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Peduru Hewa, Jeewani; Luo, Yu; Yu, Guanghui; FU, Yingyi ; He, Xinhua ; van Zwieten, Lukas ; Liang, Chao; Kumar , Amit ; He, Yan; Kuzyakov, Yakov; Qin, Hua; Guggenberger, Georg; Xu, Jianming

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Arbuscular mycorrhizal fungi accelerate carbon cycling in the plant-soil continuum: rhizodeposit stabilization and soil priming effects

Peduruhewa H. Jeewani[a,b], Yu Luo[a*], Guanghui Yu[c], Yingyi Fu[a], Xinhua He[d], Lukas Van Zwieten[e], Chao Liang[f], Amit Kumar[g], Yakov Kuzyakov [h,k], Hua Qin[i], Georg Guggenberger[j], Jianming Xu[a]

[a]Institute of Soil and Water Resources and Environmental Science, Zhejiang Provincial Key Laboratory of Agricultural Resources and Environment, Zhejiang University, Hangzhou 310058, China

[b]Department of Agriculture, Southern Province, Galle 80000, Sri Lanka

[c]Institute of Surface-Earth System Science, Tianjin University, Tianjin 300072, China

[d] College of Resources and Environment, Southwest University, Chongqing, 400716, China

[e]NSW Department of Primary Industries, Wollongbar Primary Industries Institute, NSW 2477, Australia

[f] Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, Liaoning, 110016, China

[g] Ecosystem Functioning and Services, Institute of Ecology, Leuphana University Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany

[h] Department of Soil Science of Temperate Ecosystems, Department of Agricultural Soil Science, University of Gottingen, 37077 Gottingen, Germany

[i] State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Hangzhou 311300, China

[j] Institute of Soil Science, Leibniz Universität Hannover, 30419 Hannover, Germany

[k]Agro-Technological Institute, RUDN University, 117198 Moscow, Institute of Environmental Sciences, Kazan Federal University, 420049 Kazan, Russia

Correspondence to: Dr. Yu Luo

Email: luoyu@zju.edu.cn

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Abstract

The functioning of arbuscular mycorrhizal fungi (AMF) in carbon (C) sequestration related to the abiotic and biotic processes at the root-soil interface is not well understood. To address this paucity in knowledge, we assessed the physicochemical stabilization and microbial mineralization of maize (*Zea mays* L.) rhizodeposits (rhizo-C) and soil organic C (SOC) in soil inoculated with AMF compared to a Control soil (without AMF), and also evaluated the role of goethite in these C processes. Using ^{13}C natural abundance methods, we showed that

rhizo-C derived CO_2 with AMF and AMF+Goethite inoculation decreased by 0.8 and 0.6-fold, respectively, compared to the Control. While, rhizo-C allocation into large macro-aggregate was 7.6-fold larger in soil with AMF compared to Control, which was most likely due to marco-aggregate formation stimulated by AMF hyphae. Analyses using μ-FTIR confirmed that the spatial distribution of polysaccharides overlapped with Fe-O minerals within macro-aggregate, supporting the concomitant processes of rhizodeposits stabilization and aggregate formation via hyphal-aggregate-mineral interactions. The rhizosphere priming effect (RPE) was the highest in AMF, e.g., with 2.4-fold increase compared to the Control at day 35. The intensity of the RPE induced by AMF was highly associated with several genera, i.e., *Solirubrobacter, Pseudomonas,* and *Talaromyces*, suggesting the significance of these core microbial groups in organic C mineralization. We quantified the loss and gain of C by AMF or/and Goethite addition during plant growth. For instance, AMF+Goethite addition reduced SOC mineralization and promoted rhizo-C accumulation, with 0.9-fold decrease of RPE and 1.7-fold increase of rhizodeposit stabilization compared to Control. Additionally, the inoculation of AMF in soil enhanced both RPE (by 6.1 mg C kg^{-1} day^{-1}, 74% increase compared to Control) and rhizo-C stabilization (by 6.2 mg C kg^{-1} soil day^{-1}, 47% increase compared to Control), via AMF mediated aggregate formation and microbial community shifts.

Keywords: *Arbuscular mycorrhizal fungi, Carbon sequestration, Soil organic matter, Rhizodeposition, ^{13}C natural abundance, Synchrotron-radiation-based spectro-microscopy*

1. Introduction

There is an increasing focus on soil organic carbon (SOC) storage for climate change mitigation (Lorenz and Lal, 2014; Wang et al., 2016). Arbuscular mycorrhizal fungi form mutualistic symbioses with the roots of most plants on earth contribute to terrestrial carbon (C) sequestration by acting as a conduit to transfer rhizodeposits (rhizo-C) from roots to soil (Wright et al., 1998). In these mutualistic symbioses, AMF utilizes 4-17% of the host's photosynthetically fixed C (Wright et al., 1998) and contributes to the facilitation of rhizo-C accumulation thus build up SOC through AMF hyphal extension, production, and turnover. Additionally, growing evidence suggests AMF is involved in the mineralization of rhizo-C and SOC (Cheng et al., 2012; Averill et al., 2014). There is a need to understand the role of AMF in terrestrial C sequestration by quantifying both stabilizations of rhizo-C and the simultaneous mineralization of both rhizo-C and SOC. The mechanisms driving these two processes, however, are debated in current literature.

Rhizo-C stabilization by AMF is mainly through hyphal-aggregate-mineral interactions (Averill et al., 2014; Ji et al., 2019). The hierarchical aggregation model has shown that AMF contributes to soil aggregate stability (Daynes et al., 2013; Wang et al., 2016) directly by their extraradical hyphae or indirectly via altering the biochemical properties and root morphology of host plants (Peng et al., 2013; Wu et al., 2014). The genera *Glomus* transport plant-derived monosaccharides from roots to soil aggregates (Johnson et al., 2002; Fellbaum et al., 2012) that preserves soil organic matter (SOM) (Fellbaum et al., 2012; Chen et al., 2013). Minerals such as Goethite can also promote the formation of aggregates as well as Fe-organic complexes via adsorption and/or precipitation processes, which help stabilize rhizo-C (Jeewani et al., 2020; Jeewani et al., 2021). As AMF and Goethite may regulate soil C stabilization via physicochemical processes and hyphal-

aggregate formation (Jones and Edwards, 1998; Cao et al., 2016), the interactions of hyphal-aggregate-mineral that underpin rhizo-C stabilization, however, have been rarely investigated.

AMF increases the mineralization of SOM (i.e., the rhizosphere priming effect, RPE), which is a typical response of SOM to rhizo-C additions (Carney et al., 2007; De Graaff et al., 2010). AMF induced PRE can be attributed to changes in i) C sources, i.e., rhizo-C content (Jones and Edwards, 1998; Kabir et al., 2020; Jeewani et al., 2021) and ii) edaphic variables such as nutrient status. When soils are nutrient deficient, AMF exploits N through SOM mineralization (i.e., N-mining) to meet their nutrient stoichiometric requirements and, consequently, induce a positive RPE (Kirkby et al., 2013). N-mining processes by AMF are greater under nutrient-limited conditions and are most likely caused by oligotrophic microorganisms, i.e., K-strategists, that utilize recalcitrant SOM via extracellular enzymes (co-metabolisms) (Drake et al., 2011). AMF can also enhance the trade-off between rhizo-C deposition and plant N assimilation via manipulating the microbial communities in the rhizosphere (Zhu and Miller, 2003). The interactions between AMF and bacteria maintain via the quality and quantity of available hyphal exudates, which can subsequently lead to SOM mineralization (Zheng et al., 2018). Mechanisms underlying the effects of AMF on the microbial community and, consequently, organic matter mineralization, i.e., RPE, remain unclear (Paterson et al., 2016).

There is a paucity of knowledge on how the AMF symbiosis interacts with the rhizosphere microbial community (e.g., saprotrophic fungi) (Rillig, 2004; Basu et al., 2018; Janasa et al., 2018). AMF and the associated rhizosphere microbiome has been referred to as a ‘keystone mutualist’ association (Rillig, 2004; Bonfante and Anca, 2009). This is mainly due to the consumption of AMF-spores and hyphal exudates to obtain nutrients (bacterial mycophagy) by the selected bacteria (Leveau and Preston, 2008; Bonfante and Anca, 2009). These mutualist microbes have been shown to include *Pseudomonas*, *Burkholderia*, *Bacillus*,

Actinomycetes, and protozoan communities (Drigo et al., 2010). It is noteworthy that some prokaryotes are associated not only with the hyphae of AMF but also with roots colonized by mycorrhizae and saprotrophs, e.g., the fruiting bodies of Ascomycota and Basidiomycota (Drigo et al., 2010; Bao et al., 2019). This suggests, instead of direct symbiosis, AMF might exert indirect effects on the bacterial community by influencing plant roots and other fungal communities. It awaits studies to investigate the relations between AMF and non-AMF microorganisms (Drigo et al., 2010; Frey, 2019), and their interactions could largely determine belowground C dynamics. For instance, the antagonism between AMF and associated microbiota can result in a net C sink in soil (Rillig, 2004).

Long-term SOC storage depends on the balance between gain (stabilization) and loss (mineralization). The effects of AMF on soil C storage via the opposite directional processes of both stabilization and mineralization remain rarely considered (Averill et al., 2014). For instance, there can be direct promoting effects of the hyphae and its products, such as released organic compounds, on both C stabilization and mineralization processes (Rillig, 2004; Kohler et al., 2015). Mechanisms underlying these AMF mediated C turnover processes still await investigations. Thus, we have identified such knowledge gaps that can be addressed by the current study, including 1) the role of AMF or/and Goethite on rhizo-C stabilization in the rhizosphere via aggregate formation, 2) the mechanisms involved in AMF induced RPE via shifting rhizosphere microbial community, and 3) soil C balance via compensation of SOM mineralization by rhizo-C stabilization. We hypothesized that: (i) The presence of AMF in the rhizosphere would increase rhizo-C stabilization via aggregate formation, whereas the presence of Goethite would increase stabilization through both formation of aggregates and Fe-organic complexes via precipitation, (ii) The presence of AMF will result in greater RPE due to increased rhizosphere community diversity and positive fungal-bacterial interactions, and (iii) presence of AMF will contribute to faster SOC

cycling via acceleration of both C processes of rhizo-C (new input) stabilization and SOC (native) mineralization.

2. Materials and methods

2.1 Site description

Soil (Alfisol USDA Soil Classification System) was collected in September 2018 from the top 10-cm layer of an experimental field plot located in Zhejiang, China. The location is characterized as having a subtropical monsoon climate with annual rainfall and mean temperature of 1,450 mm and 23 ^{o}C, respectively. The soil had a sandy clay loam texture, pH (Soil: H_2O 1:2.5) of 5.4, 25.6 g total C (SOC) kg^{-1}, 2.24 g total N (TN) kg^{-1}, and 29.1 g total Fe kg^{-1}. The mean $\delta^{13}C$ value of soil was -26.5 ± 0.79 ‰ (n = 4) and maize root was -12.8 ± 0.81 ‰ (n = 4).

2.2 Experimental setup

The study used a ^{13}C natural abundance approach, where a C_4 plant (Maize, *Zea mays* L. cv ND488. $\delta^{13}C$= -12.8‰) was grown on soil ($\delta^{13}C$ value of -26.5‰) previously planted solely with C_3 plants. The $\delta^{13}C$ signal from the root exudates was used as a tracer to separate plant and soil-derived CO_2 efflux. The rhizboxes were constructed from acrylic (30 cm height x 14 cm diameter, see Fig. S1) and had a layer of quartz sand (250 g) at the bottom to facilitate drainage and reduce the potential development of anaerobic conditions. Eight treatments were established, including with plants (n=4) and without plants (n=4): (1) soil only without mycorrhizal inoculum (Control), (2) soil+AMF (AMF treatment inoculated with arbuscular mycorrhizal inoculate especially containing *Glomus caledonium* 90036 obtained

from the Institute of Soil Science, Chinese Academy of Sciences, China; inoculation rate based on 10% soil weight), (3) soil+Goethite (Goethite, <0.25mm powder Sigma-Aldrich, Germany) at 1600 kg ha^{-1} and (4) soil+AMF+Goethite (AMF+Geothite, same above-mentioned doses). Additionally, four rhizoboxes filled with only 250 g of quartz sand were maintained during the experimental period as blanks. A total of 36 rhizoboxes were randomly arranged in a greenhouse. The aseptically germinated maize seeds were sown into the rhizoboxes (1 seedling per box one week after germination).

2.3 Sampling and analyses

Zea mays L. were grown for 25 days from germination to reach a uniform vegetative growth. It was previously reported that maximum vegetative growth, higher polysaccharide content and root exudation occurs around 35 days after emergence (Kuzyakov and Xu, 2013; Qiao et al., 2017). From 25 days after establishment, plant root-soil system of the rhizoboxes were isolated from the atmosphere by rubber plugs, with the holes on the top of lids being sealed by silicon gum (TACOSIL 145, Thauer & Co., Dresden, Germany) (Fig. S1). Every five days, the lids were sealed to close the rhizosphere environment, and CO_2 was trapped for a 24 h period. To achieve this, the CO_2 in the headspace was firstly removed using an alkaline trap (NaOH, 20 ml, 1.0 M) for two hours, and the CO_2 efflux from the soil was then collected using a fresh trap (NaOH, 20 ml, 1.0 M) for a 24h period. Once the NaOH traps were removed, the lids were also removed until the next sampling period. This procedure was continued until day 50. The amount of CO_2 sorbed by the NaOH solution was quantified by titration against 0.05 M HCl using an Easy Plus auto titrator (Mettler Toledo, Greifensee, Switzerland), using 20mL of the trap solution. To determine the $\delta^{13}C$ signature of the trapped CO_2, an 8 ml aliquot of NaOH solution was mixed with 8 ml 1.5 M $BaCl_2$ (Aoyama et al., 2000). The precipitated $BaCO_3$ was thrice rinsed with Milli-Q H_2O, centrifuged, and the

supernatant removed. The precipitate was freeze-dried overnight. The natural abundance of $\delta^{13}C$ in soils was measured using air-dried and sieved (<200 μm) soil, which was accurately weighed (about 0.2 mg) into tin capsules prior to analysis using an isotope ratio mass spectrometer with IAEA-600 (Caffeine); $\delta^{13}C$=-27.771‰ as standard material (Meng et al., 2013) (Thermo Fisher Scientific, DELTA V plus IRMS, Bremen, Germany) coupled with an Elemental Analyzer **(**EA NA1500-EA 1110 device, Carlo Erba and Thermo Fisher Scientific, Bremen, Germany).

Plant shoots and roots were harvested after the 50-day experiment (Figs. S3 and S7). The soil with the roots removed was homogenized by mixing and separated into two uniform batches. One batch was freeze-dried for DNA extraction. Another batch was dried at room temperature (23 ^{o}C) for further physicochemical analyses. Total carbon (C) and total nitrogen (N) was assessed using the dry combustion method (Perkin Elmer EA2400, Shelton, CT, USA). The soil was fractionated into four aggregate size classes (>2, 0.25-2, 0.053-0.25, and <0.053 mm) using wet sieving (Nimmo and Perkins, 2002). The $\delta^{13}C$ in aggregates was measured using an isotope ratio mass spectrometer coupled with an Elemental Analyzer (EA NA1500 - EA 1110 device, Carlo Erba, and Thermo Fisher Scientific, Bremen, Germany).

2.4 Calculation of the rhizosphere priming effects

The mineralization of rhizo-C was distinguished from soil organic C mineralization based on the changes in stable isotopic composition ($\delta^{13}C$) over time. The standard equation for determining $\delta^{13}C$ (‰) is derived from:

$$\delta\,^{13}C(‰) = [\left(\frac{R_{sample}}{R_{VPDB}}\right) - 1] \times 1000 \qquad (1)$$

Where R_{sample} is the mass ratio of ^{13}C to ^{12}C of the sample, and R_{VPDB} is the mass ratio of ^{13}C to ^{12}C of the Vienna Peedee belemnite (V-PDB) standard. The value of ^{13}C and ^{12}C atomic ratio of the standard material is 0.0112372.

$$C_4 = C_t \times \frac{\delta_t - \delta_3}{\delta_4 - \delta_3} \quad (2)$$

$$C_t = C_3 + C_4 \quad (3)$$

Where C_t is the total belowground CO_2, C_3 and C_4 are the respective amounts of CO_2 derived from the C_3 soil and C_4 plant, δ_t is the $\delta^{13}C$ value of the C_t (from the total CO_2), δ_3 is the $\delta^{13}C$ value of the C_3 soil without plants (-26.52‰), and δ_4 is the $\delta^{13}C$ value of the C_4 maize root (-12.71‰) (Jeewani et al., 2020).

The SOM-derived CO_2 efflux was calculated by the difference between the total CO_2 efflux and root-derived CO_2 obtained by the ^{13}C natural abundance approach.

RPE was calculated as the difference between SOM-derived CO_2 from planted ($C_{SOM(planted)}$) and unplanted ($C_{SOM(unplanted)}$) soils (Pausch et al., 2013).

$$RPE = C_{SOM(planted)} - C_{SOM(unplanted)} \quad (4)$$

2.5 Extraction of FeOM complexes

The concentration of Fe-bound OC was measured by a dithionite-citrate-bicarbonate extraction method (Lalonde et al., 2012; Wang et al., 2017). Briefly, approximately 0.50 g of freeze-dried soil was mixed with 30 mL of buffer solution (0.27 M trisodium citrate and 0.11 M sodium bicarbonate, pH 7.3) in 50-mL polycarbonate centrifuge tubes, which were then placed in a water bath (80 ^{0}C). A reducing agent (0.50 g sodium dithionite) was added to the mixture. The mixture was maintained at 80 ^{0}C for 15 min. To quantify OC released during

the heating process, controls were performed in which the soils were extracted with sodium chloride instead of trisodium citrate and sodium dithionite at an equivalent ionic strength under the same conditions. Subsequently, the mixture was separated by centrifugation at 4,000 x *g* for 10 min. The residue was washed with 5 mL of deionized water a total of five times and then freeze-dried. The TOC, TN, and $\delta^{13}C$ in the residue were analyzed using an Elementar vario micro cube elemental analyzer coupled with GV isoprime 100 isotope ratio mass spectrometer (GV Instruments, UK). The washings and supernatants were combined. The solution of the mixture from the dithionite-citrate-bicarbonate extraction was then acidified to pH 2 and filtered through a 0.45-μm PTFE membrane filter. Total soil iron oxides (Fe_d) were quantified by determining the concentration of Fe in the solution of the mixture of dithionite-citrate-bicarbonate extraction. Soil amorphous (Fe_o) and OM-complexed (Fe_p) Fe oxides were extracted with ammonium oxalate and sodium polyphosphate, respectively (Wan et al., 2018). The calculations for FeOM are provided in the supplementary information.

2.6 Synchrotron radiation-based Fourier transform-infrared (SR-FTIR)

The distribution of functional groups from SOM and minerals in soil aggregates was determined by an SR-FTIR Spectromicroscopy. Soil samples were frozen at -20 ºC and directly sectioned without embedding. Thin sections (2 μm in thickness) were cut on a cryomicrotome (Cyrotome E, Thermo Shandon Limited, UK) and transferred to infrared-reflecting MirrIR low-E microscope slides (Kevley Technologies, Ohio, USA). The SR-FTIR mapping was first obtained at the beamline BL01B1 of the National Centre for Protein Science Shanghai and Shanghai Synchrotron Radiation Facility, Shanghai, China. The spectra from 4,000 to 650 cm^{-1} were recorded in reflection mode using a Thermo Nicolet 6,700 FTIR spectrometer and a continuum infrared microscope with the following settings:

aperture size ten μm, step size 5×5 μm^2, and resolution 4 cm^{-1} (Sun et al., 2019). Spectral maps were processed using an Omnic 9.0 (Thermo Fisher Scientific Inc., Waltham, USA). Maps of the distribution of functional groups were created for dominant peak heights at 3,627 (clay-OH), 1650 (amide I), 1,511 (amide II), 1,120 (polysaccharide-OH), and 974 (Si-O-Si) cm^{-1}, respectively (Sun et al., 2017). Then, the micro-FTIR (μ-FTIR) spectra in the region of interest were rescanned with a step size of 2 μm. The spatial-related μ-FTIR imaging of soil aggregates was rebuilt using an Omnic 9.0 (Thermo Fisher Scientific Inc.).

2.7 DNA extractions and sequencing

DNA was extracted from 0.50 g of soil using a Fast DNA Spin Kit (MP Biomedicals, Santa Ana, CA, USA) according to the manufacturer's protocol. The extracted DNA was dissolved in 50 μl of Tris and EDTA (TE) buffer, and the concentration of DNA was quantified using a Nanodrop 2000 (Thermo Scientific, Willington, USA). Samples were stored at -80˚C before sequencing. The bacterial 16S rRNA gene fragments were amplified using primer sets targeting the V4-V5 variable region. The forward primer was 515F (5'- GTGCCAGCMGCCGCGGTAA-3') linked with a specific-sample 5-bp barcode sequence at the 5'end of primer, and 806R (5'-GGACTACHVGGG TWTCTAAT-3') was used as the reverse primer. The ITS1 region was amplified by the PCR for fungal genes using the 5'- CTTGGTCATTTAGAGGAAAAGTAA-3' forward primer and 5'- GCTGCGTTCTTCATCGATGC-3' reverse primer (Borneman and Hartin, 2000). Each sample was amplified in triplicate, and then the three reaction products were pooled and purified using Agincourt Ampure XP beads (Indianapolis, USA). All amplicons were pooled across all samples at equimolar concentrations (20 ng μl^{-1}) into a composite sample, and the index sequencing of paired-end 250 bp was performed on an Illumina HiSeq 2000 platform.

The procedures for bacterial and fungal DNA amplification and sequencing were performed by Major Bio, Inc. (Shanghai, China).

2.8 Soil microbial data analyses

Data from the bacterial 16S rRNA and fungal ITS gene sequencing were processed by the QIIME 1.8.0-dev pipeline (Caporaso et al., 2012). Low-quality reads (quality score < 20, read length < 200 bp, and sequence errors) were discarded. Chimeric sequences were identified by UCHIME and removed (Edgar, 2010). The remaining high-quality sequences were clustered into the operational taxonomic units (OTUs) based on a 97% pairwise identity using the UCLUST algorithm (Edgar, 2010). The representative sequences of each OTU were then chosen for subsequent alignment and taxonomic assignment with the RDP classifier. Taxonomy was assigned to bacterial phylotypes of the Green genes database and fungal phylotypes of the UNITE database (Abarenkov et al., 2010). All datasets were rarefied to prevent potential bias caused by different sequencing depths, with 39,000 sequences per sample for bacterial and 15,500 sequences per sample for fungal α- and β-diversity analyses.

We calculated the Shannon index to describe α-diversity of bacterial and fungal communities, which were conducted with vegan's function 'diversity' in R. We also performed the redundancy analysis (RDA) with fitted environmental vectors using function 'envfit' in vegan to determine the independent contributions of these selected environmental variables to the variation in community composition.

The O2PLS (Two-way orthogonal partial least squares analysis) analysis is an integrative data analysis method capable of modeling systematic variation while providing simpler models, thus aiding interpretation. The O2PLS analysis was performed using a SIMCA-P 14 (Version 14.1.0.2047) to correlate the microbial genus to C dynamics (rhizo-C

and SOM). The Y-matrix was designed as the C allocation datasets, and the X-matrix was designed as the microbial community datasets (Trygg and Wold, 2003). Distance-based linear model multivariate analysis (distLM) was conducted in a distLM_forward3 software (Anderson, 2003) and determine the relative effects of variables such as TC, TN, FeOM, pH, and aggregate size classes (>2 mm, 0.25-2 mm, 0.053-0.25 mm, and <0.053 mm) on communities of soil bacteria and fungi. If conditions were met, the Pearson's correlation coefficient was calculated with $P < 0.05$.

The analysis of important predictors of edaphic factors for rhizo-C stabilization, mineralization, and rhizosphere priming effect was done using the random forest analysis (Liaw and Wiener, 2002). Edaphic variables validation of soil physicochemical variables (>2mm aggregate size class, 0.25-2mm aggregate size class,< 0.25mm aggregate size class, total carbon, carbon: nitrogen ratio, total N, Fe organic matter complexes) and biological variables (Glomeromycota, Proteobacteria, Tremellomycetes, Eurotiomycetes, Euromycetes, Sordiomycetes, Chloroflexi, Bacteriodates, and Actinobacteria) were used in the random forest analysis to assess their relative contributions/influences to the substrate-derived C mineralization, priming, and stabilization.

A correlation network of AMF amended, and Control (non-amended) samples were separately examined to understand the effects of AMF on soil microbial networks. The co-occurrence patterns of the microbial communities were constructed by calculating multiple correlations and similarities with co-occurrence network (Co-Net) inference (Chen et al., 2019). For network constructions, the OTUs with relative abundances greater than 0.01% were kept with the dissimilarity threshold to the maximum value of the Kullback-Leibler Distance (KLD) matrix and the Spearman's correlation. The correlation threshold was greater than 0.6, and the *P*-value was below 0.01. For each edge and measure, permutation and bootstrap distributions were generated with 100 iterations. Measure-specific *P*-value was

computed as the area of the mean of the permutation distribution under a Gauss curve generated from the mean and standard deviation (SD) of the bootstrap distribution. The *P*-values were adjusted using the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995). Finally, only edges supported by two measures and with adjusted *P*-values below 0.05 were retained. The nodes in the constructed networks represent OTUs, and edges represent strong and significant correlations between OTUs. The nodes presented individual microbial taxa in the microbiome network. The network edges indicated the pairwise correlations between nodes, suggesting biologically or biochemically meaningful interactions, among which orange lines are positive connections and blue lines are negative connections. Network visualizations were conducted using Gephi (Bastian et al., 2009) and Cytoscape 3.5.1 (Shannon et al., 2003). The Network Analyzer tool was used to calculate the network topology parameters. Genera with the highest betweenness centrality scores were considered keystone species (Martín González et al., 2010). The topological characteristics of microbial networks calculated by Gephi were represented in Table S4.

2.9 Other statistical analyses

The statistical analysis of all non-microbial data was performed using SPSS 20 (SPSS, Inc., Chicago, IL, USA). A two-way ANOVA was used to analyze the C dynamics (total CO_2 efflux, rhizo-C derived CO_2, RPE) and rhizo-C in soil pools such as aggregates and FeOM complexes after the addition of AMF, Goethite, and AMF+Goethite based on the means of results. For the calculations of C balance between stabilization and RPE, cumulative rhizo-C in soil pools and cumulative SOM-derived CO_2 effluxes were used. Residues were checked for normal distribution and homogeneity by Shapiro-Wilk and Levene's tests, respectively. If conditions were met, the Tukey Post-hoc test was performed

to reveal the significance of various treatments. All comparisons were made within a sampling date. Pearson's correlation coefficient was calculated with $P<0.05$. Only the effects and differences significant at $P<0.05$ data are presented and discussed.

3. Results

3.1 Rhizo-C derived CO_2 efflux and rhizosphere priming effect

Rhizo-C derived CO_2 efflux ranged from 2.4 to 13.2 mg C kg^{-1} soil day^{-1} on day 25, reached its peak at day 35, and tended to decrease to the completion of plant growth (Fig. 1a). Rhizo-C derived CO_2 efflux, with the addition of Goethite, remained relatively stable during the whole growth period (Fig. 1a). At day 35, AMF amended soil decreased rhizo-C derived CO_2 efflux by 0.8-fold, and Goethite resulted in a 0.2-fold decrease, relative to the Control. The highest RPE (12.7 mg of C kg^{-1} soil day^{-1}) was under the AMF amendment on day 35. The other three treatments followed a similar pattern but with a smaller magnitude of changes in RPE. Total CO_2 efflux from soil increased on day 35 and then gradually declined until day 50 for all treatments (Fig. S2). The largest CO_2 efflux was observed under the AMF amendment, whereas the presence of Goethite decreased CO_2 efflux by 0.4-fold compared to AMF at day 35.

3.2 Distribution pattern of accumulated rhizo-C in aggregate size classes

The amendment of AMF and Goethite to soil increased the amount of rhizo-C accumulated in the >2 mm aggregate size class (Fig. 2a). More C accumulation was found in macroaggregates under AMF+Goethite (Fig. 2a). In contrast, the rhizo-C in the 2-0.25 mm aggregate size was the highest under the Control (0.32 g kg^{-1} of soil), and the other three

treatments were in the same range (0.17-0.18 g kg^{-1} of soil) (Fig. 2a). The rhizo-C accumulated within FeOM in the >2 mm aggregates was 2.5-fold higher under Goethite than under the Control. Accumulation of rhizo-C within FeOM fractions among treatments followed the order Goethite > AMF+Goethite > AMF > Control (Fig. 2a). The Fe-bound organic C to Fe molar ratio was between 4.3-7.1, indicating that co-precipitation (with Fe-bound organic C:Fe >6) was a dominant process under both Goethite and AMF+Goethite treatments (Table S3).

3.3 C balance between stabilization and RPE

The C balance was calculated by assessing the difference between stabilization and the RPE (Fig. S8). Rhizo-C stabilization in soils amended with AMF, Goethite, and AMF+Goethite were between 6.2-7.5 mg C kg^{-1} soil day^{-1}. In contrast, the RPE in soil inoculated with AMF was the highest (6.1 mg C kg^{-1} soil day^{-1}) while soil amended with Goethite gave the lowest SOC loss of 2.8 mg C kg^{-1} soil day^{-1}. The greatest C accumulation (7.5 mg C kg^{-1} soil day^{-1}) was in AMF+Goethite and followed by Goethite (6.9 mg C kg^{-1} soil day^{-1}).

3.4 Distribution of rhizo-C in soil aggregates

To better address, the spatial heterogeneity of mineral and organic functional groups in soil aggregates, the micro-FTIR (μ-FTIR) spectra (Fig. 2b (ii, iv)) in the region of interest (ROI, showing as a red line in Fig. 2b (ii, iii)) was further rescanned with a step size of 2 μm. We assigned a set of functional groups according to the stretching frequency attributed to specific phases (Lehmann et al., 2008; Luo et al., 2014; Saviello et al., 2014). The rebuilt spatial-related chemical imaging (Fig. 2b (ii, iv)), with a distance of 0 μm indicating the start

point of the red arrow in Fig. 2b (i, iii), across the soil (0.25-0.053 mm, >2 mm aggregate, clay minerals (3627 cm^{-1}) and secondary oxides (Si-O, 965 cm^{-1}; Al-O, 900 cm^{-1}; Fe-O, 860 cm^{-1}) were distributed homogeneously in the ROIs. The secondary oxides, such as Fe-O, Al-O, not the clay minerals, were distributed towards the surface of the aggregates, suggesting that minerals might play a critical role in supporting the integrity of soil aggregates. In contrast, amide I (C=O, 1650 cm^{-1}) and amide II (C-N, 1511 cm^{-1}) were present as patches, whereas polysaccharides (OH, 1120 cm^{-1}) had a similar distribution with Al-O and Fe-O oxides. These distribution patterns were further supported by the SR-FTIR mapping (Fig. S5), which scanned the whole soil aggregates with a step size of 10 × 10 μm^2. Based on the spatial-related μ-FTIR imaging, both clay minerals and secondary oxides (e.g., Goethite) played an essential role in sustaining the integrity of soil aggregates and potentially preserving organic matter.

3.5 Soil microbial communities

The highest bacterial diversity (Shannon index) was reported under AMF (8.18) and AMF+Goethite (8.01), while Goethite alone had a lower Shannon index value of 7.87 (Fig. 3a). The fungal diversity was similar between Goethite (3.32) and the Control (3.28) but was greater in AMF (4.03) and AMF+Goethite (3.84) (Fig. 3b). Consequently, the strongest factor affecting the bacterial and fungal diversity was AMF inoculation.

The first component of the redundancy analysis (RDA1) explained 36% of the bacterial community abundance (Fig. 3c). Soil FeOM, $\delta^{13}C$ signatures, and stability of >2 mm aggregate size class were correlated with the AMF and AMF+Goethite treated soils. RDA1 and RDA2 explained 67% and 9% of the variability in the fungal community composition, respectively (Fig. 3d). There were notable differences in the relative abundance

of bacterial and fungal phyla in the rhizosphere (Fig. S6). Bacterial phyla of Proteobacteria, Actinobacteria, Chloroflexi, and fungal classes of Sordariomycetes and Tremellomycetes were the dominant taxa (Fig. S6).

The best multivariate distance-based linear modeling (distLM) analysis showed the contributions of soil properties, including TC, TN, FeOM, and aggregate fraction distribution (>2 mm, 0.25-2 mm, 0.053-0.25 mm, and <0.053 mm), to the bacterial and fungal communities (Table 1). Soil bacterial community was affected by TC (24%), >2 mm aggregates size class (11%), and TN (10%). The fungal community was influenced by TC (12%), TN (13%), and >2 mm aggregates size class (12%) (Table 1).

3.6 Microbial interactions influenced by AMF

Co-occurrence networks were constructed to understand the interactive effects of AMF on the stimulation of the hyper-symbiont community. The ratios of the positive links (co-presence) to negative links (mutual exclusion) were the highest under the Control and lowest under AMF inoculation (Table S4). The microbial network of AMF contained 84 nodes and 91 links, and *Phenylobacterium, Claroideoglomus,* and *Solirubrobacter* were detected as keystone taxa (Table S4). Interactions between AMF and bacteria or saprotrophic fungi were identified. *Candidatus, Spingobium, Burkholderia,* and *Paenibacillus* showed positive interactions with AMF in the co-occurrence networks (Fig. 3e). *Talaromyces* (K-strategist fungi) and *Solirubrobacter* (K-strategist bacteria) showed more synergistic interactions with AMF (Fig. 3e and Table 2)

3.7 Microorganisms related to organic C mineralization and stabilization

O2PLS was used to identify the functional microorganisms associated with rhizo-C mineralization and the RPE. Three conditions were considered: (a) variable influence projection (VIP) value ≥1.3; (b) correlation coefficient ($P < 0.05$); (c) the number of microorganisms being positively correlated (|r|≥0.7). Based on these criteria, 16 genera, including fungi and bacteria, were identified as core genera related to rhizo-C allocation and mineralization (Table 2). Most importantly, bacterial genera such as *Asticcacaulis*, *Devosia*, and *Solirubrobacter*, giving the largest contribution to RPE (represented with the highest VIP value), belonged phyla, including Proteobacteria and Actinobacteria (Table 2). Core genera belonging to the phyla Firmicutes and Proteobacteria were positively correlated with the accumulation of rhizo-C (Table 2). *Solirubrobacter* was the key microbe of the rhizosphere community representing the overlap between co-occurrence networks and O2PLS analysis.

In addition, genera belonging to the phylum Glomeromycota were positively correlated with both rhizo-C stabilization and the RPE. Both the genera *Trichoderma* and *Talaromyces* had a positive contribution to rhizo-C mineralization and the RPE, while the genera *Talaromyces* overlapped between co-occurrence networks and O2PLS analysis.

3.8 Contributions of soil physical, chemical, and biological properties to C cycling

Random forest analysis showed that the stabilization of rhizo-C was mainly regulated by the FeOM content (6.9% IncMSC) (a physicochemical factor) and biological interactions with Glomeromycota (6.49% IncMSC) (Fig. 4a). Rhizo-C mineralization was governed mainly by soil pH (8.76% IncMSC) together with bacterial taxa, including the phylum of Proteobacteria (3.89% IncMSC) and Acidobacteria (2.78% IncMSC). Biological contribution towards the RPE was dominated by Proteobacteria (3.87% IncMSC), Glomeromycota (3.31% IncMSC), and Actinobacteria (2.88% IncMSC).

4. Discussion

4.1 Increased rhizo-C stabilization via aggregate formation by AMF

Presence of Goethite in the soil decreased rhizo-C derived CO_2 efflux (Fig. 1a), indicating that water-soluble root exudates and microbial metabolites of rhizo-C were stabilized by negatively charged compounds (i.e., carboxylic and some amino acids), as well as stabilization of DOC on the Fe oxide surfaces (Kaiser and Guggenberger, 2000). The Fe-bound organic C to Fe molar ratio under Goethite and AMF+Goethite treatments were 6.4 and 7.1, respectively (Table S5), indicating that co-precipitation (with Fe-bound organic C:Fe >6) was a dominant process in both goethite amended soils. Thus, freshly added goethite directly adsorbed rhizo-C and decreased the total CO_2 efflux by lowering the accessibility of C to microbes. The rhizo-C derived CO_2 efflux following AMF+Goethite addition had the same pattern as with AMF, but with a lower magnitude (Fig. 1a). This indicated that AMF accelerated rhizo-C release was mostly sorbed by the presence of goethite in the soil.

Rhizo-C accumulation in the >2 mm aggregate size class with AMF inoculation was 0.54 g kg^{-1} soil after 50 days of plant growth, which was 1.4 fold higher than without AMF inoculation (Fig. 2a). AMF hyphae served as transport conduits of rhizo-C, which accounted for up to 15% of the SOC pool (Leake et al., 2004; Lehmann and Rillig, 2015). We also found a direct effect of AMF on soil aggregation (Fig. 2a), which consequently contributed to rhizo-C stabilization, especially within macroaggregates. Biopolymers increase the aggregate formation and stabilization (Awad et al., 2013), thus stabilizing SOM (Jones et al., 2009; Mueller et al., 2017; Xiao et al., 2019). AMF stimulate soil aggregation (Iversen et al., 2012; Lehmann and Rillig, 2015; Ji et al., 2019) by attaching or binding soil particles (especially

clay particles) via the adhesion of hyphal wall-associated exo-polymers (e.g., exo-polysaccharides, glycoprotein mucilage) (Ji et al., 2019). Exo-polysaccharides cause particle alignment on the hyphal surface by cross-linking, entanglement, and gluing microaggregates together via physical and chemical bonds (Wilson et al., 2009; Ji et al., 2019). We observed a well-distributed hyphal network (Fig. S1), which could stabilize soil aggregates via the glomalin released by the hyphal enmeshment called a 'string-bag' (Miller and Jastrow, 2000). Also, AMF increased rhizo-C stabilization by translocating the rhizo-C away from the rhizosphere hotspot that has high microbial biomass towards non-rhizosphere soil with less activity and accessibility for microbes, thus resulting in lower mineralization (Zhu and Miller, 2003). We postulate that AMF acts as the conduit for the supply of rhizo-C to surrounding bulk soil and facilitated binding agents for physicochemical stabilization of rhizo-C by increasing macroaggregate formation.

Submicron level organo-mineral interactions were further confirmed by the homogenous distribution of organic compounds and the links between clay clusters and biopolymers (Fig. 2b). Macroaggregates (>2 mm) had a distinct distribution pattern of rhizo-C distribution compared to microaggregates, indicating that the proteins were mainly scattered at the surface of the microaggregates. In contrast, polysaccharides were associated with goethite distributed throughout the whole microaggregate (Fig. 2b). Rhizodeposits consist of a large number of negatively charged compounds (i.e., carboxylic and some amino acids, lignin, and polyphenols), which could be stabilized through co-precipitation with goethite via the formation of organo-mineral complexes (Rasmussen et al., 2010; Chen et al., 2014; Dippold et al., 2014). These results confirmed the second hypothesis that the presence of AMF+Goethite in the rhizosphere was responsible for allocating more biopolymers into the >2 mm aggregate size class. The AMF hyphae were responsible for the spatial distribution of rhizo-C, resulting in its stabilization, while co-precipitation with goethite

contributed to the stabilization of rhizo-C with freshly added Fe-oxides (Wilson et al., 2009; Yu et al., 2017; Dippold et al., 2014;). Further, redundancy analysis revealed a significant correlation between soil properties such as FeOM, $\delta^{13}C$ of >2 mm aggregates, and their distribution within macroaggregates (Fig. 4), indicating that AMF had a positive influence on aggregate formation and rhizo-C stabilization. Therefore, soil aggregation protected rhizo-C through co-precipitation in the presence of AMF+Goethite via the formation of aggregates as influenced by hyphal activities.

4.2 Organic matter mineralization influenced by interactions between AMF, Goethite and other microorganisms

Soil C storage is the balance between inputs of rhizo-C and output via mineralization of rhizodeposition and SOM. The largest RPE occurred with AMF inoculation (Fig. 1b) and was influenced by the inoculated Glomeromycota and associated microorganisms (Fig. 4c). The main mechanism underlying priming by AMF is due to the breakdown of SOM to meet nutrient demand using a well-distributed hyphal network (Fig. S1). Notably, we observed 5.7% of the total reads from the genera *Claroideoglomus* that belong to Glomeromycota (Table S2). Previous findings suggest that the genera *Claroideoglomus* prime SOM by mining N (Staddon et al., 2002; Jansa et al., 2013). AMF hyphae that accelerated the SOM mineralization increase nutrient availability via well-distributed hyphae (Staddon et al., 2002; Soudzilovskaia et al., 2019).

However, AMF alone is unable to mineralize SOM (Bunn et al., 2019) as they are not capable of producing the lytic enzymes necessary to mineralize SOM (Tisserant et al., 2013). Thus, AMF-driven SOM mineralization most likely results from interactions between AMF and other microorganisms. AMF promotes SOM priming by boosting the activity of

rhizosphere bacteria called ‘hyper symbionts’ (Jansa et al., 2013). Bacteria able to utilize polysaccharides and biopolymers such as chitin, glucosamine, and proteins include *Pseudomonas* (Gammaproteobacteria), *Burkholderia* (Betaproteobacteria), *Asticcacaulis*, *Mucilaginibacter*, *Solirubrobacter*, and are located on the outer spore layer of AMF (Bonfante and Anca, 2009; Nanjundappa et al., 2019). It was reported that several genera belonging to Gammaproteobacteria (e.g., *Pseudomonas*) increased their abundance in response to AMF hyphal exudates (Toljander et al., 2007; Herman et al., 2012). The AMF hyphal exudates induced bacterial growth and frequency of occurrence of some genera (e.g., *Phenylobacterium*) that belong to Betaproteobacteria and Alphaproteobacteria (Bonfante and Anca, 2009; Hashem et al., 2016). Furthermore, Alphaproteobacterial genera, such as *Devosia* and *Rhodoplanes*, are known as mycorrhiza helper bacteria (Battini et al., 2017). These taxa mainly involve bacterial mycophagy and their ability to obtain resources from AMF and transform them into bacterial biomass.

AMF is associated with not only bacteria but also with fungi based on nutritional strategies (Bonfante and Anca, 2009). This is consistent with the keystone microbiota, i.e., *Talaromyces*, revealed by the co-occurrence network (Fig. 3e and Table S4). *Talaromyces* (Phylum Ascomycota, ericoid mycorrhizal fungi, and known as phosphate-solubilizing fungi) dominated and interacted with AMF (Figs. 3e and 3f). *Claroideoglomus* is engaged in an intriguing relationship with saprotrophs (Phylum Ascomycota), as they offer rhizo-C resources for saprotrophs and simultaneously trade for nutrients (Boer et al., 2005; Chen et al., 2019). These interactions between *Talaromyces* and AMF could increase soluble P to the host plant (Arshad and Frankenberger, 1997). Further, AMF affects key microbial, fungal groups associated with litter decomposition and strongly altered the fungal community (Arshad and Frankenberger, 1997; Della Mónica et al., 2014).

Contrasting to AMF, the limited rhizo-C availability following the amendment of soil with Goethite modulated the community demonstrated less bacterial and fungal diversity (Fig. 3a and 3b). These microbiomes, especially Sordariomycetes, Actinobacteria, are a functionally diverse group of organisms that are known to have a high substrate versatility and metabolic diversity thus better able to adapt to oligotrophic conditions (De la Cruz-Barrón et al., 2017; Dini-Andreote et al., 2015; Goldfarb et al., 2011; McCarthy and Williams, 1992). It seems the ability of Goethite to lower diversity in the microbiome community in soils following amendment with Goethite.

We therefore conclude that the organic matter mineralization results from the following two mechanisms: 1) AMF modified hyper-symbiont bacteria dominated in the AMF amended soils, thus adapting quickly to utilizing organic matter mineralization; and 2) lower diversity of bacteria and fungi dominated in Goethite amended soils, demonstrating lower organic matter mineralization where rhizo-C availability is limited.

4.3 Implications for terrestrial C sequestration

The role of AMF in the rhizosphere has been considered critical to terrestrial C cycling. Mycorrhizal fungi provide a dominant pathway for C transfer from plants to the soil, contributing more than half (50-70%) of root-derived soil C to the SOM pool in boreal and temperate forests (Godbold et al., 2006; Clemmensen et al., 2015). A recent study showed that 107 g C m^{-2} (2.3 g C kg $soil^{-1}$ $year^{-1}$) of AMF-derived C accumulated in soil annually (Godbold et al., 2006; Zhang et al., 2020). Similarly, this study revealed 6.2 mg C kg $soil^{-1}$ day^{-1} (2.3 g C kg $soil^{-1}$ $year^{-1}$) accumulated in the *Zea mays* L planted soil with AMF inoculation (Table 3). However, the absolute rates of C input in ecosystems by AMF may differ (Řezáčová et al., 2018). We collected previous publications and these findings

demonstrated that between 30-700 g C m^{-2} $year^{-1}$ of mycorrhiza-derived C enter into soils (Summarized in Table S9), depending on difference in climatic and edaphic variables (Godbold et al., 2006; Clemmensen et al., 2015).

Although the importance of external mycorrhizal hyphae in C input to soils is evident (Ji et al., 2019; Zhou et al., 2020), AMF induced primed SOC losses should be considered as their presence and activated other microorganisms can lead to SOM mineralization (Leifheit et al., 2015; Li et al., 2015). While most studies report net C sequestration resulting from AMF, a few studies suggest that the AMF might lower soil C stocks by enhancing organic C priming to provide mineral nutrients for host plants (Hodge et al., 2001; Tu et al., 2006; Ji et al., 2019). Yet, limited studies have assessed the balance between input and output of C associated with mineralization and stabilization. Here, we quantified the influence of AMF or/and Goethite on stabilization (rhizo-C) and mineralization (rhizo-C and RPE), and assess C balance based on daily input (rhizo-C stabilization) and output (RPE). Our study revealed that AMF inoculation caused close magnitude of rhizo-C stabilization (6.2 mg C kg^{-1} soil day^{-1}, Table 3) and priming of SOM (6.1 mg C kg^{-1} soil day^{-1}). Comparably, this led to larger RPE (with extra increase of 2.6 mg C kg^{-1} soil day^{-1}, compared to Control) and rhizo-C stabilization (with extra increase of 2.0 mg C kg^{-1} soil day^{-1}, compared to Control) (Fig. 5). Consequently, our findings support the emerging view that AMF-induced changes on the C budget via considering loss and gain are important in addressing C sequestration in the soil-plant-microbe continuum, but it certainly requires future investigations.

5. Conclusions

AMF, as a conduit, contributed to the stabilization of rhizo-C within soil macroaggregates, which were formed by organo-mineral complexes. Simultaneously, AMF increased SOM priming via stimulation of symbiotic microorganisms, mainly from the genera of *Burkholderia*, *Solirubrobacter*, and *Talaromyces*. AMF+Goethite drove SOM cycling via acceleration of microbial mineralization of SOM and Fe regulated physicochemical stabilization of new rhizodeposits. Quantitative assessments of the C budget were conducted considering both rhizodeposition and SOM priming based on 25 days of *Zea mays* L growth period. For example, AMF are an essential regulator of terrestrial C cycling by controlling two opposing processes: increasing the stabilization of rhizodeposits (by 6.2 mg C kg^{-1} day^{-1}, compared to 4.2 mg C kg^{-1} day^{-1} in Control), while simultaneously increasing the mineralization of SOM (by 6.1 mg C kg^{-1} day^{-1}, compared to 3.5 mg C kg^{-1} day^{-1} in Control). Our results highlight the contribution of AMF amendment to faster SOM cycling via accelerating both processes of C stabilization (gain) and mineralization (loss).

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Figure Captions

Fig 1. Root derived CO_2 efflux (a) and rhizosphere priming effect (RPE) (b) from the soil without additions (Control), soil+AMF (AMF), soil+goethite (Goethite), soil+AMF+goethite (AMF+Goethite) during the 45 days of maize growth. Values show means (n=4) ± standard deviation. Different lower case letters close to the legend indicate significant differences between the treatments at each sampling date (Tukey's test, $P<0.05$).

Fig 2. Distribution of rhizo-C in various aggregate size classes and organic matter associated with Fe oxides (FeOM) (a) after 45 days of maize growth: soil without additions (Control), soil+AMF (AMF), soil+goethite (Goethite), soil+AMF+goethite (AMF+Goethite). Values (means n = 4, ± SE) followed by letters above bars indicate significant differences between treatments (Tukey's test, $P < 0.05$). The spatial-related micro-FTIR (μ-FTIR) imaging in the ROI in soil micro-aggregates (i, ii) and macro-aggregates (iii, iv) from AMF+Goethite at the end of experiment (b).

Fig 3. Soil bacterial and fungal alpha diversity by the Shannon index (a, b), the Redundancy analysis for bacteria and fungi (c, d) and the construction of co-occurrence networks with and without AMF inoculation (e, f), with the highest relative abundance 200 OTU's (both bacterial and fungal) based on the Spearman threshold (0.8). In the co-occurrence network, circles in green, orange, and purple color represent the bacterial genera, fungal genera, and bacterial and fungal genera interact with AMF, respectively; green, orange and purple colored lines represent a node, and their links belong to bacterial genera, fungal genera, and bacterial and fungal genera interact with AMF.

Fig 4. The random forest represents the relative importance of soil physical, chemical, and biological variables for rhizo-C stabilization (a), mineralization (b), and rhizosphere priming effect (c). Abbreviations: >2 mm; >2 mm aggregate size class, 0.25-2 mm; 0.25-2 mm aggregate size class, < 0.25 mm; < 0.25 mm aggregate size class, C; total carbon, C:N ratio; carbon: nitrogen ratio, N; total N, FeOM; Fe organic matter complexes. Mean importance value $\leq$ 0 is not presented.

Fig 5. Conceptual diagram of the AMF-C interactions via stabilization and mineralization. Inside the figure, (1) AMF are a major conduit of rhizodeposited-C (rhizo-C) belowground, (2) organic C stabilization through interactions with soil minerals (such as Fe oxides) and (3) stabilization of C within soil aggregates, (4) AMF involving in rhizo-C mineralization and, (5) further stimulation of SOM decomposition via co-metabolism, (6) AMF biomass production, (7) release of labile exudates into surrounding soil, (8) AMF stimulated hyper-symbiont bacteria and saprotrophs. The overall balance between the loss (rhizosphere priming and rhizo-C mineralization via microbial interactions) and gain (C stabilization in

aggregates, soil minerals (Fe oxides)) determined the C stabilization in soil with the presence of AMF.