Arbuscular mycorrhizal fungi effectively enhances the growth of *Gleditsia sinensis* Lam. seedlings under glasshouse conditions

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Abstract: The Chinese honey locust tree *Gleditsia sinensis* Lam. (Fabaceae) is a tree species valuable in both an ecological and economic sense, and which has a wide range of uses. However, knowledge regarding seedling cultivation, which would be central to the development of *Gleditsia* plantations, especially the use of arbuscular mycorrhizal fungi (AMF), is scarce. A pot experiment was carried out under glasshouse conditions to estimate the effects of three AMF strains (*Funneliformis mosseae* ¹, *Funneliformis mosseae* ², and *Diversispora tortuosa*) on the growth, photosynthetic rate, and nutrient contents of *G. sinensis* seedlings. The results showed that the growth parameters (seedling height, basal diameter, biomass) of seedlings were significantly increased by each of the three AMF strains, associated with high root colonization rates (greater than 75%). The chlorophyll concentrations and photosynthetic rates were also increased by AMF, and the phosphorus (P), and potassium (K) contents in the three organs (leaf, stem, and root), and nitrogen (N) contents in the leaf and stem of AM seedlings were significantly higher than in non-AM seedlings. Mycorrhizal dependency of the AM seedlings was greater than 350%, and significantly correlated with the increased P and K contents in all three organs and the increased N contents in leaf and stem tissue. The positive effects of *F. mosseae* on the growth and nutrient contents of seedlings were higher than those of *D. tortuosa*, but no significantly different effects on *G. sinensis* seedlings were observed between the two strains of *F. mosseae*. Hence, the growth of *G. sinensis* seedlings was effectively enhanced by AMF, with *F. mosseae* being more suitable for the inoculation of *G. sinensis* seedlings. These results indicate that arbuscular mycorrhization is beneficial for the growth of young *G. sinensis* plants. Further research is needed to determine whether the effects can be reproduced in the forest situation.

Keywords: arbuscular mycorrhizal fungi; *Gleditsia sinensis*; growth parameters; nutrient concentrations; mycorrhizal dependency
1. Introduction

The genus *Gleditsia* (Fabaceae) comprises 14 species, widely distributed in Asia, America, and Africa [1]. *Gleditsia* species is a valuable tree species, in terms of both ecology and economics, and has a wide range of uses. As a shelter forest tree species, it has considerable tolerance to abiotic stresses, such as cold, drought, heat, and salt, as well as resistance to biotic stresses such as pests and pathogens, and adapts well on the plains, and in hill and mountain areas [2]. The vegetable gum extracted from *Gleditsia* species can be used in many economic areas, such as the food industry, the mining industry, wood processing, and papermaking, and the pod powder has been used in the fermentation of rice straw [3]. Furthermore, *Gleditsia* species have been widely used for centuries in local and traditional medicine [1]. Nowadays, *Gleditsia* species have become a research hotspot, focusing on the utilization of bioactive compounds extracted from the tissues of *Gleditsia* species [4,5]. Unfortunately, the increased planting of *Gleditsia* species has revealed that knowledge of the seedling cultivation technique, especially with respect to the use of plant growth-promoting rhizomicroorganisms to aid the cultivation of *Gleditsia* species, is inadequate.

Among the plant growth-promoting root-associated microorganisms, nitrogen-fixing nodules-forming bacteria and arbuscular mycorrhizal fungi (AMF) are known to be closely associated with optimal establishment and subsequent growth of these leguminous plants [6]. Considerable research has shown that rhizobial bacteria obtain carbon from the leguminous plants and, in return, supply ammonia to the plants by fixing gaseous nitrogen, thus enhancing plant growth [7,8]. However, the role of AMF in the growth of leguminous plants has received much less attention. AMF are ubiquitous and ecologically important soil microorganisms that form mutualistic symbioses with the roots of more than 80% of terrestrial plant species [9]. They are widespread from the tropics to polar regions, from wetlands to arid regions, and can enhance the ability of plants to acquire water and nutrients (in particular, immobile elements such as P) and to adapt to stressful conditions, promoting the growth of plants and their adaptability to the local environment [10,11]. Research into the positive effects of AMF on the growth of leguminous plants such as soybean (*Glycine max*) [12], fenugreek (*Trigonella foenum-graecum*) [13], and pigeon pea (*Cajanus cajan*) [14], has been reported. However, such research has focused mainly on non-woody crops, and knowledge regarding the effects of AMF on the growth of leguminous tree species is still scarce. So far, no research had been published on the effects of AMF on the growth and nutrient uptake of *Gleditsia* species.

In the current study, we conducted a glasshouse pot experiment to study the effects of three AMF strains on the growth, photosynthesis and nutrient uptake of *G. sinensis*, under low-P conditions. Our hypothesis was that the AMF could effectively promote the growth of *G. sinensis*; if successful, our research would increase the efficiency of seedling cultivation of *Gleditsia* species for use in the development of plantations.

2. Material and Methods

2.1. Plant seeds, AMF inocula and soil

The seeds of *G. sinensis* were provided by Jiangsu Forestry Station. All seeds were soaked in concentrated sulfuric acid for 10 min to achieve scarification until the color of the seeds had turned to crimson, following which they were washed with sterile distilled water until the pH value of the residual water on the surface of the seeds was approximately 7.0. After that, the seeds were soaked in distilled water for 2 days. The swollen seeds were pressed into wet yellow sand and placed in a plant incubator in the dark at 25 °C. The wet yellow sand used in the pre-germination stage had been autoclaved at 0.14 MPa and 121 °C for 2 h to sterilize it. The germinated seedlings were chosen for experimentation when the shoot reached 5 cm in length.

*F. mosseae* 1, *F. mosseae* 2, and *D. tortuosum*, used as AM fungal inocula, were obtained from the Beijing Academy of Agriculture and Forestry Science. The three inocula were propagated for three months in sterile yellow sand with maize and clover inter-crops in a controlled-environment climatic
chamber (22°C–25 °C temperature, 60%–80% relative humidity, and 14-h/10-h diurnal light/ dark cycles with a photosynthetic photon flux density (PPFD) of 800 μmol m⁻² s⁻¹). The plants were watered with modified Hoagland’s nutrient solution containing only 25% standard P concentration every week (100 mL per pot). The mycorrhizal inocula contained yellow sand, infected root fragments, mycorrhizal and spores (> 7 /g).

The nursery substrate consisted of topsoil, yellow sand and vermiculite (1:1:1, v/v/v). The topsoil was collected from Xiashu Forest Farm of Nanjing Forestry University, and had the following physicochemical properties: total C, 1.55%; total N, 0.03%; total P, 570.48 mg kg⁻¹; available P, 10.00 mg kg⁻¹; available K, 101.39 mg kg⁻¹; electrical conductivity, 0.23 mS cm⁻¹ (soil: water ratio, 1: 5); and pH, 7.15 (soil: water ratio, 1: 5). The nursery substrates were autoclaved at 0.14 MPa and 121 °C for 2 h, and were then placed in the glasshouse of Xiashu Forest Farm for transplanting of the Gleditsia seedlings.

2.2. Experimental design

The experiment conducted in the glasshouse was started at the beginning of March 2018. Four treatments were performed: seedlings inoculated with autoclaved AMF inocula (control, CK); seedlings inoculated with F. mosseae 1 (FM1); seedlings inoculated with F. mosseae 2 (FM2); seedlings inoculated with D. tortuosum (DT). For each treatment, there were three replicates per treatment, with each replicate comprised of four pots. Before transplantation, each pot was sterilized by soaking in 0.3% KMnO₄ solution for 3 h then washed with tap water. Every pot contained 2.5 kg of autoclaved nursery substrate and 80 g of the respective inoculum which was placed 5 cm beneath the surface of the nursery substrate, and one germinated seedling was transplanted into each pot. The seedlings of G. sinensis were grown in the glasshouse from March to September 2018 under the following condition: 18 °C–30 °C temperature, 50%–80% relative humidity, 10- to 14-h photoperiod with a photosynthetic photon flux density of about 700-1000 μmol m⁻² s⁻¹. The seedlings were watered with modified Hoagland’s nutrient solution containing only 25% standard P concentration (300 mL per pot every time) every month and maintained under optimal moisture condition. The seedlings were harvested at the beginning of September 2018.

2.3. Seedling growth parameters

Seedling height was measured using a steel ruler before harvesting, and basal diameter was measured using a calipers at the same time. Then, seedlings were harvested from the pots. After the fresh weights of leaf, stem and root were separated and weighed, the three organs were then dried at 105 °C for 30 min and at 70 °C for 48 h to constant weight, and then re-weighed for mycorrhizal dependency (MD) was calculated using the following formula [15]: MD (%) = 100 × (dry weight biomass of inoculated seedlings/ dry weight biomass of control seedlings).

2.4. Root mycorrhizal colonization

The harvested fine roots from each plant were washed and cut into 1-cm long segments, cleared by soaking in 10% (w/v) KOH and stained in 0.05% (w/v) trypan blue solution [16]. The AMF colonization rate was estimated based on the previously described intercept method [17].

2.5. Photosynthetic pigments and photosynthetic rate

Leaf photosynthetic pigments (Chl, total chlorophyll; Chl a, chlorophyll a; Chl b, chlorophyll b) were extracted with 80% acetone as described by Zhang et al. (2018a) [18]. Photosynthetic parameters, including leaf net photosynthetic rate (Pn, μmol CO₂ m⁻² s⁻¹), stomatal conductance (Gs, mmol m⁻² s⁻¹), and transpiration rate (Tr, mmol H₂O m⁻² s⁻¹), were measured in the third fully expanded leaf using a portable photosynthesis system (LI-6400; LI-COR, Lincoln, NE, USA) during the day of plant harvest between 09:30 and 11:30 prior to harvest [1].

2.6. Nutrient contents in different organs
The dried leaves, stems and roots were ground separately and sieved through a 0.5-mm sieve. Samples of 50 mg were used for the measurement of N concentration using an elemental analyzer (Vario MACRO cube; Elementar Trading Shanghai, Shanghai, China). Samples of 0.2 g were digested in an acid mixture (HClO₄: HNO₃ 1: 5) and diluted with double-distilled water to determine the concentrations of P and K. The concentration of P was determined using ammonium molybdate blue method in a spectrophotometer (UV 2700, SHIMADZU, Tokyo, Japan), whereas the concentration of K was determined in an atomic absorption spectrophotometer (AA900T, Perkin Elmer, Norwalk, CA, USA) [20]. Nutrient content = nutrient concentration × dry weight of organs.

2.7. Statistical analysis

The data were analyzed by analysis of variance (ANOVA), with the means of treatments being compared by pairwise multiple comparisons using Duncan’s multiple range test (p < 0.05). All data were presented as mean ± standard deviation and all data analyses were performed using SPSS 19.0 (IBM, Armonk, NY, USA), and graphical presentation of data was carried out using Origin 8.5 (OriginLab, Northampton, MA, USA). Pearson correlation coefficient was performed in the R programming language to determine the relationship between mycorrhizal dependency and increased nutrient accumulation in mycorrhized plants.

3. Results

3.1. Mycorrhizal colonization and plant growth parameters

The mycorrhizal colonization status of the roots of plants from the four treatments are presented in Figure 1. Hyphae, arbuscules, and vesicles of AMF were observed in the roots of the three inoculation treatments but not in the CK. The mycorrhizal colonization rate were 96%, 97%, and 79% in FM1, FM2 and DT, respectively. The seedling heights and basal diameters were significantly increased (relative to the CK) by each of the three AMF strains (Figure 2). The increased values of seedling heights induced by the FM1, FM2, and DT isolates were 213.44%, 214.72%, and 225.36%, respectively, relative to the CK, compared with increased values of basal diameters of 76.87%, 83.62%, and 74.62%, respectively.

Figure 2. Effects of arbuscular mycorrhizal fungi on G. sinensis seedling height and basal diameter. CK—treatment of non-inoculation. FM1—treatment inoculated with F. mosseae 1. FM2—treatment inoculated with F. mosseae 2. DT—treatment inoculated with D. tortuosum. Different lowercase letters indicate significant differences between the three AMF and control treatments.

3.2. Plant biomass and mycorrhizal dependence

Plant biomass, both fresh weight and dry weight, was significantly increased by inoculation with AMF (Table 1). The effects of AMF on dry weight were greater than on fresh weight, and the effects of AMF on organs showed the following pattern from high to low: shoot > total > root. After
inoculating with FM1, FM2 or DT, the shoot dry weights were increased by 433.58%, 439.35%, and 345.11%, respectively, and the increases in root dry weights were 255.91%, 274.80%, and 201.97%, respectively. The mycorrhizal dependencies exhibited by the three AMF strains were greater than 350%, and were in the order: FM1, FM2 > DT (Table 1).

Table 1. Effects of arbuscular mycorrhizal fungi on G. sinensis seedling biomass and mycorrhizal dependence

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Fresh weight (g/pot)</th>
<th>Dry weight (g/pot)</th>
<th>Mycorrhizal dependence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Shoot</td>
<td>Root</td>
<td>Total</td>
</tr>
<tr>
<td>CK</td>
<td>9.33±0.34b</td>
<td>9.23±0.30c</td>
<td>18.86±0.61c</td>
</tr>
<tr>
<td>FM1</td>
<td>44.62±10.71a</td>
<td>30.66±3.46ab</td>
<td>75.28±13.96ab</td>
</tr>
<tr>
<td>FM2</td>
<td>46.24±4.46a</td>
<td>33.61±4.27a</td>
<td>79.84±0.21a</td>
</tr>
<tr>
<td>DT</td>
<td>38.12±3.89a</td>
<td>26.21±3.68b</td>
<td>64.33±7.03b</td>
</tr>
</tbody>
</table>

CK—treatment of non-inoculation. FM1—treatment inoculated with F. mosseae. FM2—treatment inoculated with F. mosseae. DT—treatment inoculated with D. tortuosum. Different lowercase letters indicate significant differences between the three AMF and control treatments.

3.3. Photosynthetic pigments and photosynthesis

F. mosseae inoculation had positive effects on the concentrations of Chl a and Chl. The concentration of Chl a in leaves increased by 13.19%, 25.38%, and 12.09% following inoculation with FM1, FM2 and DT (Table 2). The values of the photosynthetic parameters $P_n$, $G$, and $T_r$ were also increased after inoculation with AMF. The values of $P_n$ increased by 15.42%, 20.45%, and 11.96%, respectively, for the FM1, FM2 and DT treatments, respectively, whereas the increased values of the transpiration rate, $T_r$, were 53.81% ($P < 0.05$), 66.95% ($P < 0.05$), and 54.24% ($P < 0.05$), respectively.

Table 2. Effects of arbuscular mycorrhizal fungi on Photosynthetic pigments and photosynthesis of G. sinensis seedlings

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Chl a (mg/g)</th>
<th>Chl b (mg/g)</th>
<th>Chl (mg/g)</th>
<th>$P_n$ (µmol m$^{-2}$s$^{-1}$)</th>
<th>$G$ (mmol m$^{-2}$s$^{-1}$)</th>
<th>$T_r$ (mmol m$^{-2}$s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CK</td>
<td>1.82±0.40a</td>
<td>0.538±0.206a</td>
<td>2.35±0.58a</td>
<td>11.54±2.03a</td>
<td>0.127±0.029a</td>
<td>2.36±0.37b</td>
</tr>
<tr>
<td>FM1</td>
<td>2.06±0.29a</td>
<td>0.446±0.062a</td>
<td>2.50±0.35a</td>
<td>13.32±2.95a</td>
<td>0.132±0.053a</td>
<td>3.63±1.28a</td>
</tr>
<tr>
<td>FM2</td>
<td>2.10±0.15a</td>
<td>0.474±0.087a</td>
<td>2.58±0.24a</td>
<td>13.90±1.88a</td>
<td>0.169±0.058a</td>
<td>3.94±1.02a</td>
</tr>
<tr>
<td>DT</td>
<td>2.04±0.17a</td>
<td>0.416±0.050a</td>
<td>2.46±0.21a</td>
<td>12.92±2.98a</td>
<td>0.130±0.067a</td>
<td>3.64±1.47a</td>
</tr>
</tbody>
</table>

CK—treatment of non-inoculation. FM1—treatment inoculated with F. mosseae. FM2—treatment inoculated with F. mosseae. DT—treatment inoculated with D. tortuosum. Different lowercase letters indicate significant differences between the three AMF and control treatments.

3.4. Nitrogen, phosphorus and potassium contents

The N, P and K contents in organs from plants grown under different inoculation treatments were significantly higher than those in the CK treatments, except for the N concentrations in stems of the FM1 and DT treatments (Table 3). The percentage increases in P content were higher in the stem and root, with the leaf, for the FM1 and FM2 treatments, but, for the DT treatment, the percentage increase in P content was higher in the leaf and stem than in the root. The percentage increase in P contents induced by the three AMF strains showed the following pattern from high to low: FM1 > FM2 > DT. However, the percentage increase in N and K content induced by the three AMF isolates showed the following pattern from high to low: FM2 > FM1 > DT. The increased N content induced by AMF occurred mainly in the leaf and root, but the increased K concentration was greater in the leaf and stem than in the root. Overall, the positive effects of AMF on the three nutrient elements in the total plant dry biomass showed the following pattern from high to low: K > P > N.
In order to determine how the contribution of AMF to nutrient accumulation affected mycorrhizal dependency, a correlation analysis was conducted (Figure 3). Our data showed that the percentage contribution of AMF to stem P, leaf N, and to leaf, stem and root K affected mycorrhizal dependency at the 0.01 level, while percentage contribution of AMF to stem N of stem, and leaf and root P affected mycorrhizal dependency at the 0.05 level.

Figure 3. Relative analysis of mycorrhizal dependence and contribution of AMF on nutrients. MD—mycorrhizal dependency; IPLeaf, IPStem, IPRoot represent the increased P contents in leaf, stem and root; INLeaf, INSStem, INRoot represent the increased N contents in leaf, stem and root; IKLeaf, IKStem, IKRoot represent the increased K contents in leaf, stem and root; *p < 0.05, **p < 0.01, ***p < 0.001.
4. Discussion

It is well known that legumes are able to form a mutualistic endosymbiosis with AMF, but the colonization rate varies among different combinations of plant and AMF species [14, 21–22]. Our results showed that the root colonization rates of the three AMF isolates were greater than 70%, with both *F. mosseae* strains resulting in higher colonization rates than *D. tortuosum*, indicating that *G. sinensis* forms a high frequency of mutualistic endosymbioses with AMF, and that *F. mosseae* might be more suitable for root inoculation of *G. sinensis* than *D. tortuosum*. The data of increased growth (seedling height, basal diameter and biomass) in FM1 and FM2 treatments than in the DT treatment confirmed that *F. mosseae* was also more effective at improving the performance of *G. sinensis*. Similar results had been reported by Zhang et al. (2018) who found that the growth of *Zenia insignis* seedlings inoculated with *F. mosseae* performed better than seedlings inoculated with *Rhizoglomus intraradices* or *Diversisspora versiformis* [23].

However, the positive effects of *F. mosseae* on plant growth were not always the best, compared to other AMF species. *Zelkova serrata* seedlings inoculated with *D. tortuosum* grew better than did seedlings inoculated with *F. mosseae* [19], and the total dry weight of mulberry seedlings inoculated with *Rhizoglomus intraradices* was 17.56% higher than that of seedlings inoculated with *F. mosseae* [24]. These studies indicated that the most effective AMF species depends on the plant species [25]. The occurrence of different ideal combinations of host plant and AMF species are important in maintaining the diversity of plant communities [26]. MD is defined as the degree to which a plant is dependent on the mycorrhizal condition in order to produce its maximum growth or yield at a given level of fertility [27]. Our results showed that mycorrhizal dependency of *G. sinensis* seedlings inoculated with each of the three AMF strains was greater than 350%, with *F. mosseae* inoculation resulting in MD values higher than those from *D. tortuosum*. High MD (greater than 350%) was also reported on five citrus rootstocks under low-P sandy soil conditions [15]. The high mycorrhizal dependency values indicated that the growth of *G. sinensis* seedlings was highly dependent on AMF, particularly on *F. mosseae*, compared to *D. tortuosum*.

Photosynthetic pigments and photosynthetic parameters could be enhanced by AMF has been reported by a number of researchers [12, 19]. Our results showed that Chl and Chl a concentrations were increased after inoculation with each of the AMF isolates. The higher photosynthetic pigments concentrations were associated with greater plant photosynthetic rate, which, in turn, resulted in greater biomass accumulation.

Macronutrients especially P, N, and K, are of vital importance in the growth of plants. Numerous studies have reported that AMF increased nutrient (P, N, K) uptake by various plant species under particular conditions [23, 28–29]. Mycorrhizae create links between roots and the soil, the fungal hyphae being functionally analogous to fine root hairs, and acquire nutrients, especially relatively immobile elements such as P, by altering the uptake dynamics, whereas mycelia extend the effective absorption surfaces of plant roots [30]. In the present study, the P, N, and K contents in the seedlings inoculated with AMF were far higher than those in the seedlings without AMF, with *F. mosseae* exerting a greater beneficial effect on the uptake of nutrients, especially P and K, compared to *D. tortuosum*.

It was interesting to note that the positive effect of AMF species on nutrient contents differed markedly between organs. For example, the increase in P content induced by *F. mosseae* was far higher in the stem and root than in the leaf, but the increased P content induced by *D. tortuosum* was far higher in the leaf and stem than in the root. Similar results were also presented by Lu et al. [24] who investigated the effects of two AMF species on the growth and nutrient contents of *Morus alba* [24]. These findings from the current study indirectly demonstrated that the effects of AMF species on the nutrient distribution differed between the various organs of the plant. The *F. mosseae* 1 and *F. mosseae* 2 strains, isolated from different soil conditions by staff at the Beijing Academy of Agriculture and Forestry Science, showed no significantly different effects on the growth and nutrient concentrations of *G. sinensis* seedlings. Similar results were also found on *Z. serrata* seedlings [19]. The correlation analysis between mycorrhizal dependency and increased nutrient accumulation indicated that
increased biomass by AMF was significantly associated with increased P and K contents in all three organs, and with N contents in the leaf and stem. The greater biomass reflected a larger root system, which, in turn, increased the amount of N, P, and K taken up.

5. Conclusions

AMF inoculation significantly increased the growth (seedling height, basal diameter and biomass) and nutrient contents (P, K and N) of *G. sinensis* seedlings, and increased the concentration of photosynthetic pigments and the photosynthetic rate of leaves. Of the AMF species investigated, *F. mosseae* appeared to be more suitable for the inoculation of *G. sinensis* seedlings than *D. tortuosum*.

Author Contributions: J.Z. and J.W. conceived the experiments. J.W., H.Z., L.Z., L.X., L.Z., and L.Y conducted the experiments. J.W. and Y.Y. interpreted the data. J.W. wrote the manuscript. G.G.W. revised the manuscript. All authors read and approved the final manuscript.

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

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attributes, but only arbuscular mycorrhizal fungi increase biomass in woody species of a semiarid environment. *Tree Physiol.*, 2018, 38, 25–36.


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