ARBUSCULAR MYCORRHIZAL FUNGUS INOCULATION PROMOTING *IDESIA POLYCARPA* SEEDLING GROWTH BY REGULATION OF NUTRIENT ABSORPTION AND ENDOGENOUS HORMONE LEVELS

HONG, J. – SHI, K. – WAN, X. – WU, G. – HUANG, C.*

Hubei Key Laboratory of Biological Resources Protection and Utilization, Hubei Minzu University, 445000 Enshi, China
(phone: +86-071-8843-7326; fax: +86-071-8843-7326)

**Corresponding author*
e-mail: 2024102@hbmzu.edu.cn

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Abstract. Arbuscular mycorrhizal fungi (AMF) enhance root architectures and promotes the growth of plants. However, the mechanisms through which AMF inoculation influences vegetative growth, nutrient assimilation, and endogenous phytohormone regulation in *Idesia polycarpa* seedlings remain unclear. In this study, a pot experiment was conducted to investigate the impacts of four distinct AMF species on the seedling growth, root configuration, mineral nutrient uptake, and phytohormone profiles of *I. polycarpa*, with non-inoculated seedlings serving as the control group. The results indicated that AMF inoculation significantly improved the plant height, aboveground biomass, stem diameter, leaf count, and root biomass. The enhanced root architecture was evidenced by increases in the total root length, surface area, and root volume. Notably, treatments with *Funneliformis mosseae* and a mixed AMF consortium markedly elevated the mineral nutrient concentrations of the seedling roots. Furthermore, the AMF species differentially modulated phytohormone levels within the root tissues. Collectively, AMF inoculation induced significant shifts in correlations between morphological indices, nutrient assimilation efficiencies, and hormonal dynamics. Specifically, *Funneliformis mosseae*, *Rhizoglomus intraradices*, and the mixed AMF consortium demonstrated superior efficacy in the promotion of plant growth metrics. These findings provide valuable insights for the cultivation of high-quality *I. polycarpa.*

Keywords: *root system structure, infection rate, nutrient uptake, root growth, biomass accumulation*

Introduction

Arbuscular mycorrhizal fungi (AMF) are mutualistic soil microorganisms that form symbiotic associations with approximately 80% of terrestrial plant species (Fan et al., 2024). In this symbiosis, host plants supply carbohydrates to sustain AMF growth, while the extensive extraradical hyphal networks of AMF enhance the acquisition of water and mineral nutrients for host plants, thereby promoting vegetative development (Bisht et al., 2022). The growth-stimulating effects of AMF have been extensively documented across diverse plant taxa. For instance, Coriandrum sativum colonized by Funneliformis mosseae exhibited superior growth performance in contrast with non-mycorrhizal seedlings, which suggested that AMF inoculation reduced the requirements of phosphorus fertilizers for coriander cultivation (Al-Amri et al., 2016). Similarly, inoculation with Rhizoglomus irregularis significantly increased the root dry mass and stem heights of Avena sativa seedlings (Xun et al., 2015). A study by Boyer et al. (2015) demonstrated that strawberry plants inoculated with Funneliformis mosseae (BEG25), Funneliformis geosporus (BEG11), or a mixed AMF consortium exhibited marked improvements in the accumulation of aboveground biomass and root system development.

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Preceding studies demonstrated that AMF enhanced plant growth by improving the acquisition of root-mediated mineral nutrients (Ranjan et al., 2022). Root architectures, which represent the spatial configurations of root systems, play a critical role in the regulation of plant growth, yield potentials, and stress tolerance. Studies have confirmed that AMF symbiosis modifies the architectures of roots to optimize nutrient absorption efficiencies, thereby promoting plant development. For example, tomato (*Solanum lycopersicum*) seedlings colonized by AMF exhibited a greater root volumes and enhanced lateral root branching, which translated to significant improvements in their phosphorus (P) uptake capacities (Gamalero et al., 2004). Furthermore, *Citrus junos* seedlings inoculated with *Diversispora spurca* showed elongated primary roots, expanded root surface areas, and denser lateral root proliferations compared with non-mycorrhizal controls (Wu et al., 2013).

Beyond nutrient acquisition, AMF modulates endogenous phytohormone homeostasis in plants, thereby influencing growth regulation, developmental processes, and stress adaptation (Buendia et al., 2019). For instance, AMF symbiosis enhanced plant disease resistance through multiple mechanisms, including the activation of systemic defenses mediated by jasmonic acid and salicylic acid, transcriptional regulation of ethylene response factors, and synergistic improvements in nutrient uptake efficiencies and root architectures (Tang et al., 2023). Moreover, maize (*Zea mays*) plants inoculated with AMF exhibited significant modifications in their root concentrations of zeatin riboside (ZR), indole-3-acetic acid (IAA), and abscisic acid (ABA) (Wang et al., 2024). Collectively, these findings highlighted the pivotal role of AMF in orchestrating phytohormonal networks to optimize the physiological performance of plants.

Idesia polycarpa is a deciduous tree species of the family Salicaceae, native to East Asia, which has been globally introduced in various regions (Wang et al., 2022). This species is distinguished by its bright red berries, which hold significant ornamental value, which makes it widely cultivated as an ornamental tree (Wang et al., 2015). Additionally, its fruits are rich in lipids, particularly linoleic acid (a polyunsaturated fatty acid with a remarkably high content (>80%)), which contributes to their notable nutritional and health-promoting properties (Ping et al., 2025). In China, *I. polycarpa* is extensively planted as a woody oil crop; thus, the development of high-quality seedlings is critical for enhancing productivity. The current large-scale cultivation of *I. polycarpa* still faces certain limitations, primarily arising from two factors. Firstly, the species itself exhibits dormancy constraints, resulting in a very low germination rate under natural conditions, secondly, in environments with poor soil conditions, the root system develops inadequately and is susceptible to root rot (Niu et al., 2025). Studies indicate that increasing the fruit yield of *I. polycarpa* requires prioritizing tree growth. This can be achieved either by optimizing the environmental conditions at the planting site (such as soil, temperature, and light) or by enhancing the plant's overall growth status (Li et al., 2023). The identification of viable strategies for improving its growth performance and soil nutrient utilization efficacies (Rana et al., 2020) has become a primary focus for the operators of *I. polycarpa* seed orchards (Zhang et al., 2024). Although AMF are well-documented for their role in stimulating plant growth, detailed research into AMF applications for *I. polycarpa* remains scarce. Further, specific AMF taxa that exhibits the highest symbiotic affinity for this species has yet to be identified.

For this study, a controlled pot experiment was conducted to investigate the effects of different AMF species on the growth, morphological root traits, mineral nutrient acquisition, and endogenous phytohormone profiles of *I. polycarpa* seedlings. We hypothesized that: (1) Different AMF strains exhibit varying affinities for *I. polycarpa* roots. Mixed-AMF inoculations result in higher mycorrhizal colonization rates; (2) AMF inoculation enhances root growth and increases root biomass accumulation in *I. polycarpa*.

Materials and methods

Plant materials

This study was conducted at the experimental station of Yangtze University to investigate the effects of AMF on the growth of *I. polycarpa*. The experimental design included a non-inoculated control (CK) group (non-AMF) and four AMF inoculant treatments (Diversispora versiformis (DV), Funneliformis mosseae (FM), Rhizoglomus intraradices (RI), mixed AMF consortium (DV + FM + RI)) (*Fig 1*). All treatments were replicated five times (n = 5) in a randomized complete block design.

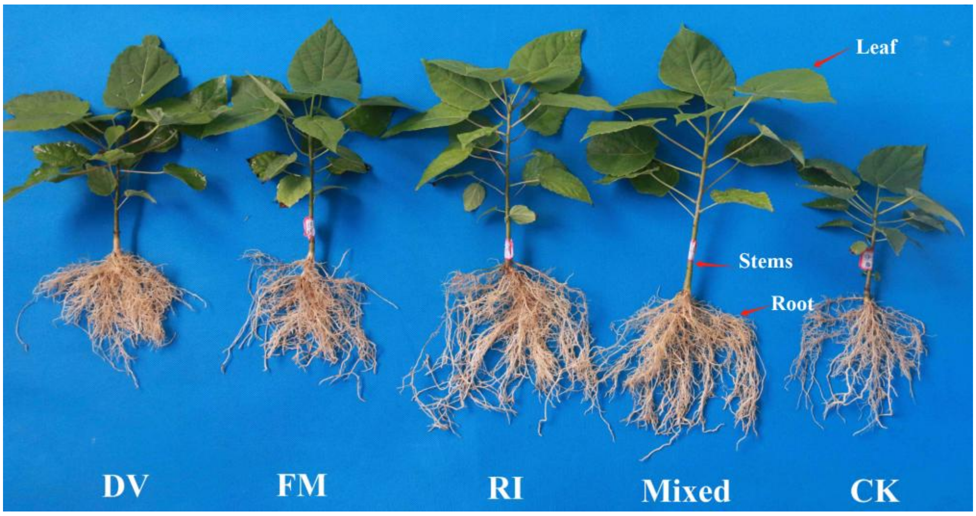

Figure 1. *Whole-plant morphology of Idesia polycarpa under experimental treatments*

AMF inoculation

I. polycarpa seeds were surface-sterilized in 70% ethanol for 15 min, rinsed with sterile distilled water, and sown in trays containing sterilized (121°C, 0.11 MPa, 1 h) substrate (peat – vermiculite – perlite = 2:1:1, v/v/v). Seedlings were watered every two days. At the fourth-leaf stage (80% emergence), seedlings were transplanted into 1.5 L plastic pots (top Diameter 15.5 cm × base Diameter 12 cm × height 14.5 cm) containing a sterilized sand mixture (1:1, v/v). Each pot received 80 g of AMF inoculum (15 spores/g). All cultures were obtained from the Culture Preservation Center of China. These fun-gal strains were propagated using Trifolium repens as a host plant, and the inoculum con-sisted of spores, infected roots, and culture material.

Measurement of physiological parameters

Prior to harvesting, the *I. polycarpa*. seedling heights, stem diameters, and leaf counts were measured. At harvest, the fresh weights of the roots and aboveground parts

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were quantified. The entire root systems were scanned using an Epson Perfection V700 Photo dual-lens system and analyzed using 2007 WinRHIZO professional software (Regent Instruments Inc, Quebec, Canada).

Measurement of mycorrhizal colonization rate

At harvest, the fine roots of the *I. polycarpa* seedlings were thoroughly rinsed and then cut into 1 cm long segments. The root segments were stained using the 10% KOH clearing–Trypan blue dyeing method and observed under a microscope (Han et al., 2019). The mycorrhizal colonization rate was calculated using Mycocalc (https://www2.dijon.inrae.fr/mychintec/Mycocalc-prg/download.html).

Determination of root elements

The nitrogen (N) contents of the roots were determined using an elemental analyzer (Vario MICRO CUBE, Elementar Analysensysteme GmbH, Germany) following established protocols (Shao et al., 2018). The phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), zinc (Zn), iron (Fe), and boron (B) concentrations were quantified via inductively coupled plasma optical emission spectrometry (ICP-OES) (Zhang et al., 2014).

Determination of root hormones

The root samples were processed according to the extraction protocols described by Liu et al. (2018). The concentrations of endogenous phytohormones, including abscisic acid (ABA), zeatin riboside (ZR), indole-3-acetic acid (IAA), and Gibberellins (GA), were quantified using enzyme-linked immunosorbent assay kits (Plant Growth Regulator Engineering Research Center, China Agricultural University, Beijing, China).

Statistical analysis

Data organization was performed using Microsoft Excel 2019. First, normality, independence, and Homogeneity of variance test were conducted on all observed data in SPSS Statistics 21. Then, one-way analysis of variance (ANOVA) was used to compare differences in seedling growth (aboveground and underground parts), photosynthetic pigment content, photosynthetic physiology, leaf element content, and hormone levels among AMF mycorrhizal inoculation treatment groups. Pairwise significance was evaluated using the post hoc least significant difference (LSD) test, $p < 0.05$. In R 4.1.3, Pearson correlation analysis and Mantel tests were used to quantify relationships between mycorrhizal infection rates of seedling roots, growth of underground and aboveground parts, element content of leaves, hormone content, and biomass components of seedlings. All graphical representations were generated in R 4.1.3 using the “ggplot2”, “vegan”, “dplyr”, and “ggcor” packages.

Results

Mycorrhizal infection characteristics

Mycorrhizal colonization analysis revealed distinct structural patterns across treatments. No arbuscular mycorrhizal structures were detected in the Non-AMF (CK), whereas all AMF-inoculated seedlings exhibited characteristic symbiotic features, including intraradical hyphae, arbuscules, and vesicles (*Fig. 2*).

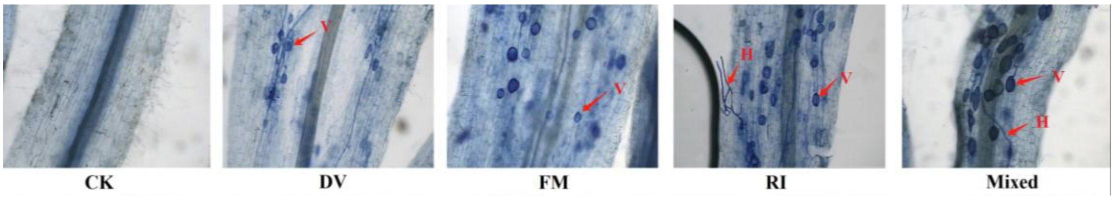

Figure 2. *Microscopic photos of root samples infected by AMF. H, hyphae; V, vesicle*

The root colonization rates followed the hierarchical order: Mixed-AMF > *R. intraradices* > *F. mosseae* > *D. versiformis* (*Fig. 3A*). Furthermore, extraradical hyphal density in the rhizosphere soil varied significantly between treatments, with the Mixed-AMF group demonstrating the greatest hyphal length density, while the *R. intraradices* treatment showed the lowest values (*Fig. 3B*).

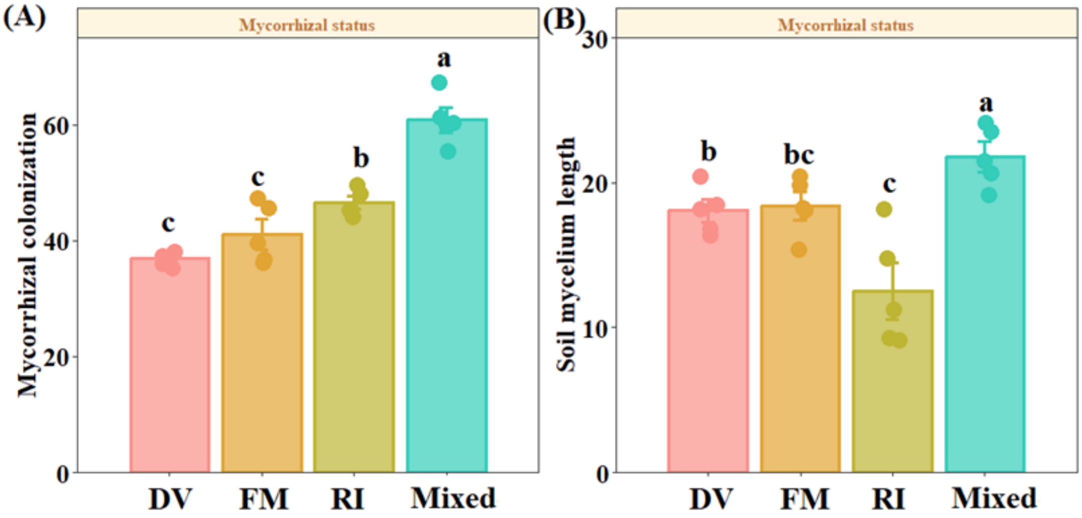

Figure 3. *Root mycorrhizal colonization rate (A) and soil mycelium length (B) of I. polycarpa seedlings under AMF conditions. Different letters on the bars indicate significant differences between treatments (p < 0.05)*

Changes in plant growth performance

Compared to the CK, AMF inoculation significantly enhanced the growth performance and accumulation of biomass in *I. polycarpa* seedlings, with *F. mosseae* and the Mixed-AMF consortium eliciting the most explicit growth-promoting effects ($p < 0.05$) (*Fig. 4A–E*). AMF colonization markedly improved the root system architecture metrics relative to the CK treatments ($p < 0.05$), including the total root length, root surface area, average root diameter, and root volume (*Fig. 4F–I*). Notably, *R. intraradices* inoculation significantly enhanced the development of root systems, which resulted in a 14.70% increase in the total root length, 9.67% greater root surface area, 17.91% expansion in root diameter, and 136.53% augmentation in root volume compared with the CK.

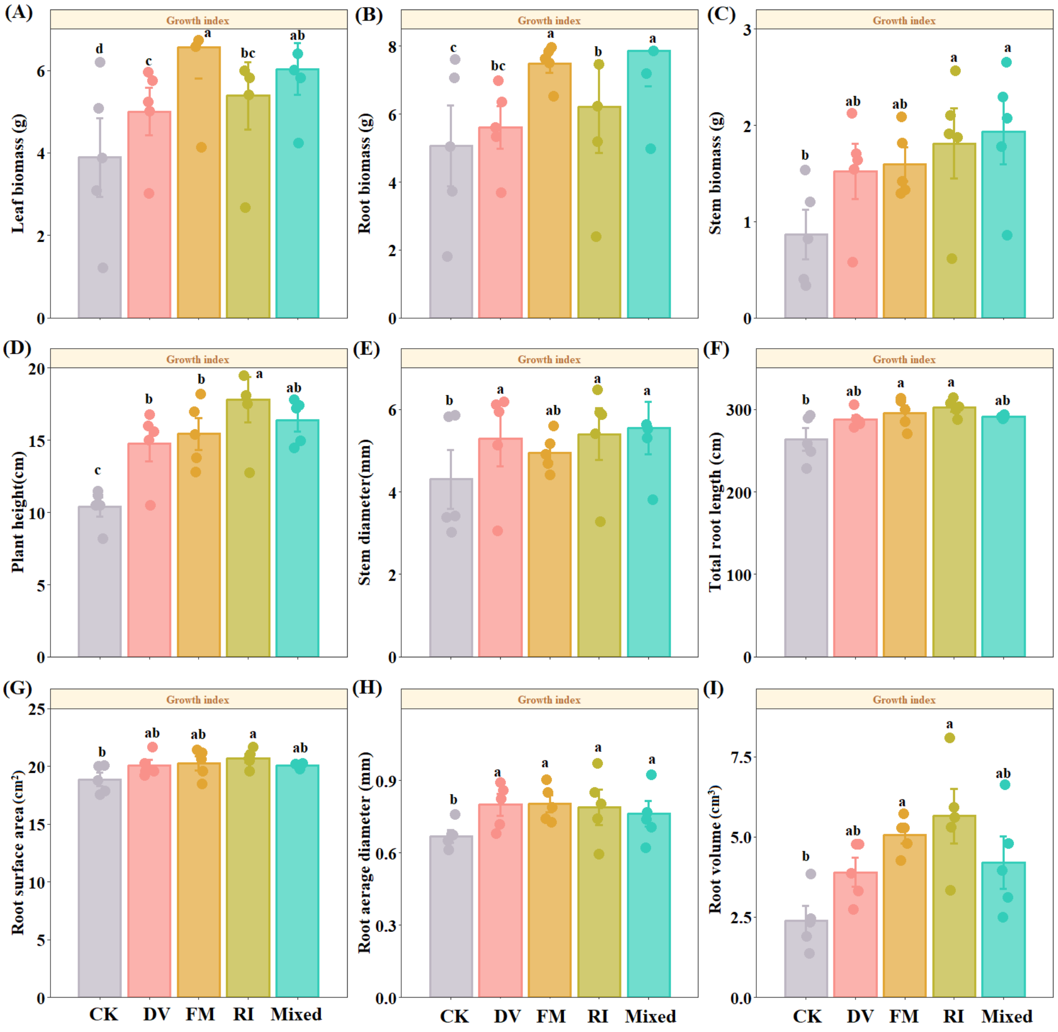

Figure 4. *Effects of AMF on leaf biomass (A), root biomass (B), and stem biomass (C) plant height (D), stem diameter (E), total root length (F), root surface area (G), average diameter (H), and root volume (I) of I. polycarpa seedlings. Different letters on the bars indicate significant differences between treatments (p < 0.05)*

Changes in plant growth performance

AMF inoculation significantly enhanced the accumulation of mineral elements in *I. polycarpa* root systems (*Fig. 5*). Compared with the CK, *F. mosseae* and the mixed AMF consortium exhibited the most prominent enhancement in the acquisition of mineral nutrients ($p < 0.05$). Under the *F. mosseae* treatment, the root N, P, K, Ca, Mg, Cu, Zn, and B concentrations increased by 53.38%, 150.17%, 52.64%, 29.09%, 44.47%, 184.54%, 71.07%, and 50.31%, respectively. Similarly, the mixed AMF consortium elevated these elements by 74.15%, 127.88%, 51.89%, 32.20%, 46.71%, 218.20%, 88.92%, and 59.42%, respectively.

Changes in plant root hormones

Inoculation with AMF significantly affected the concentrations of IAA, ABA, GA, and ZR in the *I. polycarpa* root system (*Fig. 6*). In contrast to the CK, the *F. mosseae*, *R. intraradices*, and Mixed AMF treatments increased the root ABA levels by 23.89%, 21.19%, and 18.16%, respectively. Compared with the CK seedlings, the root ZR concentrations of seedlings colonized by *D. versiformis* and *F. mosseae* were reduced by 52.73% and 66.62%, respectively. Compared with the CK plants, the root IAA concentrations of those treated with *D. versiformis* and F. mosseae were reduced by 23.32% and 20.21%, respectively. The concentration of root GA under the Mixed AMF treatment was higher, while compared with the CK, the *D. versiformis*, *F. mosseae*, and *R. intraradices* reduced the root GA concentrations.

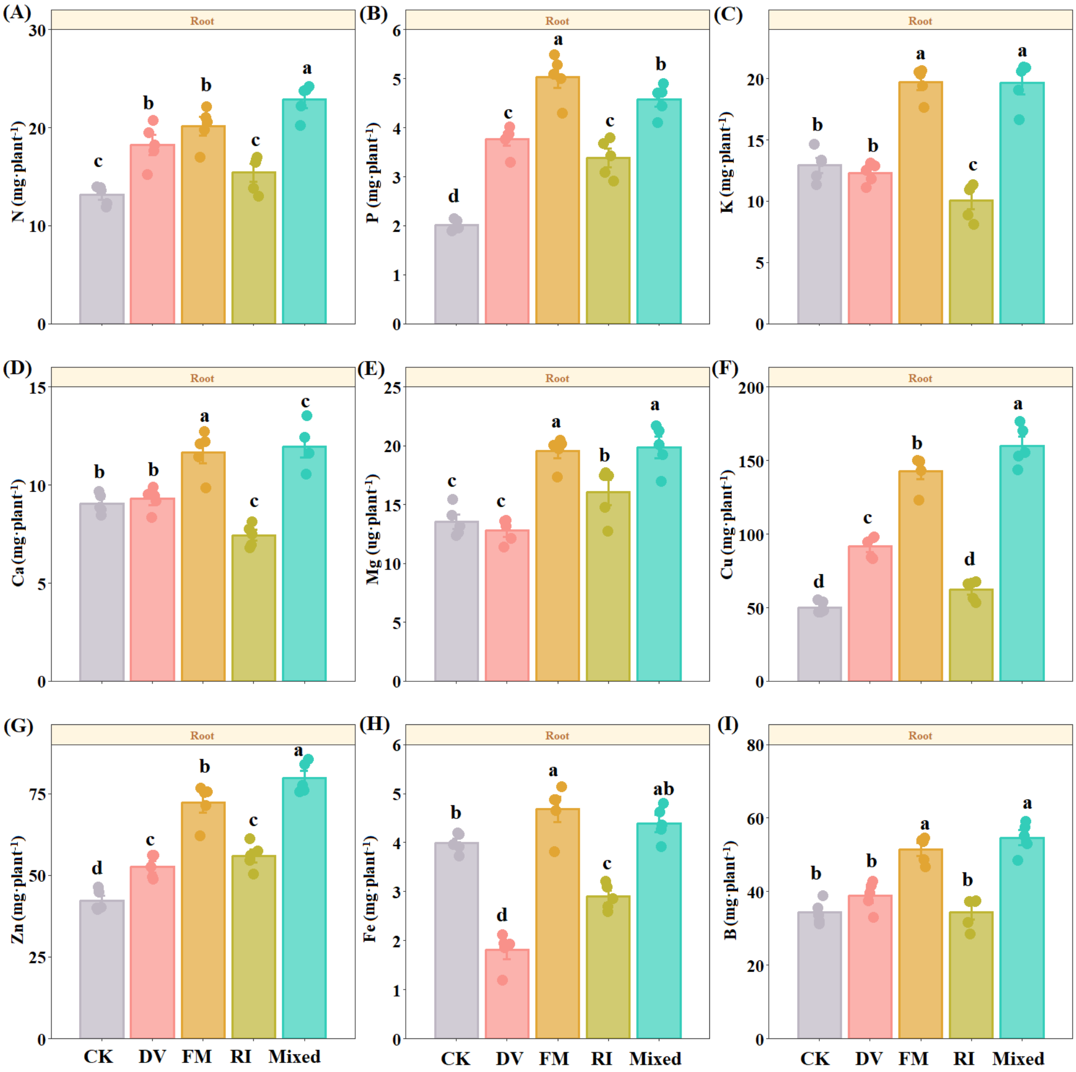

Figure 5. *Title of the given figure, graph or image included in the document Effects of AMF on N (A), P (B), K (C), Ca (D), Mg (E), Cu (F), Zn (G), Fe (H), and B (I) concentrations in the root systems of I. polycarpa seedlings. Different letters on the bars indicate significant differences between treatments (p < 0.05)*

Primary factors for the accumulation of seedling biomass

Pearson correlation analysis and Mantel test results revealed that the accumulation of biomass in discrete *I. polycarpa* seedling compartments (leaves, stems, and roots) exhibited significant positive correlations with the architectural traits of roots, as well as their nitrogen N and P concentrations ($p < 0.05$) (*Fig. 7*). Specifically, the root Mg and B contents showed substantial positive associations with the foliar biomass ($p < 0.05$), while K, Cu, Mg, and B were strongly correlated with the accumulation of stem biomass ($p < 0.05$). Further, the mycorrhizal colonization rates, soil hyphal lengths, and seedling heights demonstrated significant positive relationships with the root biomass ($p < 0.05$).

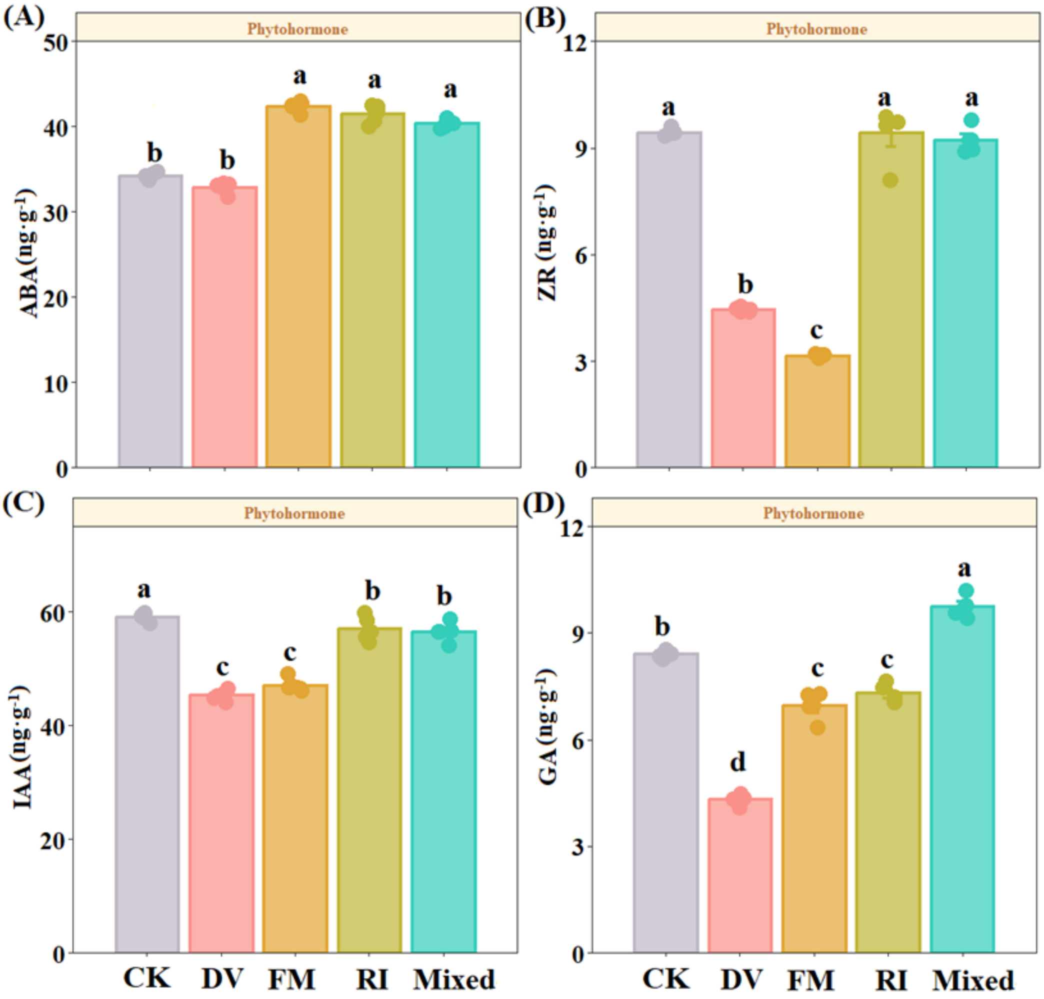

Figure 6. *Effects of AMF inoculation on abscisic acid (A), zeatin riboside (B), indole-3-acetic acid (C), and Gibberellins (D) levels in I. polycarpa seedlings. Different letters on the bars indicate significant differences between treatments (p < 0.05)*

Discussion

Effects of AMF on Idesia polycarpa growth performance

In this study, the presence of characteristic mycorrhizal structures in *I. polycarpa* roots under AMF inoculation confirmed its classification as a mycorrhizal plant. However, significant differences in the root colonization rates and soil hyphal lengths were observed between treatments, which could be attributed to the symbiotic affinity between the AMF and host plants (Koch et al., 2012). These results indicated that mixed AMF inoculation exhibited superior efficacy compared with single AMF species, which

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was consistent with previous reports (Wagg et al., 2011), thereby validating hypothesis 1. The enhanced colonization efficiency and stimulated growth via mixed AMF may have emerged from functional complementarity between different AMF species (Maherali et al., 2007).

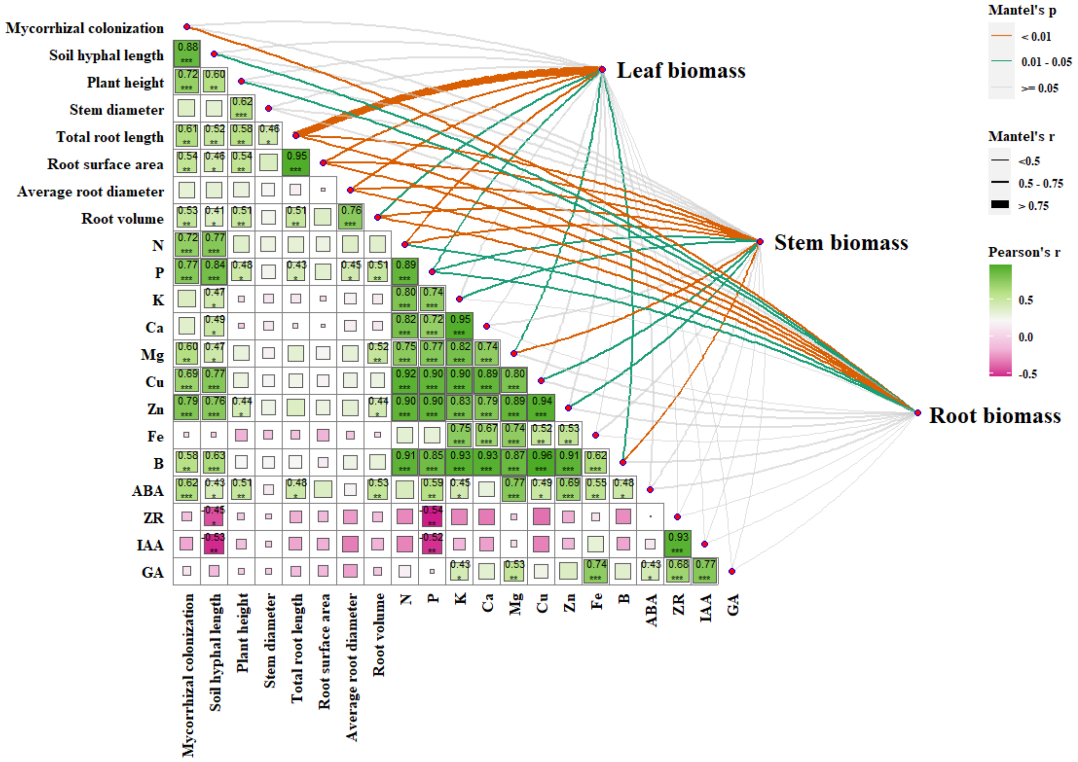

Figure 7. *Effects of mycorrhizal inoculation on the seedling biomass accumulation in relation to physiological and growth parameters. Edge colors denote statistical significance based on 9999 permutations, while edge widths represent Mantel correlation statistics for distance-based associations*

Numerous studies have reported that inoculation with only a single AMF species improved the parameters of plant growth (Singh et al., 2010). For this study, *I. polycarpa* seedlings inoculated with *D. versiformis*, *F. mosseae*, and *R. intraradices* exhibited significant increases in growth metrics (e.g., plant height, root length, leaf number, and biomass), which was consistent with the findings for other plant species. For instance, inoculation with *Glomus mosseae*, significantly enhanced the growth parameters of tea (Camellia sinensis), including the leaf number, leaf area, root length, plant height, shoot length, and root/shoot biomass (Wu et al., 2024). Similarly, inoculation with *F. mosseae* markedly increased the plant height and biomass of peanuts (*Arachis hypogaea*), thereby influencing their yield potential (Cui et al., 2019).

Effects of AMF on the morphological characteristics of roots

The morphological traits of roots are critically linked to the adaptability, fitness, and productivity of plants. Their optimal architectural parameters indicate enhanced efficiencies for the acquisition of water and nutrients from the soil (Huang et al., 2019). As an environmentally sensitive and perceptive plant system for soil, roots can undergo significant morphological plasticity to minimize physiological costs while maximizing nutrient foraging efficiencies (Mishra et al., 2017). This study demonstrated that AMF-inoculated *I. polycarpa* seedlings exhibited superior total root lengths, root surface areas, and root volumes compared with the CK, which was consistent with hypothesis 2. For example, Sun et al. (2024) reported an increased root projected area, root surface area, average root diameter, root density, RV, and root tip number in AMF-colonized *Robinia pseudoacacia* relative to non-mycorrhizal seedlings. Furthermore, Zhang et al. (2020) found that symbiosis with *R. intraradices* under arsenic stress stimulated the proliferation of fine roots in *R. pseudoacacia* seedlings, while enhancing soil resource capture via increased living root lengths, root branching frequencies, and root tip densities. Additionally, AMF colonization was shown to mitigate the inhibitory effects of auxin antagonists on the TRL, root diameter, root projected area, RSA, and RV in trifoliate orange (*Poncirus trifoliata*) (Liu et al., 2014).

Effects of AMF on mineral elements of root systems

Extraradical hyphae enhance the mineral nutrient acquisition efficiency of host plants through the “mycorrhizal pathway” (Durney et al., 2024), with improved plant growth correlating strongly with the AMF-mediated mobilization of soil nutrients (Gamalero et al., 2004). In this study, the absorption of mineral elements such as total N, P, K, Ca, Mg, Cu, Zn, Fe, and B varied depending on the type of AMF. The *F. mosseae* and Mixed-AMF treatments significantly enhanced the uptake of all nine elements for plants.

These findings aligned with reports that AMF strain identity governed micronutrient (Fe, Mn, Cu, Zn) accumulation patterns (Cosme et al., 2014). Similarly, *Glomus mosseae* inoculation elevated the concentrations of P, K, Mg, Cu, Zn, and Mn in licorice (*Glycyrrhiza uralensis*) seedlings (Chen et al., 2017). Our results confirmed the AMF species-specific modulation of mineral acquisition in *I. polycarpa*, with *F. mosseae* and Mixed-AMF inducing the most stimulated nutrient uptake.

Effects of AMF on root hormones

As pivotal secondary metabolites, phytohormones play an irreplaceable role in the modulation of plant phenotypic traits (Bilal et al., 2019). Earlier studies established that the beneficial symbiosis between plants and AMF involved AMF-mediated phytohormones, which served as signaling intermediaries for sustained molecular crosstalk between plant cells and fungal hyphae (Liu et al., 2019).

In the present investigation, the four AMF treatments differentially modulated the root phytohormone profiles. The Mixed-AMF consortium significantly elevated the GA levels, which aligned with earlier findings (Shaul et al., 2002). We found that GA concentration increase in AMF-inoculated plants positively correlated with the rise in mycorrhizal colonization. Studies indicate that GA exerts a dual effect on AMF colonization in plant roots: exogenous GA application inhibits mycelial formation, whereas endogenous GA deficiency inhibits the formation of symbiotic structures. Consequently, maintaining appropriate endogenous GA levels has a positive influence on AMF colonization. (Takeda et al., 2015). We also found that *D. versiformis*, *F. mosseae*, *R. intraradices*, and Mixed-AMF significantly reduced IAA content in *I. polycarpa* seedlings. However, previous studies suggested that AMF colonization in plants significantly increases IAA levels. (Wiriya et al., 2020). Further, *D. versiformis* and *F. mosseae* significantly decreased the ZR levels, whereas *R. intraradices* and Mixed-AMF showed no significant ZR modulation. The biological functions and mechanistic pathways of AMF-induced ZR, GA, IAA, and ABA fluctuations in *I. polycarpa* roots remain unclear. This will necessitated targeted investigations into hormone-signaling crosstalk and the transcriptional regulatory networks that govern these symbiotic interactions.

Conclusions

The experiment confirmed the positive effect of AMF fungal inoculation on the growth and development of *I. polycarpa* seedlings. Inoculation with AMF enhanced the vegetative growth and nutrient uptake of *I. polycarpa* seedlings, while simultaneously influencing the levels of phytohormone metabolism. The colonization ability of mixed arbuscular AMF on the root system of *I. polycarpa* was stronger than that of a single fungal species. Seedlings inoculated with *F. mosseae*, *R. intraradices*, and mixed AMF inoculum exhibited varying degrees of improvement in biomass accumulation, root growth, and mineral element accumulation in leaves.

The results of this study can provide a reference for screening beneficial microorganisms in the cultivation of high-quality I. polycarpa seedlings. However, limitations arise from differences between field and experimental environments; whether AMF inoculation treatments can still exert excellent effects in large-scale cultivation applications requires further verification. Additionally, we will continue experiments to verify whether AMF inoculation has a positive impact on the yield and quality of I. polycarpa, which will be a critical factor for the practical application of this technology.

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