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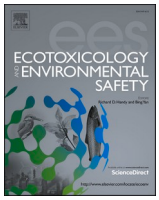

Influence of arbuscular mycorrhizal fungi on mercury accumulation in rice (*Oryza sativa* L.): From enriched isotope tracing perspective

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ABSTRACT

The microorganisms that co-exist between soil and rice systems in heavy metal-contaminated soil environments play important roles in the heavy metal pollution states of rice, as well as in the growth of the rice itself. In this study, in order to further examine the effects of soil microorganisms on the mercury (Hg) uptake of rice plants and determine potential soil phytoremediation agents, an enriched ^{199}Hg isotope was spiked in a series of pot experiments to trace the absorption and migration of Hg and rice growth in the presence of arbuscular mycorrhizal fungi (AMF). It was observed that the AMF inoculations significantly reduced the Hg concentration in the rice. The Hg concentration in rice in the AMF inoculation group was between 52.82% and 96.42% lower than that in the AMF non-inoculation group. It was also interesting to note that the presence of AMF tended to cause Hg (especially methyl-Hg ($Me^{199}Hg$)) to migrate and accumulate in the non-edible parts of the rice, such as the stems and leaves. Under the experimental conditions selected in this study, the proportion of $Me^{199}Hg$ in rice grains decreased from 9.91% to 27.88%. For example, when the exogenous Hg concentration was 0.1 mg/kg, the accumulated methyl-Hg content in the grains of the rice in the AMF inoculation group accounted for only 20.19% of the $Me^{199}Hg$ content in the rice plants, which was significantly lower than that observed in the AMF non-inoculated group (48.07%). AMF also inhibited the absorption of Hg by rice plants, and the decrease in the Hg concentration levels in rice resulted in significant improvements in growth indices, including biomass and micro-indexes, such as antioxidant enzyme activities. The improvements occurred mainly because the AMF formed symbiotic structures with the roots of rice plants, which fixed Hg in the soil. AMF also reduce the bioavailability of Hg by secreting a series of substances and changing the physicochemical properties of the rhizosphere soil. These findings suggest the possibility of using typical co-existing microorganisms for the remediation of soil heavy metal contamination and provide valuable insights into reducing human Hg exposure through rice consumption.

1. Introduction

Heavy metal pollution of soil has become a global environmental problem of great concern in recent years. It is estimated that approximately 235 million ha of farmland soil has been polluted by heavy metals (Wang et al., 2021). Nearly one-fifth of farmland regions in China are contaminated by heavy metals, with cadmium (Cd), arsenic (As) and mercury (Hg) being the most prominent contaminants in farmland soil (Chen et al., 2018; Wu et al., 2022; Yuan et al., 2021). Hg-contaminated farmland accounts for 1.6% of all heavy metal-contaminated farmland in China. Previous studies have found that the average Hg pollution concentration in contaminated farmland soil in China is 0.074 mg/kg, with concentration in farmland soil located near Hg mining areas reaching 335 mg/kg Hg (Dai et al., 2013; Ren et al., 2022; Yuan et al., 2021). Biomagnification and bioaccumulation results in Hg accumulation in the farmland food chain. For example, rice (*Oryza sativa* L.) is

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more likely to absorb and accumulate Hg from the soil and transfer it to edible plant parts (Zhao et al., 2016, 2020). Previous studies reported that the total Hg and methylmercury content of rice grown in former Hg mining sites ranged from 17.5 to 608 μg/kg and 7.31–62.3 μg/kg, respectively, and the methylmercury absorbed by rice accounted for over 30% of the total Hg. Both these ranges far exceed the national food safety limit of 20 μg/kg (Feng et al., 2008; Qiu et al., 2008). Moreover, when compared to bran and straw, rice grains were found to be more likely to take up Hg (Meng et al., 2014), indicating that the Hg content of rice grains may be higher than that of the rhizosphere soil environment and other non-edible parts of the plants (Hang et al., 2018). Therefore, the high accumulations of Hg in rice could result in heavy metal exposure in human consumers and present considerable health risks to those who rely on rice as a staple food (Chowdhury et al., 2020; Gao et al., 2021; Zhao et al., 2020). Typical neurological symptoms of Hg intake include memory loss, depression, and anger (Kim et al., 2016). Hg can also potentially enter the human blood stream and increase the contractility of heart muscles by blocking calcium ions from entering heart muscle cells, which can lead to high blood pressure (Castoldi et al., 2008). To reduce the risks of human Hg exposure, it is important to study related behaviors of Hg in soil–plant systems, and effectively controlling and decreasing Hg accumulation in the food chain (especially in the crop food chain).

Previous studies regarding the behavior of Hg in soil–plant systems and the related control methods have mainly focus on simple laboratory soil preparation systems and the effects of exogenous additives on the absorption and transport of Hg in soil–plant systems (Cozzolino et al., 2016). However, the absorption and transformation processes of Hg in complicated soil environments are inevitably affected by symbiotic microorganisms within soil–plant systems. Many studies have shown that symbiotic microorganisms in the soil can affect the absorption and transportation of heavy metals in soil–plant systems (Bellabarba et al., 2019; Efe, 2020; Jach et al., 2022; Solís-Ramos et al., 2021). For example, arbuscular mycorrhizal fungi (AMF) are typical soil microorganisms which are widely distributed in natural environments. AMF can form symbiotic systems with over 80% of terrestrial plant species (Leonie et al., 2017; Ma et al., 2022; Zhang et al., 2019a). AMF are also widely distributed in paddy–type soil, with as many as 30 species identified in the paddy soil of Sichuan, China. Majority of these species belonged to the family Glomeraceae (Panneerselvam et al., 2020; Wang et al., 2008). In addition, many studies have shown that the presence of AMF can reduce the negative effects of external stress (such as salinization, drought and heavy metal pollution) on plant growth and physiological indicators by changing the root structures of plants and exerting other effects (Chen et al., 2018; Pavithra and Yapa, 2018; Riaz et al., 2021). For example, symbiotic systems between AMF and host plants can increase the surface area of plant roots to facilitate nutrient and water absorption by plants. Chen et al. (2018) found that Cd primarily accumulates and stabilizes in the mycelium of AMF–plant symbiotic systems, thereby limiting its transfer to plant cells. Furthermore, AMF can alter the availability and related activities of heavy metals in the soil by secreting specific substances that inhibit the transport of heavy metals into plants. For example, Hu et al. (2019) found that *Rhizophagus intraradices*, *Glomus versiforme* and *Funneliformis mosseae* can increase the total glomalin-related soil protein (GRSP) content in the soil and decrease the accumulation of lead (Pb) and Cd in maize. Special substances secreted by AMF can also change the physical and chemical properties of the rhizosphere soil (such as pH, soil redox potential and other factors), which then affects the bioavailability of heavy metals in the soil, thereby reducing the transport of heavy metals into plants (Liu et al., 2020; Riaz et al., 2021; Shen et al., 2006). Overall, the presence of AMF, which includes distributed soil microorganisms, could potentially affect the absorption and transfer of heavy metals by plants and improve plant growth under heavy metal stress (Shen et al., 2022). It is highly likely that AMF (co-existing in soil–plant systems) could be utilized as an effective microbial remediation method for soil Hg contamination. Therefore, researching about the absorption and transfer on soil Hg in plants and the effect of plant growth and physiological indexes under AMF inoculation can help propose a feasible soil Hg pollution remediation method. This method has important practical significance in reducing the risk of heavy metal exposure in food crops and the human body. However, studies on the absorption and transfer of soil Hg in plant–microorganism symbiotic systems and the impact of AMF inoculation on plant growth in Hg-contaminated soil are relatively scarce. Compared with other heavy metals, Hg is a trace element that exists in complicated and diverse forms (example.g., inorganic Hg^{2+}, Hg^0, methylmercury, ethylmercury and dimethylmercury) in natural environments, and the presence of special gaseous Hg can cause Hg vapor volatilization. Those factors tend to elevate the complexity and difficulty of Hg detection (Da Silva et al., 2022).

The present study aimed examine the absorption and migration processes of Hg in plants and to investigate the effects of Hg on plant growth under AMF inoculation conditions. We adopted a technique of single enrichment stable Hg isotope labeling combined with inductively coupled plasma-mass spectrometry (ICP-MS) Among them, single-enrichment stable Hg isotope labeling technology can be utilized to distinguish newly added Hg from Hg already present in the environment, and can accurately and clearly distinguish the biogeochemical behavior of exogenous Hg in complex soil environmental media (Harrisa et al., 2007). The integration of ICP-MS and Hg isotope pre-enrichment technologies has substantially increased the accuracy and efficiency of trace Hg analysis and detection technologies (Strickman and Mitchell, 2017; Zhang et al., 2021). In the present study, we selected ^{199}Hg as the labeled Hg isotope, rice (*Oryza sativa* L.) as the test plant, and *Glomus etunicatum* and *Glomus mosseae* (AMF with strong adaptability) as inocula. In this study, the absorption and migration behavior of Hg in rice plants in the presence of AMF and the effects of Hg on rice growth and physiological indices were investigated using greenhouse experiments. Then, through the explorations of the AMF–plant symbiotic system, the rhizosphere secretions, rhizosphere soil environments, and other related environmental media were examined to clarify the mechanism of the effects of AMF on rice grown in Hg-contaminated soil. The results of this study can assist in clarifying the role of symbiotic soil microorganisms in the treatment of soil Hg pollution in farmland regions, which will also provide a convenient and rapid in situ remediation method for the treatment of soil Hg pollution.

2. Materials and methods

2.1. Soil preparation, fungi, and plant cultivation

In the present study, soil samples were collected from a flooded paddy field surface layer (1–20 cm) at Changshu, Jiangsu, China (Latitude: 31°43′35″N; Longitude: 120°45′43″E). The collected soil was air-dried for two weeks and then passed through a 2-mm sieve. The characteristics of the collected soil samples are listed in Table S1. To remove microorganisms, the soil was sterilized using steam at 120 °C and 0.1 MPa for 2 h and then air dried in a sterile environment.

Two types of AMF inocula consisting of infective propagules of *Glomus etunicatum* and *Glomus mosseae* (1:1 m/m) provided by the Beijing Academy of Agriculture and Forestry Sciences were used in the experiment. The inoculant was composed of a mix of rhizosphere soil containing mycorrhizal fungal spores, hyphae and host plant root segments. Each experimental pot was amended with 25 g of AMF at a depth of 5 cm.

The rice cultivar Zhennuo 20 was selected for the experiment. The seeds of Zhennuo 20 were obtained from the Agricultural Circulation Park of Yi'an District in Tongling, China. After the seeds were disinfected with 10% H_2O_2 for 15 min, they were washed three times with sterile distilled water. The seeds were germinated under dark conditions for 48 h, raised in sterilized nutrient soil, and grown to the four-leaf stage for transplantation. The plants were grown for 150 days in a

greenhouse under day/night temperatures of 28/20 °C, with a relative humidity of 80–90%. In addition, to ensure that the plants received sufficient nutrition, Hoagland solution was added twice a week; the compositions of Hoagland are shown in Table S2 (Ren et al., 2014).

2.2. Pot experiment design and Hg^{2+} spiking experiment

Rice plants were used as the host plants for the pot culture experiment, and a mixture of *G. etunicatum* and *G. mosseae* (1:1 m/m) was used as the inoculum. Two treatments were employed, which included AMF inoculation groups (+M) and AMF non-inoculation groups (-M), and four series of Hg(II) concentrations (0, 0.1, 1 and 2 mg/kg) were employed to investigate the absorption and transfer of Hg across the soil–plant interface and the subsequent fate of Hg. In this study, a ^{199}Hg tracer is used. The configured $^{199}Hg^{2+}$ tracer solution in ultrapure water was spiked into the sterilized soil to obtain the target soil Hg concentration. Each experimental group contained three replicates. All of the plastic pots used in this experiment were 22 cm in height and 16 cm in diameter and contained 2.5 kg of soil. The configured $^{199}Hg^{2+}$ tracer solution in ultrapure water was spiked into the sterilized soil to obtain final soil Hg concentrations of 0.1, 1 and 2 mg/kg. All $^{199}Hg^{2+}$ pollutants were added one month before the completion of the incubation. Greenhouse pot experiments were conducted at the Chinese Research Academy of Environmental Sciences. After 150 days, the rice plants were harvested.

2.3. Determination of plant growth and physiological indexes and scanning electron microscope (SEM) analysis

After harvest, the rice plants were cleaned four times with deionized water. The height of the intact rice plants was measured thrice using a tape measure. The plants were then cut and separated into roots, stems, leaves and rice grains. All parts of the plants were freeze dried using freeze dryer (FD-1A-50, Biocool, China) for 72 h. Thereafter, the dry biomass of each rice part was measured. The heights and dry biomass values were measured three times and averaged.

The photosynthetic rate and chlorophyll content were measured during the experiment two months after the plants had been transplanted. The total chlorophyll content of the leaves was determined using a chlorophyll tester (TYS-B, Sai Mio, China). Three pieces of parietal leaves were selected from each pot of rice to measure the chlorophyll content. Photosynthetic rates were determined using a photosynthetic apparatus (3051D, Sai Mio, China). Photosynthetic indices were measured from 10:00–12:00 (noon) local time. The chlorophyll content and photosynthetic rates were measured three times, and the mean values were calculated.

A plant enzyme-linked immunoassay was used to determine the activities of antioxidant enzyme systems and malondialdehyde (MDA) concentrations in the plant roots and leaves. Briefly, 1.00 g of fresh rice roots or leaves were sampled and homogenized in 3 mL of 50 mmol/L phosphate buffer (PBS, pH 7.8) in an ice water bath. Subsequently, the extracts were centrifuged at 10,000 r/min and 4 °C for 20 min (3 K-15, Sigma, Germany). Supernatants were removed to measure superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and MDA levels using commercial ELISA kits (Thermo Fisher Scientific, USA) according to the manufacturer's instructions. A sample solution of 10 μL, sample diluent of 40 μL and horseradish peroxidase of 100 μL were added to the sample holes in this order, which was then sealed with a sealing plate membrane and incubated for 1 h at 37 °C under dark conditions. The solution was poured out and the samples were cleaned five times with a washing buffer. Thereafter, substrates (50 μL) were added into the sample holes. Incubation was performed in the dark for 15 min at 37 °C. Finally, the sealing film was unwrapped and 50 μL of termination solution were added into each hole, after which absorbance of the solution was measured.

For SEM analyses, the materials were fixed with 2.5% glutaraldehyde (0.1 M PBS, pH 7.2) for 24 h at 4 °C (Wu et al., 2015). The samples were then rinsed thrice in PBS and post-fixed in buffered 1% OsO_4 for 2 h. The samples were dehydrated using gradient concentrations of ethanol solutions of 30%, 50%, 70%, 80%, 90% and 95% for 15 min at each concentration. After removing OsO_4, the samples were treated twice with 100% ethanol for 20 min for each treatment. The samples were treated with a mixture of ethanol and isoamyl acetate (1:1 v/v) for 30 min. After treatment with pure isoamyl acetate for 1 h, the samples were observed using a scanning electron microscope (FEI Quanta 450, FEI, USA).

2.4. Determination of AMF colonization rate, soil properties and root exudates

One month after transplantation, root samples were collected to measure mycorrhizal infection rates. Root samples were stained following the procedure described by Phillips and Hayman (1970). Briefly, root samples were heated at 90 °C in 10% KOH for 30 min, washed with tap water, acidified with 30% HCl, and stained with 0.05% trypan blue. Excess staining was removed using lactic acid and glycerol. Subsequently, 100 roots were randomly collected from each subsample to observe AMF colonization. The soil samples were air-dried and passed through a 2-mm sieve. Soil pH was determined using a pH meter (PHB-4, Lei Ci, China), and the samples were soaked in deionized water (1:2.5 v/v). The soil and water mixture were shaken vigorously for 5 min and allowed to settle for 30 min. The pH of the supernatant was determined using a pH meter. The measurement process was repeated three times, and the average value was calculated.

Root samples were collected after 150 days of growth. The rice roots were gently rinsed using ultrapure water and soaked in a 0.5 mmol/L $CaCl_2$ solution for 30 min. The root samples were cultured for 4 h under sufficient light conditions. Next, the samples were removed and washed three times with ultrapure water. The washing solution was then combined with a $CaCl_2$ solution to soak the plants and form rice root exudates. For the measurement of organic acids, the mixed samples were ultrasonically extracted for 30 min, bathed in water at 60 °C for 1 h, and centrifuged using 10 mmol/L K_2HPO_4. The supernatant was analyzed using liquid chromatography (LC Thermo 300, Thermo Fisher, USA). Amino acid concentrations were determined using an automatic amino acid analyzer (LA 8080, Hitachi, Japan). Prior to the analysis, the samples and 1.5 mL 0.02 mol/L HCl were added to the activated C^{18} pretreatment column, passed through a 0.45-μM filter membrane, and then placed onto the machine. GRSP concentration was determined according to the procedure described by Wright et al. (1998), with some modifications (Tian et al., 2020). Each soil sample was placed into a centrifuge tube and leached with 50 mmol/L sodium citrate (pH 8.0) at 121 °C for 60 min. The samples were centrifuged (4500 r/min) for 5 min and stored at 4 °C for further analyses. Coomassie Brilliant Blue G-250 (0.10 g) was dissolved in 50 mL of 95% ethanol, and 100 mL of 85% phosphoric acid and distilled water were added to increase the volume to 1 L. The absorbance was measured at a wavelength of 595 nm and the GRSP concentration of the sample was determined using the standard curve.

2.5. Determination of Hg concentration in plants

After harvesting, rice tissue samples were cleaned in the laboratory using ultrapure water and freeze-dried for 72 h. The mass of each rice plant sample was recorded after the completion of the drying process. Freeze-dried rice plant tissues were triturated and then ground using a 200-mesh sieve. To accurately analyze the total-Hg ($T^{199}Hg$) concentrations in rice samples, each rice tissue sample (0.20 g) was digested by 5 mL of aqua regia (3:1 v(HCl)/v(HNO_3)), then heated in a water bath for 5 min at 95 °C. The digestion solution was then supplemented with 10 mL BrCl and kept in the water bath for 30 min at 95 °C. An appropriate volume of the digested sample was collected for $T^{199}Hg$

determination by ICP-MS (Agilent 7700X, Agilent Technologies Inc., USA) following preconcentration with deuterium-depleted water (DDW), HCl, and $SnCl_2$, purging with N_2, and thermal desorption.

For methyl-Hg ($Me^{199}Hg$) analysis processes, 0.20 g of dried samples were digested with 25% KOH/CH_3OH and heated at 75 °C in a water bath for 3 h. Samples were digested and acidified using concentrated HCl. The digested samples were shaken for 30 min and centrifuged for 30 min at 3000 r/min after adding 10 mL of CH_2Cl_2, back-extracted from the solvent phase into water, and subjected to aqueous-phase ethylation. Hg separated from the samples was then purged with N_2 using a Tenax trap. Next, the Tenax was heated to 80–120 °C to decompose various forms of Hg to Hg^0 for ICP-MS detection (Liu et al., 2022, 2021; Meng et al., 2010).

2.6. Quality control and data analysis

In this study, triplicate treatment samples were assessed to ensure the quality of the results. Certified reference materials (CRM) were used. All of the procedure blanks determined were found to be below the method detection limits (0.2 ng/g for $T^{199}Hg$ and 0.01 ng/g for $Me^{199}Hg$ in rice tissues), and the recoveries of $T^{199}Hg$ and $Me^{199}Hg$ were both between 80% and 120% for all matrix spikes and CRM (Table S3).

The concentrations of $T^{199}Hg$ and $Me^{199}Hg$ in the rice tissues that originated from the spiked ^{199}Hg tracer were calculated based on the measured concentrations of ^{202}Hg and ^{199}Hg isotopes of $T^{199}Hg$ and $Me^{199}Hg$ and the natural abundances of ^{199}Hg and ^{202}Hg (Liu et al., 2021; Mao et al., 2013) using Eq. (1) and Eq. (2):

$$C_{T199Hg}(tracer) = C_{total-199Hg} - P_{199}C_{total-202Hg}/P_{202} \quad (1)$$

$$C_{Me199Hg}(tracer) = C_{methyl-199Hg} - P_{199}C_{methyl-202Hg}/P_{202} \quad (2)$$

where, $C_{total-199Hg}$ and $C_{total-202Hg}$ are the measured concentrations of the ^{199}Hg and ^{202}Hg isotopes of $T^{199}Hg$ at the end of rice culture, respectively; $C_{methyl-199Hg}$ and $C_{methyl-202Hg}$ represent the measured concentrations of the ^{199}Hg and ^{202}Hg isotopes of $Me^{199}Hg$, respectively; P_{199} and P_{202} indicate the natural isotopic abundances of ^{199}Hg and ^{202}Hg, respectively (Table S4); and CT199Hg(tracer) and CMe199Hg(tracer) are the concentrations of $T^{199}Hg$ and $Me^{199}Hg$, respectively, in samples that originated from the spiked ^{199}Hg tracer. The distribution and transfer of Hg among different tissues of rice were represented by transfer factors (TFs), which were calculated as follows:

TF = Ctissue1/Ctissue2, where Ctissue1 and Ctissue2 refer to the Hg content in different parts of the rice plant.

In this study, the transient signals recorded by ICP-MS and all figures were processed and plotted using Origin 9.0, and Hg isotopes were quantified based on the peak areas of the corresponding species. In addition, statistical analysis was performed using SPSS 24.0, with all data shown as the means ± standard derivations (means ± S.D.) (n = 3). One-way analysis of variance at a confidence level of 95% was used to test the differences between the treatments, followed by comparisons of the treatment means using the least significant difference tests ($p < 0.05$).

3. Results and discussion

3.1. Inoculation with AMF significantly inhibited the uptake of heavy metals by rice

The experimental results revealed that the Hg concentration in rice increased with increasing Hg concentration in the soil, whereas AMF inoculation reduced the uptake rate and amount of Hg by rice (Fig. 1 and Table S5). In general, with an increase in the Hg concentration in the soil, the amount of Hg absorbed by rice ($T^{199}Hg$ and $Me^{199}Hg$) showed a linearly increasing trend (Fig. 1). However, AMF inoculation significantly reduced the slope at which heavy metals entered plants. As shown in Fig. 1a and b, for $T^{199}Hg$, the linear growth slope of the AMF non-inoculation group was 1352.69, while that of the AMF inoculation group was 454.91, which was significantly lower than that of the AMF non-inoculation group, which suggests that AMF inoculation significantly reduces the incorporation of Hg taken up by plants. AMF inoculation also significantly inhibited the concentrations of Hg taken up by the plants when the concentrations of Hg in the soil were consistent. As detailed in Fig. 1a, when the concentrations of Hg in the soil were 0.1, 1 and 2 mg/kg, the $T^{199}Hg$ concentrations in rice without AMF inoculation were 27.94, 5.72 and 2.52 times that those in rice with AMF

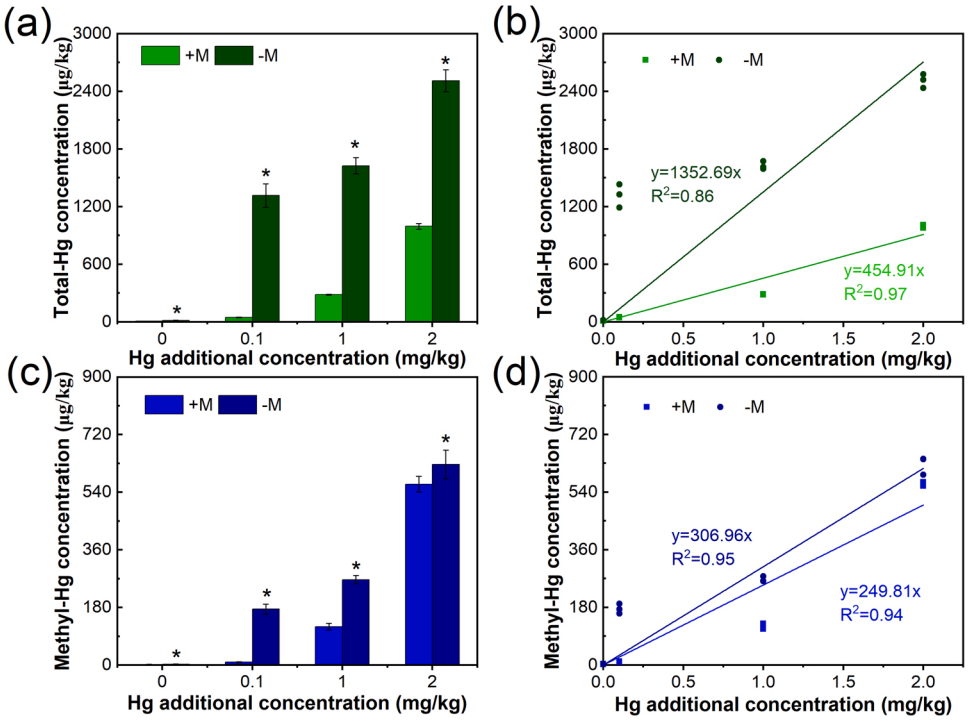

Fig. 1. Effects of AMF on the Hg concentration of rice (means ± S.D., n = 3) under different Hg concentrations, and linear fitting diagram of Hg. (a) total-Hg ($T^{199}Hg$) concentration; (b) linear fitting diagram of $T^{199}Hg$; (c) methyl-Hg ($Me^{199}Hg$) concentration; (d) linear fitting diagram of $Me^{199}Hg$. +M: AMF inoculation groups. -M: AMF non-inoculation groups. The "* " represents significant differences between inoculation and non-inoculation under the same exogenous Hg concentration ($p < 0.05$).

inoculation.

Methylmercury is the most toxic form of Hg (Beauvais-Fluck et al., 2018a; Cosio and Renault, 2020). Therefore, the toxicity of methylmercury to plants differs from that of the other forms of Hg (Beauvais-Fluck et al., 2018a). Previous studies have confirmed that the inhibition of metabolic pathways (Cosio and Renault, 2020) and the induction of oxidative stress responses under methylmercury exposure are much more severe than those induced by inorganic Hg (Beauvais--Fluck et al., 2018b), which directly inhibits normal growth activity and aggravates plant damage (Farooq et al., 2019; Ran et al., 2022). Therefore, this study investigated the $Me^{199}Hg$ concentration in rice. The $Me^{199}Hg$ intake trends in rice in the AMF inoculation and non-inoculation groups were similar to those of $T^{199}Hg$ (Fig. 1 and Table S6). For example, the linear growth slope of the AMF inoculation group was 248.81, which was significantly lower than that of the AMF non-inoculation group ($k = 306.96$) (Fig. 1d). In addition, as shown in Fig. 1c, when treated with a series of doses (0.1, 1 and 2 mg/kg) of Hg, the $Me^{199}Hg$ concentrations in rice without AMF inoculation were 18.46, 2.23 and 1.11 times those in rice with AMF inoculation, respectively. The findings indicated that AMF inoculation significantly inhibited the uptake of $Me^{199}Hg$. Overall, the above-described phenomena demonstrate that AMF inoculation could inhibit Hg absorption by plants, possibly due to the immobilization of heavy metals by the symbiotic structures between host plants and AMF (Amir et al., 2013).

3.2. *Inoculation with AMF significantly improved the growth indicators of rice under heavy metal stress*

Plant growth indicators are the most intuitive means for examining the effects of heavy metal stress. To better understand the impact of heavy metal exposure on rice, this study assessed the effects of AMF inoculation on rice growth indexes under Hg stress. The effects of AMF inoculation on rice growth indices (Fig. 2a and b) were in the same way to the effects of AMF inoculation on rice uptake of the heavy metal Hg (Fig. 1). In other words, under the same heavy metal stress conditions, AMF inoculation reduced the absorption of heavy metals by rice plants, thereby reducing the damage caused to plant growth. As shown in Fig. 2a and b, with an increase in Hg concentration, the basic growth indices of rice, such as biomass (including aboveground biomass and underground biomass) and plant height, decreased. However, under the same concentration of Hg stress, the growth indices of rice in the AMF inoculation group were significantly better than those in the AMF non-inoculation group. When the Hg concentrations were 0, 0.1, 1 and 2 mg/kg, the biomasses of the AMF inoculation group were 76.00, 70.26, 48.08 and 27.10 g/pot, respectively; these values were 1.27–1.66 times that of the AMF non-inoculation group (Fig. 2a). The same was true for the height of rice plants (Fig. 2b). When the Hg concentrations were 0, 0.1, 1 and 2 mg/kg, the plant heights of the AMF inoculation group were 116.00, 112.33, 96.67 and 77.33 cm, respectively, which were significantly higher than the AMF non-inoculation group (107.33, 102.00, 90.67 and 73.67 cm, respectively). Therefore, the results showed that although inoculation with AMF can improve the growth conditions of rice in the absence of Hg stress or the presence of minor Hg stress, the changing trend of the rice growth index was consistent with the Hg content in rice, regardless of whether the plants were inoculated with AMF (e.g., the higher the Hg content, the worse the growth index), which further indicated that the content of heavy metals entering the plant body was a direct factor affecting the growth indices.

In rice, photosynthesis is an important biochemical reaction that determines plant growth indices (Teng et al., 2022). In this study, further evidence was found that the effects of AMF inoculation on rice photosynthesis (Fig. 2c) were consistent with the effect of AMF inoculation on rice growth indices and Hg concentrations absorbed by rice (Figs. 1, 2a and b). As shown in Figs. S1 and 2c, with an increase in Hg concentration in the soil, the chlorophyll content and photosynthetic rate in rice leaves significantly decreased, accompanied by significant increases in MDA in the rice leaves (Fig. 2d). MDA is a product of cell membrane lipid peroxidation, and its content is an important indicator of the strength of cell membrane lipid peroxidation and the degree of plasma membrane destruction (Lenoir et al., 2016). Generally, MDA concentrations increase with the intensification of abiotic or biotic stress. It was observed in this study that with an increase in the Hg concentrations in the soil, the MDA concentrations increased (Fig. 2d), which indicated that heavy metal stress conditions would result in

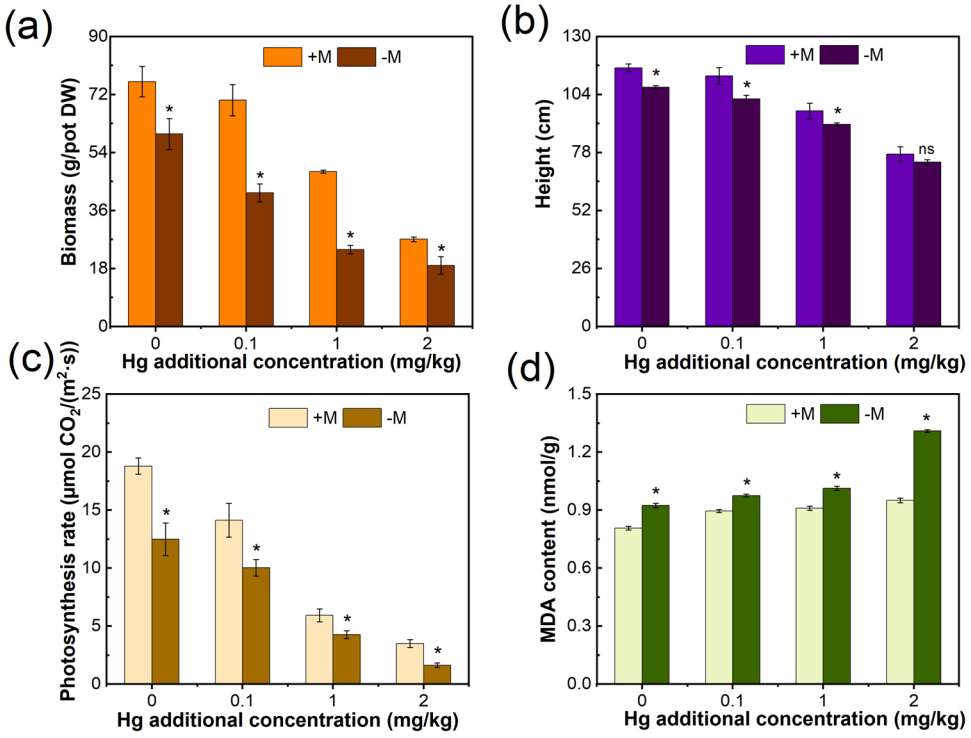

Fig. 2. Effects of AMF on rice physiological and biochemical indexes (means ± S.D., n = 3) under different Hg concentrations. (a) biomass; (b) height; (c) photosynthetic rate; (d) MDA concentrations. +M: AMF inoculation groups. -M: AMF non-inoculation groups. DW: dry weight. The "* " represents significant differences between inoculation and non-inoculation under the same exogenous Hg concentration ($p < 0.05$). The "ns" indicates that there is no significant difference between inoculation and non-inoculation under the same exogenous Hg concentration ($p > 0.05$).

damage to rice leaves, leading to a significant decrease in the chlorophyll content and photosynthetic rate (Figs. S1 and 2c). The final intuitive conclusion was that all basic growth indices of the plants were reduced by exposure to heavy metal stress (Fig. 2a and b). The SEM results also revealed the aforementioned outcome. As shown in Fig. 3, with an increase in Hg concentration (0, 0.1, 1 and 2 mg/kg), rice mesophyll cells gradually began to appear deformed, damaged and eventually ruptured (Fig. 3a–d). However, under Hg stress at the same concentration, AMF inoculation increased photosynthesis in rice by reducing the generation of MDA in the rice leaves, thus alleviating the effect of heavy metal stress on rice. For example, when the concentrations of Hg in the soil were 0.1, 1 and 2 mg/kg, the MDA concentrations of rice leaves in the AMF inoculation group were only 72.58–91.78% of the MDA concentrations in the AMF non-inoculation group (Fig. 2d), which significantly reduced the degree of damage to rice leaves in the AMF inoculation group compared to the AMF non-inoculation group. When the Hg concentration was 0.1 mg/kg, the vascular cells and parenchyma cells of rice leaves were split, mesophyll cells were slightly damaged, and inhomogeneity was increased, while the cell walls of rice mesophyll cells in the AMF inoculation group were relatively more uniform (Fig. 3b and f). When the Hg concentration was 1 mg/kg, the cell walls of the mesophyll cells of rice leaves in the AMF non-inoculation group were severely uneven and cracked. For the AMF inoculation group, the cell wall of the rice leaves was also significantly uneven, but the cell wall remained intact (Fig. 3c and g). Subsequently, when the Hg concentration was increased to 2 mg/kg, the volume of mesophyll cells in the AMF non-inoculation group increased and became severely cracked, whereas the volume of mesophyll cells in rice leaves inoculated with AMF increased; however, the cell structure was relatively intact without obvious fragmentation (Fig. 3d and h). The results indicated that under the same heavy metal stress conditions, the photosynthetic intensity of rice inoculated with AMF was significantly higher than that of the AMF non-inoculation group. At Hg concentrations of0.1, 1 and 2 mg/kg, the photosynthetic rate of rice inoculated with AMF was 1.39–2.15 times that of the AMF non-inoculation group (Fig. 2c). As previously mentioned, these results demonstrated that AMF inoculation could improve the growth state of plants under heavy metal stress, and this phenomenon was directly related to the reduction in heavy metal content in plants via AMF inoculation.

3.3. Inoculation with AMF significantly improved the physiological and biochemical indexes of plants under heavy metal stress

To further verify that AMF inoculation mainly affects plant growth by changing the concentrations of Hg entering rice plants, we examined the effects of AMF inoculation on the physiological and biochemical indices of rice (antioxidant enzyme system activities). The results revealed that inoculation significantly enhanced the activity of several typical antioxidant enzymes in rice roots. This effect was closely related to the reduction of Hg uptake in rice after AMF inoculation (Figs. 1 and 4). Fig. 4 shows that with an increase in Hg concentration in the soil, the activities of four typical antioxidant enzymes (SOD, CAT, POD and APX) in rice roots gradually increased. The effects of heavy metals on plants mainly affect the production of reactive oxygen species such as H_2O_2 and $O_2^{\bullet-}$, which destroy the oxidative balance of plant cells, thereby inhibiting growth (Riaz et al., 2021; Rizwan et al., 2019). The stress resistance system in rice reduces the damage caused by heavy metals to the cellular oxidation balance by increasing the activity of antioxidant enzymes. SOD in rice root cells is involved in the first step in which antioxidant enzymes clear ROS to generate H_2O_2, which is immediately decomposed into completely harmless water by CAT and POD (Yang et al., 2020). APX uses H_2O_2 as an oxidant to catalyze the production of monodehydroascorbic acid and H_2O (Caverzan et al., 2012). Thus, the four antioxidant enzymes in the rice roots form a relatively complete antioxidant chain.

After AMF inoculation, the activities of antioxidant enzymes increased. When the Hg concentrations were 0, 0.1, 1 and 2 mg/kg, SOD activity in the AMF inoculation group was 596.15, 627.43, 667.73 and 683.93 U/g, respectively, which was significantly higher than the AMF non-inoculation group (576.93, 609.00, 653.22 and 670.89 U/g, respectively) (Fig. 4a). The activities of CAT and POD in the AMF inoculation group were 84.16 and 3.96, 89.78 and 4.44, 95.99 and 4.73 and 101.83 and 5.11 U/g, respectively, and higher than the AMF non-inoculation group (78.63 and 3.90, 86.76 and 4.28, 92.79 and 4.59 and 98.66 and 4.87 U/g, respectively) at Hg concentrations of 0, 0.1, 1 and 2 mg/kg, respectively (Fig. 4b and c). The same was true for APX, for which the enzyme activity of the AMF inoculation group was 5.06, 5.38, 5.65 and 6.38 U/g, respectively, and significantly higher than the AMF non-inoculation group (4.05, 4.73, 5.08 and 5.35 U/g,

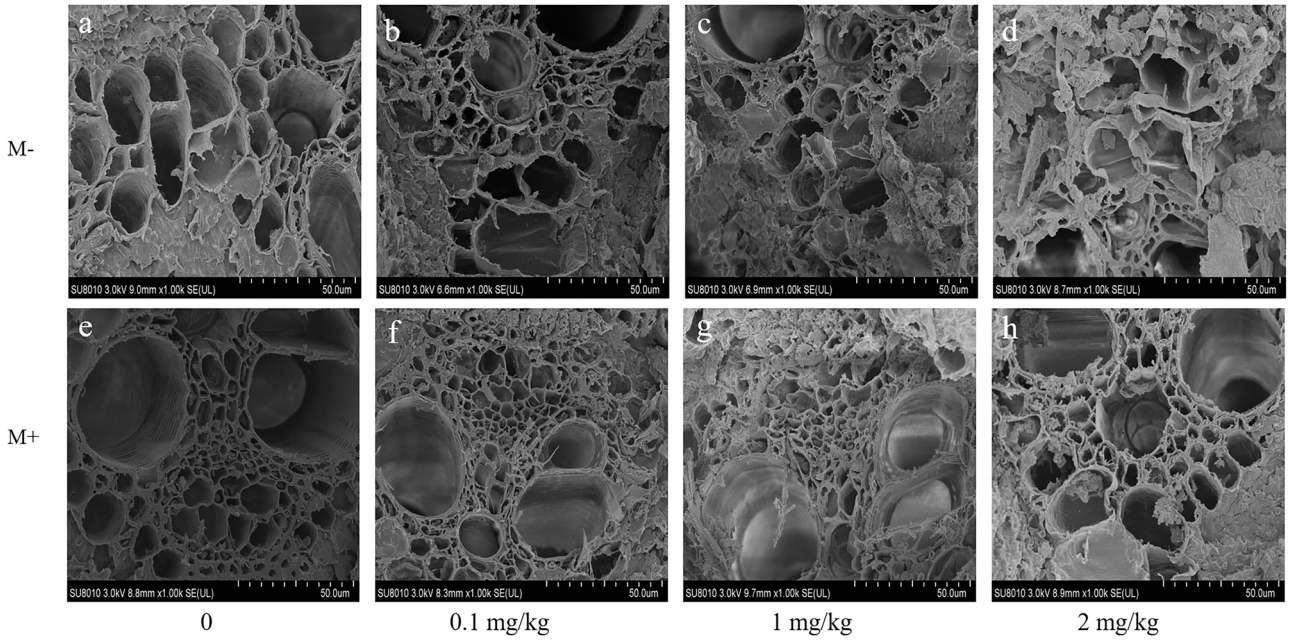

Fig. 3. SEM of the leaves of rice under different Hg concentrations. (a) -M, Hg 0; (b) -M, Hg 0.1 mg/kg; (c) -M, Hg 1 mg/kg; (d) -M, Hg 2 mg/kg; (e) +M, Hg 0; (f) +M, Hg 0.1 mg/kg; (g) +M, Hg 1 mg/kg; (h) +M, Hg 2 mg/kg. +M: AMF inoculation groups. -M: AMF non-inoculation groups.

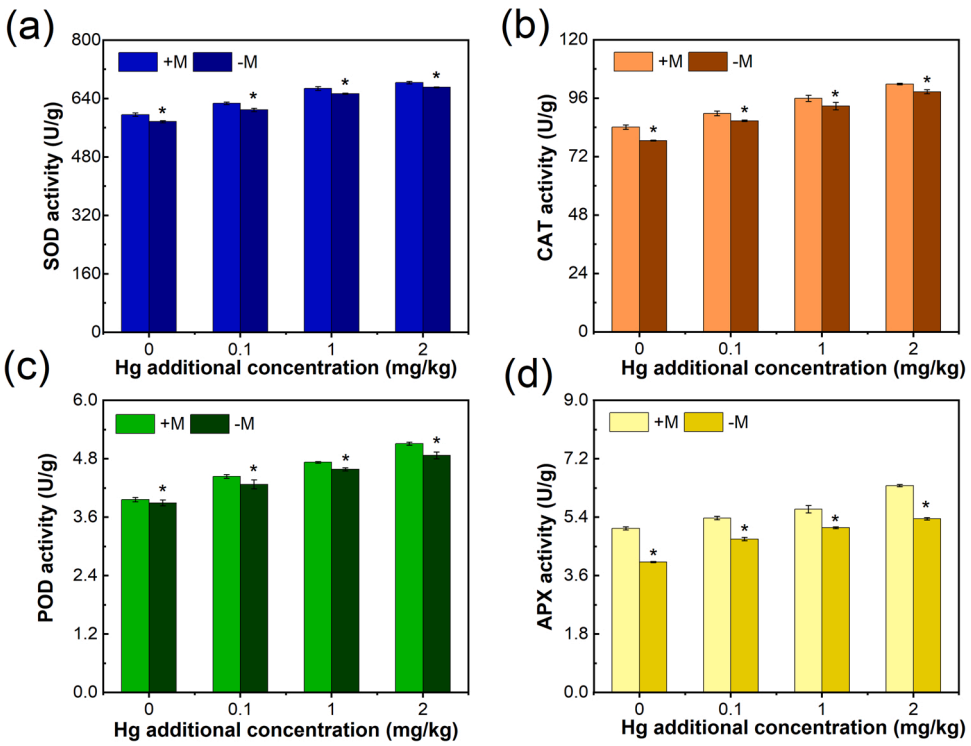

Fig. 4. Effects of AMF on antioxidant enzymes activity of rice root (means ± S.D., n = 3) under different Hg concentrations. (a) SOD; (b) CAT; (c) POD; (d) APX. +M: AMF inoculation groups. -M: AMF non-inoculation groups. The "* " represents significant differences between inoculation and non-inoculation under the same exogenous Hg concentration ($p < 0.05$).

respectively) at Hg concentrations of 0, 0.1, 1 and 2 mg/kg (Fig. 4d). In addition, this study detected the effect of AMF on antioxidant enzyme activity in rice leaves, and found that the effect of AMF on antioxidant enzyme activity in rice leaves was similar to that in the roots (Fig. S2). These results indicate that the presence of AMF could enhance the strength of the rice antioxidant system by reducing the concentrations of heavy metals entering the plant body, thus improving rice stress resistance, which could help the rice maintain its growth under stress.

3.4. Inoculation with AMF reduced heavy metal uptake by plants by forming a symbiotic network with plants and affecting soil properties

The above experiments demonstrated that after AMF inoculation, both the growth indices and physiological and biochemical indices of plants where improved when compared with those of the AMF non-inoculation group, which was directly related to the reduction in Hg uptake by plants after AMF inoculation. Therefore, based on the aforementioned findings, the present study investigated why Hg uptake by plants decreased after AMF inoculation. As shown in Fig. 5, clear symbiotic structures were observed between the AMF and roots of the host plant in the AMF inoculation group, including additional root hyphae and vesicles. It was found that the AMF had the ability to retain and fix Hg by forming symbiotic structures with the roots of rice plants, thereby inhibiting the transport of Hg from rice roots to other rice tissues. This may be one of the main reasons why AMF inoculation reduced Hg uptake by rice (Riaz et al., 2021; Wu et al., 2015). At the same time, the appearance of mycorrhizal infection in rice roots was also a basic indicator of the successful establishment of symbiosis between AMF and host plants (Table S7). In addition, because the root of a rice plant is the main organ involved in both nutrient absorption and blocking harmful pollutants, the symbiosis between AMF and rice roots could potentially enhance the resistance of rice to harmful external factors by changing the structural characteristics of rice roots, thereby inhibiting the entry of metals into rice to improve various rice growth indicators. This also

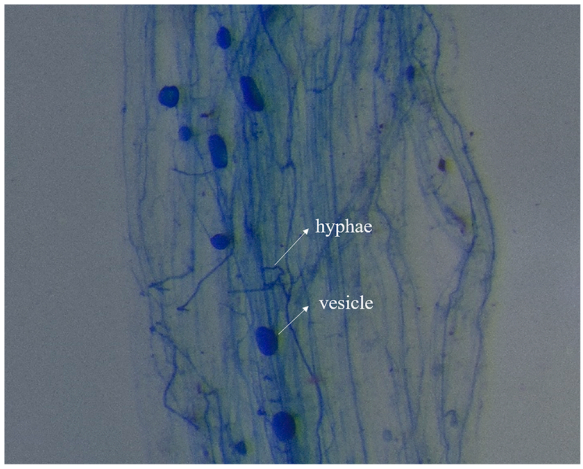

Fig. 5. AMF microstructure infecting the root of rice.

suggested that the "dilution effect" caused by the increase of plant growth under AMF inoculation was another factor in the mechanism of AMF detoxification of heavy metals (Zhang et al., 2019b). This study found that at the same Hg pollution concentration, AMF inoculation significantly increased the biomass of rice (Fig. 2a), which diluted the Hg absorbed by the rice, and the tolerance of plants to heavy metals was relatively enhanced. For example, it was observed that when the additional concentration of Hg was 1 mg/kg, the $T^{199}Hg$ of the AMF non-inoculation group was 38,812.70 μg, far more than the $T^{199}Hg$ of the AMF inoculation group, which was 13,653.37 μg. At the same time, the biomass of the AMF non-inoculation group was 24.20 g/pot, which was lower than that of the AMF inoculation group (48.08 g/pot). The Hg concentration in the AMF non-inoculation group was much higher than that in the AMF inoculation group, which was referred to as the dilution

effect of AMF inoculation. In addition, as shown in Table S7, with an increase in Hg concentration, the mycorrhizal colonization rate between AMF and rice roots showed a downward trend. This may have occurred because with the increase in Hg concentration, the inhibitory effects of Hg on the growth of rice roots gradually increased and the contact area between rice roots and AMF was reduced. However, under high concentrations of Hg pollution, inoculation with AMF still significantly improved various physiological indicators of plant growth (Figs. 2 and 3), indicating that AMF could play a role in mitigating the toxic effects of heavy metals even under low infection conditions.

This study also found that AMF could affect the migration of heavy metals into plants by changing the basic properties of the rhizosphere soil (Table 1), thereby alleviating the damage to rice plants caused by Hg. Rhizosphere soil pH is one of the dominant factors determining the form and available concentrations of heavy metals in soil. Increases in pH in the rhizosphere soil cause heavy metals in the soil to transform from exchangeable to stable states, which also leads to decreases in the concentrations of bioavailable heavy metals in the soil that can be easily absorbed by plants (Walker et al., 2004), thereby inhibiting the entry of heavy metals into plants through roots (Rehman et al., 2016). As shown in Table 1, when the Hg concentrations were 0.1, 1 and 2 mg/kg, the pH of the rhizosphere soil in the AMF inoculation group was higher than that in the AMF non-inoculation group. The increase in pH in the rhizosphere soil converted Hg in the soil from available Hg to carbonate-bound Hg, which was unfavorable for absorption by the rice plants, resulting in a decrease in rice Hg concentrations compared with the AMF non-inoculation group (Table 1, Fig. 1 and S3). Moreover, the increases in the pH values of the rhizosphere soil enhanced the electrostatic adsorption sites and stability between soil and heavy metals (Gabriel and Williamson, 2004; Vaňková et al., 2021), thus further immobilizing heavy metals.

This study further found that AMF secreted a series of specific substances (including organic acids, amino acids, GRSP and similar factors) to immobilize heavy metals in the rhizosphere soil, which also effectively inhibited the migration of soil heavy metals into plants (Table 1 and S7). It was important to note that AMF inoculation had also significantly increased the concentrations of aspartic acid, lysine, glutamic acid, citric acid, succinic acid and fumaric acid in the rhizosphere soil (Table 1). It has been found that aspartic acid and lysine can chelate heavy metal ions to fix soil heavy metals, reduce the biological toxicity of heavy metals, and effectively promote plant growth (Plohl et al., 2021; Wang et al., 2020). In addition, glutamate reduces the concentrations of available heavy metals in the soil by increasing the soil pH (Yang et al., 2018), which is consistent with the findings of increased rhizosphere soil pH after AMF inoculation in the present study (Table 1 and Fig. S3). Also, citric acid, succinic acid and fumaric acid all have the ability to convert the available Hg in the rhizosphere soil into carbonate-bound and iron-manganese oxides, which are known to be less easily absorbed by rice (Pinto et al., 2008; Rao et al., 2019). In addition, AMF can bind to Hg in the soil by secreting GRSP (Table S7), which is a widely distributed AMF. When the concentration of Hg in soil is high, GRSP can form a binding state with Hg, thus inhibiting the transfer of Hg from the roots to the shoots of rice (Ghasemi et al., 2017). Generally speaking, a series of root exudates produced by inoculation were found to play a role in fixing Hg in the rhizosphere soil, which was consistent with the reductions in the overall Hg content of rice after inoculation with AMF.

3.5. *Inoculation with AMF promoted Hg localization on non-edible parts of rice plants*

The aforementioned results indicated that AMF inoculation can reduce the concentrations of Hg in rice, thereby reducing the toxic effects of Hg on rice plants. Accordingly, this study further investigated the effects of AMF inoculation on the migration and distribution of Hg, which has already been taken up by rice. Interestingly, after AMF inoculation, the Hg in the rice tended to be distributed in the non-edible parts of the rice, such as the stems and leaves, while the proportion of Hg accumulated in the edible parts of the rice decreased significantly (Fig. 6). Fig. 6 indicates that when the Hg pollution concentration in the soil was 0.1 mg/kg, the effects of AMF on the reduction of $Me^{199}Hg$ concentrations were the most obvious. For edible rice grains, the proportion of $Me^{199}Hg$ in the AMF inoculation group was 20.19%, which was significantly lower than that in the AMF non-inoculation group (48.07%). It was also determined that the proportions of $Me^{199}Hg$ in the rice stem and leaf tissues inoculated with AMF were 12.61% and 2.88%, respectively. Those values were significantly higher than the proportions of $Me^{199}Hg$ in the stem and leaf tissues of rice in the AMF non-inoculation group (2.76% in the stem tissues, and 0.47% in the leaf tissues). A similar phenomenon was observed at Hg concentrations of 1 and 2 mg/kg, where it was found that the inoculation with AMF had also reduced $Me^{199}Hg$ concentrations in rice grains and increased the

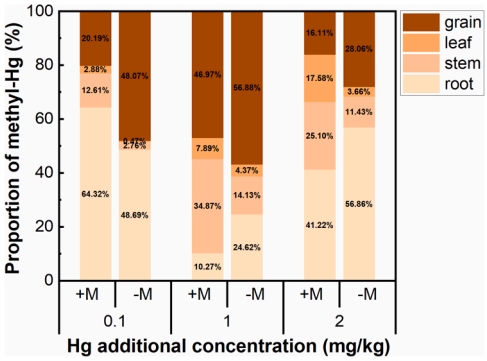

Fig. 6. Effect of AMF on the methyl-Hg ($Me^{199}Hg$) proportion of different parts of rice under different Hg concentrations. +M: AMF inoculation groups. -M: AMF non-inoculation groups.

Table 1
Effects of AMF on rice roots and rice rhizosphere properties (means ± S.D., n = 3) under different Hg concentrations.

Hg (mg/kg)	Treatments	pH	Aspartic acids (mg/L)	Glutamic (mg/L)	Lysine (mg/L)	Citric acid (mg/L)	Succinic acid (mg/L)	Fumaric acid (mg/L)
0	+M	7.89 ± 0.01	0.04 ± 0.01	0.06 ± 0.02	0.04 ± 0.01	55.29 ± 2.11	199.25 ± 34.40	5.98 ± 2.21
	-M	8.00 ± 0.01*	0.03 ± 0.01*	0.04 ± 0.01*	0.02 ± 0.01*	42.35 ± 0.68*	89.20 ± 15.78*	4.31 ± 0.11*
0.1	+M	7.94 ± 0.03	0.05 ± 0.02	0.11 ± 0.06	0.02 ± 0.01	53.72 ± 12.44	475.15 ± 24.77	12.58 ± 3.28
	-M	7.58 ± 0.06*	0.03 ± 0.01*	0.04 ± 0.01*	0.02 ± 0.00*	24.06 ± 2.46*	258.46 ± 30.25*	3.28 ± 0.68*
1	+M	7.86 ± 0.02	0.04 ± 0.02	0.10 ± 0.01	0.03 ± 0.00	62.37 ± 16.68	313.76 ± 46.81	7.86 ± 0.02
	-M	7.67 ± 0.02*	0.04 ± 0.01*	0.07 ± 0.02*	0.02 ± 0.01*	57.54 ± 4.72*	218.24 ± 22.84*	6.88 ± 0.14*
2	+M	7.65 ± 0.02	0.06 ± 0.02	0.11 ± 0.05	0.03 ± 0.00	21.33 ± 5.23	340.58 ± 10.22	1.04 ± 0.42
	-M	7.42 ± 0.03*	0.03 ± 0.01*	0.06 ± 0.02*	0.03 ± 0.02 ^{ns}	12.37 ± 1.28*	238.16 ± 26.99*	0.59 ± 0.01*

+M: AMF inoculation groups. -M: AMF non-inoculation groups. The "* " in the same table column indicates significant differences between inoculation and non-inoculation groups ($p < 0.05$). The "ns" in the same table column indicates there is no significant difference between inoculation and non-inoculation groups ($p > 0.05$).

$Me^{199}Hg$ concentrations in the stems and leaves. Taken together, these results indicated that AMF inoculation can reduce the concentrations of $Me^{199}Hg$ distributed in the edible parts of rice plants, which could greatly reduce the hidden danger to food safety caused by soil heavy metal pollution.

To confirm the above results, we further calculated $Me^{199}Hg$ TFs among different parts of rice to determine how $Me^{199}Hg$ migrated through the rice after entering rice under AMF inoculation. As shown in Table S8, when the concentrations of additional Hg were 0.1, 1 and 2 mg/kg, the TFs of rice roots, stems and leaves to rice grains were significantly lower than those of the AMF non-inoculation groups. The findings are consistent with the observed decrease in the concentrations and ratio of $Me^{199}Hg$ in rice grains (Fig. 6). In addition, when the concentrations of additional Hg were 0.1, 1 and 2 mg/kg, the TFs of the plant roots to stems and leaves were 0.19 and 0.05, 3.34 and 1.00 and 0.51 and 1.61, respectively, which were significantly higher than those found in the AMF non-inoculation treatments (0.06 and 0.02, 1.15 and 0.58 and 0.34 and 0.20, respectively). The concentrations and ratio of $Me^{199}Hg$ in rice leaves and stems were higher than those in the AMF non-inoculation treatments. Overall, AMF inoculation inhibited the transfer of $Me^{199}Hg$ from the roots, stems, and leaves to rice grains and significantly reduced $Me^{199}Hg$ concentrations in the rice, particularly in the rice grains. Therefore, it was considered that the presence of AMF could reduce the human intake of $Me^{199}Hg$ through rice and the risk of human exposure to $Me^{199}Hg$, which has great significance in ensuring the food safety of rice. In addition, this study analyzed the TFs of $T^{199}Hg$ from different organs to rice grains under the influence of AMF and found that AMF did not hinder the migration of $T^{199}Hg$ between various rice tissues (Table S9). Recent studies on Hg migration and accumulation in rice in Hg mining areas have shown that $Me^{199}Hg$ is more likely to accumulate in grains than in stems and leaves (Aslam et al., 2022; Meng et al., 2014). This is mainly due to the fact that the methylmercury in rice generally binds with cysteine, and the methylmercury-cysteine associations behaves like a mobile nutrient, and tend to accumulate in the final fruit during the growth and development of rice grains (Zhao et al., 2020). Our research findings are in contrast to those of previous studies (Fig. 6), possibly due to the addition of AMF affecting the main mechanism of methylmercury accumulation in rice grains, resulting in a significant reduction in food risk.

4. Conclusions

This study used an enriched ^{199}Hg isotope tracer technique to study the effects of AMF on the absorption and migration of Hg in rice as well as plant growth in a soil–microbe–rice system. AMF are able to form symbiotic structures with the rice plant roots and secrete various amino acids and other special substances; they also adjust the physical and chemical properties of the rhizosphere soil and other related mechanisms, thereby reducing the amount of Hg entering rice plants via roots. Hence, the growth trend of rice in Hg-contaminated soil was improved from the perspective of both macro growth index as well as micro physiological and biochemical indices. Furthermore, the experimental results revealed that AMF promoted the distribution of $Me^{199}Hg$ in non-edible parts such as stems and leaves, as opposed to rice grains, which are known to easily accumulate $Me^{199}Hg$. Specifically, compared with the AMF non-inoculation group, the maximum reduction of Hg content in the AMF inoculation group was 96.42%, and the corresponding rice biomass was 1.69 times of that observed in the AMF non-inoculation group. It was also determined that the proportion of methylmercury content in grain was 20.19%, which was significantly lower than that in the AMF non-inoculation group (48.07%). This further reduces the potential risk of Hg pollution in the food chain. Furthermore, this study successfully confirmed the application potential of Hg isotope technology for studying the environmental geochemical behaviors of Hg and a feasible microbial approach for reducing the toxicity of Hg in food crops was proposed. Valuable insights that could assist in the reduction of human Hg intake through rice consumption were also provided, which could help ensure future food safety. In addition, the findings of this study indicate that detailed assessments of the application of typical symbiotic microorganisms for soil Hg remediation should be conducted.

CRediT authorship contribution statement

Xinru Li: Conceptualization, Methodology, Data analysis, Visualization, Writing. **Min Zhou**: Methodology, Data analysis, Revision. **Feng Shi**: Sampling, Formal analysis. **Bo Meng**: Conceptualization, Methodology. **Jiang Liu:** Methodology, Data analysis. **Yidong Mi**: Sampling, Investigation. **Cuimin Dong**: Sampling. **Hailei Su**: Funding acquisition. **Xuesong Liu**: Data curation. **Fanfan Wang**: Conceptualization, Research design, Writing – review & editing, Funding acquisition, Supervision. **Yuan Wei**: Conceptualization, Writing – review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgments

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ecoenv.2023.114776.

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