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RESEARCH ARTICLE

Arbuscular mycorrhizal colonization increases plant above-belowground feedback in a northwest Chinese coal mining–degraded soil by increasing photosynthetic carbon assimilation and allocation to maize

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Abstract

A three-compartment culture system was used to study the mechanism by which the AM fungus *Funneliformis mosseae* influences host plant growth and soil organic carbon (SOC) content in a northwest China coal mining area. A $^{13}CO_2$ pulse tracing technique was used to trace the allocation of maize photosynthetic C in shoots, roots, AM fungus, and soil. Carbon accumulation and allocation in mycorrhizal (inoculated with *Funneliformis mosseae*) and non-mycorrhizal treatments were detected. AM fungal inoculation significantly increased the ^{13}C concentration and content in both above- and below-ground plant parts and also significantly enhanced anti-aging ability by increasing soluble sugars and catalase activity (CAT) in maize leaves while reducing foliar malondialdehyde content (MDA) and leaf temperature and promoted plant growth. AM fungi also increased P uptake to promote maize growth. Soil organic carbon (SOC), glomalin, microbial biomass carbon (MBC), and nitrogen (MBN) contents increased significantly after inoculation. A mutually beneficial system was established involving maize, the AM fungus and the microbiome, and the AM fungus became an important regulator of C flux between the above- and below-ground parts of the system. Inoculation with the AM fungus promoted plant growth, C fixation and allocation belowground to enhance soil quality. A positive above-belowground feedback appeared to be established.

Keywords AM fungi · Carbon allocation · Positive feedback · Stress resistance · Soil carbon content · $^{13}CO_2$ pulse labeling

Introduction

In a natural system, there is positive above-belowground feedback that is essential for a healthy ecosystem (Mariotte et al. 2018). However, some artificial practices such as coal mining disrupt this and lead to environmental degradation (Rocha-Nicoleite et al. 2017). Mining subsidence induces cracks in the soil surface and damage to plant roots leading to plant death and vegetation degradation (Guo et al. 2011). It is therefore important to devise methods for the ecological restoration of mining areas (De and Mitra 2002; Shrestha and Lal 2006). Inoculation with arbuscular mycorrhizal fungi has been demonstrated to be an effective biotic method to achieve ecological restoration of degraded mining areas (Bi et al. 2018, 2019; Vahter et al. 2020; Wang 2017). AM fungi may play an important role in building a sustainable ecosystem with vegetation cover and enhance soil properties (Levy and Cumming 2014; Cavagnaro et al. 2015). However, how AM fungal inoculation influences the positive above-belowground feedback of mining areas remains unclear.

The soil organic carbon (SOC) pool is an important part of soil fertility, productivity, and quality (Schlesinger 1999; Wiesmeier et al. 2019). Changes in SOC are considered indicators of feedback effects (Kirschbaum 2000; Liu et al. 2019). Carbon is derived mainly from the allocation of primary productivity of higher plants to below ground (Malhi et al. 2011). A large portion of the C fixed by photosynthesis

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is distributed directly to plant roots and root-associated soil microorganisms which indirectly affect soil C sequestration (Zhu and Miller 2003; Heinemeyer et al. 2007; Dijkstra and Cheng 2007). Microbially mediated plant-soil feedback affects plant growth and community assembly (van der Heijden et al. 1998; Kardol et al. 2007). However, some previous studies have demonstrated that coal mining significantly decreased SOC content and further plant-soil feedback (Delschen 1999; Pagliai et al. 2004; Qiang et al. 2007; Six et al. 2004). In addition, it was difficult and time-consuming to achieve the same level as before the onset of mining activities (Pihlap et al. 2019). Inoculation with arbuscular mycorrhizal (AM) fungi accelerates this reclamation process (Qiu et al. 2019).

AM fungi form a symbiotic association with 80% of terrestrial plant species, and 4–20% of plant photosynthetic products are transferred to the AM fungi to build hyphae that extend into the soil and influence soil C storage (Bago et al. 2000; Godbold et al. 2006). Hyphae, spores, and vesicles of AM fungi are widely present in soils and the extraradical biomass can form up to 32% of the total soil microbial biomass, contributing up to 15% of SOC (Miller and Kling 2000). A ^{13}C labeling experiment has found that AMF received 4.3% plant fixed C in 24 h (Tomè et al. 2015). Kaiser et al. (2015) found that mycorrhizal fungi directly transported C from plant photosynthetic products to the soil and even to soil microbes (Kaiser et al. 2015). AM fungi therefore play an important role in C cycling from above- to below-ground (Miller et al. 2002; Zhu and Miller 2003). AM fungi also promote host plant growth and photosynthetic C fixation (Rodrigues and Rodrigues 2014) by influencing plant physiological traits enhancing nutrient uptake, water supply, and C source-sink relations (Bethlenfalvay et al. 1982, 1988; Andrade et al. 1998; Black et al. 2000; Baier et al. 2010). In particular, an increase in root biomass may increase the space for colonization by AM fungi while AM inoculation decreases the root-to-shoot ratio by ameliorating plant nutrient status (Veresoglou et al. 2012; Goicoechea et al. 2014). The AM fungal hyphae extend and exert important effects on the soil environment (Zhu and Miller 2003; Godbold et al. 2006).

Previous studies show that AM fungi affect the association between roots and soil by increasing nutrient uptake and the resistance of host plants to a range of environmental stresses and by promoting plant growth and development (Evelin et al. 2009; Hajiboland et al. 2010; Lee et al. 2012; Klein et al. 2016). A number of mechanisms are involved. Mycorrhizal inoculation can increase the chlorophyll content and the rate of photosynthesis and furtherly increase plant C accumulation (Talaat and Shawky 2014). Plants inoculated with AM fungi show decreased H_2O_2 and increased malondialdehyde (MDA) contents compared to non-AM plants and increased soluble proteins and sugars, thereby increasing both their resistance to environmental stress and productivity (Latef et al. 2016). Furthermore, inoculation facilitates the acquisition of mineral nutrients, especially P (Řezáčová et al. 2018). The establishment of mycorrhizal association often increases the allocation of C to the roots and further to the mycorrhizal fungi (Řezáčová et al. 2017). As feedback, the roots and AM fungi exude sugars and organic acids to the soil and thus to soil microorganisms, which may be activated to metabolize accumulated soil mineral nutrients for the growth of the host plants (Zhang et al. 2016). When hyphae die a portion of their C is rapidly decomposed by other microorganisms and converted to CO_2 which may enter the atmosphere or some recalcitrant organic compounds such as chitin and glomalin that can remain in the soil for years to decades (Gleixner et al. 2002; Wilson et al. 2009; Smith and Read 2010; Treseder 2013). In addition, the contribution of AM fungi to the C cycle also depends on both the extraradical hyphae (ERH) and exudates from AM fungal hyphae such as glomalin which can contribute to soil C aggregation and soil quality enhancement (Wright and Upadhyaya 1996; Tisdall et al. 1997; Zhu and Miller 2003; Zhang et al. 2016). However, several studies show that plant C allocated to hyphae was high enough to cause depression of host plant growth in some experiments, especially in nutrient-limited areas or at the establishment stages of roots and hyphae (Jakobsen 1999; Gavito et al. 2019). Thus, understanding the mechanisms by which AM fungi promote soil C storage is helpful. However, most studies have been conducted under field conditions and factors such as soil heterogeneity and climatic variability have had a substantial impact on the results. Recent efforts have been made to quantify how AM associations affect overall C balance and C fluxes in different types of photosynthetic metabolism using stable ^{13}C isotopes, but have ignored how much C the AM fungi receive because of the paucity of available methods to quantify this directly (Lendenmann et al. 2011; Slavíková et al. 2017; Řezáčová et al. 2017; 2018).

In previous studies, quantification of the contribution of AM fungi to the exchange of photosynthetic products between above- and below-ground pools have been based mainly on $\delta^{13}C$ and C% values, methods which cannot give a direct indication of the allocation of primary products. Here, a greenhouse experiment was conducted and $^{13}CO_2$ pulse labeling was used to quantify the effects of AM inoculation on the allocation of photosynthetic products above- and below-ground and the effects of AM fungal inoculation on C storage in plants and soil. The effects of hyphae on C allocation were studied using three-compartment microcosms to collect AM fungal biomass and then calculate the amount of ^{13}C in the biomass. The present work aimed to unveil the mechanisms by which AM fungi promote C sinks in plants and soil under controlled conditions and to provide a theoretical basis for the role of AM fungi in C storage in

the soil and in photosynthate allocation above- and belowground in a nutrient-poor soil from a coal mining area in northwest China.

Materials and methods

Soil, plants, and AM fungus

Sandy soil collected from Daliuta mining area, Yulin, Shanxi Province, China, was sieved (< 2 mm), sterilized at 121 ℃ and 103 kPa for 2 h, and air-dried for three days before used. Selected soil physicochemical properties were: available phosphorus (AP, $NaHCO_3$ extracted), 2.97 mg kg^{-1}; available potassium (AK), 12.9 mg kg^{-1}; organic matter content, 1.25 g kg^{-1}; pH, 7.39; electrical conductivity, 834 μS cm^{-1}; and water holding capacity, 18.6%. The low AP, AK, and conductivity indicate a nutrient-limited environment for plants. Maize (*Zea mays* L., cultivar Nuoyu 2) was selected as the host plant and seeds were provided by the Seeds Company of the Chinese Academy of Agricultural Sciences. They were surface sterilized by immersion in 10% (v/v) H_2O_2 for 10 min, rinsed several times with distilled water, and germinated at 25℃ for 48 h in the dark. The AM fungal inoculum, *Funneliformis mosseae*, was provided by the Institute of Plant Nutrition and Resources, Beijing Academy of Agriculture and Forestry Sciences, Beijing, China, and propagated at the State Key Laboratory for Coal Resources and Safe Mining, China University of Mining and Technology (Beijing). The inoculum consisted of spores (2000 spores per 100 g inoculum), external hyphae, and mycorrhizal root fragments.

Experimental design and management

The experiment was conducted using 55 × 28 × 26 cm three-compartment microcosms (Fig. 1a). On the left was the root compartment (RC), in the middle the buffer zone (BC) and on the right the hyphal compartment (HC). We used a 1-mm nylon mesh to allow hyphae and fine roots (but not coarse roots) into the BC in order to avoid the roots extending to the HC and ensuring enough hyphae in the HC for collection. The BC and HC were separated by 30-μm pore nylon mesh to allow hyphae in and exclude all roots. The soil in the RC and BC was sterilized sandy soil sieved to < 2 mm and the medium in the HC was 0.8–1.2 mm glass beads immersed

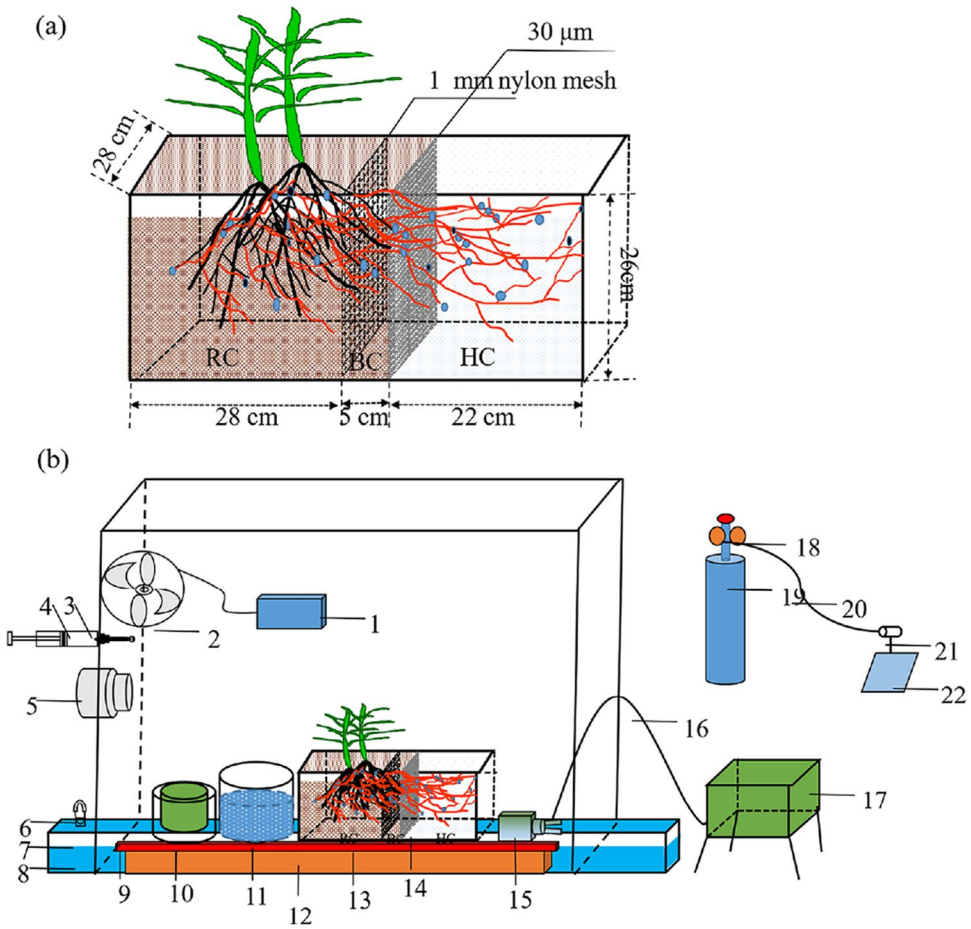

Fig. 1 Schematic diagrams of **a** the three-compartment microcosm and **b** the pulse labeling device. RC, root compartment; BC, buffer compartment; HC, hyphal compartment. One-mm nylon mesh was used to separate the RC and BC and 30 μm nylon mesh was used to separate the BC and HC. 1, rechargeable battery; 2, electric fan; 3, U-shaped silicone plug; 4, injector; 5, semiconductor refrigerator; 6, clip; 7, sink; 8, water; 9, plastic film; 10, thermometer; 11, silica gel; 12, board; 13, three-compartment microcosm; 14, nylon mesh; 15, LI-6400 handheld probe; 16, wire; 17, LI-6400 host; 18, pressure reducing valve; 19, $^{13}CO_2$ cylinder; 20, plastic catheter; 21, cock valve; 22, vacuum bag

in 5% HCl for 24 h and washed with distilled water several times before use to collect clean hyphae. There were 25 kg, 5 kg, and 22 kg soil, respectively, in the RC, BC, and HC of each pot. Two treatments were established, mycorrhizal (inoculated with *F. mosseae*) and non-mycorrhizal controls (CK). One hundred grams of inoculum were applied to the root compartment of the mycorrhizal treatment by layering and the non-mycorrhizal treatment received 100 g sterilized inoculum. The effects of AM fungi on maize growth, stress resistance, and C allocation were determined compared with the control. There were three replicates of each treatment and a total of six microcosms were used.

We added 100 mg N (as NH_4NO_3), 30 mg P (as KH_2PO_4), and 150 mg K (as K_2SO_4) per kg to the RC to meet the basic nutrient demand of maize at the seedling stage. Before transplanting, the soil was watered to maximum water holding capacity and preconditioned the soil for 24 h. Maize seeds were sown in plastic seedling pots and then transplanted to the RC at the three-leaf stage on April 5th, 2017. There were two maize plants in each RC. An EM50 data logger (ICT International, Armidale, NSW, Australia) was used daily to maintain the soil moisture content within 75 to 80% of the water holding capacity. Deionized water (100 ml) was added to the HC every day plus 100 ml 1/10 Hoagland's nutrient solution every three days to ensure hyphal growth. Maize growth was maintained by adding 50 mg N (as NH_4NO_3), 15 mg P (as KH_2PO_4), and 75 mg K (as K_2SO_4) to the RC soil for 25 days after transplanting to alleviate plant nutrient deficiency.

$^{13}CO_2$ pulse labeling chamber and procedure

Previous studies indicate that ^{13}C from photosynthesis may be transferred to each plant part, AM fungi and soil and even to soil microbes within one day (Kuzyakov and Cheng 2004; Kaiser et al. 2015). $^{13}CO_2$ stable isotope pulse labeling for three days starting at the tasseling stage 63 days after transplanting was used to trace the distribution of maize photosynthetic C among plant parts, AM fungus, and soil. The labeling chamber was 110 × 110 × 75 cm in size (Fig. 1b). The mycorrhizal treatments and non-mycorrhizal controls were randomly placed in two labeling chambers with good light transmission and repositioned randomly each day to minimize variation due to the labeling process. LI-6400 handheld probes (LI-COR Biosciences, Lincoln, NE; to probe the real-time concentration of CO_2), air fans, silica gel, and thermometers (to determine the real-time temperature) were placed in the airtight chambers before labeling as shown in Fig. 1b. The $^{12}CO_2$ in the labeling chamber was consumed by placing maize pots in the glasshouse chambers at 08:00 in the morning. When the CO_2 concentration in the labeling chambers was < 50 ppm at 09:00 the $^{13}CO_2$ (atom > 99.99%) gas was injected at 30-min intervals into the chambers to maintain a constant $^{13}CO_2$ concentration of 300–450 ppm. At 15:00 $^{13}CO_2$ gas was injected for the last time and the concentration of $^{13}CO_2$ was ≤ 450 ppm. The labeling chambers were opened at 17:00 when labeling ended to ensure maize respiration during the night. The experiment was conducted in Beijing at the China University of Mining and Technology (40°N, 116°E). The weather was sunny and the temperatures on the three ^{13}C-tracing days were, respectively, 40.7, 37.5, and 37.3 ℃.

Sampling and measurement

The photosynthetic rates of the third and fourth fully expanded leaves (from the top) were measured at 10:00 one day before labeling to test the effects of the AM fungus on plant photosynthetic ability. An LI-6400 handheld probe (Licor Biosciences, Lincoln, NE) was used and the built-in red and blue light source, with a red light photosynthetic effective radiation flux density of 1000 μmol m^{-2} s^{-1} was used. The leaf chlorophyll content was measured with a SPAD-502 chlorophyll meter (Konica Minolta, Tokyo, Japan; Ling et al. 2011). Leaf starch and soluble sugar contents (fresh samples) were determined by anthrone colorimetry (Leach and Braun 2016) to indicate plant stress resistance. Soluble protein was determined by the Coomassie brilliant blue G-250 staining method (Murphey et al. 1989) and malondialdehyde (MDA) content by the thiobarbituric acid (TBA) method (Schmedes and Hølmer 1989). Catalase (CAT) activity was determined by the potassium permanganate titration method (Chen et al. 2015). The plant and soil samples were collected after three days of labeling. The plants were divided into six parts to determine the allocation of carbon among plant parts, namely young leaves (leaves not fully expanded), intermediate leaves, senescent leaves (leaves with yellow edges and signs of senescence), dry leaves (completely withered leaves), stems, and roots. Leaf areas and shoot and root biomass were determined. All plant parts were oven-dried to constant weight and ground to 0.15 mm. Shoot P and K concentrations were determined by digestion with H_2SO_4-H_2O_2 and analysis using ICP-AES (Thomas et al. 1967). Rhizosphere soil was sampled by the quartering method and then passed through a 2-mm sieve. The soil was divided into two portions to determine the carbon allocation to the soil and the effects of the AM fungus on soil properties. One portion was stored at 4℃ to determine microbial biomass and the remainder was air-dried outdoors. Wet sieving was used to collect hyphae. The glass beads in the hyphal compartment were transferred to buckets and washed five times with distilled water. Glass rods were used to mix the glass beads and water. The supernatant was immediately passed through a 30-μm pore sieve to collect the hyphae. The AM fungal hyphae were dried at 80℃, ground to 0.15 mm, and homogenized before analysis.

The carbon allocation, $\delta^{13}C$ value, and C% content of each plant part and soil and hyphal samples were fully quantified using a Deltaplus XP mass spectrometer (Thermo Fisher, Waltham, MA) and an elemental analyzer at the stable isotope laboratory of the Chinese Academy of Agricultural Sciences. The carbon allocation, $\delta^{13}C$ value, and C% content in soil included the C incorporated in rhizodeposition, residual AM fungi, soil bacteria, and soil substrate. The accuracies of measurement of C content and C isotopic composition were 0.1% and 0.2‰, respectively (Deniro and Epstein 1978).

Root segments were stained with 0.05% Trypan blue and examined under a microscope (Nikon, Tokyo, Japan) to determine the percentage of root length colonized (Phillips and Hayman 1970). The mycorrhizal colonization in each compartment was calculated as the number of mycorrhizal root segments/total number of root segments examined × 100%, which may be described as the percentage of root length colonized or the colonization frequency. The hyphal length density was determined by the method of Jakobsen et al. (1992). SOC content was determined by standard dichromate oxidation (Bremner and Jenkinson 1960). Briefly, the easily extractable soil glomalin (EEG) was extracted with alkaline citrate (20 mM, pH 7) by autoclaving for 30 min (121 °C) followed by centrifuging at 4000 rpm for 5 min and collecting the supernatant. The supernatant was stained with Coomassie brilliant blue G-250 and detected by UV spectrophotometry. Total glomalin (TG) was extracted with alkaline citrate (50 mM, pH 8) by autoclaving for 90 min (121 °C) and centrifuging at 4000 rpm for 5 min. The cycle of extraction and centrifugation was repeated four times until the supernatant was almost transparent. The supernatants extracted each time were combined and estimated as TG (Wright and Upadhyaya 1996). AP and AK, respectively, were extracted with 0.5 M $NaHCO_3$ and 1 M ammonium acetate (Zebec et al. 2017) and then determined by ICP-AES. Soil microbial biomass C (MBC) and soil microbial biomass N (MBN) were determined by chloroform fumigation and extraction with 0.5 M K_2SO_4 solution. MBC was determined using a total C analyzer and MBN using an automatic Kjeldahl nitrogen analyzer (Nguyen et al. 2016). Some glass beads were extracted from the hyphal compartment 40 and 60 days after inoculation and observed microscopically after staining with 0.05% Trypan blue (Nikon E100, 40×) to ensure successful establishment of hyphae in the hyphal compartment (Fig. 2).

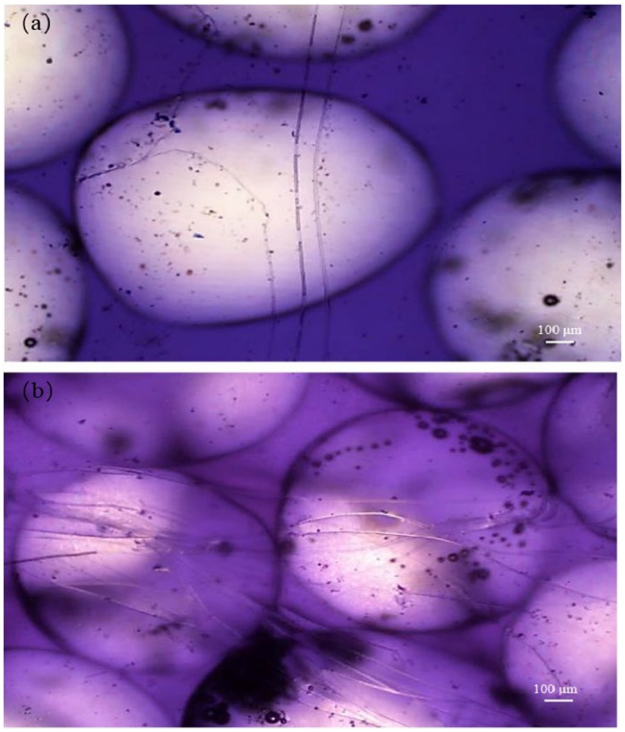

Fig. 2 Photographs of the hyphal compartment **a** 40 and **b** 60 days after inoculation at × 40 magnification

Data calculations

The effects of AM fungi on photosynthetic leaf area and total area of maize leaves (green leaves only) were determined using the following equations.

$$S_i = \text{leaf length} \times \text{maximum leaf width} \times 0.75 \quad (1a)$$

$$S = \sum_i^1 Si \quad (1b)$$

where Si is the area of a single leaf I and S is the total leaf area.

To determine ^{13}C distribution rate in each plant part, $\delta^{13}C$ was calculated by the following equations:

$$\delta^{13}C = \frac{R_{\text{samples}} - R_{PDB}}{R_{PDB}} \times 1000 \quad (2)$$

where R, ^{13}C concentration/^{12}C concentration; PDB, Peedee belemnite in the Cretaceous Peedee formation, South Carolina, $R_{PDB} = (11{,}237.2 \pm 90) \times 10^{-6}$.

To determine the absolute C allocation of ^{13}C in plant and soil, C%, c(^{13}C), and m(^{13}C) were calculated.

$$C\% = \frac{13 \times {}^{13}C + 12 \times {}^{12}C}{M} \times 100 \quad (3)$$

M, dry weight of samples; ^{13}C, the ^{13}C content in samples; ^{12}C, the ^{12}C content in samples

$$c\left({}^{13}C\right) = \frac{13 \times \frac{C\%}{100}}{\frac{12 \times 1000}{\left(\delta^{13}C + 1000\right) \times R_{PDB}}} \quad (4)$$

c(^{13}C), indicates the ^{13}C concentration in each plant and soil part

$$m\left({}^{13}C\right) = \frac{m \times \frac{C\%}{100}}{13 + \frac{12\times1000}{(\delta^{13}C+1000)\times R_{PDB}}} \times 13 \quad (5)$$

m (^{13}C), ^{13}C content; indicates the ^{13}C weight in each plant and soil part.

The mycorrhizal contribution of each plant biomass and shoot P and K nutrition (MC%) were calculated by the following equation:

$$MC\% = \frac{index(inoculated) - index(CK)}{index(inoculated)} \times 100\% \quad (6)$$

Data analysis

All results in the tables and figures are mean value ± standard error. The mean values of all data were compared to determine the difference between the inoculated treatment and uninoculated control. Student's t-test was used to determine the effects of inoculation at $P < 0.05$ using the IBM SPSS 20.0 software package (IBM, Armonk, NY).

Differences between mycorrhizal treatment and non-mycorrhizal control of mycorrhizal colonization, hyphal length density, shoot and root biomass, P and K concentration, TG/SOC, EEG/SOC, MBC/MBN, MBC/SOC, SPAD value, total leaf area, MDA, CAT, soluble protein, soluble sugar, and starch were compared. The differences in photosynthetic indexes and soil physical and chemical properties between mycorrhizal and non-mycorrhizal treatments were compared by Student's t-test. Differences in δ^{13}C, C%, ^{13}C concentration, and ^{13}C content in plants and soil samples between mycorrhizal and non-mycorrhizal treatments were also examined using Student's t-test. The root mycorrhizal colonization data, TG/SOC, EEG/SOC, MBC/SOC, δ^{13}C, and C% were normalized by arcsine-transformation before statistical analysis.

The factors important in carbon allocation were examined using the sPearson-correlation analysis between carbon allocation and other factors at $P < 0.05$.

Results

Mycorrhizal colonization, hyphal length density and plant biomass, and P and K concentrations

As shown in Table 1, the roots in the inoculated treatment were colonized by *F. mosseae* in both the root and buffer compartments in which the root mycorrhizal colonization rate reached 77 and 81%, respectively. The hyphal length density was 1.56 m g^{-1} soil in the root compartment with no colonization or mycelium found in the non-mycorrhizal control. Both mycorrhizal colonization and hyphal length density indicate that the AM fungus colonized the maize roots and the hyphae extended into the soil. Shoot, root, and total biomass values were significantly higher in the mycorrhizal treatment than in the non-mycorrhizal control. The mycorrhizal contributions to shoot, root, and total biomass were 13.6, 25.4, and 17.3%, respectively. In addition, AM fungal inoculation significantly increased and contributed 45.4% to shoot P concentrations, with 3.5 mg g^{-1} in mycorrhizal treatment but only 1.9 mg g^{-1} in non-mycorrhizal treatment. There was no influence of AM fungal inoculation observed on K concentrations (Table 1).

Soil properties

As shown in Table 2 the SOC, EEG, and TG values in the inoculated treatment were, respectively, 640, 173, and 515 mg kg^{-1} and increased by 21.2, 85.9, and 62.4% compared to the non-mycorrhizal control. Inoculation also promoted the biomass of soil microorganisms. The MBC and MBN values in the mycorrhizal treatment were 100 and 46.7 mg kg^{-1} and were significantly higher than in the non-mycorrhizal control. Soil AP in the mycorrhizal treatment

Table 1 Mycorrhizal colonization, hyphal length density, maize biomass and mycorrhizal contribution. Values are mean values ± standard errors. Different lowercase letters represent significant differences between Myc (inoculated treatment) and Ctrl (uninoculated control) at $P < 0.05$. RC, root compartment; BC, buffer compartment; and MC%, mycorrhizal contribution

Treatment	Mycorrhizal colonization (%)		Hyphal length density (m g^{-1})	Shoot biomass (g plant^{-1})	Root biomass (g plant^{-1})	Total biomass (g plant^{-1})	Shoot P concentration (mg g^{-1})	Shoot K concentration (mg g^{-1})
	RC	BC						
Myc (*F. mosseae*)	76.67 ± 3.33	81.11 ± 3.85	1.56 ± 0.05	20.5 ± 0.77^{a}	9.46 ± 0.28^{a}	30.0 ± 0.85^{a}	3.50 ± 0.32^{a}	80.7 ± 9.43
Ctrl	None	None	None	17.7 ± 0.48^{a}	7.06 ± 0.32^{b}	24.8 ± 0.45^{b}	1.91 ± 0.34^{b}	73.3 ± 8.34
MC %	None	None	None	13.6	25.4	17.3	45.4	9.15

Table 2 Effect of mycorrhizal inoculation on soil properties. Values are mean values ± standard errors. Different lowercase letters represent significant differences between Myc (inoculated treatment) and Ctrl (uninoculated control) at $P < 0.05$. *AK*, available potassium; *AP*, available phosphorus; *SOC*, soil organic carbon; *TG*, total glomalin; *EEG*, easily extractable glomalin; *MBC*, soil microbial biomass carbon; *MBN*, soil microbial biomass nitrogen

Treatment	AK (mg kg^{-1})	AP (mg kg^{-1})	SOC (g kg^{-1})	TG (mg kg^{-1})	EEG (mg kg^{-1})	MBC (mg kg^{-1})	MBN (mg kg^{-1})
Myc	148 ± 18.37[a]	9.05 ± 0.87[b]	0.64 ± 0.03[a]	515 ± 50.05[a]	137 ± 32.65[a]	100 ± 11.65[a]	46.7 ± 3.21[a]
Ctrl	166 ± 14.77[a]	13.3 ± 0.48[a]	0.53 ± 0.04[b]	317 ± 52.24[b]	73.9 ± 16.69[b]	62.4 ± 6.89[b]	27.2 ± 3.94[b]

Table 3 Effect of mycorrhizal inoculation on ratios of soil parameters. Values are mean values ± standard errors. Different lowercase letters represent significant differences between Myc (inoculated treatment) and Ctrl (uninoculated control) at $P < 0.05$. *EEG/SOC*, the ratio of easily extractable glomalin to soil organic carbon; *TG/SOC*, the ratio of total glomalin to soil organic carbon; *MBC/MBN*, the ratio of microbial biomass carbon to microbial biomass nitrogen; *MBC/SOC*, the ratio of microbial biomass carbon to soil organic carbon

Treatment	EEG/SOC	TG/SOC	MBC/MBN	MBC/SOC
Myc	0.22 ± 0.06	0.80 ± 0.08[a]	2.15 ± 0.36	0.16 ± 0.02
Ctrl	0.14 ± 0.03	0.60 ± 0.07[b]	2.33 ± 0.42	0.11 ± 0.03

was significantly lower than in the control but there was no significant difference in soil AK between mycorrhizal and non-mycorrhizal treatments. This may be related to the higher shoot biomass and larger microbial biomass in the mycorrhizal treatment. Here, mycorrhizal inoculation increased soil C deposition and the biomass of soil microorganisms while reducing soil's available P and K contents. EEG/SOC and TG/SOC were calculated to illustrate the contribution of glomalin to soil organic carbon. As shown in Table 3, there were higher EEG/SOC and TG/SOC values in the mycorrhizal treatment, especially TG/EEG which was significant at $P < 0.05$. MBC/MBN and MBC/SOC were calculated to show the activity and metabolism of soil microorganisms. Mycorrhizal inoculation increased MBC/SOC but decreased MBC/MBN.

Physiological characteristics and photosynthetic indices of maize

Inoculation with *F. mosseae* increased plant resistance to environmental stress and photosynthetic efficiency. As shown in Table 4, inoculation significantly increased CAT activity and the soluble protein, soluble sugar and starch contents of leaves ($P < 0.05$), by 2 U g^{-1} FW min^{-1}, 0.02 mg g^{-1}, 0.5%, and 0.11%, respectively. MDA, which can indicate plant senescence, also decreased significantly in the mycorrhizal treatment. In addition, inoculation significantly promoted plant photosynthetic ability. Furthermore, the Pn significantly increased from 31.0 to 33.5 µmol CO_2 m^{-2} s^{-1} because of AM fungal inoculation (Table 5). Inoculation also increased plant resistance to high temperatures by increasing the Tr and decreasing leaf temperature (Table 5). Inoculation decreased the Ci owing to decreased respiration and increased photosynthesis. Thus, inoculation

Table 4 Physiological characteristics of maize in the mycorrhizal and non-mycorrhizal treatments. Values are the mean values ± standard errors. Different lowercase letters represent significant differences between Myc (inoculated treatment) and Ctrl (uninoculated control) at $P < 0.05$. *SPAD*, leaf chlorophyll content; *MDA*, malondialdehyde content; *CAT*, catalase activity

Treatment	SPAD	Total leaf area (m^2)	MDA (µmol g^{-1})	CAT (u g^{-1} FW min^{-1})	Soluble protein (mg g^{-1})	Soluble sugar (%)	Starch (%)
Myc	38.2 ± 0.56[a]	0.15 ± 0.01[a]	6.16 ± 1.31[b]	4.93 ± 0.64[a]	0.22 ± 0.01[a]	1.02 ± 0.09[a]	0.58 ± 0.02[a]
Ctrl	33.7 ± 1.00[b]	0.13 ± 0.00[b]	15.7 ± 0.10[a]	2.95 ± 0.21[b]	0.20 ± 0.00[b]	0.70 ± 0.00[b]	0.47 ± 0.02[b]

Table 5 Photosynthetic indices of maize. Values are mean values ± standard errors. Different lowercase letters represent significant differences between Myc (inoculated treatment) and Ctrl (uninoculated control) at $P < 0.05$. *Pn*, net photosynthetic rate; *Gs*, stomatal conductance; *Ci*, intercellular CO_2 concentration; *Tr*, transpiration rate; *T*, leaf temperature

Treatment	Pn (µmol CO_2 m^{-2} s^{-1})	Gs (mmol H_2O m^{-2} s^{-1})	Ci (µmol CO_2 m^{-2} s^{-1})	Tr (mmol H_2O m^{-2} s^{-1})	T (℃)
Myc	33.5 ± 0.58[a]	0.042 ± 0.00[a]	84.8 ± 9.07[a]	4.39 ± 0.11[a]	32.7 ± 0.18[b]
Ctrl	31.0 ± 1.44[b]	0.046 ± 0.00[a]	91.2 ± 1.89[a]	4.14 ± 0.10[b]	33.27 ± 0.20[a]

promoted both resistance of maize to stress and photosynthetic C fixation.

^{13}C assimilation and allocation

AM fungal inoculation significantly influenced the δ^{13}C, C%, ^{13}C concentration and ^{13}C content of intermediate leaves, roots, soil, and hyphae at $P < 0.05$ and significantly increased the C% of the soil (Fig. 3). The ^{13}C concentration and content of maize and soil were significantly higher in the mycorrhizal treatment than in the non-mycorrhizal control, indicating that the AM fungus promoted C fixation in both maize and soil. The ^{13}C concentration of maize followed the sequence: young leaves > stems > intermediate leaves > senescent leaves > roots. The ^{13}C concentration in the hyphae of the AM fungus was about 100 μg g^{-1}, equivalent to that in the intermediate and senescent leaves of maize and much higher than in the roots (Fig. 3c). The sum of ^{13}C fixation in above- and below-ground parts in the mycorrhizal treatment was 4.00 mg while it was 3.02 mg on the non-mycorrhizal control (Fig. 3d). The MC% to the sum of ^{13}C content in all parts was 25% and was 24% to ^{13}C content only in soil (Fig. 3d). Although the ^{13}C content in maize shoots increased, the percentage of the ^{13}C in maize shoots declined by 5.89%, possibly indicating that inoculation promoted C accumulation and allocation to the belowground parts. Compared to the non-mycorrhizal control, mycorrhizal inoculation reduced the proportion of the ^{13}C distribution to the stems but increased the percentages of the distribution to the roots, soil, and hyphae (Fig. 4). The ^{13}C content belowground involved soil, hyphae, and roots, accounting for about 17.7% of the total ^{13}C content and much higher than the 11.8% in the non-mycorrhizal control (Fig. 4). As a result, the AM fungus increased photosynthetic C fixation and soil C content. Inoculation also changed the distribution of photosynthetic products among shoots, roots, and

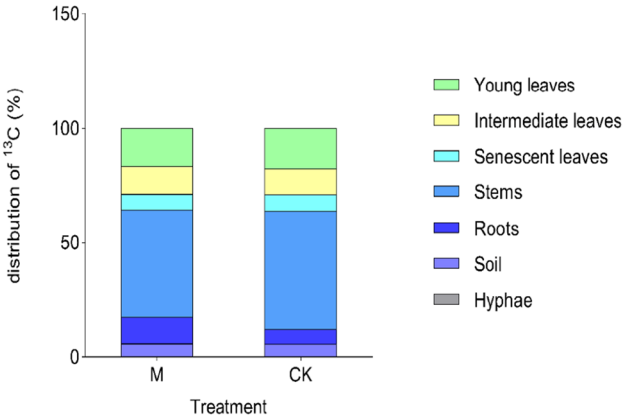

Fig. 4 Distribution of ^{13}C in different plant parts and the soil; bars are mean values + standard errors ($n = 3$); different lowercase letters indicate a significant difference between mycorrhizal and non-mycorrhizal treatments at $P < 0.05$

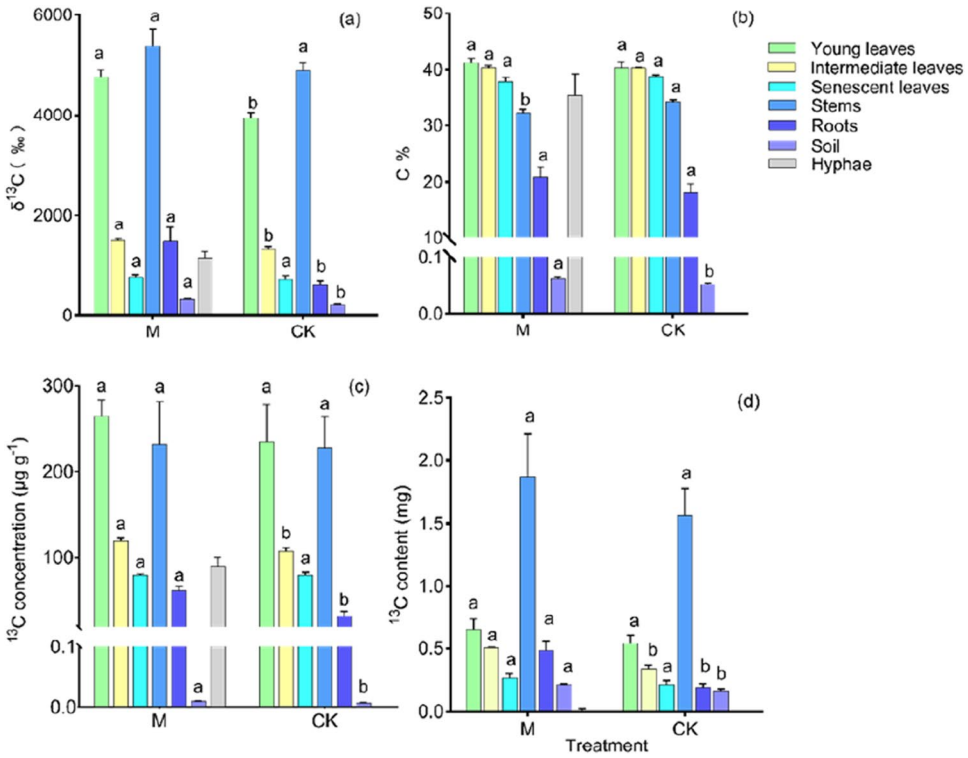

Fig. 3 **a** δ^{13}C, **b** C%, **c** ^{13}C concentration, and **d** ^{13}C contents in different plant parts and the soil; M, mycorrhizal treatment; CK, non-mycorrhizal control; bars are mean values + standard errors ($n = 3$); different lowercase letters indicate a significant difference between mycorrhizal and non-mycorrhizal treatments at $P < 0.05$

soil and tended to promote the allocation of photosynthetic C belowground.

Correlation between carbon allocation and physiological characteristics and soil properties

As shown in Fig. 5, Pn showed positive correlations with ^{13}C allocation to roots and hyphae. Mycorrhizal inoculation increased the Pn and then increased the carbon allocation to roots and AM fungal hyphae. CAT was positively correlated with ^{13}C allocation to the hyphae, indicating that mycorrhizal association increased antibiotic resistance and further promoted the ^{13}C allocation to hyphae for the growth of AMF. However, the soluble protein and sugar contents and starch content showed no significant correlation with carbon allocation. Soil AK and AP are important nutrients for maize growth. Here, AK was positively correlated with ^{13}C allocation to the stems but negatively to ^{13}C allocation to the intermediate leaves and soil. AP was positively correlated with the ^{13}C allocation to young leaves.

As a feedback, soil C properties were influenced by C allocation. The carbon allocated to hyphae was positively related to SOC accumulation. MBN was also positively correlated to C allocation to AMF fungi, as more C allocation to the AM fungal hyphae increased the microbial biomass and microbial activity. Soil EEG was positively correlated with C allocation to roots but negatively to C allocation to the young leaves.

Discussion

Validation of a novel method for full quantification of carbon allocation in the plant-AM fungus-soil system

The contribution of AM fungi to C allocation and sequestration belowground has long been a matter of interest and debate because accurate quantification, especially in realistic conditions, is very difficult (Parihar et al. 2020). There are a number of approaches to the estimation of the amount of C allocated to mycorrhiza. Numerous recent efforts have been made to quantify how AM symbiosis would affect the overall C balance and C fluxes in different types of photosynthetic metabolism using the stable ^{13}C isotope (Lendenmann et al. 2011; Slavíková et al. 2017; Řezáčová et al. 2017, 2018). The amounts of plant and soil carbon have been calculated and it has been reported that AM fungi increased assimilation by plants and the carbon allocation to the soil. However, how much carbon AM fungi receive is unclear because it is difficult to collect hyphae from the soil. In addition, NanoSIMS has demonstrated that AM fungi transferred C to soil and soil microbes (Kaiser et al. 2015). However, it is difficult to calculate the absolute amount of carbon. Here, we used a compartment culture system and mixed glass beads with soil to collect AM fungal hyphae, and combined with hyphal weight, the carbon allocation to the AM fungus was calculated. In addition, the carbon content of different plant parts was studied to understand carbon allocation in more detail. Numerous studies report that aboveground respiration levels in mycorrhizal treatments declined coincident with increased C drain belowground (Řezáčová et al. 2017; 2018). Here, we focus on the carbon assimilated to organic matter. Although a large percentage of carbon assimilated by photosynthesis is used for respiration, it is related to the carbon in organic matter (Smith and Dukes 2013).

The AM fungus increased plant growth and C allocation by enhancing the potential of plant stress resistance and nutrient uptake

Numerous previous studies have shown plant growth responses to mycorrhizal inoculation including positive (mutualism), neutral (commensalism), and negative (parasitism) effects (Johnson et al. 1997; Klironomos 2003). AM fungi form potentially symbiotic relationships with host plants based on the exchange of nutrients, especially relatively immobile nutrients such as P, and plant primary

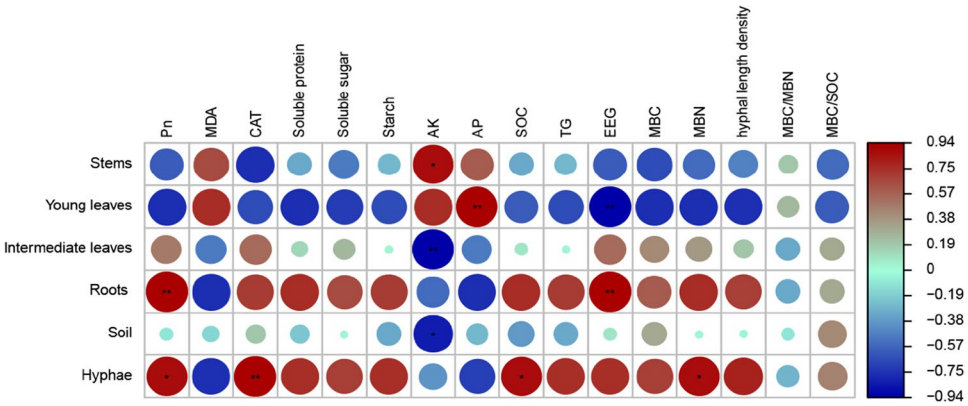

Fig. 5 Pearson correlation of ^{13}C allocation with physiological characteristics and soil properties. *, significant correlation at $P < 0.05$; **, significant correlation at $P < 0.01$

products (Kiers et al. 2011). According to the assumption of the bio-market model the effect of AM fungi on the growth of host plants lies in the trade-off between the C cost and the nutrient acquisition by the host plants (Kiers et al. 2011). Here, the AM fungus formed large amounts of hyphae and increased the biomass, leaf area, and P level of maize while decreasing soil available P and K (Tables 1, 2, and 4). These results indicate that the mycorrhizal benefits of nutrient uptake exceeded the C cost to the plant to construct the hyphal network. Especially, the shoot P concentration in mycorrhizal treatment was much higher than it in non-mycorrhizal treatment which was lower than the threshold of shoot P concentration from silking stage to mature stage of maize (Jones 1983). In addition, high concentrations were attained in the mycorrhizal maize (Wen et al. 2017).

Inoculation with the AM fungus also significantly increased leaf chlorophyll content and plant net photosynthetic rate resulting in the accumulation of primary products such as starch, while the intercellular CO_2 concentration decreased in the mycorrhizal treatment and this is consistent with previous studies (Borde et al. 2010; Talaat and Shawky 2014). In addition, soluble sugars and soluble proteins increased as a result of mycorrhiza-mediated enhanced photosynthesis (Table 4). When soluble sugars and soluble proteins increase the resistance to stress of the host plants is enhanced (Latef and Huang 2011; Sheng et al. 2011). Furthermore, the MDA content in the leaves decreased significantly while CAT in the leaves increased in the mycorrhizal treatment (Table 4). Lower H_2O_2 and MDA contents compared to non-mycorrhizal controls reduce oxidative (or other) stresses (Latef and Huang 2011; Talaat and Shawky 2014; Yang et al. 2014). Here, mycorrhizal inoculation reduced the temperature of leaf surfaces and increased the ability of the plants to resist high temperatures that might occur in northern Chinese coal mining areas (Table 5), perhaps by increasing the transpiration rate (Lee et al. 2012). Above all, AM fungi may increase the potential resistance to environmental stress in coal mining areas and increase their nutrient uptake capacity, as well as contributing to plant growth and the accumulation of photosynthetic products (Xie et al. 1995; Hajiboland et al. 2010).

AM fungi regulate the allocation of photosynthetic products

Symbiotic associations between AM fungi and plants affect the transportation and allocation of photosynthetic products in plants (Lendenmann et al. 2011; Slavíková et al. 2017; Řezáčová et al. 2018). Here, the $^{13}CO_2$ pulse labeling method was used to label the maize and quantitatively determine the allocation of photosynthetic C in various plant parts and in the soil and the inoculated AM fungus and this is consistent with previous studies. Inoculation with the AM fungus increased the concentration and total amount of ^{13}C in the plants (Figs. 3 and 4). This is supported by previous studies showing that AM fungi increase the C fixation capacity of their host plants by enhancing photosynthesis (Hoeksema et al. 2010; Jakobsen and Rosendahl 1990; Al-Karaki 2000; Drigo et al. 2010; Olsson et al. 2010). We also observed significantly higher ^{13}C concentrations in the intermediate leaves and roots in the mycorrhizal treatment as well as higher concentrations of ^{13}C in the young and senescent leaves and stems than in non-mycorrhizal controls (Fig. 3c). Higher ^{13}C concentrations in plant parts indicate stronger photosynthesis in young leaves than in the intermediate and senescent leaves. Here, inoculation with the AM fungus increased the ^{13}C content in the plants and soil and also significantly changed the allocation of ^{13}C between the above- and below-ground parts of the system (Fig. 4). Although inoculation increased the concentration of total ^{13}C and each part of the ^{13}C, the above-ground ^{13}C allocation ratio in the inoculated treatment decreased by 5.89%. The Pn was positively correlated to the ^{13}C to the roots and hyphae as shown in Fig. 4. In the correlation analysis, AK was negatively correlated with ^{13}C allocation to soil, and CAT was positively correlated with the ^{13}C allocation to the AM fungal hyphae (Fig. 5). This indicates that inoculation promoted photosynthesis and altered plant physiology while promoting the transportation of photosynthetic products belowground. This is supported by studies in which associations between AM fungi and host plants have accelerated the transport of photosynthetic products from leaves to roots and through stems. Here, the C% and ^{13}C concentrations in the hyphae were equivalent to those in the leaves and were higher than in the roots (Fig. 3b and c). This is consistent with a previous study in which ^{14}C was fixed by plants and then transferred to AM fungi within a few minutes (Clemmensen et al. 2013). In fact, AM fungi contain 5 to 20% of the photosynthetic C (Jakobsen and Rosendahl 1990; Johnson et al. 1997). Therefore, AM fungi are regulators of C flux pools from above- to below-ground (Zhu and Miller 2003).

AM fungi enhance C flux to soil microorganisms

Mycorrhizal inoculation significantly increased SOC and glomalin in the soil by increasing the ^{13}C allocation to roots or hyphae (Table 2 and Fig. 4). When a symbiotic relationship has formed a portion of the photosynthetic products is allocated to the AM fungi for extension of hyphae and development of spores in the soil (Gavito et al. 2005; Godbold et al. 2006). Previous studies show that the turnover time is usually 5–6 days. When the AM fungi die, part of their C may be decomposed by other microorganisms and then released to the atmosphere or enter the soil C cycle (Staddon et al. 2003; Treseder 2013). There were significantly higher MBC and MBC/SOC values in the mycorrhizal treatment

(Tables 2 and 3). This is direct evidence of AM fungal enhancement of C flux to soil microorganisms. There is also a portion of C produced by AM fungi, for example in their cell walls, in the form of chitin that can remain in the soil for decades. The soil average organic C content in the inoculated treatment increased by 21.3% compared with the uninoculated control (Table 2). Thus, although the AM fungus had a rapid turnover rate in the soil the C stored by the fungus in the soil was measurable, maintaining a stable hyphal network that is important in soil C sequestration (Friese and Allen 1991). In the mycorrhizal treatment, the soil contents of EEG and TG increased significantly (Table 2), indicating that the content of soil glomalin was closely related to the AM fungus (Wright and Upadhyaya 1996). The EEG/SOC and TG/SOC values increased in the mycorrhizal treatment, showing that inoculation enhanced the contribution of glomalin to soil organic carbon (Table 3). Studies show that AM fungi can produce exudates such as glomalin that are stable in the soil and influence the soil C storage indirectly by stabilizing soil aggregates (Steinberg and Rillig 2003; Rillig and Mummey 2006). This indicates that soil C deposition is not only affected by the C turnover in the mycelium but also by the protection of exudates of AM fungi and hyphal networks (Miller and Jastrow 2000; Zhu and Miller 2003). Readily broken down carbon sources include sugars, organic acids, phenols (Zhang et al. 2016). These may be rapidly used by soil microorganisms and increase soil MBC directly (Zhang et al. 2016) and this also suggests that AM fungi enhance C flux to soil microorganisms.

AM fungi regulate above-belowground feedback

It is reported that soil organisms are important drivers of plant growth and then the effect of plants on soil community may influence the plants that grow later in the soil (Van der Putten et al. 2013; Wilschut et al. 2019). Once a symbiotic relationship is established it can extend the range of uptake by plant roots from a few millimeters to 12 cm, increasing the efficiency of soil nutrient utilization (Li et al. 1991). Therefore, in the mycorrhizal treatment, the contents of available P in the soil declined significantly (Table 2). The results support the prevalence of a positive plant-soil feedback in the AM system (Bahram et al. 2020). Interaction between the host plants and the AM fungus increased the nutritional status of the host plants in nutrient-limited soils and also promoted plant growth and nutrient especially P status and the distribution of photosynthetic products belowground to supply both the roots and the AM fungus (Tables 1 and 3). The results support the promotion of the accumulation of C in the soil by the AM fungal association by promoting the distribution of photosynthetic products from the above-ground parts of the host plant to the intra- and extraradical mycelium (Leake et al. 2004). ^{13}C allocation to hyphae was significantly positively correlated to MBN

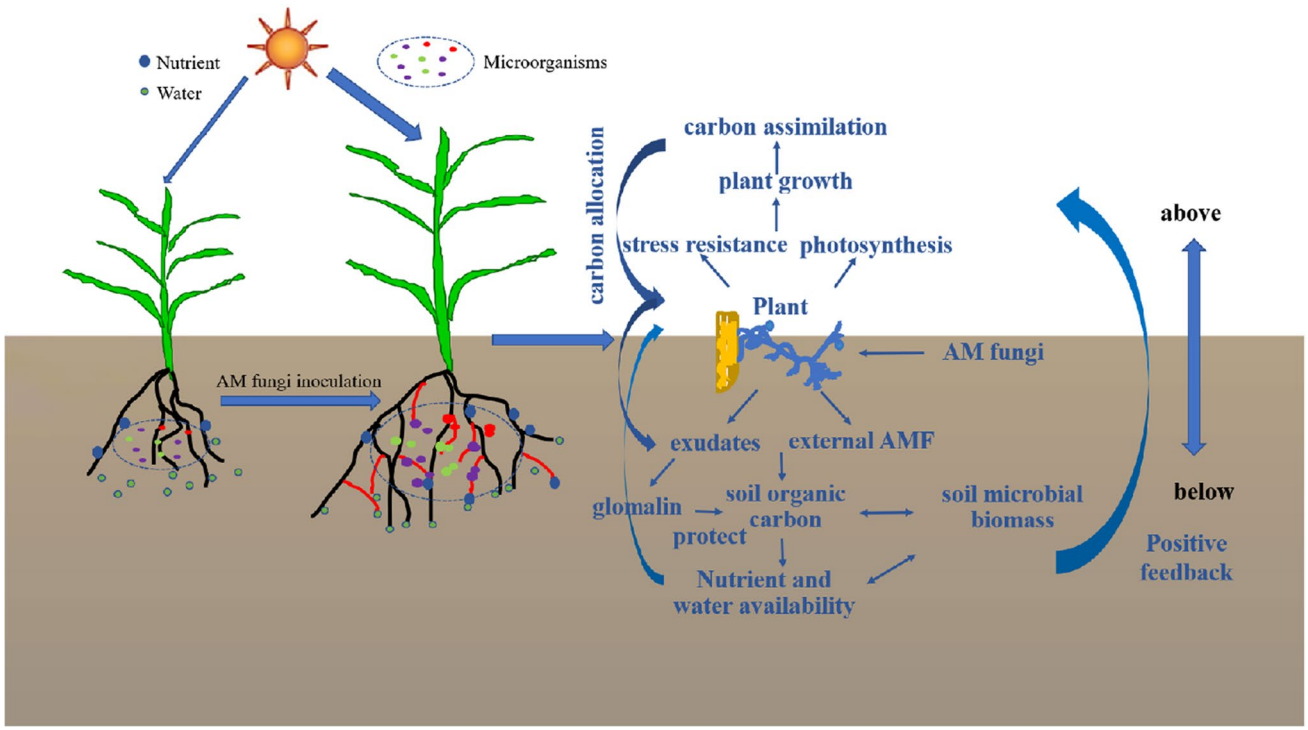

Fig. 6 Schematic representation of increased above-belowground feedback through enhanced plant carbon assimilation and allocation

(Fig. 5). This stimulates the accumulation of microbial biomass. The hyphae release exudates and stabilize the soil structure and can also provide C sources for the soil microbial community and promote the growth of soil microorganisms (Toljander et al. 2007; Jones et al. 2009). Soil microorganisms are the most active part of the soil. They play an important role in soil nutrient acquisition and organic matter mineralization to meet the growth needs of plants and AM fungi (Hodge et al. 2001; Scheublin et al. 2010; Jansa et al. 2013; Wang et al. 2016; Zhang et al. 2018). Therefore, a mutually beneficial system is formed among host plants, AM fungi, and soil microorganisms which affects the soil C cycle and enhances soil nutrient conditions. The enhanced microbial and environmental conditions in the nutrient-poor soil regulated a good feedback mechanism to increase plant growth.

Conclusions

Here, we established a suitable method to quantify the carbon allocation in plants, AM fungus and soil, and additionally in different plant parts. We also determined soil nutrient and SOC change caused by the AM fungus to detect above-belowground feedback regulated by the AM fungal association. Our results indicate that mycorrhizal colonization aided in the promotion of plant growth through increased stress resistance and mineral nutrient uptake. The AM fungus regulated the carbon allocation to functional leaves and increased plant photosynthetic activity. Mycorrhizal colonization also stimulated C allocation belowground to roots, hyphae, and microorganisms. Soil available P and K contents decreased significantly because of the mycorrhizal nutrient uptake pathway to host plants. The positive feedback regulated by the AM fungus was established (Fig. 6). Mycorrhizal inoculation may therefore be a useful technique for ecological restoration and land reclamation in mining areas of northwest China, acting through above-belowground interactions and positive feedback. However, the current pot experiment was conducted in greenhouse conditions and further studies are required to verify the results under field conditions.

Author contribution YL Bi, P Christie, Y Cai, and X Wang designed the study. Y Cai performed the plant culture and chemical analysis. YL Bi, P Christie, and X Wang contributed to the statistical interpretation of results and wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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