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Differential response of root traits to arbuscular mycorrhizal fungi in two maize varieties alters cadmium speciation and migration in soil solution

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) form symbiotic associations with crop roots, but their effects on the root traits of crops with different root system sizes and the subsequent influence of these traits on the migration of cadmium (Cd) within the maize-soil system remain unclear. In this study, two maize varieties with relatively large roots (Jingdian 8) and relatively small roots (Enyu 98) were selected as test plants. A compartmentalized soil culture experiment (Cd 17.4 mg/kg) was conducted to investigate the effects of AMF inoculation on the root traits, plant Cd content and accumulation, soil aggregates, preferential flow distribution, and solution Cd loss in both maize varieties. Compared with the non-inoculated treatment, AMF inoculation significantly promoted root growth of both maize varieties, resulting in increases in root length, root tip number, and branch number by 27–161%, and an increase in glomalin-related soil protein (GRSP) concentration by 57–84%. The number of large soil aggregates in the mycorrhizal compartment of Enyu 98 increased by 29% compared with the root compartment, and the distribution area of soil preferential flow increased by 23–185%. AMF significantly reduced soil available Cd concentration by 26–40%, soil solution Cd loss by 35–87%, and plant Cd content by 41–60%. Cd speciation in soil interflow and leachates were dominated by Cd^{2+} (96–98%), followed by $CdSO_4$(aq) (1–2%). Partial least squares structural equation modeling revealed that AMF promoted root growth in Jingdian 8, but weakened the mycorrhizal control on soil Cd loss; in contrast, AMF promoted root architecture and GRSP secretion in Enyu 98, and directly inhibited soil Cd loss through the "AMF-root traits-GRSP" pathway. This study identifies divergent root responses to AMF inoculation among different maize varieties and reveals how AMF reshapes cadmium migration pathways via differential regulation of root traits, while also providing theoretical support for applying AMF to remediate Cd-contaminated soils.

1. Introduction

Mining and metallurgical activities, such as lead-zinc mining, smelting, and tailings accumulation, are key sources of cadmium (Cd) pollution in soil (Zhang et al., 2016). Cd in soil is stable, highly toxic, and moves easily. Over time, its accumulation can directly inhibit plant growth (Haider et al., 2024). Cd can also spread both horizontally and vertically with soil water, increasing pollution and harming ecosystem stability (Yang et al., 2025(a)).

The environmental behavior and biological effects of Cd in soil primarily depend on its chemical forms, which undergo dynamic processes such as adsorption-desorption, precipitation-dissolution, and ion exchange (Tack and Verloo, 1995; Stephan et al., 2008). Among common Cd forms, the ionic form (Cd^{2+}) has the strongest bioavailability and mobility, exerting the most significant toxic effect on crops, and is also the main form causing secondary soil pollution (Islam et al., 2023). Cd^{2+} enters the soil and migrates under external forces, such as rainfall and runoff, causing inestimable impacts and damages to surrounding soils (Desogus et al., 2013; Imoto et al., 2018). Therefore, the soil interflow and leachate are important carriers for exploring the migration of Cd in different directions within the soil.

Arbuscular mycorrhizal fungi (AMF), a key group of microorganisms

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that form symbiotic relationships with plant roots in soil, are widely distributed in barren and heavy metal-contaminated soils, playing an irreplaceable role in maintaining soil ecosystem functions (Kumar et al., 2015; Tiwari et al., 2020). AMF can form mycorrhizal symbionts with maize roots, and their extraradical hyphae can significantly extend the spatial absorption range of roots, altering root structure, thus mitigating the inhibitory impact of Cd on plant growth and facilitating biomass accumulation (Simard et al., 2012; Halim et al., 2020). During this symbiotic process, AMF are also involved in the migration and transformation of Cd at the root-soil interface: (1) they immobilize Cd ions through direct pathways such as adsorption on the hyphal surface and intracellular storage in spores, reducing their transport to roots (Wei et al., 2023; González-Guerrero et al., 2008); (2) they reshape the microenvironment of the root-soil interface through indirect pathways, promoting the cementation of soil microaggregates to form large aggregates and reducing the release risk of Cd through physical encapsulation (Frey et al., 2019). Furthermore, the growth-promoting effect of AMF on roots can also enhance the modification of soil structure by roots, exerting a positive or inhibitory effect on Cd leaching (Lu et al., 2020).

Maize, as a globally important food crop, occupies a core position in maintaining agricultural ecosystem productivity and material cycling (Rizwan et al., 2017). However, significant genetic differences exist among different maize varieties, leading to obvious differentiation in their root traits and tolerance to Cd stress, which in turn affects the efficiency of symbiotic response to AMF (Yu et al., 2021). For example, root traits of the two maize varieties were differentially modulated by AMF, Fanyu 3 and Ludan 8, with comprehensive response indices to AMF of 753.6% and 389.4%, respectively (Chen et al., 2023). However, research on the effects of varietal differences in root trait responses to AMF on soil structure, Cd speciation, and soil Cd migration is limited, and how root trait differences affect Cd migration via AMF remains unknown, particularly in Cd-contaminated soils affected by mining and smelting activities.

Huize, Yunnan, is a typical lead-zinc mining area in China. Long-term mining and smelting activities have resulted in significant Cd pollution in the surrounding farmland soils. As the primary cultivated crop in the area, the growth status and productivity of maize are influenced by soil Cd stress, and the migration of soil Cd also exacerbates the ecological risk to regional soils. Based on this, this study used Cd-contaminated farmland soil around a lead-zinc mining area in Huize as the test soil, and selected two maize (*Zea mays* L.) varieties with different root development characteristics: Jingdian 8 (relatively large roots) and Enyu 98 (relatively small roots) as research objects (Yu et al., 2021). A compartmentalized leaching pot experiment device was adopted to systematically investigate the effects of AMF inoculation on maize (root traits, plant Cd content, and accumulation), rhizosphere soil (Cd chemical forms, aggregate size distribution, and preferential flow distribution), and chemical properties of leachate and soil interflow (dissolved and particulate Cd contents, Cd loss and speciation). The Integrated Biomarker Response (IBR) method was employed to elucidate the differential responses of AMF in regulating root growth, Cd absorption, and migration in the two maize varieties. This was combined with the PLS-SEM model to investigate the effect of AMF on Cd migration in the maize-soil system by modifying maize root traits. This study hypothesized that the regulatory effects of AMF on maize root growth and soil Cd migration vary among maize cultivars. By modulating maize root traits, AMF alter rhizosphere soil structure and Cd migration characteristics, thereby differentiating Cd accumulation in plants and Cd loss in soil among different maize cultivars.

2. Materials and methods

2.1. Experimental materials

The experimental soil was collected from a Cd-polluted farmland plot (26°51'75"N, 103°60'22"E) near the Huize lead–zinc mining area. The soil was naturally air-dried, and impurities were removed. It was screened with a 2 mm sieve, sterilized (121℃ for 2 h) for use. The Cd content in soil was 17.4 mg/kg, and the other basic physical and chemical properties of the soil were shown in Table S1.

The two maize varieties (*Zea mays* L.) were Jingdian 8, which has relatively large roots, and Enyu 98, which has small roots. The seed surface was disinfected by the method of You et al. (2023), with 10% (v/v) sodium hypochlorite applied for 10 min, followed by immersion in 75% (v/v) ethanol for 1 min. After sterilization, the seeds were germinated under controlled conditions (28°C, 3 days). Seedlings with homogeneous growth vigor were selected and reserved for subsequent experiments.

The AMF inoculum consisted of the strain *Funneliformis mosseae*, which was isolated from contaminated farmland near the Huize lead–zinc mining area, with a spore concentration of 18 spores per gram.

2.2. Experimental design

Pots were constructed of 30 × 20 × 30 cm (L × W × H) that were divided into two equal compartments by an organic glass plate, further details of pot design in Supplementary Material (Text S1 and Fig. S1). Cd-contaminated farmland soil was sterilized, and each pot contained approximately 10 kg of soil (5 kg in each of the left and right compartments). Jingdian 8 and Enyu 98 maize were used as host plants, and 2 sterilized germinated seeds with white radicals were transplanted per pot. The experiment consisted of AMF inoculation (treatment group) and non-AMF inoculation (control group), with five replicates per treatment, totaling 20 pots. The two compartments in the non-AMF inoculation treatment were designated as the soil compartment and root compartment, respectively, while those in the AMF inoculation treatment were the hyphal compartment and mycorrhizal compartment,. For the inoculated group, the AMF inoculant was fully blended with sterilized soil prior to being filled into the pots (Fig. 1). Maize was grown under natural light, and deionized water was applied to maintain a soil water content of 60–70%. Samples were collected after 50 days of maize growth. First, the plastic culture container was carefully cut open, and soil adhering to the root system was gently shaken off. Rhizosphere soil tightly attached to the roots was collected, air-dried naturally, and sieved through a 2 mm mesh for subsequent analysis. Afterwards, intact maize plants were separated into aboveground and underground parts. These plant tissues were rinsed 2–3 times successively with tap water and deionized water to remove surface contaminants before further treatment.

An artificial simulated rainfall experiment was conducted when the maize was 30 days old. Leaching tests were performed on the soil with distilled water, with an irrigation rate of 500 mL in 10 min, equivalent to a rainfall intensity of 50 mL/min.

2.3. Determination of maize root morphology, plant Cd concentration and uptake

Root morphological parameters, including total root length, surface area, mean diameter, volume, tip count, and branch number, were determined using a Win RHIZO analyzer following image acquisition with a root scanner. The Cd concentration in plant tissues was determined by wet digestion (Chaturvedi et al., 2019). The calculation formula for Cd accumulation in corresponding plant parts is as follows (Zhang et al., 2018):

Cd accumulation in corresponding plant parts (μg/plant) = Biomass of corresponding plant part (g/plant) × Cd content of corresponding plant part (mg/kg) (1).

2.4. Determination of AMF-related indicators

Spore counts were obtained by employing the wet

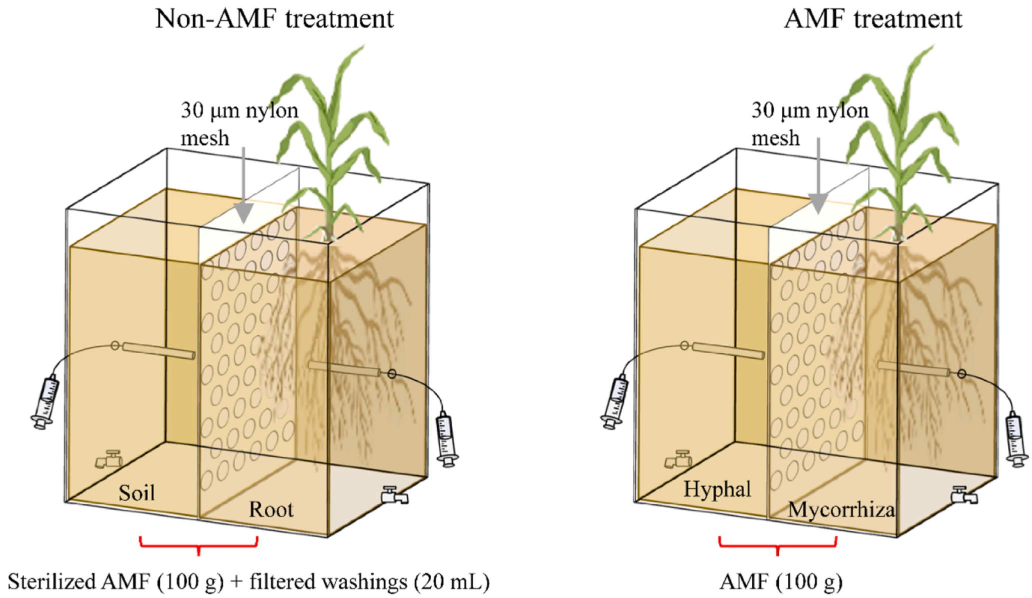

Fig. 1. The system of interventricular septum culture.

sieving-decantation protocol (An et al., 2018). The content of easily extractable glomalin-related soil protein (EE-GRSP) and total glomalin-related soil protein (T-GRSP) were determined via the Bradford method (Wright et al., 1996). The AMF colonization rate was determined using the cross method to calculate the rate (Shi et al., 2025). The details of experimental procedure were given in the Text S2.

2.5. Determination of soil Cd forms and aggregates

The total content of heavy metal Cd in soil was analyzed by the aqua regia-perchloric acid digestion method, and the Cd content was determined using an ICE−3000-SERIES flame atomic absorption spectrophotometer. The available heavy metal content was determined using the DTPA extraction method. The chemical forms of Cd (weak acid extractable, reducible, oxidizable, and residual forms) were determined by the modified BCR sequential extraction method, and the extractants of each form were quantitatively determined using a Thermo ICETM 3300 AAS atomic absorption spectrophotometer (Rauret et al., 1999). Three replicates were set for all determinations.

The distribution of soil aggregates was determined by the dry sieving-wet sieving method, with detailed operational procedures provided in Text S3.

2.6. Soil interflow and leachate sampling

After the leaching test was completed, the soil interflow was collected using a soil interflow sampler, and the leachate was collected via the drainage valve. The pH of both soil interflow and leachate was determined using a pH meter. 5 mL of filtrate along with the soil particles adhering to the filter were transferred into separate boiling tubes. After adding HNO_3 (5 mL) and H_2O_2 (5 mL), the mixture was digested. Subsequently, the samples were placed into flasks together with distilled water and soaked to a volume of 25 mL (He et al., 2020). The Cd loss was calculated as the product of concentration and leachate volume, with the formula as follows:

$$\text{Cd loss } (\mu g) = \text{Cd concentration } (\mu g/mL) \times \text{Leachate volume } (mL) \quad (2)$$

.

Speciation analysis of heavy metals was performed via Visual MINTEQ 3.1 modeling. Parameters entered into the model included pH, ionic concentrations, and Cd content. Total Cd leaching loss was estimated by multiplying Cd concentration by the volume of leachate.

2.7. Statistical analysis

Data analysis was performed using SPSS 21. Graphical plots were created using Origin 2021. The IBR index was calculated for indicators of maize roots, soil structure, and soil solution under Cd stress with AMF inoculation (Ma et al., 2022). Detailed calculation procedures are provided in Text S4 to quantify the effect of AMF on Cd migration by regulating root traits of different maize varieties. PLS-SEM was established using the plspm and vegan packages in R software to analyze the differential regulation of AMF inoculation on Cd migration and transformation in the plant-soil system of the two maize varieties (Yang et al., 2025(b)).

3. Results and analysis

3.1. AMF colonization and glomalin-related soil protein content in maize roots of two varieties

AMF inoculation resulted in successful colonization of roots in both maize varieties (Fig. 2A-B). The AMF infection rates of Jingdian 8 and Enyu 98 roots were 31.4% and 28.5%, respectively, and the number of spores per gram of soil in the mycorrhizal compartment and hyphal compartment ranged from 13.6 to 19.5 and 12.7–17.9, respectively (Table S2).

Compared to the root compartments, the soil in the mycorrhizal compartments of the maize varieties Jingdian 8 and Enyu 98 exhibited increases in EE-GRSP of 84% and 75%, respectively, and T-GRSP increased by 71% and 80%, respectively. Compared with the soil compartment, the EE-GRSP in the soil of Jingdian 8 and Enyu 98 in the hyphal compartment increased by 75% and 82%, respectively, and the T-GRSP increased by 57% and 62%, respectively. Two-way ANOVA analysis showed that AMF had an extremely significant effect on EE-GRSP and T-GRSP (Fig. 2C).

3.2. Effects of AMF on root traits, Cd content and accumulation

Compared with CK, AMF inoculation increased the root length, root surface area, average root diameter, root volume, root tip number, and branch number of Jingdian 8 and Enyu 98 by 27%, 55%, 34%, 105%,

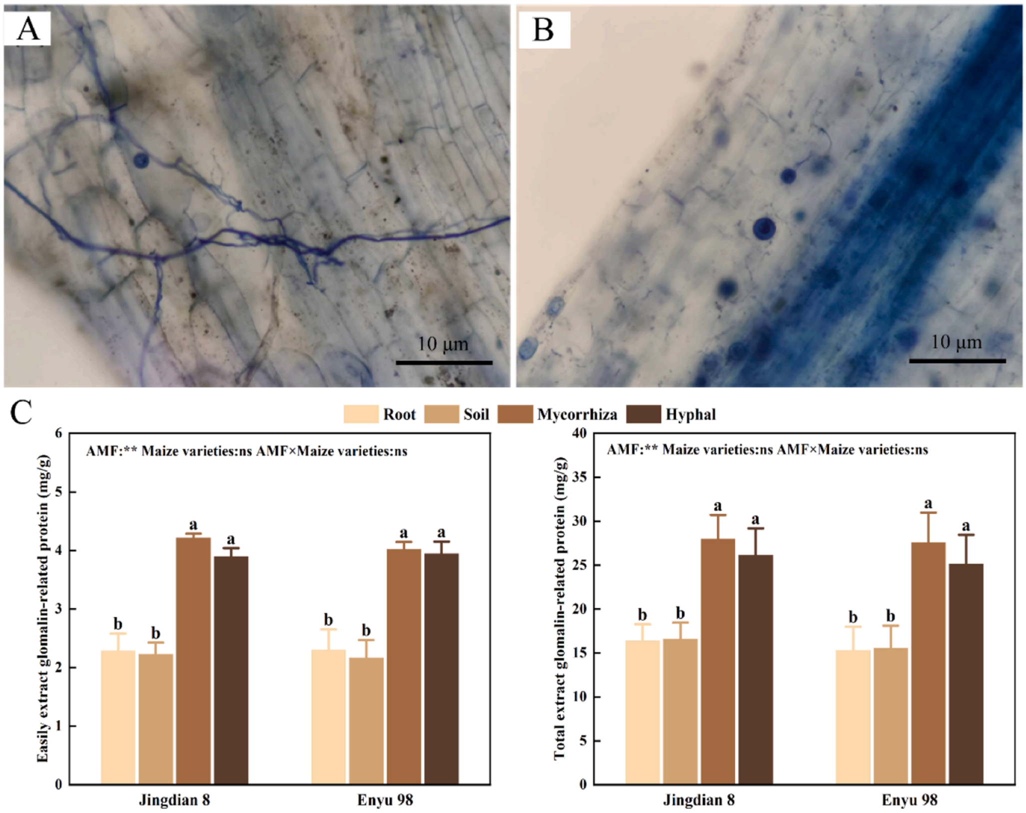

Fig. 2. Colonization of AMF in the roots of two maize varieties. A-B, Structure staining of AMF mycelium (A) and vesicle (B) maize roots; C, The content of glomalin-related protein.

161%, 53% and 35%, 127%, 64%, 219%, 65%, 91%, respectively (Fig. 3A-F). In addition, the Cd content in shoots and roots decreased by 41%, 49% and 60%, 41%, respectively, while the root Cd accumulation increased by 48% and 93%, respectively (Fig. 3G-H).

IBR analysis showed that the responses of different varieties to root traits and Cd uptake after AMF inoculation were different. Jingdian 8 exhibited a higher response than Enyu 98 (IBRv2 values were 34.43 and 18.48, respectively) (Fig. 3I-J).

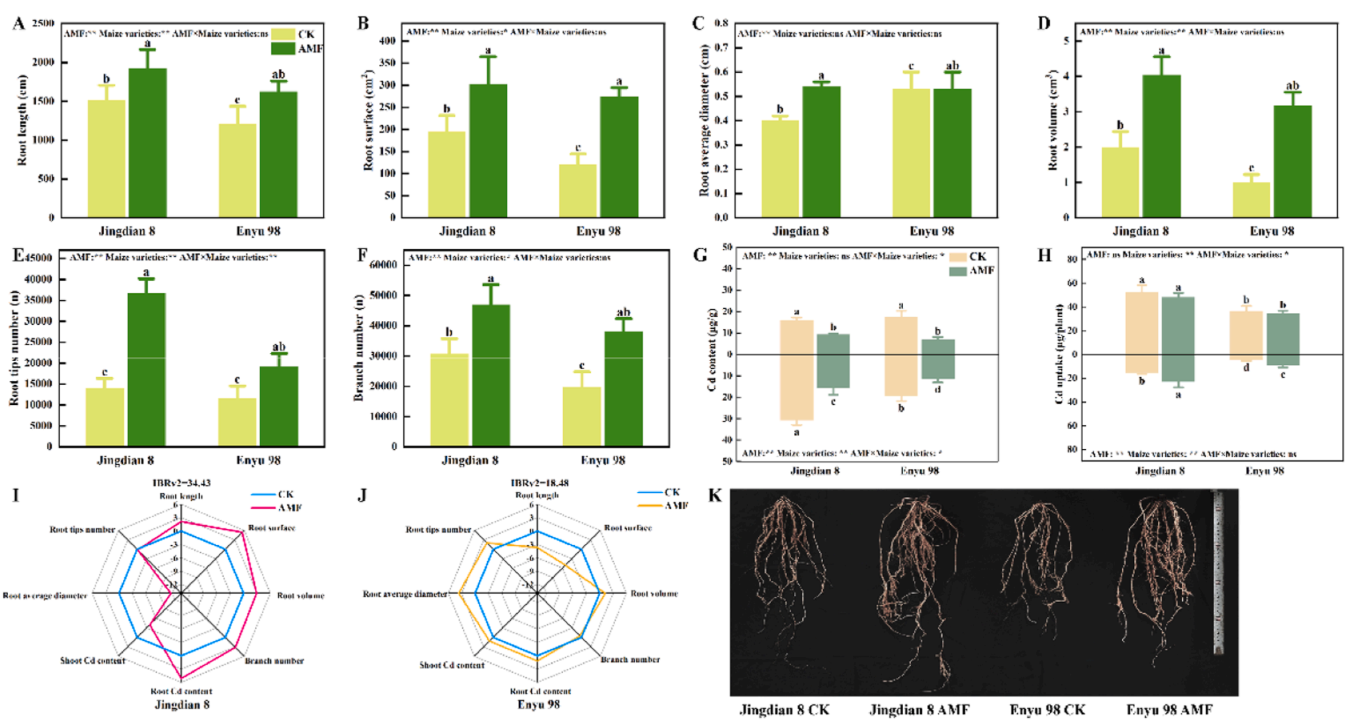

Fig. 3. Root traits (A-F), Cd content (G), uptake (H), IBR values (I and J) and root growth photo (K) of two varieties maize.

3.3. Rhizosphere available Cd and different chemical forms

Compared with the root compartment, the content of available Cd in the rhizosphere soil of Jingdian 8 and Enyu 98 in the mycorrhizal compartment decreased by 30% and 40%, respectively; the proportion of oxidizable Cd increased by 23% in both varieties, and the proportion of reducible Cd decreased by 21% and 30%, respectively. Compared with the soil compartment, the content of available Cd in the soil of Jingdian 8 and Enyu 98 in the hyphal compartment decreased by 27% and 26%, respectively, and the proportion of residual Cd in the soil of Enyu 98 increased by 27%. Two-way ANOVA analysis revealed that both AMF and maize variety had a highly significant effect on soil available Cd content, and there was an interactive effect between them (Fig. 4A-B).

3.4. Soil aggregate and preferential flow distribution characteristics

AMF inoculation facilitated the formation and stabilization of soil aggregates. Compared with the root compartment, the content of soil aggregates (> 0.25 mm) in the mycorrhizal compartment of Enyu 98 significantly increased by 29%. Compared to the soil compartment, the total content of soil aggregates (>0.25 mm) in the rhizosphere of Jingdian 8 and Enyu 98 in the hyphal compartment increased significantly by 34% and 36%, respectively (Table S3).

With the increase of soil depth, the stained area gradually decreased, showing funnel-shaped or dendritic flow patterns (Fig. 5A). As a result, the stained area of both maize varieties decreased with increasing soil depth. In the 0–10 cm, 10–20 cm, and 20–30 cm soil layers, compared with the root compartment, the proportion of stained area in the mycorrhizal compartment of Jingdian 8 and Enyu 98 increased by 40%, 59%, 80% and 30%, 38%, 36%, respectively. Compared with the soil compartment, the proportion of stained area in the hyphal compartment of both varieties increased by 40%, 73%, 185% and 23%, 60%, 95%, respectively (Fig. 5B).

3.5. Effects of AMF on interflow Cd concentration

Compared with the root compartment, the interflow Cd concentration in the mycorrhizal compartment showed a significant decreasing trend. Specifically, the Cd concentrations of Jingdian 8 and Enyu 98 in the three leaching experiments decreased by 22–43% and 31–42%, respectively. Compared to the soil compartment, the Cd concentrations of Jingdian 8 and Enyu 98 in the hyphal compartment decreased by 30–35% and 32–33%, respectively (Fig. 6A). IBR analysis revealed that there was no significant difference in the regulation of Cd horizontal migration between the two varieties following AMF inoculation (Fig. 6B-E).

3.6. Soil leachate Cd concentration and Cd loss

Compared with the root and soil compartments, the concentration of both dissolved Cd and particulate Cd in the soil leachates generated from the three leaching experiments in the mycorrhizal and hyphal compartments, and the extent of reduction varied among different maize varieties (Fig. S1A). IBR analysis indicated that AMF exhibited differential regulatory effects on the vertical migration of Cd among maize varieties. The response intensity to Cd migration was higher in Enyu 98 than in Jingdian 8 (Fig. S1B-E).

Compared with the root compartment, the losses of dissolved and particulate Cd in the three leachates from the mycorrhizal compartment decreased by 42–52% (Jingdian 8), 30–43% (Enyu 98) and 75–87% (Jingdian 8), 63–85% (Enyu 98), respectively. Compared with the soil compartment, the losses of dissolved and particulate Cd in the three leachates of Jingdian 8 and Enyu 98 from the hyphal compartment decreased by 36–61% (Jingdian 8), 58–83% (Enyu 98) and 37–47% (Jingdian 8), 45–77% (Enyu 98), respectively (Fig. 7A).

IBR analysis clarified the differences in the regulation of vertical leaching and migration of Cd by AMF in different maize varieties and compartments. Compared with the root compartment, the mycorrhiza of Enyu 98 exhibited a stronger response than that of Jingdian 8 (IBRv2 values were 31.81 and 17.34, respectively) and had an inhibitory effect on particulate Cd (Fig. 7B-E).

3.7. Cd speciation in soil interflow and leachates

During the second leaching event, Cd^{2+} concentrations in the mycorrhizal compartments of both maize cultivars were significantly lower than those in the root compartments, while $CdSO_4$(aq) and $CdCl^+$ were significantly increased (Fig. 8B). In soil leachates, the proportions of $CdSO_4$(aq) and $CdCl^+$ were significantly higher than those in the root compartments during the first and third leaching events. In addition, for Enyu 98, the proportions of Cd^{2+} in the mycorrhizal and hyphal compartments were significantly lower than those in the root and soil compartments during the first leaching event (Fig. 8D and F). Inoculation with AMF resulted in an overall slightly higher pH in Enyu 98 than in Jingdian 8 (Fig. S2), whereas the pH variations caused by leaching frequency did not significantly alter the speciation distribution overwhelmingly dominated by Cd^{2+}(96–98%), followed by $CdSO_4$(aq) (1–2%) and $CdCl^+$ (0.3–1.1%), and $CdOH^+$ (0.05–0.68%) and CdF^+ (0.03–0.08%) were the least abundant.

3.8. Relationship between AMF, maize roots of different varieties and soil Cd migration

Compared with the soil compartment, the hyphae of Jingdian 8 could significantly inhibit the vertical loss of dissolved and particulate Cd by promoting the formation of GRSP and large aggregates. AMF

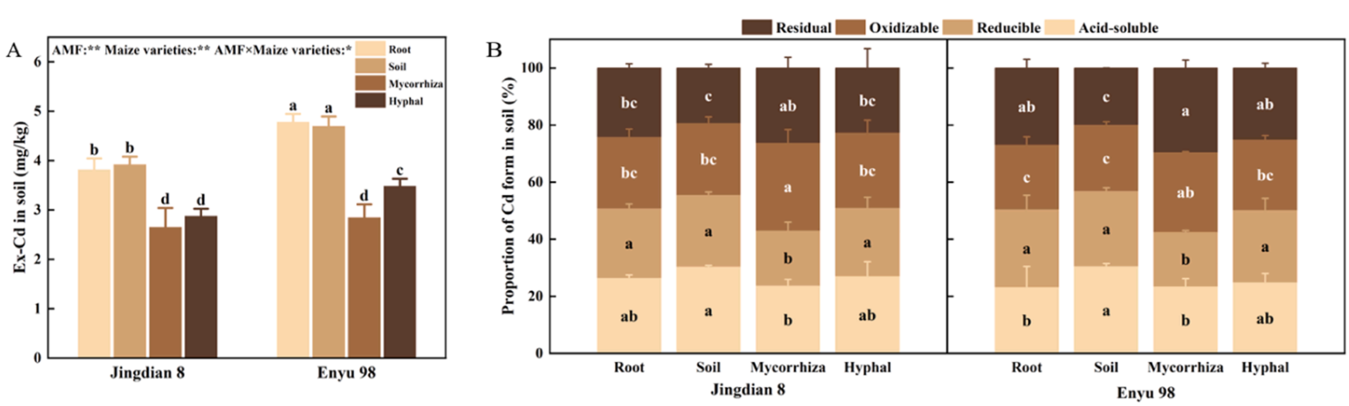

Fig. 4. The ex-Cd (A) and proportion of Cd forms (B) in rhizosphere soil.

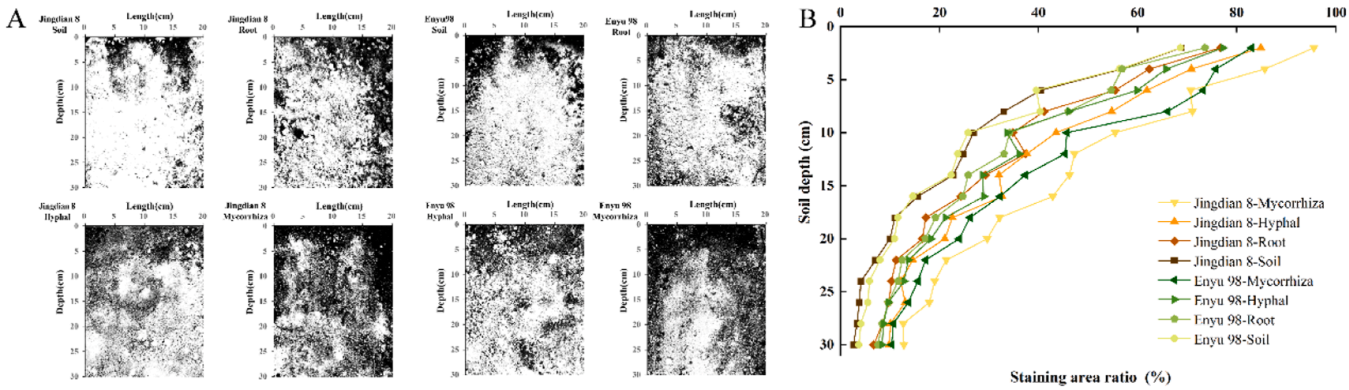

Fig. 5. Soil vertical profile staining image of two maize varieties (A) and colored area ratio of soil vertical profile at different depths (B).

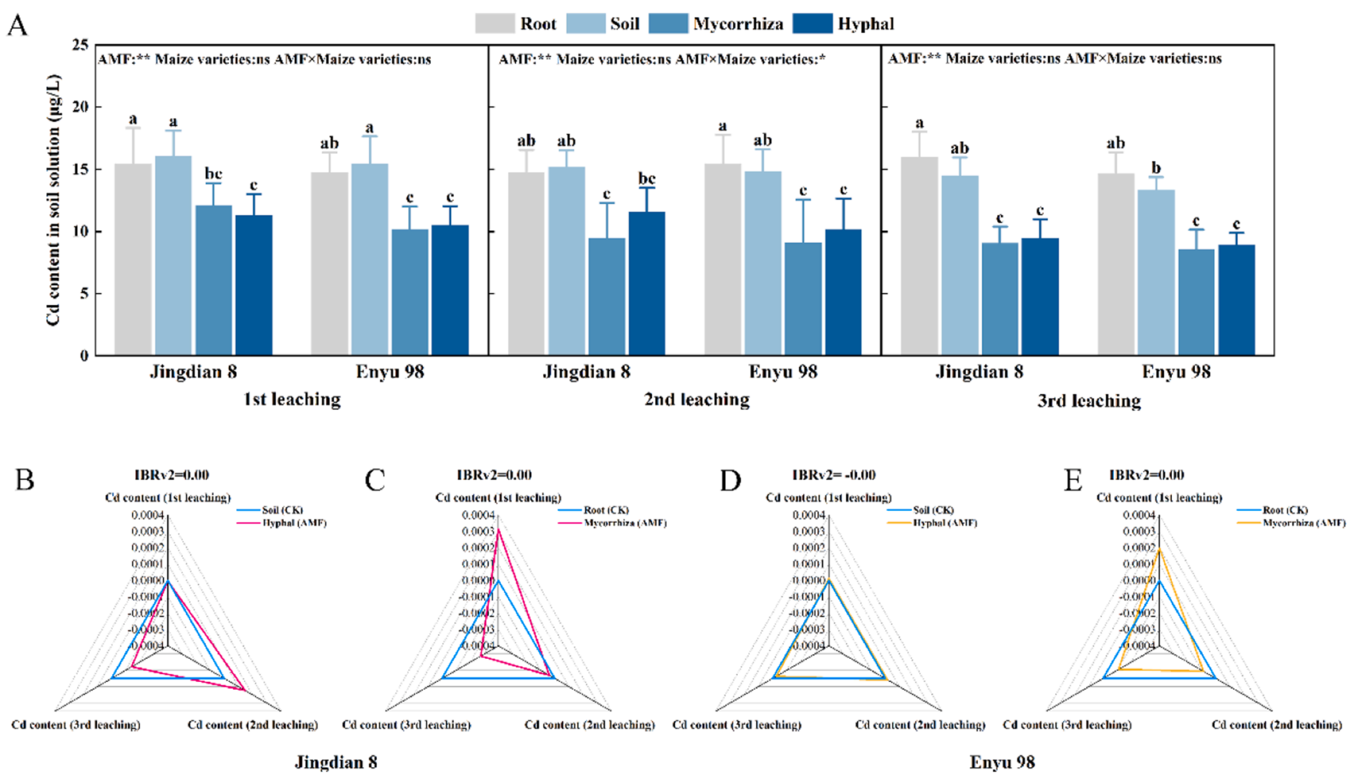

Fig. 6. Cd content in interflow of two maize varieties and IBR values of Cd content in solution for hyphal and mycorrhiza of Jingdian 8 (B and C) and Enyu 98 (D and E).

hyphae had a significant inhibitory effect on the loss of particulate Cd (total effect coefficient: −0.99; Table S4), but the inhibitory effect in the horizontal direction was not significant (Fig. 9A). AMF hyphae of Enyu 98 had a significant effect on GRSP secretion and ex-Cd in soil (total effect coefficient: −0.98; Table S5) (Fig. 9B).

Compared with the root compartment, AMF inoculation mainly inhibited the content of ex-Cd in soil for Jingdian 8 through direct effects (total effect coefficient: −0.90; Table S6) (Fig. 9C). Enyu 98 root growth and GRSP secretion are significantly promoted, and through the direct effects of roots and GRSP, as well as the indirect effects of roots promoting the formation of soil aggregates, the migration of ex-Cd in soil, dissolved and particulate Cd in both horizontal and vertical directions is further inhibited (Fig. 9D; Table S7).

4. Discussion

4.1. Differential regulation of AMF on root traits and plant Cd accumulation characteristics

Root traits are important indicators for evaluating plant growth status. They demonstrate diverse physiological and morphological modifications under stressful conditions (Lynch et al., 1995; Yang et al., 2014). The symbiotic relationship between AMF and plant roots regulates plant growth and heavy metal uptake. Differences in root morphology among maize varieties often result in varied responses following AMF inoculation (Yin et al., 2021). In this study, we used Jingdian 8, which has relatively large roots, and Enyu 98, which has relatively small roots. We confirmed varietal differences in the regulation of maize root traits by AMF. IBR analysis showed AMF inoculation promoted root length, root surface area, root volume, root branch number, and root tip number of Jingdian 8, with increases of 27%, 55%,

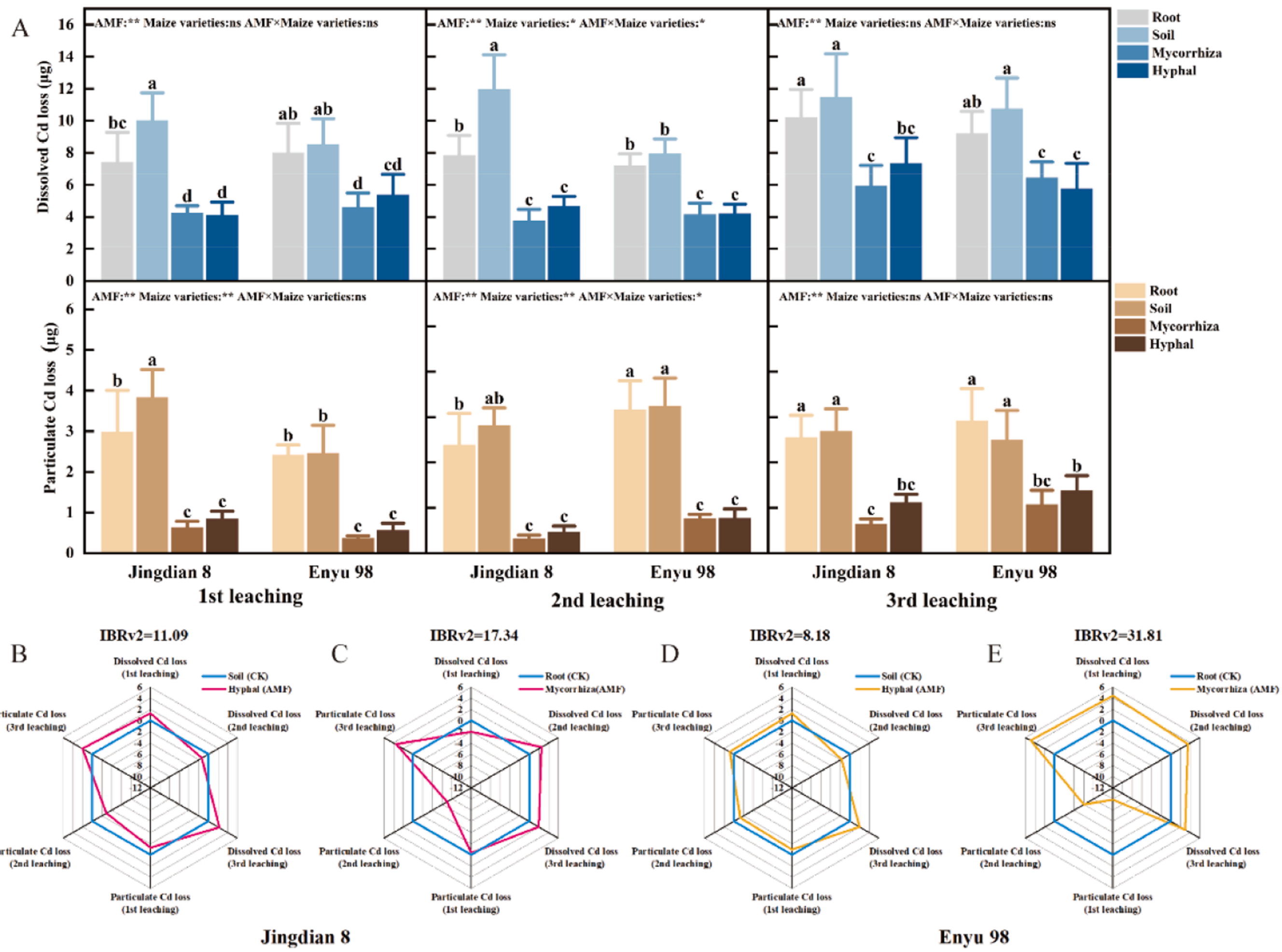

Fig. 7. Effects of AMF inoculation on the loss of dissolved Cd and particulate Cd in two varieties of maize (A) and IBR values of Cd loss for hyphal and mycorrhiza of Jingdian 8 (B and C) and Enyu 98 (D and E).

105%, 161%, and 53% respectively. For Enyu 98, it promoted average root diameter, root tip number, and root volume, with increases of 64%, 219%, and 65% respectively. Jingdian 8 had a higher response than Enyu 98.

Plant root growth provides more absorption sites, improving the plant's ability to absorb water and nutrients. It also enhances the absorption efficiency for substances such as Cd (Zhang et al., 2022). Cd usually exists in ionic form in soil and can be actively absorbed by roots. Therefore, root growth further promotes Cd absorption efficiency (Wasson et al., 2012; Herath et al., 2023). AMF can enhance the expression of metal transporters in roots, promote the production of organic compounds, and combine with Cd^{2+} to form complexes. This reduces the biotoxicity of Cd^{2+} in plants (Wang et al., 2022). Thus, more larger roots carry a higher risk of Cd uptake. Our results also show that Jingdian 8, which responded more to AMF, had a greater promoting effect on Cd uptake by roots than Enyu 98. However, Jingdian 8 showed an inhibitory effect on Cd uptake in shoots, consistent with previous studies (Zhan et al., 2018).

4.2. Effects of AMF on soil Cd forms

The chemical form of soil Cd determines its mobility and bioavailability. AMF regulation of Cd forms is influenced by the host variety (Liang et al., 2023; Li et al., 2023). Two-way ANOVA analysis confirmed that AMF inoculation, maize variety, and their interaction all significantly affect the content of available Cd in rhizosphere soil. This means that Cd form regulation by AMF depends on the characteristics of the maize variety. Among compartments, the available Cd in soil reduction was stronger in the mycorrhizal compartment than in the hyphal compartment. Comparing varieties, Enyu 98 showed a greater reduction in available Cd in the mycorrhizal compartment. This may be due to the stronger synergy between its root morphology and AMF.

AMF not only reduces the available Cd content in soil. It also drives the transformation of Cd between different chemical forms, enhancing stability (Yang et al., 2026. Zhao et al., 2025) found that AMF inoculation improved soil available Cd removal and promoted the conversion of Cd to more stable forms. This study showed that compared with the root compartment, the proportion of oxidizable Cd in the rhizosphere soil of Jingdian 8 and Enyu 98 maize increased significantly by 23%, while the proportion of reducible Cd decreased by 21% and 30%, respectively. Compared with the soil compartment, the proportion of residual Cd in the hyphal compartment of Enyu 98 increased significantly by 27%. Oxidizable Cd mainly combines with soil organic matter, like GRSP and humus. Its mobility and bioavailability are significantly lower than those of reducible Cd. Residual Cd, the most stable form in soil, is almost immobile and has no bioavailability (Zhao et al., 2020). In summary, AMF inoculation improves the chemical form of Cd in rhizosphere soil and reduces Cd stress on plant growth.

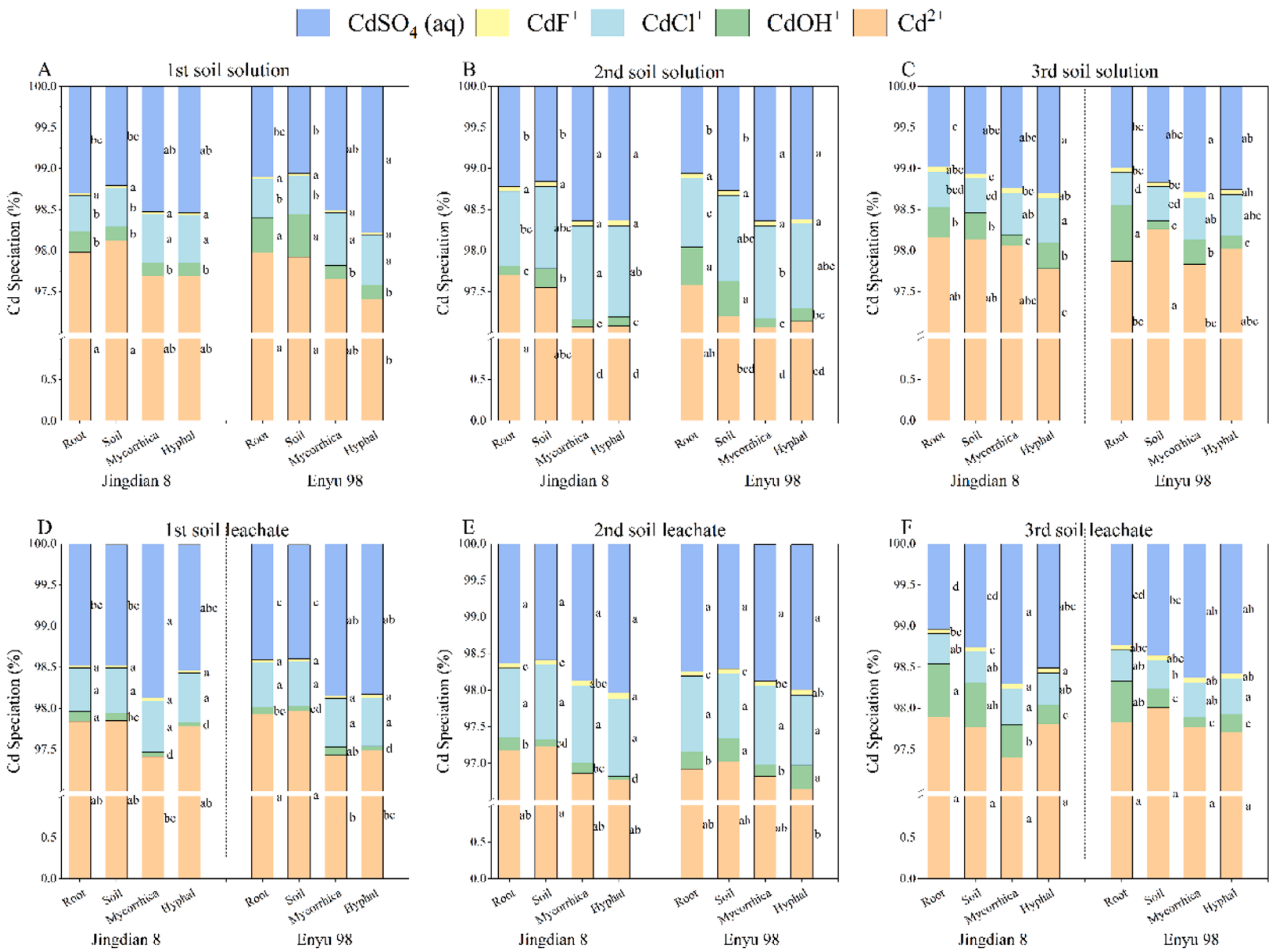

Fig. 8. The chemical speciation percentage of Cd in soil interflow (A-C) and leachate (D-F).

4.3. Effects of AMF-regulated maize root traits on soil Cd forms and Cd loss

Soil solutions contain a diverse array of inorganic anionic ligands (Wang et al., 2012). Among these, Cl^- and SO_4^{2-} exhibit strong binding affinities and can preferentially form stable complexes with Cd^{2+} through coordination reactions, thereby altering the chemical speciation of cadmium in the soil environment (Chien et al., 2009). Such complexation processes exert critical effects on the migration potential of Cd and further modify its bioavailability, environmental mobility, and ecotoxicity. These findings indicate that Cd^{2+} was identified as the predominant species in both soil interflow and leachates. Moreover, AMF inoculation significantly increased the relative proportions of $CdSO_4$(aq) and $CdCl^+$ in mycorrhizal compartments.

Plant roots play a crucial role in influencing soil structure, water behavior, and Cd migration (Lu et al., 2020). AMF symbiosis and plant roots synergistically regulate Cd speciation by facilitating the transformation of highly mobile free Cd^{2+} into more stable and less bioavailable complex forms, which may effectively restrict Cd leaching and bioaccumulation within the soil–plant system. We found that AMF affects GRSP secretion and soil structure by regulating root morphology in maize varieties. This regulation differentially impacts Cd migration and transformation in soil. For Jingdian 8, which has relatively large roots, AMF promotes root branching and elongation. This increases preferential flow distribution. As a result, Jingdian 8 exhibited a larger stained area in different soil layers within both hyphal and mycorrhizal compartments compared with Enyu 98; the most prominent increase occurred in the 20–30 cm layer. The PLS-SEM model showed that AMF hyphae inhibited particulate Cd loss (Fig. 9A). However, since AMF promotes Jingdian 8 root growth, the mycorrhizal symbiosis had no significant inhibitory effect on Cd loss (Fig. 9C). This indicates that Jingdian 8's large roots cause more soil disturbance. This reduces the AMF hyphae's inhibitory effect on Cd migration, allowing Cd to rapidly move through soil via preferential flow.

Enyu 98, with relatively small roots, depends more on mycorrhizal symbiosis. PLS-SEM analysis showed that GRSP, soil aggregates, and roots all inhibited soil interflow Cd concentration, as well as Cd loss in leachate (Fig. 9D). This inhibited both horizontal and vertical migration of Cd in soil. Enyu 98's roots can better synergize with AMF hyphae. This triggers the "AMF-GRSP-root traits-soil aggregates " pathway in the mycorrhizal compartment, reducing soil Cd loss. GRSP is a key protein secreted by AMF (Wright and Upadhyaya, 1998). The functional groups in GRSP, such as carboxyl and hydroxyl groups, can form stable complexes with available Cd (Zhou et al., 2023). This converts exchangeable Cd into less mobile bound Cd (Nihal et al., 2021; Li et al., 2022). Wu et al. (2014) found that GRSP can bind Cd^{2+} in soil, forming GRSP-Cd complexes. In summary, AMF induces several changes: (1) directly promoting GRSP secretion to immobilize dissolved Cd through complexation; (2) promoting root growth, which inhibits particulate Cd migration and reduces Cd concentration through root interception; (3) indirectly promoting aggregate formation to reduce particulate Cd migration by physical encapsulation.

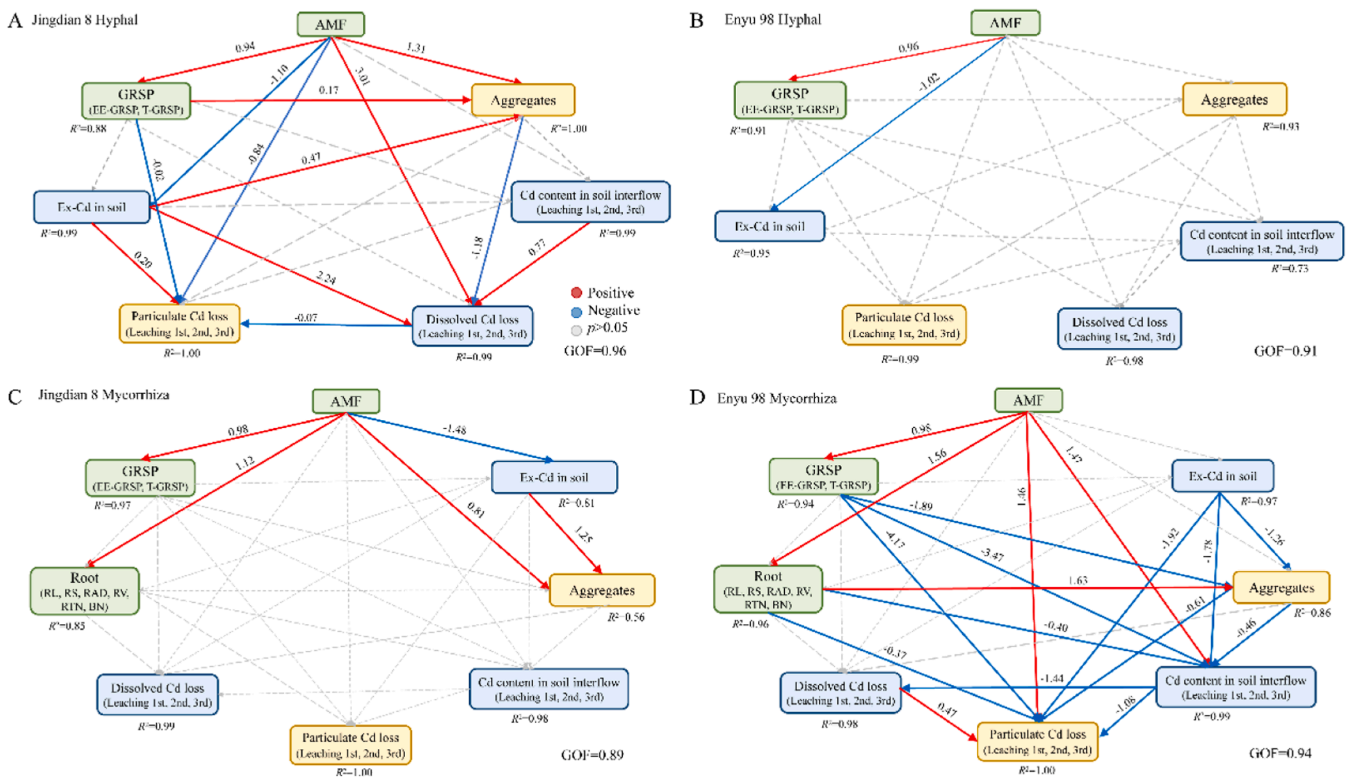

Fig. 9. PLS-SEM path diagram. Solid- and dashed-line arrows represent significant and insignificant effects, respectively.

5. Conclusion

This study revealed the differential processes by which roots of different maize varieties respond to AMF, thereby affecting Cd migration. Jingdian 8 exhibited a stronger root response to AMF, which altered soil structure and preferential flow paths, and inhibited the regulatory effect of mycorrhizal on the vertical migration of particulate Cd. In contrast, Enyu 98 with underdeveloped roots showed stronger mycorrhizal dependence, and synergistically inhibited the horizontal and vertical migration processes of different forms of Cd through AMF-regulated GRSP secretion, root growth, and soil aggregates. Future research should further strengthen in-depth studies on the mechanism of AMF on heavy metal migration during different growth stages of maize.

Abbreviations used

AMFarbuscular mycorrhizal fungi.
Cdcadmium.
GRSPglomalin-related soil protein.
PLS-SEMpartial least squares structural equation modeling.
IBRintegrated biomarker response.
EE-GRSPeasily extractable glomalin-related soil protein.
T-GRSPtotal glomalin-related soil protein.

CRediT authorship contribution statement

Pan Yunfeng: Writing – review & editing, Supervision, Methodology. **Wang Ruibo:** Supervision, Software, Formal analysis. **Yang Qian:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **Yang Yijie:** Methodology, Data curation, Conceptualization. **Shan Yuanyuan:** Supervision, Data curation. **He Yongmei:** Visualization, Supervision, Project administration, Investigation. **Zhan Fangdong:** Writing – review & editing, Validation, Resources, Project administration, Conceptualization. **Gilles Colinet:** Writing – review & editing, Methodology, Conceptualization.

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.

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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.indcrop.2026.123913.

Data Availability

Data will be made available on request.

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