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Parasitic plant infection shifts arbuscular mycorrhizal fungal community and increases organic carbon decomposition

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ABSTRACT

The role of arbuscular mycorrhizal fungi (AMF) in the decomposition of soil organic carbon (C) may be substantial. However, how species at high trophic levels, such as parasitic plants, regulate the effects of AMF on decomposition remains unknown. We hypothesized that parasitic plant infection would shift the composition of AMF community and hyphosphere bacterial community, and affect decomposition of soil organic C. We conducted two independent container experiments with the herbaceous plant *Bidens pilosa* as host and *Cuscuta australis* as the parasitic plant and provided ^{13}C-enriched maize leaves as organic material in in-growth bags. In-growth bags had either 25-μm nylon mesh to allow penetration by AMF hyphae but block root growth or 0.5-μm nylon mesh to prevent penetration of both AMF hyphae and roots. Parasitic plant infection significantly changed AMF community composition and decreased ^{13}C remaining in in-growth bags. The ^{13}C remaining was significantly positively related to the relative abundance of the AMF genus *Glomus*, but was significantly negatively related to that of *Sclerocystis*. Additionally, with maize leaves addition, parasitic plant infection significantly decreased hyphal density and increased copy numbers of the N-cycle gene *amoB* in the hyphosphere. The ^{13}C remaining was significantly related to the relative abundances of the dominant hyphosphere bacterial phyla *Bacillota* and *Pseudomonadota*. Thus, we conclude that parasitic plant infection can shift composition of AMF community and hyphosphere bacterial community, and increase soil C loss. Our research highlights the potential role of parasitic plants in shaping soil nutrient cycling.

1. Introduction

Soil organic carbon (C) is a major terrestrial C pool and the main source of atmospheric carbon dioxide, exerting crucial influence on ecosystem productivity as well as climate regulation (van Groenigen et al., 2014). Carbon inputs originating from plants and C outputs resulting from decomposition are the main factors regulating the dynamic balance of soil organic C (Vesterdal et al., 2012; Sun et al., 2019). Studies indicate that soil arbuscular mycorrhizal fungi (AMF) have key roles in driving soil organic C decomposition (Cheng et al., 2012; Qiu et al., 2021). Arbuscular mycorrhizal fungi can protect organic C from decomposition via glomalin and hyphal enmeshment or increase decomposition via cooperation with hyphospheric saprophytic microbes (Hodge and Fitter, 2010; Cheng et al., 2012; Leifheit et al., 2015). However, most host plants are attacked by higher trophic-level species such as herbivores and parasites (Price et al., 1980). How such attacks on host plants regulate the effects of AMF on soil organic C decomposition remains unknown.

Parasitic plants obtain all or part of their C, nutrients, and water from host plants, which can heavily suppress host plant growth (Press and Phoenix, 2005; Bardgett et al., 2006; Yuan et al., 2021). The C-limitation hypothesis suggests that the loss of photosynthetic tissue impairs AMF symbiosis by reducing C availability for AMF (Gehring and Whitham, 1994; Frew et al., 2024a). Infection of host plants by parasitic plants would therefore be expected to have important effects on the AMF symbiosis, because host species reallocate C resources between parasitic plants and the root system. Indeed, in recent studies, the parasitic plant *Cuscuta australis* significantly decreased colonization of the AMF species *Rhizophagus intraradices* in roots of the host plant *Bidens pilosa* (Yuan and Li, 2022; Yuan et al., 2023). However, host plants form symbiotic relations with a variety of AMF species, and there is currently a lack of relevant research on how parasitic plants regulate the diversity of AMF

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communities in host plant root systems.

In other types of attacks (e.g., herbivory) on host plants, the C loss can shift AMF community composition and increase host plant nutrient uptake (Frew et al., 2024a). This pattern may develop because reduced C availability intensifies competition among AMF taxa, thereby favoring taxa with lower C demands or those more competitive for host-derived C, which in turn may influence overall nutrient acquisition by the host (i.e., C-limitation hypothesis; Frew et al., 2024b). In addition, the effects of AMF on soil organic C decomposition can vary among taxa (Arcidiacono et al., 2024; Basiru and Hijri, 2024). For example, Arcidiacono et al. (2024) found that members of the *Gigasporaceae* increased litter decomposition, whereas *Funneliformis mosseae* had no significant effect. Therefore, shifts in AMF community composition induced by C loss in host plants may subsequently alter organic C decomposition. Because parasitic plants also induce C loss in host plants, we expect that parasitic plant infection may regulate AMF community composition and influence organic C decomposition.

When AMF extraradical hyphae encounter patches of organic matter, they may establish close associations with bacteria in the hyphosphere (Jiang et al., 2021). Hyphosphere bacteria can utilize C derived from hyphal exudates and produce extracellular enzymes involved in organic matter decomposition (Zhang et al., 2016, 2022). However, the composition and functional potential of bacterial communities in the AMF hyphosphere can vary among AMF taxa. For example, Zhou et al. (2023) found that the hyphosphere bacterial community of the AMF species *Gigaspora margarita* was rich in genes encoding alkaline phosphatase, suggesting increased potential for organic phosphorus mineralization, whereas the hyphosphere of *Funneliformis mosseae* contained relatively few such genes. These findings indicate that the species of AMF can shape the functional potential of associated bacterial communities. Therefore, we expect that parasitic plant infection not only alters AMF community composition but also shifts that of hyphosphere bacterial communities. The shift may influence organic matter decomposition and nutrient release, ultimately influence nutrient acquisition by both host and parasitic plants.

In this study, we used the stem holoparasite *Cuscuta australis* R.Br. and its host plant *Bidens pilosa* L. to investigate whether and how parasitic plant infection regulates AMF community composition, hyphosphere bacterial community composition, and soil organic C decomposition. *Cuscuta australis* is rootless and leafless and develops haustoria to obtain C, nutrients, and water from host plants (Sun et al., 2018). Because *C. australis* parasitizes host stems rather than roots, its effects on soil organic C decomposition are likely mediated indirectly through host roots and extraradical AMF hyphae. Additionally, *Cuscuta australis* can parasitize a variety of herbaceous plants, including *B. pilosa*, and cause severe damage. We previously demonstrated that *C. australis* can significantly inhibit the root colonization rate of *B. pilosa* by the AMF species *Rhizophagus intraradices* (Yuan and Li, 2022; Yuan et al., 2023). Building on these observations, we hypothesized that parasitic plant infection would shift composition of AMF community and hyphosphere bacterial community, and alter decomposition of soil organic C.

2. Materials and methods

We conducted two independent greenhouse container experiments to investigate whether parasitic plant infection influenced composition of the host-plant AMF community and hyphosphere bacterial community, and affected decomposition of soil organic C. The stem holoparasite *C. australis* and its host plant *B. pilosa* were used in the study system.

2.1. Soil substrate

Soil was collected from an abandoned field on the Zijingang campus of Zhejiang University in Hangzhou, Zhejiang Province, China (30°28′N, 120°15′E). The soil was air-dried, homogenized, and sieved using a metal screen with 1.0-cm mesh. The soil had the following properties: pH: 7.46; organic C: 5.81 g kg^{-1}; total nitrogen: 0.82 g kg^{-1}; total phosphorus: 0.49 g kg^{-1}; and available phosphorus: 15.53 mg kg^{-1}.

2.2. Seedling culture

Seeds of *B. pilosa* were obtained from the seed collection at Taizhou University, Taizhou, Zhejiang Province, on October 25, 2024, and then air-dried and stored at 4 °C. Before planting, seeds were surface sterilized with 0.5% sodium hypochlorite for 15 min, rinsed three times with distilled water, and then sown into plastic trays (54 cm (length) × 27 cm (width) × 4.5 cm (height)) filled with sterilized peat (QTS, CompaQpeat Sia, Latvia). The sterilized peat was obtained by ^{60}Co γ-irradiation at a dose of 32 kGy for 3 day at the Zhejiang Academy of Agricultural Sciences (Hangzhou, China). When height of aboveground parts reached approximately 2 cm, seedlings were individually transplanted into separate containers.

Seeds of *C. australis* were purchased from Bozhou Medicinal Materials Company, Bozhou, Anhui Province, China. Stems of *C. australis* were propagated by parasitizing soybean (*Glycine max*) as the host plant. First, soybean seeds were sown in microcosms filled with peat on April 3, 2025. After 5 weeks, *C. australis* seeds were sown in the substrate close to soybean stems. After a few days, germinated *C. australis* seedlings began to coil around soybean plants, form haustoria, and produce new stems. Five weeks later, new, 10-cm long stem segments of *C. australis* were collected and used to infect *B. pilosa*.

All containers and plastic trays were maintained in the greenhouse at the Agricultural Station of Zhejiang University, Hangzhou, Zhejiang Province, China (30°28′N, 120°15′E), with natural light and temperature and adequate water supplied daily. No additional fertilizers were applied in this study.

2.3. Experiment 1

Experiment 1 was conducted to test whether parasitic plant infection shifts AMF community composition and affects organic C decomposition. On April 26, 2025, 20 experimental containers (26 cm (length) × 12 cm (width) × 12 cm (height)) were filled with 2.5 kg of field soil, and one *B. pilosa* seedling was transplanted into one side of each container. Six weeks later, one 10-cm long stem segment of *C. australis* was twined around each host plant to establish parasitism. Half of the containers received the parasitism treatment, while the other half were unparasitized controls (Yuan et al., 2023). Immediately after introducing *C. australis*, one in-growth bag was buried in the soil on the other side of each container (Fig. S1). In-growth bags were made of either 25-μm or 0.5-μm nylon mesh (Jiuding High-Tech Filtration Equipment Co., Ltd, Beijing, China). The 25-μm nylon mesh allows AMF hyphae to enter but blocks plant roots, while the 0.5-μm mesh prevents both AMF hyphae and plant roots from entering bags. Each in-growth bag was filled with 50 g of field soil and 0.5 g of oven-dried maize leaves. Maize leaf nutrient concentrations were 45.96% C, 1.74% N, and 0.27% P. Maize leaves were cut into 1-mm pieces and uniformly mixed with the field soil. Because maize is a C_4 plant, its natural $^{13}C/^{12}C$ ratio ($\delta^{13}C = -12.971‰$) is higher than that of C_3 plants (Smith and Epstein, 1971). Therefore, maize leaves can be regarded as a natural ^{13}C stable isotope-labeled material. In total, the 20 experimental containers comprised two parasitic plant infection treatments (with [P+] or without [P-]) × two AMF treatments (present [AMF] or excluded [None] in in-growth bags) × 5 replicates.

The experiment was completed on July 20, 2025. All in-growth bags were carefully removed from the containers, and the samples inside bags were air-dried and then ground to a fine powder in a ball mill (Retsch Technology GmbH) for ^{13}C measurement. The *C. australis* plants were harvested by detaching them from *B. pilosa* host plants. Plant aboveground samples were harvested at the soil surface and oven-dried at 65 °C to constant weight. Plant roots were washed to remove all surface soil and then divided into two parts on the basis of fresh weight. One part

was oven-dried at 65 °C to constant weight, and the dried root sample was subsequently used to determine the AMF colonization rate of *B. pilosa* using the gridline-intersection method (Giovannetti and Mosse, 1980). Briefly, root segments were cleared in 10% KOH, acidified in 1% HCl, and stained with acid fuchsin. The AMF colonization was quantified using the modified gridline-intersection method by evaluating 200 intersections per root sample using a 20x microscope. The other part was stored at −80 °C for analysis of AMF community composition.

2.4. Experiment 2

Experiment 2 was conducted to determine whether parasitic plant infection shifts hyphosphere bacterial community composition and affects organic C decomposition. Twenty containers (20 cm (length) × 10 cm (width) × 11.5 cm (height)) were used, with one plastic core (10 cm (height) × 8.5 cm (diameter)) dug into one side of each container (Fig. S2). Each container was filled with 1.3 kg of field soil, while each plastic core was filled with 500 g of field soil. A quarter of the lateral surface area of the plastic core was cut out and then covered with the 25-μm nylon mesh to prevent roots but allow AMF hyphae to penetrate. The opening of each plastic core was directed toward the other side of the container (Fig. S2) (Yuan et al., 2021, 2023).

On April 26, 2025, one seedling of *B. pilosa* was transplanted into the plastic core of each container. Four weeks later, one 10-cm long stem segment of *C. australis* was twined around each host plant to establish parasitism. Half of the 20 containers received the parasitic plant infection treatment, while the other half were unparasitized controls (Yuan et al., 2023). Immediately after parasite addition, one in-growth bag was buried in the other side of the container 7 cm from *B. pilosa* (Fig. S2). The in-growth bags were made of 25-μm nylon mesh, with bags filled with either 50.5 g of sand or a mixture of 50 g of sand and 0.5 g of oven-dried maize leaves (Fig. S2). The experiment had 20 total containers (2 parasitic plant infection treatments [presence or absence] × 2 organic material treatments [with or without maize leaves in in-growth bags] × 5 replicates).

The experiment was completed on July 20, 2025. All in-growth bags were carefully removed from each container, and a 5-g sample from each in-growth bag was air-dried, ground using a ball mill (Retsch Technology GmbH), and then measured for ^{13}C. A second 5-g sample was taken from each bag and immediately transferred to a −80 °C refrigerator for DNA analysis. The hyphal density in each bag was determined using a modified membrane filter technique (Jakobsen and Robson, 1992; Wang et al., 2013; Yuan and Li, 2022). Samples from four in-growth bags were randomly selected from each treatment for analysis of hyphosphere bacterial community composition. Because of the important effect of soil nitrogen on soil organic C decomposition (Ye et al., 2018), we also randomly selected three in-growth bags to determine copy numbers of the N-cycle genes *amoA* and *amoB*. Gene abundance was determined using quantitative real-time PCR (qPCR).

2.5. Measurement of ^{13}C

The $\delta^{13}C$ (‰) values and the percentage of total C concentration were determined using a continuous-flow isotope-ratio mass spectrometer (CF-IRMS, Delta Plus, Thermo Finnigan). The $\delta^{13}C$ (‰) values were converted to absolute isotope ratios ($R = {}^{13}C/{}^{12}C$) using the Vienna Pee Dee Belemnite (VPDB) standard according to the following equation:

$$R_{sample} = R_{VPDB} \times \left(\frac{\delta^{13}C}{1000} + 1\right)$$

The ^{13}C concentrations of samples were then calculated using the following equation:

$$^{13}C\ \text{concentration} = \frac{R_{sample}}{1 + R_{sample}} \times \text{amt\%(C)} \Big/ 100 \times 1000\ \text{mg g}^{-1}$$

where amt % (C) is the percentage of total C concentration.

Then, the percentage of ^{13}C remaining within each in-growth bag was calculated by dividing the amount of ^{13}C in samples at the end of the experiment by the initial values in samples when the in-growth bags were added to the containers (Cheng et al., 2012; Yuan et al., 2023).

2.6. Analysis of AMF and bacterial communities

Extraction of DNA, polymerase chain reaction (PCR) amplification, and sequencing were performed at Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China) (Method S1). Mycorrhizal fungal DNA was extracted from fresh roots of *B. pilosa* (Experiment 1), and the 18S ribosomal RNA (rRNA) gene of AMF was amplified using nested PCR, with the two pairs of primers AML1F and AML2R and AMV4.5NF and AMDGR (Lumini et al., 2010) (Table S1). Bacterial DNA was extracted from the samples in in-growth bags (Experiment 2), and the V3–V4 region of the bacterial 16S rRNA gene was amplified with the primer pair 338F and 806R (Liu et al., 2016) (Table S1). After amplification, PCR products were purified, pooled, and then sequenced on an Illumina Nextseq2000 platform (Illumina, San Diego, CA, USA) by Majorbio Bio-Pharm Technology Co. Ltd. The raw sequences are deposited in the National Center for Biotechnology Information (NCBI) under BioProject accession numbers PRJNA1337623 and PRJNA1337633.

The Maarj*AM* (Öpik et al., 2010; Stefani et al., 2020; Qiu et al., 2021) and SILVA (v138) (https://www.arb-silva.de/) databases were used for taxonomic assignment of amplicon sequence variants. Bioinformatic analysis of the AMF and bacterial communities was conducted using the Majorbio Cloud platform (https://cloud.majorbio.com). Shannon, Simpson, and Pielou's evenness alpha diversity indices were calculated. Principal co-ordinates analysis (PCoA) and permutational analysis of variance (PERMANOVA) were used to determine the influence of different treatments on the similarity among mycorrhizal and bacterial communities (Method S1).

2.7. Real-time quantitative PCR

Total DNA was extracted from samples in in-growth bags (Experiment 2). Copy numbers of *amoA* and *amoB* genes were quantified using a qPCR instrument (ABI7300, Applied Biosystems, CA, USA) with the respective primer pairs CHEND-arch-*amoA*-23F and CHEND-arch-*amoA*-616R and CTO189f and CTO654r (Table S1). Detailed information on the PCR reaction system and reaction conditions is included in Supplementary Information (Method S1). A standard curve was generated by constructing plasmid standards, and then, the gene copy number per gram of sample was calculated.

2.8. Statistical analyses

All statistical analyses were performed in R v4.5.1 (R Core Team, 2025). In Experiment 1, the differences in aboveground biomass, root biomass, AMF colonization rate of *B. pilosa*, the ^{13}C remaining in in-growth bags, and the relative abundance of AMF taxa between treatments were evaluated using independent-sample *t*-tests. The associations between the ^{13}C remaining in in-growth bags and the relative abundances of *Glomus* and *Sclerocystis* were determined using Pearson's correlation analysis. In Experiment 2, the effects of parasitic plant infection, maize leaves addition, and their interaction on aboveground and root biomass, total C remaining, hyphal density, bacterial alpha diversity indices, and copy numbers of *amoA* and *amoB* genes were tested using two-way ANOVAs. The effect of parasitic plant infection on the ^{13}C remaining in in-growth bags and the effect of maize leaves addition on *C. australis* biomass were examined using independent-sample *t*-tests. Pearson's correlation analysis was used to evaluate associations between total C remaining and ^{13}C remaining and the relative abundances of the major phyla *Bacillota* and

Pseudomonadota. Before statistical analyses, data were tested to determine whether they were normally distributed and had homogenous variance. Data sets not meeting those criteria were transformed. Only the *amoB* gene copy numbers failed to meet these assumptions and were therefore cube-root transformed before analysis. Significant differences were accepted at $P < 0.05$.

3. Results

3.1. Experiment 1

Parasitic plant infection significantly reduced *B. pilosa* aboveground biomass (−40.5%; $t = 5.958$, $df = 17.935$, $P < 0.001$) (Fig. 1a), root biomass (−29.7%; $t = 2.468$, $df = 10.953$, $P = 0.031$) (Fig. 1b), and AMF colonization rate (−18.6%; $t = 5.589$, $df = 17.859$, $P < 0.001$) (Fig. 1c). The presence of AMF in in-growth bags significantly decreased the ^{13}C remaining by −39.5%. Parasitic plant infection significantly reduced the ^{13}C remaining by −15.7% in the presence of AMF (Fig. 1d).

According to PCoA and PERMANOVA, parasitic plant infection significantly affected AMF community composition ($R = 0.1446$, $P = 0.048$) (Fig. 2). The AMF communities were dominated by the genera *Glomus* and *Sclerocystis* (Fig. S3). Parasitic plant infection significantly decreased the relative abundance of *Glomus* ($t = 5.481$, $df = 11.687$, $P < 0.001$) (Fig. 3a) but significantly increased that of *Sclerocystis* ($t = -5.540$, $df = 10.762$, $P < 0.001$) (Fig. 3c). In the presence of AMF, the ^{13}C remaining in in-growth bags was significantly positively related to the relative abundance of *Glomus* (Fig. 3b) but significantly negatively related to that of *Sclerocystis* (Fig. 3d). By contrast, with AMF excluded, the ^{13}C remaining in in-growth bags was not significantly related to *Glomus* or *Sclerocystis* relative abundance.

3.2. Experiment 2

Parasitic plant infection significantly reduced *B. pilosa* aboveground biomass (−22.8%) (Fig. 4a) and root biomass (−31.8%) (Fig. 4b). The biomass of *B. pilosa* was not significantly affected by the addition of maize leaves in in-growth bags. However, *C. australis* biomass increased significantly with in-growth bags filled with maize leaves (+127.5%; $t = -2.9007$, $df = 7.8029$, $P = 0.02041$) (Fig. 4c).

The addition of maize leaves in in-growth bags significantly

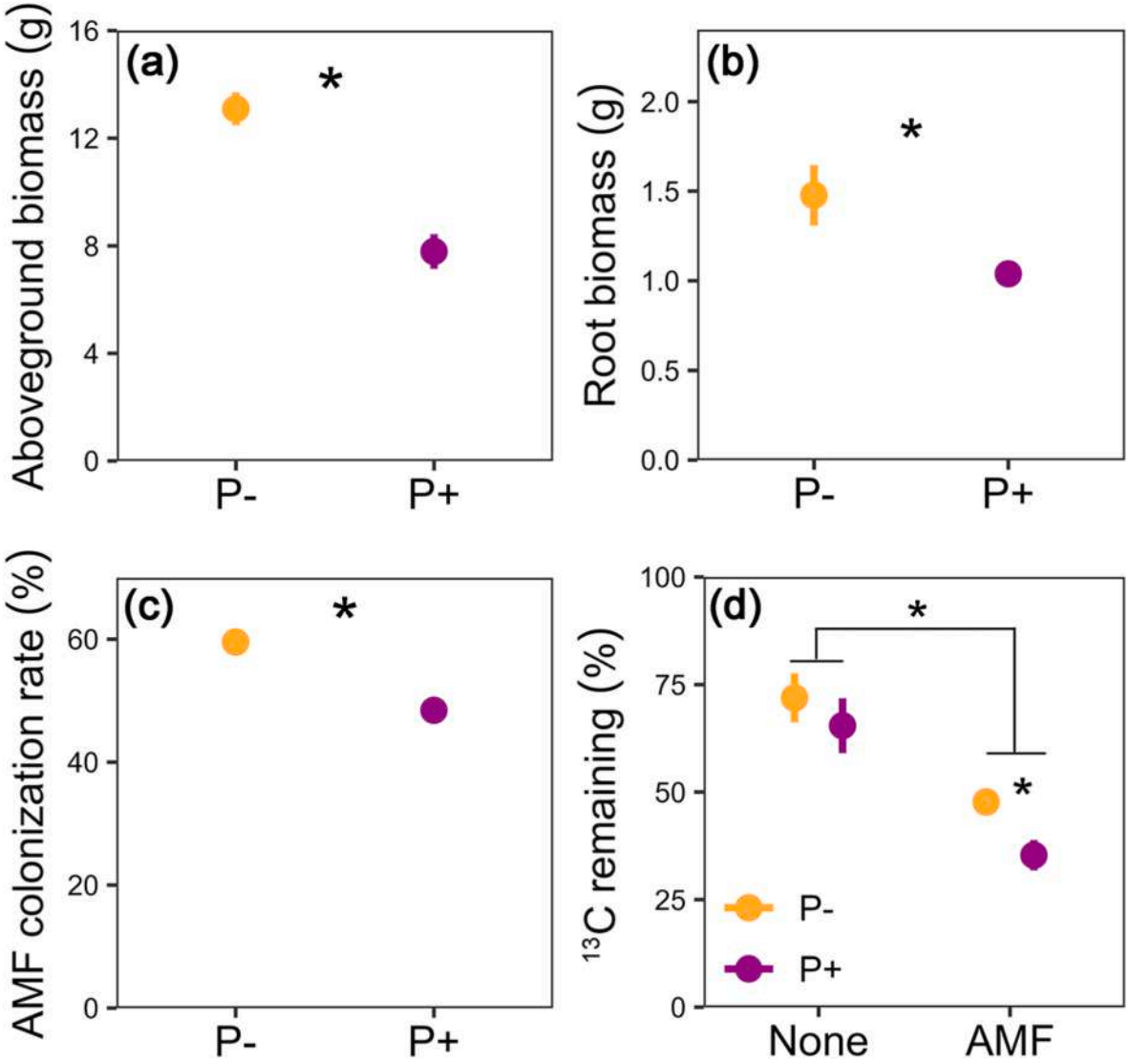


Fig. 1. Effect of parasitic plant infection on host plant *Bidens pilosa* (a) aboveground biomass, (b) root biomass, and (c) arbuscular mycorrhizal fungal (AMF) colonization rate, and effects of parasitic plant infection and AMF on (d) ^{13}C remaining (%) in in-growth bags in Experiment 1. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism; None: both roots and AMF excluded in in-growth bags; AMF: AMF present but roots excluded in in-growth bags. Values are the mean ± SE. *$P < 0.05$.

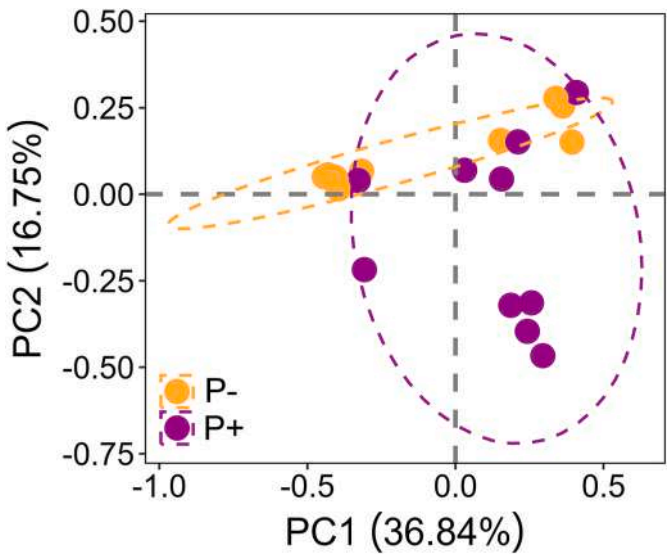


Fig. 2. Principal co-ordinates (PC) analysis of the effects of parasitic plant infection on the composition of arbuscular mycorrhizal fungal communities colonizing roots of *Bidens pilosa*. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism.

increased total C remaining (+40.1%) and hyphal density (+63.3%) (Table S2; Fig. 4d and f). Parasitic plant infection significantly decreased total C remaining (−27.7%) and hyphal density (−35.9%) with the addition of maize leaves but not without their addition (Table S2; Fig. 4d and f). Parasitic plant infection also significantly decreased the ^{13}C remaining (−27.5%) (Fig. 4e).

Shannon, Simpson, and Pielou's evenness alpha diversity indices of the bacterial community were not significantly affected by parasitic plant infection. However, addition of maize leaves significantly affected Simpson and Pielou's evenness indices (Tables S3 and S4). According to PCoA and PERMANOVA, the addition of maize leaves in in-growth bags significantly changed composition of the hyphosphere bacterial community (R = 0.57483, P = 0.001) (Fig. 5a); whereas parasitic plant infection did not significantly affect bacterial community composition (R = 0.03306, P = 0.204) (Fig. 5a).

The dominant bacterial phyla were *Bacillota* and *Pseudomonadota* (Fig. 5b). Maize leaves addition significantly increased the relative abundance of *Bacillota* by 85.9% (Fig. 6a). Without maize leaves addition, parasitic plant infection did not significantly affect the relative abundance of *Bacillota* and *Pseudomonadota*. However, with the addition, parasitic plant infection significantly increased the relative abundance of *Bacillota* by 31.5% but significantly decreased that of *Pseudomonadota* by 31.1% (Fig. 6a and b). Additionally, without maize leaves addition, the total C remaining was not significantly related to the relative abundance of *Bacillota* and *Pseudomonadota* (Fig. 6c and d).

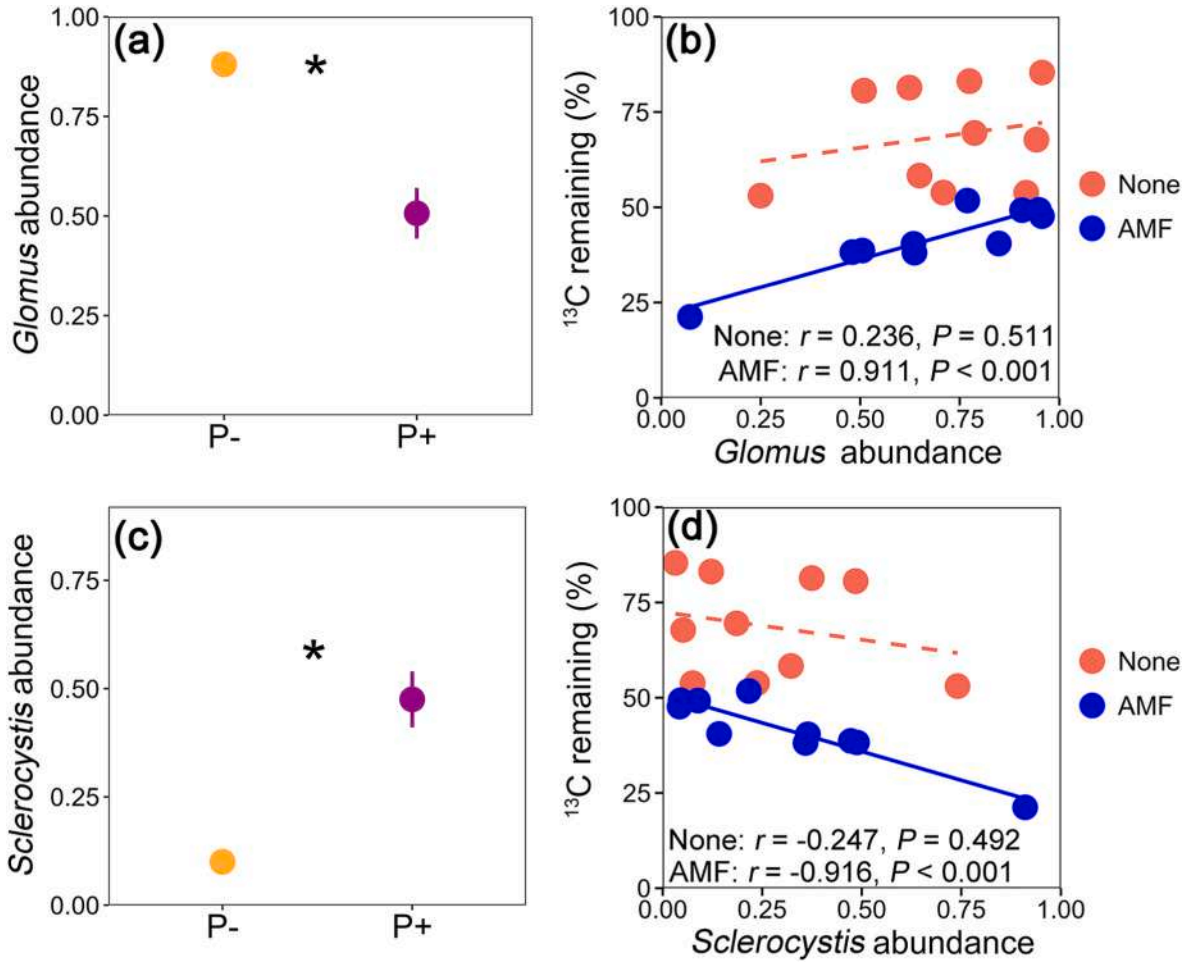


Fig. 3. Effect of parasitic plant infection on relative abundances of the dominant arbuscular mycorrhizal fungi (AMF) genera (a) *Glomus* and (c) *Sclerocystis* in Experiment 1. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism. The correlations between ^{13}C remaining in in-growth bags and relative abundance of (b) *Glomus* and (d) *Sclerocystis* in Experiment 1. None: both roots and AMF excluded in in-growth bags; AMF: AMF present but roots excluded in in-growth bags. Values in (a) and (c) are the mean ± SE. *P < 0.05. Significant correlations (P < 0.05): solid lines; nonsignificant correlations (P > 0.05): dashed lines.

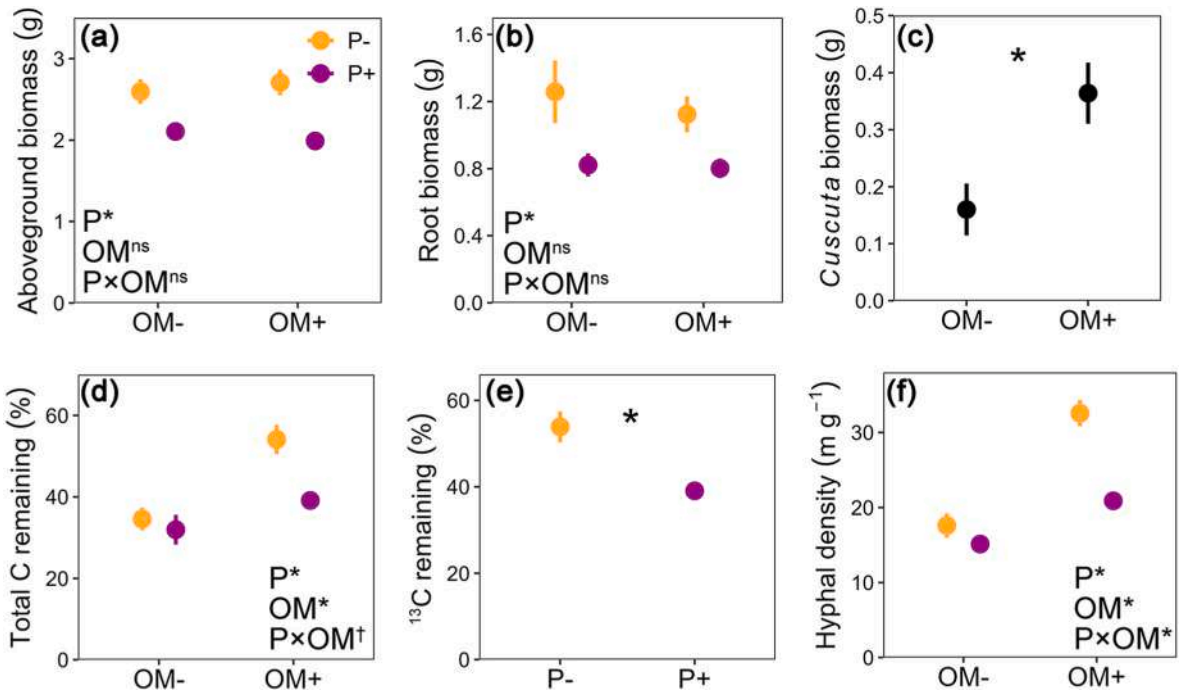


Fig. 4. Host plant *Bidens pilosa* (a) aboveground and (b) root biomass, (c) *Cuscuta australis* biomass, (d) total C and (e) ^{13}C remaining, and (f) hyphal density in in-growth bags in Experiment 2. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism; OM−: in-growth bags without maize leaves as organic material; OM+: in-growth bags with maize leaves. Values are the mean ± SE. $^{*}P < 0.05$; $^{\dagger}0.05 < P < 0.1$; $^{ns}P > 0.1$.

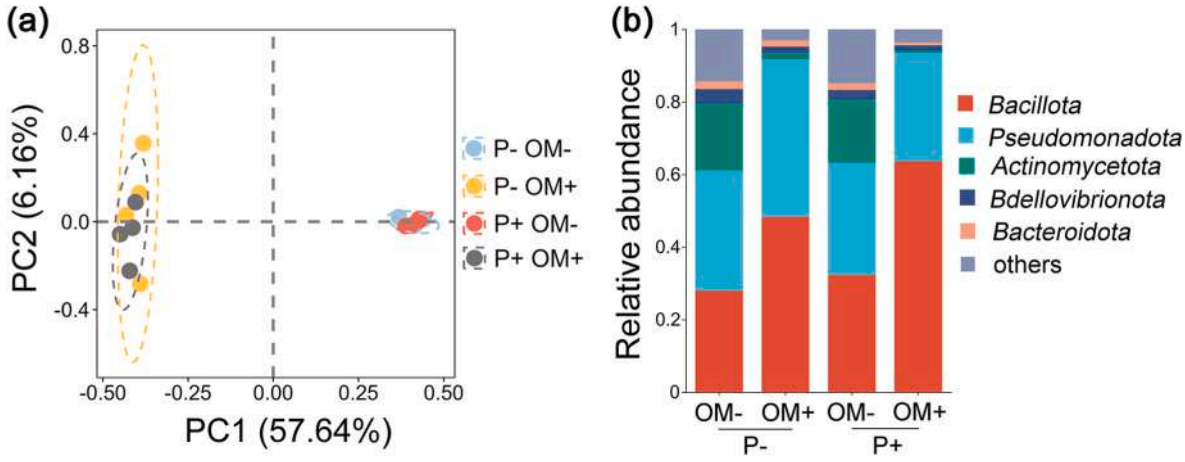


Fig. 5. Effects of parasitic plant infection and maize leaves addition on (a) principal co-ordinates (PC) analysis of bacterial community composition and (b) relative abundance of the major phyla of bacteria in in-growth bags under different treatments in Experiment 2. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism; OM−: in-growth bags without maize leaves as organic material; OM+: in-growth bags with maize leaves.

However, with the addition, both total C and ^{13}C remaining were significantly negatively related to the relative abundance of *Bacillota* (Fig. 6c and e) but significantly positively related to the relative abundance of *Pseudomonadota* (Fig. 6d and f).

Parasitic plant infection and the addition of maize leaves did not significantly affect *amoA* gene copy number (Fig. 7a) but did significantly affect *amoB* gene copy number individually and interactively (Fig. 7b). Specifically, maize leaves addition significantly increased *amoB* gene copy number. Without the addition, parasitic plant infection did not significantly affect *amoB* gene copy number. However, with the addition, parasitic plant infection significantly increased the copy number (Fig. 7b).

4. Discussion

We propose a conceptual framework illustrating potential mycorrhizal pathways linking parasitic plant infection and soil organic C decomposition based on our findings (Fig. 8). In this framework, parasitic plant infection alters host C allocation patterns and shifts competitive interactions among AMF taxa, potentially favoring taxa associated with increases in organic C decomposition. Changes in AMF community composition are in turn accompanied by shifts in hyphosphere bacterial communities, influencing decomposition dynamics and nutrient release. The nutrients released from organic patches can then be absorbed by extraradical AMF hyphae and transferred to the host plant, indirectly benefiting the parasitic plant.

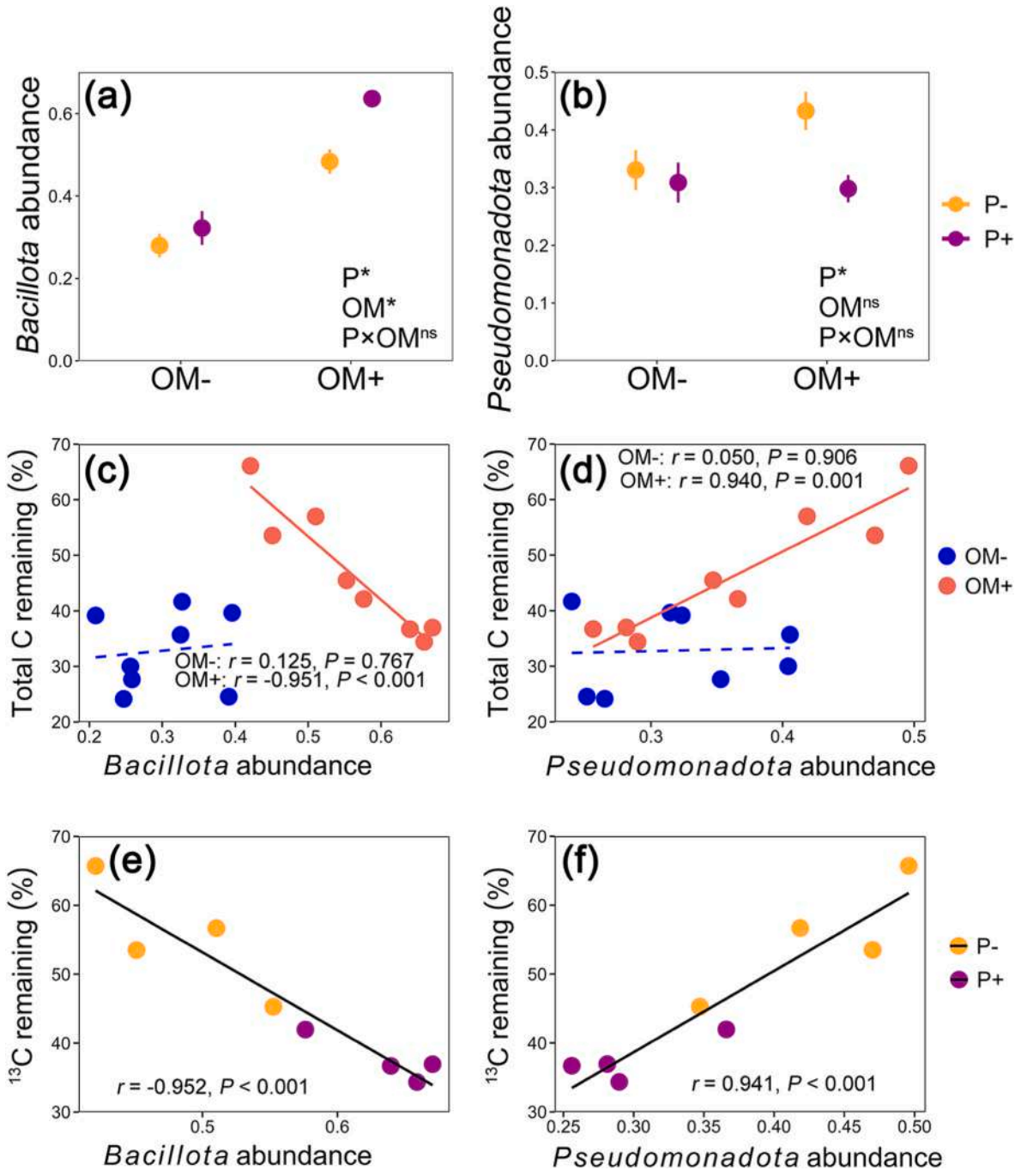


Fig. 6. Effects of parasitic plant infection and maize leaves addition on relative abundance of the dominant bacterial phyla (a) *Bacillota* and (b) *Pseudomonadota*; the correlations between total C (c, d) or ^{13}C (e, f) remaining in in-growth bags and the relative abundances of *Bacillota* and (c, e) and *Pseudomonadota* (d, f) in Experiment 2. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism; OM−: in-growth bags without maize leaves as organic material; OM+: in-growth bags maize leaves. Values in (a) and (b) are the mean ± SE. $^{*}P < 0.05$; $^{ns}P > 0.05$. Significant correlations ($P < 0.05$): solid lines; nonsignificant correlations ($P > 0.05$): dashed lines.

4.1. Arbuscular mycorrhizal fungal community composition and decomposition

In Experiment 1, *Glomus* and *Sclerocystis* were the primary AMF genera we detected in roots of host plant *B. pilosa* (Fig. S3), which accounted for more than 90% of total AMF abundance. We suspect the two genera were preferred by *B. pilosa*, because they remained dominant even when we grew *B. pilosa* in soil collected from different ecosystems and sites (unpublished). Furthermore, according to PERMANOVA results, parasitic plant infection significantly changed AMF community composition (Fig. 2). Particularly, parasitic plant infection significantly decreased the relative abundance of *Glomus* (Fig. 3a) but significantly increased that of *Sclerocystis* (Fig. 3c). *Sclerocystis* is phylogenetically closely related to the genus *Glomus* and was historically classified within *Glomus* based on morphological characteristics (Almeida and Schenck, 1990; Redecker et al., 2000). Therefore, the close phylogenetic relation between the two genera and the parasitic plant infection-induced reduction in C availability for AMF may lead to the competitive exclusion of *Glomus* by *Sclerocystis*, explaining their opposite changes in relative abundance (Frew et al., 2024). However, the mechanism by

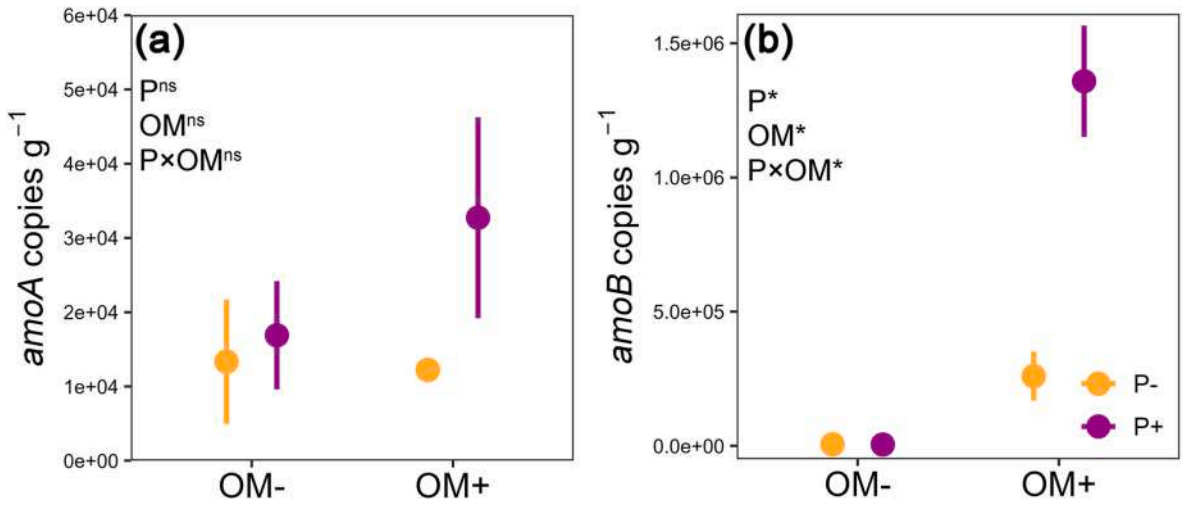


Fig. 7. Effects of parasitic plant infection and maize leaves addition on copy numbers of the N-cycle genes (a) *amoA* and (b) *amoB* in in-growth bags in Experiment 2. P−: without parasitic plant infection; P+: with *Cuscuta australis* parasitism; OM−: in-growth bags without maize leaves as organic material; OM+: in-growth bags with maize leaves. Values are the mean ± SE. $^{*}P < 0.05$; $^{ns}P > 0.05$.

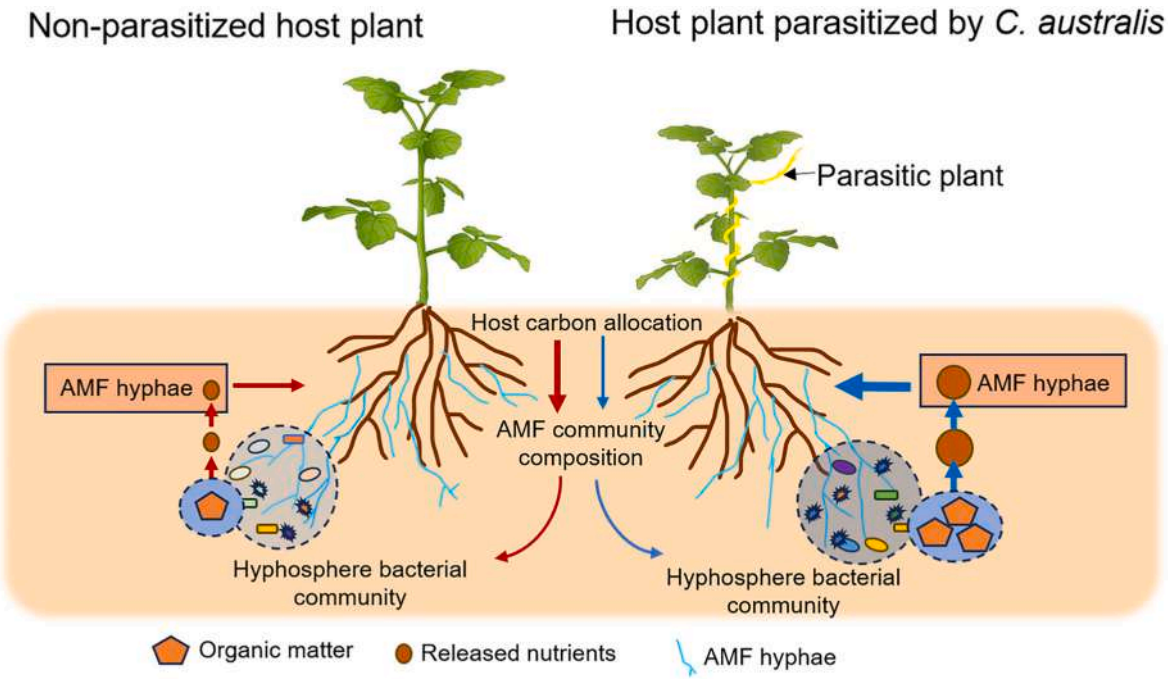


Fig. 8. Conceptual framework illustrating potential pathways by which arbuscular mycorrhizal fungi (AMF) link parasitic plant infection and soil organic carbon dynamics. Parasitic infection may alter host carbon allocation patterns and modify competitive interactions among AMF taxa. Shifts in AMF community composition may be accompanied by changes in hyphosphere bacterial communities, potentially favoring bacterial taxa associated with organic matter decomposition. Nutrients released from organic patches may be taken up by extraradical AMF hyphae and transported to host plants, with possible implications for parasitic plant performance. Red arrows: without parasitism; blue arrows: with parasitic plant infection. Increased arrow thickness indicates relative increase in carbon allocation or nutrient flux through AMF hyphae.

which *Sclerocystis* gained a competitive advantage remains to be further explored.

The presence of the AMF community in in-growth bags significantly decreased ^{13}C remaining (Fig. 1d), which is consistent with previous studies in which AMF influence soil organic C decomposition (Cheng et al., 2012; Gui et al., 2017). Additionally, the ^{13}C remaining in in-growth bags was positively related to the relative abundance of *Glomus* colonizing roots of *B. pilosa* but negatively related to that of *Sclerocystis* (Fig. 3), indicating taxon-specific differences in AMF-related organic C decomposition. Earlier studies proposed that members of *Glomus* contribute to soil aggregation through the production of glomalin-related soil proteins (GRSP), potentially affecting soil organic matter stabilization (Miller and Jastrow, 1990; Wright and Upadhyaya, 1998). However, recent research suggests that AMF-mediated soil C dynamics involve multiple interacting pathways, including effects on microbial community structure, mineral-associated organic matter formation, and resource allocation processes (Hodge and Fitter, 2010; Cheng et al., 2012; Leifheit et al., 2015), and cannot be attributed solely to GRSP-related stabilization mechanisms. Therefore, further experimental work is required to explain the taxon-specific differences in the influence of AMF on organic C decomposition. Overall, these results indicate that parasitic plant infection results in changes in AMF

community composition and soil organic C loss.

4.2. Hyphosphere bacterial community and decomposition

The addition of maize leaves to in-growth bags significantly increased extraradical hyphal density and altered the hyphospheric bacterial community (Fig. 4f and 5), which is consistent with previous studies in which organic C addition promotes the growth of extraradical AMF hyphae (Cheng et al., 2016; Yuan and Li, 2022). The increase in hyphal density may be related to changes in resource availability following organic material addition, because as previous studies demonstrate, AMF hyphae can proliferate in response to nutrient-enriched patches (Hodge et al., 2001; Hodge and Fitter, 2010). Such increases in hyphal density are likely linked to changes in the hyphosphere bacterial community structure due to the interactions with AMF (Zhang et al., 2016). However, further experimental work is needed to determine the mechanisms underlying these patterns.

Parasitic plant infection significantly affected hyphal density and the hyphospheric bacterial community in in-growth bags when maize leaves were added but had only negligible effects in their absence (Fig. 4f). These results may reflect differences in resource conditions between treatments. In the absence of maize leaf addition, the in-growth bags likely represented a relatively resource-poor environment, in which extraradical hyphal density was low and parasitic plant infection had limited effects. By contrast, when maize leaves were added, the in-growth bags represented a relatively resource-enriched environment, coinciding with increases in hyphal density. The increase in hyphal density may increase the responsiveness of AMF to changes in host plant status, including that caused by parasitic plant infection. However, nutrient availability and plant C allocation were not directly measured in this study. Future studies incorporating direct measurements of nutrient dynamics and plant C allocation will be required to explicitly test these proposed mechanisms.

Parasitic plant infection significantly reduced hyphal density but increased the decomposition of organic C in in-growth bags (Fig. 4e). One potential explanation is that parasitic infection shifted composition of the AMF community and hyphosphere bacterial communities. Interactions between AMF and hyphosphere bacteria may influence organic matter turnover (Hodge, 2001; Cheng et al., 2012). For example, Jiang et al. (2021) found that AMF can carry bacteria along their extraradical hyphae to organic patches to increase decomposition. In our study, parasitic plant infection significantly increased the relative abundance of the dominant phyla *Bacillota* and the copy number of the N-cycle *amoB* gene in the hyphosphere (Fig. 7). The abundance of these phyla of hyphosphere bacteria was significantly related to organic C decomposition (Fig. 6), indicating a potential link between shifts in hyphosphere bacterial communities and decomposition dynamics. In addition, in a previous study, *Bacillota* and *Pseudomonadota* were also the dominant bacterial phyla in maize hyphosphere soils and harbored genes encoding alkaline phosphatase, which may contribute to organic matter transformation (Zhang et al., 2020). Together, these results suggest that parasitic plant infection is associated with shifts in composition of the AMF community and hyphosphere bacterial community and increases in soil organic C decomposition.

Organic C in soil is often patchily distributed (Hinsinger et al., 2005; Kuzyakov and Blagodatskaya, 2015), and AMF can acquire 20% of the nitrogen required by their host plants from such organic C patches (Leigh et al., 2009). In our study, nutrient concentrations in maize leaves were higher than those in the bulk soil, suggesting that decomposing maize leaves represented a relatively nutrient-rich substrate compared with the surrounding soil matrix. Although maize leaf addition did not significantly affect host plant biomass (Fig. 4a and b) or nutrient contents (Fig. S4), it increased the biomass (Fig. 4c) and nutrient contents of the parasitic plant *C. australis* (Fig. S5). Given that *C. australis* acquires all its C and nutrients from its host, this pattern is consistent with the possibility that nutrient release from decomposing maize leaves altered nutrient dynamics within the host–parasite system.

Although we only examined one parasitic plant–host plant system, our results revealed that parasitic plants can regulate AMF communities and soil organic C decomposition. In the future, we will focus on additional parasitic and host plant pairs to gain a more comprehensive understanding of the regulatory mechanisms of parasitic plants on soil nutrient cycling. Furthermore, although our results suggest that parasitic plants may influence decomposition processes by regulating hyphosphere bacterial communities, those communities involved in decomposition processes need to be investigated in greater depth. For example, the DNA-stable isotope probing (DNA-SIP) method can be used to explore the microbial communities involved in the regulation of decomposition by parasitic plants. In addition, we used the 0.5-μm mesh to isolate AMF-specific effects. Although 0.5-μm mesh has been widely applied in previous studies to isolate AMF contributions (Qiu et al., 2021; He et al., 2025), it does not completely exclude potential influences from non-mycorrhizal fungi. To better isolate AMF-specific effects, future studies could combine soil sterilization with controlled AMF inoculation.

5. Conclusions

The results of this study are consistent with our hypotheses that parasitic plant infection shifts composition of the AMF community and hyphosphere bacterial community and increases decomposition of soil organic C. These results suggest that parasitic plants may influence soil C dynamics through alterations in belowground microbial communities. Our study highlights the potential importance of parasitic plants in shaping soil nutrient processes via multitrophic interactions, although the underlying mechanisms require further investigation.

CRediT authorship contribution statement

Xintao Wang: Data curation, Investigation, Methodology, Writing – original draft. **Haonan Feng:** Writing – review & editing. **Dingjun Jiang:** Writing – review & editing. **Shijin Huang:** Writing – review & editing. **Yongge Yuan:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Hangjun Zhang:** Writing – review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2026.110183.

Data availability

Data are available from Figshare https://doi.org/10.6084/m9.figshare.31440631.

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