, flooding, salinity, pests and diseases, change root system architecture, and increase photosynthesis, soil structure, and fruit quality of plants, thus, playing an important role in sustainable agriculture and environment (Wu *et al.*, 2017; Zhang *et al.*, 2019; Xie *et al.*, 2021; Zou *et al.*, 2021a, 2021b). According to morphology and anatomy, mycorrhizae can be divided into three major groups: ectomycorrhizae, endomycorrhizae, and ectendomycorrhizae (Jin *et al.*, 2004; Lin *et al.*, 2013). Of them, arbuscular mycorrhiza fungi (AMF), the most widespread fungi in the soil, can form arbuscular mycorrhiza (one of endomycorrhizae) with most plants (Wu *et al.*, 2013). The fruit tree species with arbuscular mycorrhizae include citrus, apple, plum, pear, date, peach, grape, apricot, avocado, pear, pistachio, pomegranate, fig, pistachio, persimmon, loquat, hawthorn, kiwi, walnut, cherry, strawberry, banana, lychee, pineapple, longan, and mango. There are about 32 species of AMF studied and utilized in China. Liu *et al.* (2002) indicated that walnut is also capable of producing ectomycorrhizae, while He *et al.* (2013a, 2013b) proposed that walnut is a woody plant with a strong mycorrhizal dependence. As a result, walnut belongs to the plant having ectomycorrhizae and endomycorrhizae (Figure 1a, 1b), which deserves to be noticed. These mycorrhizal fungi have been found in the rhizosphere of walnut cultivated in the field, and many potted experiments also revealed various positive impacts of the inoculation with mycorrhizal fungi on walnut, as shown in Figure 2.

AMF can significantly and effectively improve plant growth of the host. Zou *et al.* (2021b) concluded through potted experiments that inoculation of AMF under soil water deficit conditions could dramatically increase growth responses of citrus plants, along with the improvement of root hairs and hormone balance (Zhang *et al.*, 2019). Song *et al.* (2005) proved that the plant height, ground diameter and total biomass of the poplar inoculated with AMF were considerably higher than those of the uninoculated poplar. Chen *et al.* (2018) proved the stimulated effect of AMF on iris, and the positive effect mainly reflected on the plant growth, chlorophyll content, nitrate reductase activity, peroxidase activity, total root length, root specific surface area, root volume, and root average diameter that were significantly increased. Such experimental results fully reveal the positive effect of mycorrhizal fungi on the host.

The purpose of this review is to simply summarize the physiological roles of walnut plants by AMF, ectomycorrhizal (ECM) fungi, and arbuscular mycorrhizal like fungus *Piriformospora indica* (Figure 3), so as to promote the application of mycorrhizal fungi in the walnut industry.

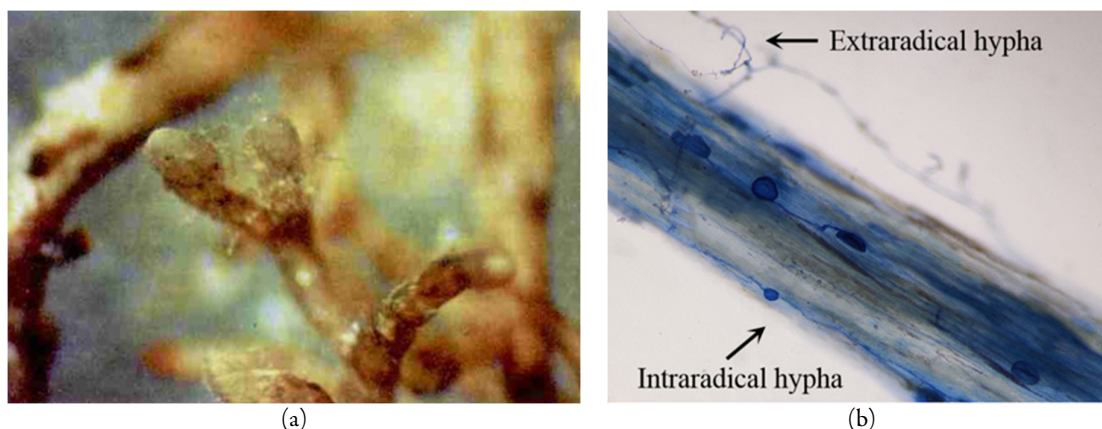


Figure 1. Mycorrhizal colonization of walnut plants. (a) *Carya illinoensis* after inoculated with ectomycorrhizal *Tuber* spp. (Yang *et al.* 2015); (b) *Juglans regia* L. Liaohe 1 after inoculated with an arbuscular mycorrhizal fungus *Diversispora spurca* (unpublished data)

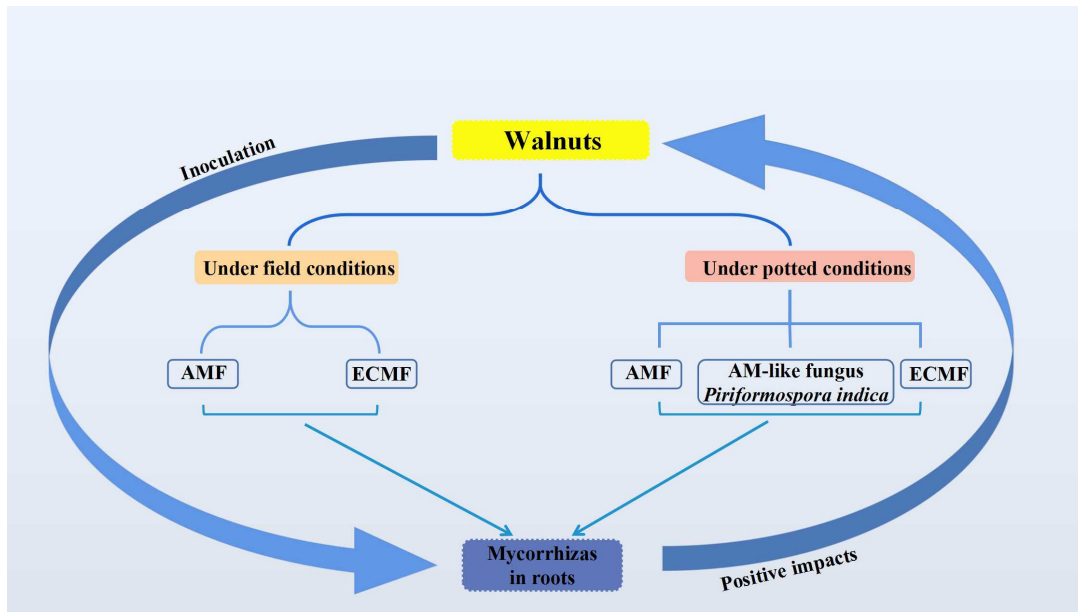


Figure 2. Overall overview on walnut and mycorrhizal fungi

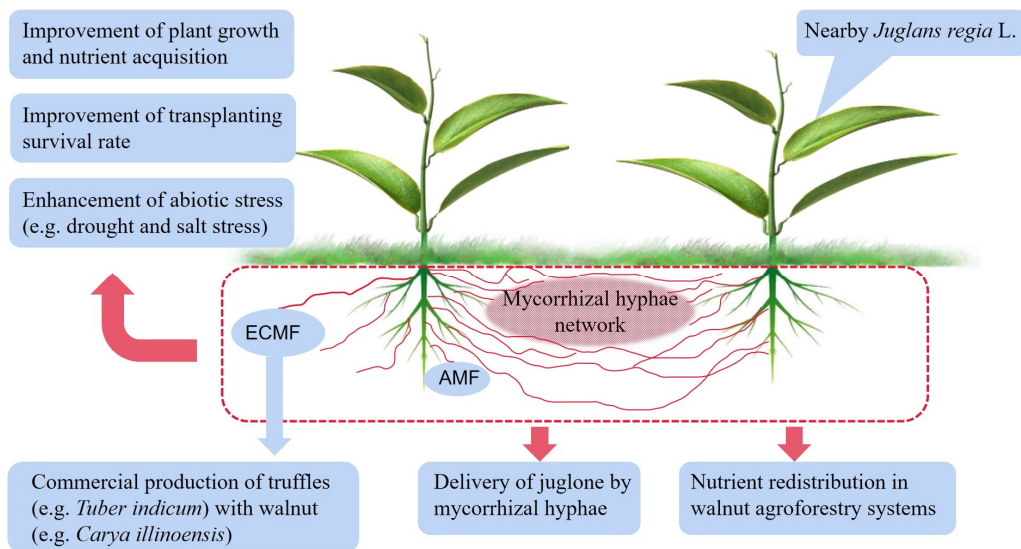


Figure 3. A diagram regarding mycorrhizal fungal roles in physiological activities of walnut plants. The rhizosphere of walnut inhabits both ectomycorrhizal fungi (ECMF) and arbuscular mycorrhizal fungi (AMF), which have positive effects on plant growth, nutrient uptake and redistribution, abiotic stress tolerance, and delivery of juglone by mycorrhizal hyphae network between plants. In addition, walnut e.g. *Carya illinoensis* becomes an important host used for commercial production of truffles (e.g. *Tuber indicum*)

Physiological roles of arbuscular mycorrhizal fungi in walnut

Improvement of growth and nutrient acquisition

A huge spectrum of previous investigations have proved that AMF are of great help to plants under stress, and it has also been documented that AMF can co-exist with walnut root systems, which is helpful to walnut seedling growth. Wang (2015) inoculated potted walnut seedlings with three different AMF species, namely, *Glomus versiforme*, *G. intraradices*, and *Diversispora suprcum*, and found that the root colonization rate of *G. versiforme* to walnut seedlings was the highest, and thus this mycorrhizal fungus might be one of the dominant strains of walnut seedlings. And, the AMF-inoculated walnut plants showed greater plant height, stem diameter, biomass production, and leaf number and lower root:shoot ratio than non-AMF-inoculated plants, dependent on AMF species. However, although AMF-colonized walnut plants recorded higher tissue water content and contents of chlorophyll, starch, soluble sugar and soluble protein in leaves than non-AMF controls, there was no significant difference among the three mycorrhizal fungi-inoculated seedlings. In addition, if AMF (e.g. *G. fasciculatus*) inoculation combined with foliar-fertilized N, P, and N+P fertilizer in black walnut (*Juglans nigra* L.), such treatment would be an important factor in increasing growth and survival of outplanted walnut seedlings (Ponder, 1984). So AMF can shorten the time to the seedling stage of walnuts. Mortier *et al.* (2020) summarized that the AMF-improved nutrient absorption of walnut is associated with lateral roots, but not with pioneer roots.

Cheng *et al.* (2020) analyzed the effects of five AMF species (*Acaulospora scrobiculata*, *D. spurca*, *G. etunicatum*, *G. mosseae*, and *G. versiforme*) on biomass and leaf physiological activity of walnut seedlings. These AMF accelerated the production of stem and root biomass of walnut, and also increased the content of P, K, Mg, B, Fe, Zn, and Cu in leaves, whilst *G. versiforme* represented the potential effect. The stimulated nutrient acquisition also was found in drought-stressed walnut plants after AMF inoculation. *G. mosseae*, *G. etunicatum*, and the mix of both collectively increased leaf N, P, and Zn contents of walnut under normal water and drought stress conditions (Behrooz *et al.*, 2019). In *Juglans regia* L. Liaohe 1, Huang *et al.* (2020) used five AMF species (*A. scrobiculata*, *D. spurca*, *G. etunicatum*, *G. mosseae*, and *G. versiforme*) and found that the AMF inoculations could improve plant growth performance, dependent on AMF species. Similarly, nutrient improvement after AMF inoculation was dependent on AMF species and nutrient elements. Dolcet-Sanjuan *et al.* (1996) also showed that the survival rate of micropropagated walnut seedlings inoculated with *G. mosseae* and *G. intraradices* was significantly improved after being transferred to the nursery. As a result, AMF could confer protection against stress situation due to the transplant process. In Eastern black walnut seedlings, inoculation with *G. microcarpus*, *G. mosseae*, or *G. microcarpus* + *G. fasciculatus* showed superior growth and development of seedlings (Melichar *et al.*, 1986). Hence, early application of AMF may be beneficial in stimulating early growth and survival of outplanted walnut stock, which is due to the improvement of lateral roots and P contents, dependent on AMF and host species (Mortier *et al.*, 2020).

Variable root mycorrhizal colonization and nutrient redistribution under interplanting patterns

Li *et al.* (2021) studied the correlation between soil factors and arbuscular mycorrhizae of walnut under different interplanting patterns. They found that walnut formed a good mycorrhizal symbiosis with soil AMF in Yunnan Plateau mountainous area. In addition, the highest mycorrhizal colonization rate of walnut roots was found in the interplanting pattern of walnut and tea tree, followed by the interplanting of walnut and maize, the interplanting of walnut and wheat, and the interplanting of walnut and pea in the decreasing order. This implies that interplanting plant species strongly influence the mycorrhizal status of walnuts. Therefore, the selection of interplanting plants in walnut orchards for mycorrhizal growth has to be studied in the future.

Tuinen *et al.* (2020) further found that in a walnut-maize agroforestry system, a common mycorrhizal network linked roots of both plants. Moreover, the part C from walnut trees could be transferred to maize plants, suggesting nutritional redistribution in such agroforestry ecosystems. The nutrient transferring would facilitate the redistribution of resources, which in turn promotes the recycling and reuse of nutrients.

Table 1. Physiological roles of mycorrhizal fungi in walnut plants

Walnuts	Mycorrhizal types	Mycorrhizal fungi	Mycorrhizal effects on walnut	References
<i>Juglans regia</i> L.	Arbuscular mycorrhiza	<i>Glomus versiforme</i> , <i>G. intraradices</i> , and <i>Diversispora suprcum</i>	growth target↑; chlorophyll↑; soluble sugar content↑; starch content↑; protein content↑; malondialdehyde↓	(Wang <i>et al.</i> , 2015)
<i>J. regia</i> L. var. 'Liaoh 1'		<i>Acaulospora scrobiculata</i> , <i>D. spurca</i> , <i>G. etunicatum</i> , <i>G. mosseae</i> , and <i>G. versiforme</i>	shoot and root biomass↑; chlorophyll a↑; chlorophyll b↑; total chlorophyll↑; glucose↓; fructose↓; sucrose↑	(Cheng <i>et al.</i> , 2020)
<i>J. regia</i> L.		<i>G. mosseae</i> and <i>G. intraradices</i>	survival↑	(Dolcet-Sanjuan <i>et al.</i> , 1996)
<i>J. regia</i> L. var. 'Liaoh 1'		<i>A. scrobiculata</i> , <i>D. spurca</i> , <i>G. etunicatum</i> , <i>G. mosseae</i> , and <i>G. versiforme</i>	root length↑; projected area↑; surface area↑; volume↑; plant growth↑; nutrient improvement and gas exchange depended upon AMF species	(Huang <i>et al.</i> , 2020)
<i>J. regia</i> L.		<i>Rhizophagus irregularis</i>	juglone transport↑	(Achatz <i>et al.</i> , 2014a)
<i>J. regia</i> L. var. 'Jizhuamian'		<i>Piriformospora indica</i>	salt resistance↑	(Gao <i>et al.</i> , 2019)
<i>J. regia</i> L. var. 'Jizhuamian'		Ectomycorrhiza	<i>Suillus tomentosus</i>	resistance↑
<i>Carya illinoensis</i>	<i>Tuber melanosporum</i> , <i>T. aestivum</i> , <i>T. sinoaestivum</i> , and <i>T. indicum</i>		growth↑; root vitality↑; soil organic content↑	(Zou <i>et al.</i> , 2019)

↑ and ↓ mean the significant ($P < 0.05$) increase and reduction of the parameter after inoculation with mycorrhizal fungi.

Enhancement of drought tolerance

The walnut tree has a high-water demand, so its production and tree growth can be influenced by soil drought stress (Vahdati *et al.*, 2009). Behrooz *et al.* (2019) tried to use *G. mosseae*, *G. etunicatum*, and a mixture of both inoculated into one-year-old *J. regia* cv. 'Chandler' seedlings, and found that these AMF species significantly improved the contents of some metabolites under drought stress, such as total phenolic, proline, total soluble sugar, and starch, and also enhanced activities of peroxidase. In addition, among the AMF strains used by Behrooz *et al.* (2019), *G. etunicatum* was a more efficient mycorrhizal fungus for alleviating drought symptoms than either *G. mosseae* or the mix of both fungi. This positive role of AMF in walnut plants stimulates plant growth responses and nutrient acquisition, which would benefit drought adaptation of walnut plants. The enhancement of drought tolerance in mycorrhizal walnut plants is dependent on AMF species.

Delivery of juglone by mycorrhizal hyphae

Walnut is a typical tree species with allelopathic effects, whilst juglone is a secondary metabolite of walnut in allelopathy (Ma *et al.*, 2019). Juglone is found in leaves, roots, pericarp, exocarp, and bark of walnuts, and has been widely used for the treatment of cancer, stomach pain, cardiovascular diseases, and antitumor diseases (Binju *et al.*, 2018; Ahmad *et al.*, 2020). Achatz *et al.* (2014a) found that AMF (e.g. *Rhizophagus irregularis*) increased the soil-to-soil transfer of the allelochemical substance juglone, and mycorrhizal hyphae

network could increase the juglone transfer between walnut plants. Juglone is slightly hydrophilic and thus occurs via water flowing along hyphae, as well as also dissolves in a liquid layer surrounding hypha in the soil matrix, which is absorbed and transported within the mycelium (Querejeta *et al.*, 2003; Achatz *et al.*, 2014b). However, whether this process is active or passive absorption by the hyphae is not yet clear.

Physiological roles of an arbuscular mycorrhizal like fungus *Piriformospora indica* in walnut

Some coastal saline areas have been planted with walnuts, and the soil salinity in these areas is high. Walnut is less salt tolerant and more sensitive to salinity (Zhang *et al.*, 2002). *P. indica*, an arbuscular mycorrhizal like fungus, was discovered by Verma and other Indian scientists (1998) in the Thar Desert of northwestern India, and can colonize in the roots of many crops. The mycorrhizal like fungus has been documented the various role in plants, including enhancing plant growth, promoting the uptake of N, P, and other minerals, and enhancing crop tolerance to stresses (Zhang *et al.*, 2002; Li *et al.*, 2015; Wang *et al.*, 2017; Yang *et al.*, 2021). Gao *et al.* (2019) investigated the effects of *P. indica* on salt tolerance of walnuts. They found that the plant height, stem diameter, and leaf water content of *P. indica*-inoculated walnuts were higher than those of uninoculated treatments at high salt concentrations. Moreover, inoculation with *P. indica* also accelerated photosynthetic rate, chlorophyll content, and superoxidase activities, thereby, enhancing photosynthetic utilization efficiency of mycorrhizal walnuts and antioxidant defense systems, which in turn promoted the growth of the plants. The effect of *P. indica* in enhancing salt tolerance of walnuts would be better if combined with *Suillus tomentosus* (Gao *et al.*, 2019). Future studies should further clarify the colonization characteristics of *P. indica* in walnut roots and the physiological benefits of mycorrhizas such as nutrient acquisition, water uptake and drought tolerance potential of walnut.

Ectomycorrhizal fungi and walnut

Diversity of ectomycorrhizal fungi in rhizosphere of walnut

Ectomycorrhizal (ECM) fungi form special structures with roots of most deciduous trees (e.g. oaks, beech trees, and conifers), including mycorrhizal snares, harting net, and extraradical mycelium (Smith and Read 2008; Ge *et al.*, 2021). Ectomycorrhizae have been less studied in walnuts (Haug *et al.*, 1991; Rivero *et al.*, 2009). Tedersoo and Brundrett (2017) showed both ECM fungi and non-ECM fungi in the walnut family. Ge *et al.* (2017) used the pyrosequencing technology and identified 96 ECM fungi species associated with walnut (*Carya illinoensis*), belonging to 14 families. In these fungi, *Scleroderma* sp., *Tomentella* sp., *Inocybe radiata*, *Russula pectinatoides*, *I. cf. calospora*, and *Tuber lyonii* were the dominant species. Bonito *et al.* (2011) studied the ECM fungi diversity in *C. illinoensis* in southern Georgia (USA) in terms of ITS and SSU rDNA sequence-based methods. They identified 44 ECM phylotypes, whilst Ascomycete genera included *Cenococcum*, *Elaphomyces*, *Pachyphloeus*, and *Tuber* and basidiomycete genera consisted of *Hebeloma*, *Hymenogaster*, *Inocybe*, *Russula*, *Scleroderma*, *Sebacina* *Thelephora*, and *Xerocomus*. *Tuber* and *Scleroderma* were abundant in these taxa, and *T. lyonii* and *Tubersp.* were the two most abundant species.

Physiological roles of ectomycorrhizal fungi in walnut

Ectomycorrhizae have characteristics such as mycorrhizal sheaths, mycorrhizal nets, and mycelium that do not enter the cells. Ectomycorrhizal fungi have the following effects on plants: a nutrient enrichment, stimulating nutrient (e.g. N, P, and K) and water absorption, improvement of soil structure, and enhancement of metabolisms and immunity of the host. He *et al.* (2013a) isolated *Boletus edulis*, *Calvatia uiacina*, and *Cantharellus cibarius* from walnut orchards. They further found that under the optimum combination (temperature of 20°C, relative humidity of 70%, and pH 6.0), average mycelia biomass was up to 127.81 mg. In *Carya illinoensis*, inoculation with *Tuber melanosporum*, *T. aestivum*, *T. sinoaestivum*, and *T. indicum* showed root mycorrhiza after four months and the highest root mycorrhizal colonization was observed in six

months by inoculation with *T. indicum* (Zou *et al.*, 2019). The ectomycorrhizal fungi-inoculated *C. illinoensis* represented greater shoot g and root peroxidase activity than non-inoculated plants, suggesting that different *Tuber* strains especially *T. indicum* accelerated plant growth and stress tolerance of walnut trees. Further studies conducted by Yang *et al.* (2015) showed that *T. indicum* formed ectomycorrhiza after inoculated with *T. indicum*, along with light milky root tip, light yellow root base, yellowish brown root, and Hart's nets. Therefore, *C. illinoensis* is a very good host plant for *T. indicum*. Moreover, *C. illinoensis* is the only pecan species suitable for low altitude cultivation, and thus *C. illinoensis* becomes an important host used for commercial production of truffles, especially *T. indicum*.

Conclusions

Current information adequately displays the ability of walnut roots to establish symbiotic associations with both ectomycorrhizal fungi and AMF, and walnut roots can also be symbiotic with an arbuscular mycorrhizal like fungus *P. indica*. Since there are multiple mycorrhizal types in roots of walnut, it is not clear which mycorrhiza is dominant and how such mycorrhizal occurrence is associated with climate, soil conditions, and tree growth. The mycorrhizal symbiosis has been shown to promote nutrient uptake and plant growth, enhance drought resistance, and regulate nutrient transfer in walnut agroforestry systems (Figure 3). In particular, the symbiosis between walnut and truffle (an ECM fungus) produces more edible for truffle production, and such symbiosis not only increases economic benefits, but also has positive impacts on the growth of walnut. However, compared to mycorrhizae in other plants such as maize and citrus, the literature on walnut mycorrhizae is scarce. This provides the opportunity to understand walnut mycorrhizae. Future mycorrhizal research on walnut should focus on the following points:

(1) Mycorrhizal fungal diversity of walnuts must be identified, especially AMF communities, so as to provide a basis for walnut industry and healthy tree management along with few pesticides and other chemicals.

(2) How mycorrhizal fungi improve the uptake of P by walnuts, especially under soil P deficit conditions should be clarified.

(3) How mycorrhizal fungi enhance drought and salt tolerance of walnuts at the molecular level would be studied.

(4) Further studies need to increase the commercial production of truffles (e.g. *T. indicum*) using *Carya illinoensis* as a suitable host and also optimize the growth condition of the *T. indicum*-*C. illinoensis* system.

(5) Many of walnut trees are planted in the mountainous areas where the soil is relatively poor, so the soil management of walnut is relatively important. In addition, AMF also release glomalin into the soil, contributing to soil nutrients such as soil organic carbon and nitrogen (He *et al.*, 2020; Meng *et al.*, 2020). The study of Cheng *et al.* (2020) showed the elevation of easily extractable glomalin-related soil protein in the soil after AMF inoculation in walnut. In the future, we also need to assess the benefits of glomalin in walnut orchard.

Authors' Contributions

Conceptualization: WYM and QSW; Data curation: WYM and QSW; Funding acquisition: YJX, KK and QSW; Project administration: YJX; Supervision: QSW; Writing - original draft: WYM and QSW; Writing - review and editing: QSW and KK. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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