



Research article

Effects of arbuscular mycorrhizal fungi inoculation on plant growth, root morphology, and interspecific interactions in a ginger-pepper intercropping system

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Abstract: In this study, we aimed to investigate the regulatory role of arbuscular mycorrhizal fungi (AMF) in interspecific interactions in a ginger–pepper intercropping system, using the ginger cultivar ‘Luoping Yellow Ginger’ and the pepper cultivar ‘King 336’ as plant materials. A two-factor pot experiment was conducted involving monoculture versus intercropping and AMF inoculation with *Funneliformis mosseae*. The results revealed that the mycorrhizal colonization rate was significantly higher in ginger (96.6%) than in pepper (45.0%). AMF inoculation increased the total biomass of ginger in the monoculture by 49.8% and enhanced the dry weight of pepper fruits. However, under intercropping conditions, AMF inoculation did not significantly enhance system productivity, as land equivalent ratio (LER) values (1.03–1.08) did not differ from those of non-inoculated controls ($P > 0.05$). Instead, AMF inoculation caused a decrease in the partial LER (PLER) of ginger from 0.34 to 0.29 ($P < 0.05$), whereas the PLER of pepper remained stable at 0.74. Morphologically, AMF promoted root branching and elongation in ginger, while in pepper it induced root thickening and modulated shoot architecture by increasing stem diameter and reducing plant height, leading to a more compact growth habit. Consistent with our hypothesis that AMF would differentially affect the two species and that stronger morphological responses would not necessarily confer competitive advantage, these results demonstrate that AMF does not provide synergistic benefits to this system and that its ecological

function is highly dependent on crop combinations. Therefore, its application requires a precise evaluation of interspecific interactions.

Keywords: arbuscular mycorrhizal fungi; intercropping; biomass; interspecific competition; land equivalent ratio

1. Introduction

Ginger (*Zingiber officinale* Roscoe) and pepper (*Capsicum annuum* L.) are globally important spice crops that are commonly used in culinary, medicinal, and agricultural processing [1,2]. However, both crops are prone to replanting problems [3,4], as continuous cultivation leads to the accumulation of soil-borne diseases, enhanced allelopathic effects from root exudates, and soil nutrient imbalances, which collectively limit yield and quality improvement [5,6]. Intercropping is a sustainable and intensive planting system that offers significant advantages for land utilization, resource optimization, and pest and disease suppression [7]. Yet, in intercropping systems, different crops compete for key resources, such as light, water, and nutrients, to varying degrees [8–10]. When interspecific relationships become unbalanced, weaker crops often experience suppressed growth because of limited resource availability, which affects the overall productivity and stability of the system [11].

In production practice, intercropping systems involving ginger and crops such as citrus, grapes, corn, and pepper have been implemented [12–15]. Different intercropping combinations exhibit significant differences in plant structure, light energy utilization, and nutrient preferences, which directly affect system yield and resource use efficiency [16]. Generally, differences in plant structure and light resource utilization can create complementary effects on both temporal and spatial scales [17], whereas differences in nutrient absorption preferences help alleviate root-zone competition and improve soil nutrient use efficiency [18]. In the ginger–pepper intercropping system, ginger plants typically reach heights of 0.5 m to 1.0 m, grow upright, and can create shaded environments in later growth stages. Some pepper varieties can maintain good growth under moderate shading at the mature stage [19]. Additionally, ginger has high nitrogen and potassium requirements [20], whereas pepper requires relatively more phosphorus and calcium [21,22], indicating significant differences in nutrient utilization profiles. Although this ecological niche differentiation provides a theoretical foundation for synergistic effects in intercropping, the regulation of interspecific interactions remains poorly understood, particularly regarding how microbial symbionts, such as arbuscular mycorrhizal fungi (AMF) inoculation, can optimize resource allocation, alleviate competition, and enhance growth.

AMF are widespread symbiotic microorganisms in terrestrial ecosystems that form mutualistic relationships with approximately 80% of vascular plants [23]. AMF extend the root absorption capacity of host plants through their hyphal networks, enhancing their ability to acquire phosphorus, nitrogen, and water [24]. In multi-species coexistence systems, AMF mediate nutrient transfer and signal exchange between plant roots, reshaping interspecific competition dynamics and promoting cooperative growth [25]. Previous studies have shown that both ginger and pepper can be colonized by AMF [26,27]. However, systematic research on how AMF regulate the growth coordination, root morphology, and interspecific relationships of ginger and pepper in intercropping systems is lacking.

Addressing this gap is essential to unlock the full potential of AMF for enhancing productivity and stability in ginger–pepper intercropping systems.

Based on the above research background and existing knowledge gaps, we propose the following two hypotheses: (H1) In the ginger–pepper intercropping system, AMF inoculation will differentially affect the growth and root morphology of the two species, with the more mycorrhiza-dependent species expected to exhibit greater root morphological plasticity and higher aboveground biomass. (H2) This differential response to AMF may alter the balance of interspecific interactions between ginger and pepper; however, the species exhibiting stronger morphological and growth responses to AMF is not necessarily the one that achieves greater competitive dominance in the intercrop.

In this study, we aimed to evaluate the regulatory effects of AMF on interspecific relationships in a ginger–pepper intercropping system. ‘Luoping Yellow Ginger’ and the pepper variety ‘King 336’ were used as experimental materials in a pot experiment with monoculture / intercropping and AMF inoculation / non-inoculation treatments. Plant growth and morphology were assessed, including mycorrhizal colonization, agronomic traits, biomass allocation, and root architecture. Herein, we focused on investigating whether AMF can alleviate growth suppression caused by niche overlap through modulating both above- and below-ground plant morphology (e.g., plant height, leaf area, root length, and root diameter), enhance resource acquisition strategies, and promote complementary and coordinated resource utilization between ginger and pepper, which may help improve the overall resource use efficiency and stability of the system. Our findings contribute to a deeper understanding of the ecological functions of mycorrhizal symbiosis in spice–vegetable intercropping systems and provide a theoretical basis for developing an efficient ginger–pepper intercropping model based on mycorrhizal regulation.

2. Materials and methods

2.1. Experimental materials

The ginger variety ‘Luoping Yellow Ginger’ and the pepper variety ‘King 336’ were selected for this experiment. Soil was collected from the arable layer (0–20 cm) of a farmland at Weixing Lake, Yongchuan District, Chongqing (105°52′49″E, 29°14′41″N). The previous crop was sweet potatoes (*Ipomoea batatas* (L.) Lam.). The basic chemical properties of the soil were as follows: pH 7.41, organic matter 65.13 g·kg⁻¹, alkali-hydrolyzable nitrogen 155.79 mg·kg⁻¹, available phosphorus 45.10 mg·kg⁻¹, available potassium 283.75 mg·kg⁻¹, total nitrogen 2.98 g·kg⁻¹, total phosphorus 1.10 g·kg⁻¹, and total potassium 17.92 g·kg⁻¹. After sampling, the soil was air-dried indoors, sieved through a 2.0-mm mesh to remove stones and plant residues, and thoroughly mixed. The soil was then spread out in a greenhouse under natural light and ventilation for 15 days (with a soil layer thickness of approximately 5 cm). The soil was turned regularly, and the average daily temperature was maintained at 28 ± 3 °C. This treatment aims to reduce weed germination and native microbial activity while minimizing disturbances to the physical and chemical properties of the soil, as well as to nutrient availability, by avoiding high-temperature sterilization [28]. After the treatment, the soil was stored in a cool, dry place for later use.

The AMF used in this experiment was *Funneliformis mosseae* (Nicol. & Gerd.) C. Walker & A. Schüßler [29], provided by the Subtropical Arbuscular Mycorrhizal Fungi Resource Preservation Center, Guangxi Academy of Agricultural Sciences. The AMF was propagated for 3 months in a

sterilized substrate using white clover (*Trifolium repens* L.) as the host plant. The final inoculum consisted of a mixture of AMF-infected root segments, hyphal fragments, and spores. The spore density was approximately 100 spores per 10 g of substrate. After propagation, the inoculum was air-dried at room temperature (22–25 °C) in the dark for 7 days and stored at 4 °C in sealed polyethylene bags for 15 days before use. A preliminary colonization assay confirmed high infectivity, with approximately 83.4% of white clover roots showing typical AMF structures (arbuscules and vesicles) after staining.

2.2. Experimental design

The experiment was conducted in a multi-span greenhouse at the Chongqing University of Arts and Sciences, using natural light. A completely randomized two-factor design was used, with cropping pattern (ginger monoculture, pepper monoculture, and ginger–pepper intercropping) and AMF inoculation treatments (AMF-inoculated and non-inoculated) as the two factors, resulting in 6 treatment combinations, with 12 repetitions per treatment. Experimental units were randomly arranged within the greenhouse.

The experimental containers were nutrient pots with dimensions of 40 cm (inner diameter) × 40 cm (height). The growing medium was a mixture of farmland soil, perlite, and peat moss in a volumetric ratio of 5:3:2, with a total substrate weight of 10 kg per pot. During potting, 6.3 kg of the mixed substrate was added and leveled at the bottom of each pot, and then the crops were planted in these pots. For the AMF inoculation treatments, 700 g of the inoculum (described in Section 2.1) was evenly applied to each pot to ensure adequate contact between the inoculum and the roots or ginger seed pieces. For the non-inoculation treatments, an equal amount of heat-sterilized (121 °C for 1.0 h) inactive inoculum was applied. The remaining 3.0 kg of mixed substrate was added to cover the top layer, which was lightly compressed and leveled.

Uniform ginger seed pieces (approximately 50 g each) with 3–4 healthy buds and no mechanical damage or mold were selected. Prior to planting, the ginger pieces were washed to remove surface soil and disinfected by soaking in a 10% (v/v) hydrogen peroxide solution for 10 min. They were then thoroughly rinsed with sterile distilled water (5 times or more) and left to dry. Pepper seedlings approximately 15 cm in height, with robust growth and free from visible pests and diseases, were selected. Prior to transplanting, the roots of the seedlings were gently washed with sterile water. The planting method was as follows: in monoculture treatments, two ginger seed pieces or two pepper seedlings were planted in each pot; in intercropping treatments, one ginger seed piece and one pepper seedling were planted in each pot at diagonally opposite positions. The planting distance between the two individuals was approximately 20 cm in all treatments, ensuring that each crop occupied 50% of the planting space. This spacing represents a balanced configuration that facilitates belowground mycorrhizal interactions while minimizing excessive aboveground competition. After planting, the first irrigation was performed using distilled water equivalent to 13% of the substrate weight, ensuring that the substrate was sufficiently moistened and the plants were well-rooted. During the growing period, the substrate moisture content was monitored using a weighing method, and distilled water was added periodically to maintain the moisture content at 70–80% of field capacity.

2.3. Measurement indicators and methods

Non-destructive growth measurements were recorded every 30 days, starting from the three-leaf stage of ginger (locally known as the “three-branch stage”), throughout the crop growth period. The number of branches, plant height, and stem diameter were recorded, and the leaf area of five randomly selected functional leaves was measured using a portable leaf area meter (YMJ-B). At 150 days after planting (end of maturity), the aboveground and underground parts of both ginger and pepper were harvested. The roots were cleaned with distilled water, and the AMF infection rate was determined using the Trypan Blue staining method [30]. AMF spores were extracted from rhizosphere soil using the wet sieving and sucrose centrifugation method [31], and the number of spores was counted; the results were expressed as spores per 10 g of dry soil. Additionally, complete fibrous roots of ginger and pepper were scanned, and root system parameters, including total root length, average diameter, surface area, and volume, were analyzed using the WinRHIZO Pro 2010 software.

Ginger was harvested as a whole plant. After harvesting, plant organs were separated into aboveground (stems and leaves) and underground (roots and rhizomes) parts, and their fresh weight was measured. The samples were then blanched at 105 °C for 30 min, followed by drying at 80 °C until a constant weight was achieved for further weighing. For pepper fruits, harvests were staged according to ripeness, and the fresh and dry weights of fruits were recorded for each harvest, with the total yield accumulated.

All data were collected on a per-plant basis, with the pot serving as the experimental unit for statistical analysis.

2.4. Data analyses

Mycorrhizal growth dependency (MGD) refers to the degree to which a plant achieves its maximum biomass or yield through mycorrhizal formation at a given soil fertility level [32]. MGD was calculated using Equation (1):

$$MGD = \frac{(B_{AMF} - B_{NAMF})}{B_{AMF}} \times 100\% \quad (1)$$

where B_{AMF} and B_{NAMF} represent the total biomass of plants with and without AMF inoculation, respectively.

Land equivalent ratio (LER) [33] was calculated using Equations (2)–(4):

$$PLER_g = \frac{Y_{ig}}{Y_{mg}} \quad (2)$$

$$PLER_p = \frac{Y_{ip}}{Y_{mp}} \quad (3)$$

$$LER = PLER_g + PLER_p \quad (4)$$

where Y_{ig} and Y_{ip} are the dry weights of ginger rhizomes and chili peppers, respectively, per unit area in the intercropped plot ($\text{g} \cdot \text{cm}^{-2}$); Y_{mg} and Y_{mp} are the corresponding yields in the monoculture system; and $PLER_g$, $PLER_p$ and LER represent the partial land equivalent ratios for ginger and pepper, and the

total land equivalent ratio, respectively. Intercropping is considered advantageous when $LER > 1$, and disadvantageous when $LER < 1$.

Interspecific competitiveness [34] was determined from Equation (5):

$$A_{gp} = \frac{Y_{ig}}{Y_{mg} \times P_g} - \frac{Y_{ip}}{Y_{mp} \times P_p} \quad (5)$$

where A_{gp} represents the interspecific competitiveness of ginger relative to pepper, and P_g and P_p denote the area proportions of ginger and pepper in the intercropping system, respectively. A positive A_{gp} ($A_{gp} > 0$) indicates that ginger exhibits stronger interspecific competitiveness than pepper, whereas a negative value ($A_{gp} < 0$) suggests the opposite.

Experimental data are presented as mean $\pm$ standard deviation. Prior to the two-way analysis of variance (ANOVA), the normality of residuals was assessed using the Shapiro-Wilk test, and homogeneity of variances was evaluated using Levene's test. The data met the assumptions of normality and homoscedasticity; therefore, no data transformation was applied. The two-way analysis of variance (ANOVA) was performed to analyze the effects of the AMF inoculation treatments (inoculated / non-inoculated) and cropping system (monoculture / intercropping) on mycorrhizal infection, MGD, and plant growth indicators. For determining the LER and interspecific competitiveness in the intercropping system, independent sample t-tests were used to compare the differences between AMF-inoculated and non-inoculated treatments. All multiple comparisons were conducted using the least significant difference method, with a significance level of $P < 0.05$. Statistical analyses were performed using SPSS 27.0, and graphs were plotted using Origin 2025.

3. Results

3.1. Mycorrhizal infection rate, soil spore density, and MGD of ginger and pepper

The two-way ANOVA revealed that the mycorrhizal infection characteristics of ginger and pepper were significantly impacted by AMF inoculation ($P < 0.001$). The effect of cropping pattern varied depending on the crop, but no significant interaction between the two factors was observed ($P > 0.05$). Under the inoculation conditions, the mycorrhizal infection rate of ginger in both the monoculture and intercropping systems reached 100%, and the soil spore density in the monoculture treatment was 89 spores per 10 g dry soil, which was significantly higher than that in the intercropping treatment ($P < 0.01$; Figure 1a and b). Under non-inoculation conditions (NAMF), no significant differences were found in the mycorrhizal infection rate or soil spore density between monoculture and intercropping treatments. For pepper, inoculation significantly promoted the establishment of the symbiotic relationship. Unlike in ginger, the mycorrhizal infection rate of pepper was significantly impacted by cropping pattern, with a significantly higher infection rate under intercropping conditions than under monoculture conditions ($P < 0.05$). However, the soil spore density for pepper was influenced only by the AMF inoculation treatment, with no significant effect of the cropping pattern ($P > 0.05$). Overall, the average mycorrhizal infection rate of ginger (96.6%) was significantly higher than that of pepper (45.0%) ($P < 0.001$), indicating that ginger has a stronger symbiotic affinity for AMF. In the non-inoculated treatment, a small number of spores were detected, confirming the presence of native AMF, but the infection level was much lower than that in the inoculated treatment.

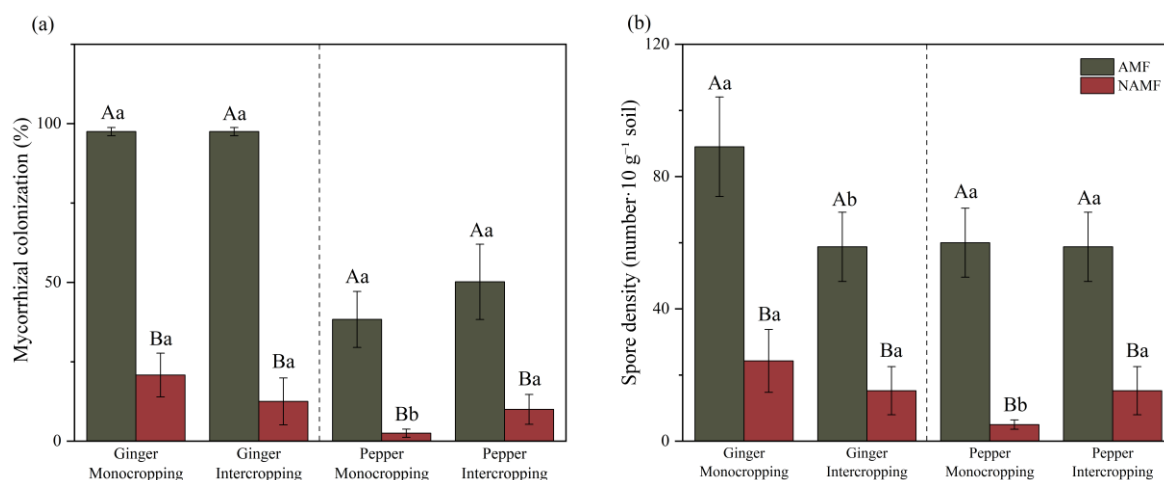


Figure 1. Mycorrhizal colonization (a) and spore density (b) of ginger and pepper under arbuscular mycorrhizal fungi (AMF) inoculation and cropping pattern treatments. Data are expressed as mean $\pm$ standard deviation (SD). Bars represent mean mycorrhizal colonization (panel a) or spore density (panel b) for each treatment. AMF and NAMF indicate AMF-inoculated and non-inoculated treatments. Lowercase letters indicate significant differences between monoculture and intercropping within the same AMF treatment ($P < 0.05$), whereas uppercase letters indicate significant differences between AMF-inoculated and non-inoculated treatments within the same cropping pattern ($P < 0.05$).

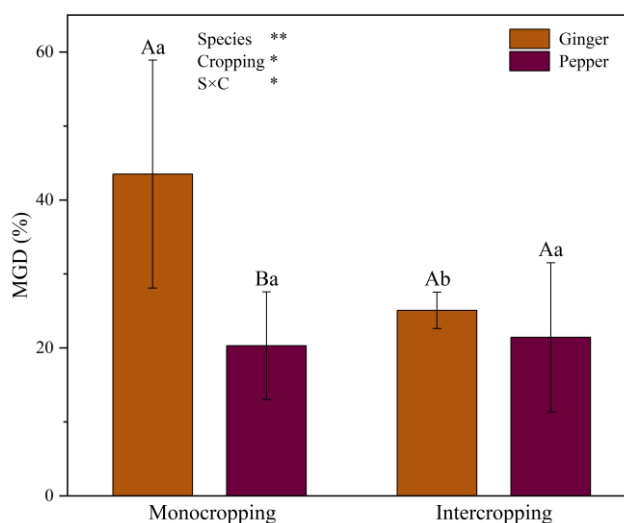


Figure 2. Mycorrhizal growth dependency (MGD) of ginger and pepper under arbuscular mycorrhizal fungi (AMF) inoculation and cropping pattern treatments. Data are expressed as mean $\pm$ standard deviation (SD). Bars represent mean MGD values for each treatment. Lowercase letters indicate significant differences in MGD between monoculture and intercropping for the same crop ($P < 0.05$), whereas uppercase letters indicate significant differences in MGD between ginger and pepper under the same cropping pattern ($P < 0.05$). Asterisks denote significance levels from two-way ANOVA: * $P < 0.05$, ** $P < 0.001$ for main effects (species [S], cropping [C]) and their interaction.

A significant interaction between species and planting treatments on MGD was observed ($F = 6.64$, $P = 0.015$), indicating that the response patterns of different crops to cropping pattern varied. The MGD of ginger under monoculture conditions was significantly higher than that under intercropping ($P < 0.05$; Figure 2), suggesting that intercropping reduced the dependency on AMF. However, no significant difference was found in the MGD of pepper between monoculture and intercropping treatments ($P = 0.99$; Figure 2). Ginger exhibited higher MGD than that of pepper under both cropping patterns, with its dependency on AMF being more responsive to the cropping pattern (monoculture/intercropping), whereas the mycorrhizal response in pepper remained relatively stable.

3.2. *Effects of AMF inoculation and cropping pattern on the agronomic traits of ginger and pepper*

The regulation of crop agronomic traits by cropping pattern and AMF inoculation primarily manifested as independent effects, with significant species differences observed (Table 1). Ginger was more sensitive to intercropping, with its plant height and stem diameter generally being lower throughout the entire growth period than in monoculture. AMF inoculation elicited phase-dependent effects on the growth of ginger plants. At 30 days of growth, AMF inoculation significantly reduced the number of branches under monoculture conditions, and at 60 days, AMF further inhibited plant height and leaf area under intercropping conditions. At the vigorous growth stage at 90 days, although AMF significantly reduced the number of branches in intercropped ginger (3.8 branches), it simultaneously significantly increased leaf area ($P < 0.05$). Under both monoculture and intercropping conditions, AMF-treated plants had larger leaf areas than the NAMF control, demonstrating a “branch number reduction and leaf area enlargement” morphological adjustment. Pepper exhibited different morphological plasticity. Under NAMF conditions, intercropping significantly suppressed plant height at 30, 60, and 120 days ($P < 0.05$). However, after AMF inoculation, this suppression was not significant during most periods ($P > 0.05$), indicating that AMF alleviated intercropping stress. Moreover, AMF significantly regulated the stem development of pepper. From 60 to 150 days, the stem diameter of intercropped pepper was significantly higher than that of monoculture ($P < 0.05$), and from 90 to 150 days, it significantly reduced the plant height of monocropped pepper (at 150 days, AMF: 14.80 cm vs. NAMF: 16.70 cm; $P < 0.05$). Between 120 and 150 days, intercropping further promoted stem diameter growth, resulting in overall compact and robust plant characteristics.

3.3. *Effects of AMF inoculation and cropping pattern on the biomass of ginger and pepper*

The changes in the fresh and dry weights of various tissues of both species showed highly consistent trends (Figure 3a–d). In this study, dry weight was primarily used to assess biomass accumulation. The effects of AMF inoculation and cropping pattern on crop biomass showed significant differences. The growth of ginger was significantly influenced by the interaction between the two factors (aboveground dry weight and total dry weight, $P < 0.05$), whereas pepper showed independent main effects of the two factors (interaction $P > 0.05$). For ginger, the growth-promoting effect of AMF was highly dependent on the cropping pattern. Under monoculture conditions, AMF inoculation significantly increased the total dry weight of ginger (AMF: 40.37 g vs. NAMF: 26.98 g; $P < 0.01$; Figure 3a). This yield enhancement was mainly driven by significant growth in aboveground stem and leaf biomass. Although the dry weight of the underground rhizome exhibited an increasing trend (AMF: 23.81 g vs.

Table 1. Agronomic traits of ginger and pepper under arbuscular mycorrhizal fungi (AMF) inoculation and different cropping patterns at different growth stages.

Cropping Pattern	Inoculation Treatment	Growth Duration	Ginger				Pepper			
			Plant Height	Stem Diameter	Branch	Leaf Area	Plant Height	Stem Diameter	Branch	Leaf Area
			(cm)	(mm)	Number	(cm ²)	(cm)	(mm)	Number	(cm ²)
Monocropping	AMF	30 d	70.30 ± 8.49 Aa	8.54 ± 1.02 Aa	3.0 ± 0.8 Ba	19.61 ± 4.27 Aa	13.09 ± 1.94 Aa	5.20 ± 0.31 Aa	6.5 ± 1.7 Aa	6.76 ± 2.01 Aa
Intercropping			56.47 ± 9.40 Ab	7.30 ± 0.73 Ab	2.3 ± 1.4 Aa	18.24 ± 2.19 Aa	11.78 ± 2.83 Aa	5.53 ± 0.69 Aa	6.0 ± 1.7 Aa	6.04 ± 1.38 Ab
Monocropping	NAMF	30 d	77.36 ± 5.96 Aa	8.68 ± 0.82 Aa	4.0 ± 0.4 Aa	19.90 ± 4.95 Aa	14.42 ± 2.51 Aa	5.03 ± 0.51 Aa	6.3 ± 1.6 Aa	6.58 ± 2.02 Aa
Intercropping			49.72 ± 14.53 Ab	7.02 ± 1.15 Ab	1.8 ± 0.7 Ab	19.82 ± 4.58 Aa	11.03 ± 2.28 Ab	5.09 ± 0.51 Aa	7.0 ± 1.8 Aa	5.79 ± 1.25 Ab
Monocropping	AMF	60 d	80.14 ± 7.24 Aa	9.43 ± 0.60 Aa	5.5 ± 1.3 Aa	35.59 ± 7.98 Aa	12.27 ± 2.02 Aa	6.13 ± 0.35 Ab	9.3 ± 1.3 Aa	10.11 ± 3.49 Aa
Intercropping			60.60 ± 10.27Bb	8.22 ± 0.70 Ab	2.7 ± 1.2 Ab	31.35 ± 7.78 Bb	11.36 ± 2.40 Aa	6.81 ± 0.66 Aa	7.7 ± 1.8 Ab	10.66 ± 3.43 Aa
Monocropping	NAMF	60 d	84.26 ± 2.16 Aa	9.13 ± 0.74 Aa	6.4 ± 1.0 Aa	36.56 ± 8.41 Aa	14.22 ± 1.65 Aa	5.93 ± 0.42 Ab	8.1 ± 1.3 Aa	10.70 ± 2.94 Aa
Intercropping			69.04 ± 10.98 Ab	8.72 ± 0.39 Aa	3.2 ± 1.3 Ab	34.62 ± 8.08 Aa	10.75 ± 2.90 Ab	6.73 ± 0.57 Aa	8.1 ± 1.9 Aa	10.16 ± 1.75 Aa
Monocropping	AMF	90 d	84.89 ± 8.78 Aa	8.94 ± 1.00 Aa	6.8 ± 1.9 Aa	34.07 ± 7.12 Aa	12.68 ± 1.42 Aa	6.00 ± 0.30 Ab	8.2 ± 1.6 Aa	8.74 ± 3.44 Aa
Intercropping			65.99 ± 12.40 Ab	7.87 ± 0.67 Ab	3.8 ± 1.5 Bb	26.95 ± 7.88 Ab	12.33 ± 2.02 Aa	6.78 ± 0.73 Aa	8.2 ± 2.0 Aa	9.38 ± 5.48 Aa
Monocropping	NAMF	90 d	84.66 ± 6.99 Aa	8.69 ± 0.40 Aa	7.4 ± 1.2 Aa	27.14 ± 9.11 Ba	14.75 ± 1.98 Ba	6.00 ± 0.54 Aa	8.5 ± 1.8 Aa	8.33 ± 3.06 Aa
Intercropping			74.62 ± 12.12 Aa	8.24 ± 0.65 Aa	5.4 ± 1.1 Ab	22.98 ± 8.14 Bb	11.08 ± 2.80 Ab	6.12 ± 0.48 Ba	6.8 ± 1.2 Ab	6.64 ± 3.08 Bb
Monocropping	AMF	120 d	78.88 ± 17.61 Aa	8.51 ± 1.14 Aa	7.1 ± 1.6 Aa	36.76 ± 7.36 Aa	12.65 ± 1.38 Aa	6.25 ± 0.54 Ab	8.9 ± 1.7 Aa	11.51 ± 3.41 Ab
Intercropping			69.34 ± 17.50 Aa	6.91 ± 1.11 Ab	3.7 ± 1.3 Ab	35.80 ± 5.22 Aa	11.58 ± 2.92 Aa	7.11 ± 0.54 Aa	8.8 ± 2.0 Aa	13.08 ± 2.97 Aa
Monocropping	NAMF	120 d	72.33 ± 12.90 Aa	7.51 ± 1.04 Aa	7.3 ± 1.4 Aa	35.30 ± 6.60 Aa	14.91 ± 2.16 Ba	6.14 ± 0.61 Aa	9.4 ± 1.6 Aa	11.75 ± 3.59 Aa
Intercropping			67.96 ± 14.67 Aa	7.04 ± 0.96 Aa	5.0 ± 2.2 Ab	33.06 ± 6.55 Aa	11.88 ± 2.68 Ab	6.41 ± 0.40 Ba	8.4 ± 1.9 Aa	12.24 ± 3.56 Aa
Monocropping	AMF	150 d	82.00 ± 9.69 Aa	9.12 ± 0.71 Aa	5.9 ± 1.5 Aa	38.66 ± 5.22 Aa	14.80 ± 1.57 Aa	6.37 ± 0.28 Ab	8.5 ± 1.0 Aa	17.5 ± 3.76 Aa
Intercropping			69.14 ± 6.82 Ab	7.89 ± 0.47 Ab	3.9 ± 1.5 Ab	37.30 ± 5.23 Aa	13.84 ± 2.41 Aa	6.93 ± 0.54 Aa	9.1 ± 1.9 Aa	16.42 ± 3.49 Aa
Monocropping	NAMF	150 d	81.54 ± 4.22 Aa	8.81 ± 0.47 Aa	5.5 ± 1.6 Aa	36.38 ± 5.61 Aa	16.70 ± 1.65 Ba	6.15 ± 0.31 Aa	8.4 ± 1.1 Aa	15.78 ± 2.89 Aa
Intercropping			69.73 ± 13.60 Ab	8.13 ± 0.63 Ab	4.0 ± 2.4 Aa	32.94 ± 5.41 Aa	13.24 ± 2.17 Ab	6.44 ± 0.35 Ba	7.7 ± 1.3 Ba	15.48 ± 3.34 Aa

Note: Within each sampling time, lowercase letters indicate significant differences between monoculture and intercropping under the same AMF treatment ($P < 0.05$), whereas uppercase letters indicate significant differences between AMF-inoculated and non-inoculated treatments under the same cropping pattern ($P < 0.05$).

NAMF:19.89 g), the two-way ANOVA revealed that its growth was primarily affected by the cropping pattern ($P < 0.001$), with no significant effect of the inoculation treatments ($P = 0.51$). Under intercropping conditions, the growth-promoting advantage of AMF disappeared, and inoculation exerted no significant effect on the dry or fresh weight of ginger ($P > 0.05$; Figure 3a and b). Additionally, under the NAMF treatment, no significant difference in total biomass was found between intercropped and monoculture ginger ($P > 0.05$), suggesting that intercropping itself had no significant effect on ginger growth. For pepper, regardless of AMF inoculation, intercropping significantly increased both aboveground and underground biomass ($P < 0.001$; Figure 3c), demonstrating a clear interspecific complementarity advantage. Moreover, AMF inoculation had a significant main effect ($P < 0.05$), overall enhancing the total dry weight of pepper. The biomass analysis of various organs revealed that AMF inoculation significantly increased fruit dry weight ($P < 0.01$; Figure 3c) and fibrous root biomass ($P < 0.05$) but exhibited no significant effects on stem and leaf biomass ($P > 0.05$), which suggests that AMF mainly optimize the allocation of resources to reproductive organs and absorbing roots, thereby enhancing the yield advantage of pepper.

3.4. Effects of AMF inoculation and cropping pattern on the root morphological characteristics and root/shoot ratio of ginger and pepper

The effects of AMF inoculation and cropping pattern on the root morphology of ginger and pepper exhibited interspecific differences (Figure 4). For ginger, AMF inoculation significantly increased root length ($P < 0.01$; Figure 4a), root tip number ($P < 0.01$; Figure 4b), and specific root length ($P < 0.05$; Figure 4d), whereas intercropping significantly increased specific root length ($P < 0.001$). This result indicates that AMF primarily promotes root extension and branching, whereas intercropping enhances root morphology by forming relatively finer, more efficient roots, collectively improving the foraging capacity of the root system.

For pepper, AMF inoculation significantly increased its total root length ($P < 0.05$; Figure 4a) and average root diameter ($P < 0.05$; Figure 4c), whereas intercropping also significantly increased the average root diameter ($P < 0.05$), demonstrating a different root structural response of pepper compared with that of ginger. This result suggests that AMF promotes ginger growth mainly by enhancing root branching and fine root proportion, whereas for pepper, AMF inoculation results in a synergistic effect of root elongation and thickening. The effects of both factors on root morphology were primarily independent main effects, with no significant interaction observed ($P > 0.05$).

The root/shoot ratio of ginger was significantly higher than that of pepper ($P < 0.01$; Figure 5). The root/shoot ratio of ginger was significantly influenced by the interaction between the two factors ($P < 0.01$). Under monoculture conditions, AMF inoculation significantly reduced the root/shoot ratio of ginger from 0.123 to 0.065 ($P < 0.01$; Figure 5a), reflecting a relative increase in aboveground biomass. Although the main effect of cropping pattern was not significant ($P > 0.05$), the interaction between cropping pattern and AMF inoculation suggested that the regulation of root/shoot allocation by AMF was only effective in monoculture systems. In contrast, there were no significant differences in the root/shoot ratio of pepper between treatments ($P > 0.05$; Figure 5b), with values ranging from 0.051 to 0.055, indicating that its root / shoot allocation was insensitive to both AMF inoculation and cropping pattern.

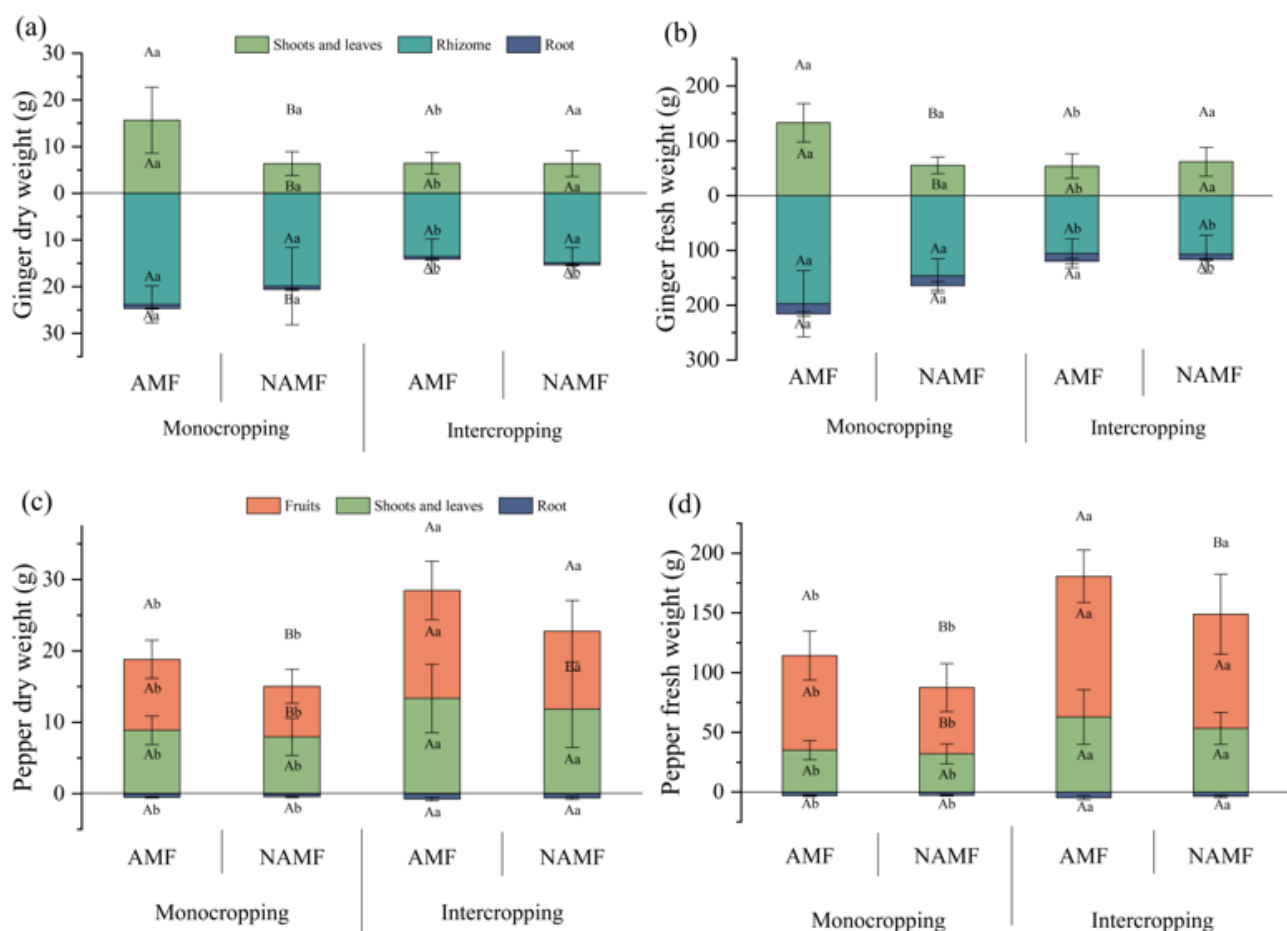


Figure 3. Biomass distribution of ginger and pepper under arbuscular mycorrhizal fungi (AMF) inoculation and cropping pattern treatments. Data are expressed as mean $\pm$ standard deviation (SD). Bars represent mean dry weight (panels a, c) or fresh weight (panels b, d) for each treatment. AMF and NAMF indicate AMF-inoculated and non-inoculated treatments. Lowercase letters indicate significant differences between monoculture and intercropping within the same AMF treatment ($P < 0.05$), whereas uppercase letters indicate significant differences between AMF-inoculated and non-inoculated treatments within the same cropping pattern ($P < 0.05$). Significance labels for individual organs are placed within their corresponding bar segments where space permits; labels for total plant dry or fresh weight are shown above the bars. Due to limited space, significance labels for roots are positioned immediately below their respective segments, adjacent to the bottom of the bars.

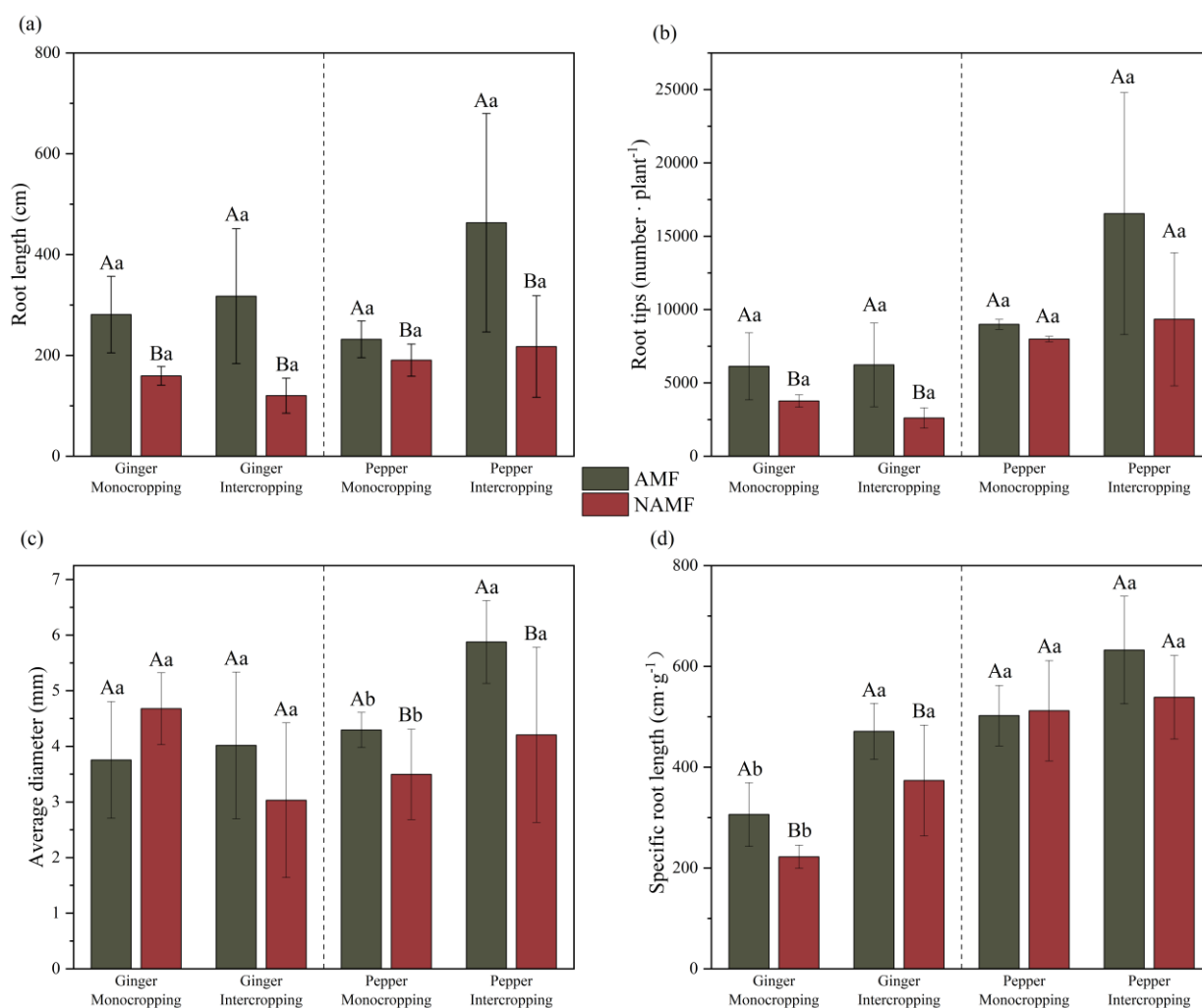


Figure 4. Root morphological characteristics of ginger and pepper under arbuscular mycorrhizal fungi (AMF) inoculation and cropping pattern treatments. Data are expressed as mean $\pm$ standard deviation (SD). Bars represent mean values for root length, root tip number, average diameter, and specific root length for each treatment. AMF and NAMF indicate AMF-inoculated and non-inoculated treatments. Lowercase letters indicate significant differences between monoculture and intercropping within the same AMF treatment ($P < 0.05$), whereas uppercase letters indicate significant differences between AMF-inoculated and non-inoculated treatments within the same cropping pattern ($P < 0.05$).

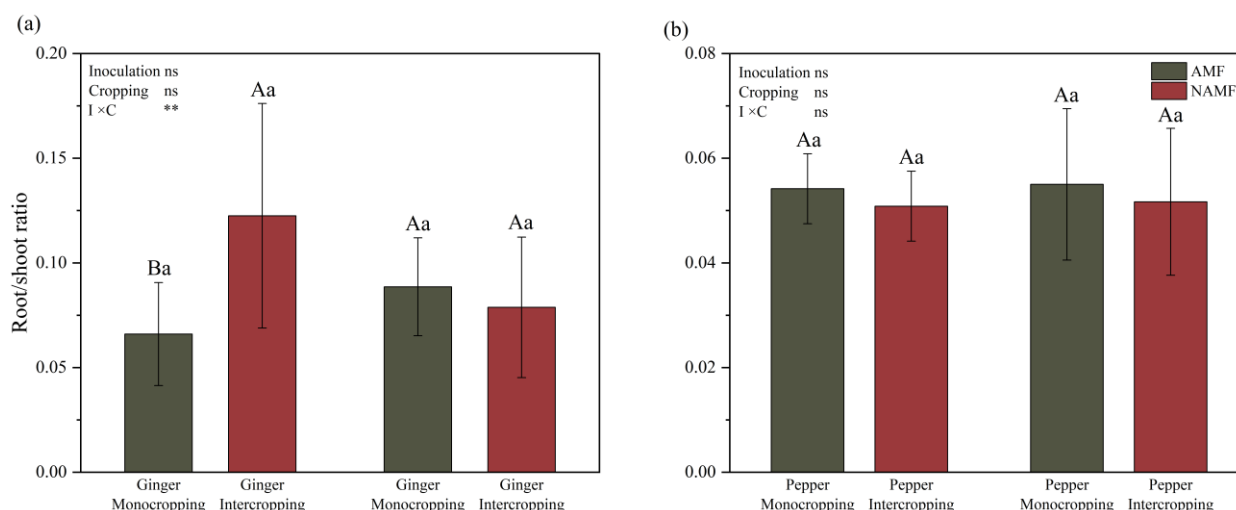


Figure 5. Root/shoot ratio of ginger (a) and pepper (b) under arbuscular mycorrhizal fungi (AMF) inoculation and cropping pattern treatments. Data are expressed as mean $\pm$ standard deviation (SD). Bars represent the mean root/shoot ratio for each treatment. AMF and NAMF indicate AMF-inoculated and non-inoculated treatments. Lowercase letters indicate significant differences between monoculture and intercropping within the same AMF treatment ($P < 0.05$), whereas uppercase letters indicate significant differences between AMF-inoculated and non-inoculated treatments within the same cropping pattern ($P < 0.05$). Asterisks and “ns” denote significance levels from two-way ANOVA: ** $P < 0.001$ for the interaction effect (AMF inoculation [I] $\times$ cropping pattern [C]); ns = not significant.

3.5. Effects of AMF inoculation on LER and interspecific competitiveness in the intercropping system

The intercropping of ginger and pepper conferred a modest but significant land-use advantage, with LER values ranging from 1.03 to 1.08 (all > 1 ; see Table 2). However, the AMF inoculation treatments did not significantly alter the overall productivity of the intercropping system ($P > 0.05$). The $PLER_p$ remained stable at approximately 0.74 under both AMF and NAMF treatments, significantly higher than the $PLER_g$ (0.29–0.34), indicating that pepper exhibited stronger resource utilization capacity in the intercropping system. The $PLER_g$ was significantly lower in the AMF treatment than in the NAMF treatment (0.29 ± 0.01 vs. 0.34 ± 0.05 ; $P < 0.05$), suggesting that the introduction of AMF weakens its growth and resource acquisition ability in intercropping. The analysis of interspecific competitiveness revealed that the competitiveness value of ginger relative to pepper (A_{gp}) was negative, further confirming that pepper is the dominant species. Additionally, AMF inoculation did not significantly alter the competitive relationship between the two species ($P > 0.05$).

Table 2. Land equivalent ratio (LER) and competitiveness (A) in the ginger–pepper intercropping system.

Inoculation treatment	PLER _g	PLER _p	LER	A _{gp} (ginger vs. pepper)
AMF	0.29 ± 0.01 b	0.74 ± 0.08 a	1.03 ± 0.09 a	−0.89 ± 0.15 a
NAMF	0.34 ± 0.05 a	0.74 ± 0.05 a	1.08 ± 0.05 a	−0.79 ± 0.16 a

Note: Lowercase letters “a” and “b” indicate differences between the different treatments (AMF vs. NAMF) at the $P < 0.05$ level.

4. Discussion

4.1. Responses of ginger and pepper growth, development, and root morphology to AMF inoculation

The contrasting strategies employed by ginger and pepper in response to AMF inoculation, reflect fundamental differences in their mycorrhizal dependency and carbon allocation priorities. Ginger exhibited higher MGD than pepper across both cropping systems, consistent with its exceptionally high colonization rate (96.6% vs. 45.0%). Under monoculture conditions, AMF increased the total biomass of ginger by 49.8%, mainly by promoting the growth of aboveground stems and leaves, a response typical of Zingiberaceae species that rely on AMF to overcome limited root hair development and improve phosphorus acquisition [35]. This pronounced responsiveness, coupled with greater plasticity in root morphology (e.g., increased root length and tip number under intercropping), demonstrates that the more mycorrhiza-dependent species exhibits stronger growth and morphological adjustments to AMF (supporting Hypothesis 1). However, this mutualism proved highly sensitive to interspecific competition. In the intercropping system, the positive effect of AMF on ginger’s overall biomass disappeared, and its partial land equivalent ratio (PLER) even declined, suggesting that interspecific competition disrupted the cost-benefit balance of the symbiosis. Notably, AMF still promoted root proliferation in intercropped ginger, yet this underground investment failed to translate into greater rhizome or shoot production, likely due to a carbon allocation trade-off where assimilates were prioritized for maintaining the symbiotic interface rather than expanding harvestable organs [36], or co-limitation by light under the pepper canopy.

In contrast, pepper plants exhibited a remarkably stable and efficient response to AMF regardless of cropping pattern. AMF increased the total dry weight, with resources preferentially allocated to fruits and fibrous roots, and it also alleviated early suppression of pepper plant height during intercropping and promoted stem thickening, resulting in the formation of stronger stems, likely an adaptive morphological adjustment to shaded conditions that enhances mechanical support for heavier fruits and reduces the risk of lodging [37]. Moreover, AMF induced root thickening rather than fine branching, indicating reliance on the external mycelial network for nutrient foraging. This phenotype is characteristic of species with moderate MGD, allowing them to minimize carbon investment in root construction while sustaining nutrient acquisition via the fungal network [38]. Notably, pepper’s responsiveness to AMF is highly context-dependent, with published evidence demonstrating improved symbiotic benefits under low phosphorus conditions yet suppressed effects under high-P soils [39], as well as strong regulation by light intensity [40]. Furthermore, AMF growth promotion effects are known to differ across pepper genotypes [41]. These findings collectively suggest that the positive AMF response observed in pepper within our study reflects the specific agroecological and genetic context of this ginger–pepper intercropping system.

In the present study, we also found that the AMF colonization rate was higher in intercropping pepper than in monoculture, suggesting that the presence of ginger may promote AMF establishment in the pepper rhizosphere. Zingiberaceae species can release flavonoids, organic acids, and other rhizosphere signaling substances that activate the expression of key AMF symbiosis genes (e.g., RAM2 and DMI3) [42,43]. Furthermore, as a highly mycorrhiza-dependent plant, ginger can improve the surrounding environment through mycelial extension [44], thereby facilitating the early establishment of AMF communities in neighboring plant roots [45]. Consequently, AMF differentially regulates root plasticity and resource allocation strategies of the two crops, with ginger mainly adopting a “root expansion and leaf promotion” strategy, whereas pepper features “stem thickening and fruit stabilization” benefiting from the inoculation effect of the neighboring plant. This asymmetry in underground symbiotic strategies not only explains the divergence in aboveground performance but also indicates that species exhibiting a stronger morphological response to AMF do not necessarily gain a competitive advantage in intercropping systems (supporting Hypothesis 2), and highlights the potential regulatory role of AMF in mediating interspecific interactions within intercropping systems.

4.2. Effects of AMF inoculation on land use efficiency and interspecific relationships in the intercropping system

The ginger–pepper intercropping system maintained a stable LER (> 1); however, AMF inoculation did not significantly enhance the overall productivity of the system. Instead, it altered the interspecific resource allocation pattern, as shown by a significant decrease in $PLER_g$, whereas $PLER_p$ remained stable. This suggests that AMF did not exert a synergistic effect in the intercropping system, but may have exacerbated the asymmetry in interspecific competition [46]. This finding contrasts with observations in classical interaction systems (e.g., maize–legume) where AMF promotes nutrient complementarity and increases system productivity [47]. This difference may be due to the significant heterogeneity in crop dependence on AMF and their carbon allocation strategies [48].

Studies have shown that when crops differ substantially in their dependence on AMF, resource allocation in common mycorrhizal networks (CMNs) may favor species with a higher photosynthetic capacity or greater carbon storage [49]. In the present study, pepper exhibited a pronounced carbon sink strength during fruit development and a high demand for mineral nutrients, particularly phosphorus, which likely enabled it to preferentially access phosphorus via CMNs. By contrast, ginger, despite its high dependence on AMF, likely incurred disproportionate carbon costs to maintaining the symbiosis under competitive intercropping conditions, thereby limiting its growth benefits. Consequently, rather than generating the anticipated complementary effect, AMF activity amplified pre-existing competitive asymmetries between the two species. This outcome directly supports Hypothesis 2, which posits that the species exhibiting stronger responsiveness to AMF is not necessarily the one that achieves greater competitive dominance in intercropping systems, particularly when CMN-mediated resource exchange is skewed toward more dominant partners like pepper. This study employed non-sterilized substrates to better reflect natural soil conditions, where crop roots interact with diverse indigenous microorganisms, which can modulate colonization and effectiveness through competitive, antagonistic, or synergistic interactions [50]. The absence of a significant LER increase following AMF inoculation may thus partly reflect these complex biotic constraints, rather than an inherent limitation in the effectiveness of AMF inoculation under field-like conditions.

5. Conclusions

In the ginger–pepper intercropping system, AMF did not deliver the expected synergistic benefits. Although ginger exhibited pronounced morphological plasticity in response to AMF colonization, its relative performance within the intercrop was not correspondingly enhanced. In contrast, pepper benefited more from AMF, disrupting the original balance in resource use between the two species. This indicates that the effectiveness of AMF in intercropping systems hinges on how well the partner crops match in terms of their dependence on mycorrhizae and their physiological traits. Therefore, to fully harness the potential of AMF for sustainable intercropping, crop combinations should be carefully selected based on complementary responses to mycorrhizal symbiosis, which jointly promote system-level outcomes such as efficient resource use or stable coexistence, rather than assuming that all component crops will benefit equally.

Author contributions

Yikai Yang: Writing–original draft, Visualization, Investigation, Funding acquisition. Lei Zhang: Writing–original draft, Methodology, Investigation. Xiaogang Wu: Writing–review & editing, Supervision. Kai Hu: Writing–review & editing, Visualization, Conceptualization. Qin Liang: Visualization, Conceptualization. Wei Wang: Supervision, Funding acquisition, Conceptualization.

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare no conflict of interest.

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