Effects of Arbuscular Mycorrhizal Networks on Growth and Nitrogen Uptake of Different Karst-Adapted Plants: Postprint

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Abstract

Arbuscular mycorrhizal fungi (AMF) can form common mycorrhizal networks (CMN) among different plant individuals through hyphal networks. To address the issue of nutrient allocation and biological trait regulation among different plant individuals via CMN in karst habitats, this study selected three well-adapted plant species from karst habitats as research subjects and constructed microecosystems that simulate natural environments. The experiment established isotope donor and receptor chambers, with Cinnamomum camphora planted in the donor compartment and subjected to 15N isotopic labeling, while the receptor compartment was planted with different growth-form plants including Cinnamomum camphora, Broussonetia papyrifera, and Bidens pilosa. The receptor compartments were treated with 20 m (M+) and 0.45 m nylon mesh (M-), the roots of donor plant Cinnamomum camphora were labeled with 15N isotope, and the leaf $ $15N values, plant nitrogen uptake, biomass, and growth trait indicators of receptor plant seedlings were measured. The experimental results demonstrated: (1) The leaf $ $15N values of the three receptor plants under M+ treatment were significantly higher than those under M- treatment; concurrently, M+ treatment significantly enhanced the aboveground, belowground, and total nitrogen uptake of Cinnamomum camphora seedlings, whereas the nitrogen uptake of Broussonetia papyrifera and Bidens pilosa did not differ significantly between treatments. (2) M+ treatment significantly increased the aboveground, belowground, and total biomass of Cinnamomum camphora, but exerted no significant effect on Broussonetia papyrifera; under M+ treatment, the seedling height, basal diameter, and leaf area of Cinnamomum camphora and the seedling height and basal diameter of Bidens pilosa were significantly higher than those under M- treatment, yet Broussonetia papyrifera showed no significant differences between M+ and M- treatments. (3) The average root diameter, root length, root surface area, and root volume of Cinnamomum camphora seedlings under M+ treatment were significantly higher than those under M- treatment, but these parameters were significantly reduced in Broussonetia papyrifera seedlings under M+ treatment. The study reveals that common mycorrhizal networks (CMN) in microecosystems asymmetrically influenced nitrogen uptake and plant growth traits among different plant individuals, with CMN being more advantageous for enhancing leaf $ $15N, plant N uptake, and promoting biomass accumulation and seedling root growth in receptor Cinnamomum camphora that shares the same species as the donor plant.

Full Text

Effects of Common Mycorrhizal Networks on Nitrogen Acquisition and Growth Traits of Different Plants in Karst Areas

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Abstract

Arbuscular mycorrhizal fungi (AMF) can form common mycorrhizal networks (CMN) through mycelial connections between different plant individuals. This study investigated how CMN regulate nutrient allocation and growth traits of three different karst-adapted plant species using a simulated microcosm system. The microcosm consisted of one donor compartment planted with *Cinnamomum camphora* inoculated with *Glomus etunicatum* and labeled with isotopic ^{15}N, and six receiver compartments planted with different growth-form plants (*C. camphora*, *Broussonetia papyrifera*, and *Bidens pilosa*). Three receiver compartments were treated with 20 m nylon mesh (M+ treatment) to allow hyphal penetration, while the other three were treated with 0.45 m nylon mesh (M- treatment) to block hyphae and roots. All receiver compartments were not inoculated with AMF. We evaluated CMN effects on plant growth and measured leaf δ^{15}N values, nitrogen acquisition, biomass, and growth traits.

The results showed: (1) Leaf δ^{15}N values of the three plant species in M+ treatment were significantly higher than those in M- treatment. Aboveground, belowground, and total nitrogen acquisition of *C. camphora* in M+ treatment were significantly higher than in M- treatment, while nitrogen acquisition of *B. papyrifera* and *B. pilosa* showed no significant differences between treatments.

(2) Aboveground, belowground, and total biomass of *C. camphora* in M+ treatment were significantly higher than in M- treatment, while *B. papyrifera* biomass showed no significant difference between treatments. Height, ground diameter, and leaf area of *C. camphora*, and height and ground diameter of *B. pilosa* in M+ treatment were significantly higher than in M- treatment. (3) Root average diameter, surface area, and volume of *C. camphora* in M+ treatment were significantly higher than in M- treatment, while these measurements in *B. papyrifera* were significantly lower in M+ treatment. Our results suggest that CMN unequally affected growth traits and nitrogen acquisition of different plant individuals in the microcosm, and were more beneficial for improving leaf δ^{15}N values, nitrogen acquisition, and biomass accumulation of *C. camphora* (the same species as the donor) than for the other two species, while also promoting root growth.

Keywords: arbuscular mycorrhizae; common mycorrhizal networks (CMN); karst; nitrogen acquisition; growth traits

Introduction

Arbuscular mycorrhizal fungi (AMF) form mutualistic symbioses with the roots of most vascular plants worldwide. The fungi obtain carbohydrates from host plants to maintain growth while absorbing soil nutrients to benefit their hosts. Extraradical hyphae can infect other plant roots through entry points, forming extensive underground common mycorrhizal networks (CMN) between different plants. CMN play important roles in nutrient transfer between plant individuals, affecting plant nitrogen and phosphorus allocation, nutrient balance, and species diversity maintenance. By altering plant functional traits such as nutritional and phenotypic characteristics, CMN influence plant performance and ecosystem stability.

China has the world' s largest karst distribution area, with the most typical carbonate karst landscapes found in southwestern China. Karst ecosystems contain various microhabitats (e.g., rock surfaces, soil patches) and exhibit high habitat heterogeneity, which affects the spatial distribution of soil microbes and aboveground plant communities. This raises an important ecological question: how do numerous species coexist in the same habitat? Plant competition may promote resource redistribution in heterogeneous habitats, facilitating multi-species coexistence. CMN may play crucial roles in regulating habitat resources and altering plant functional traits to affect ecosystem stability.

Current karst mycorrhizal research has focused on host plant physiology, drought resistance, and nutrient utilization, but studies on CMN effects on plant individuals in highly heterogeneous karst habitats remain limited. Karst plant communities comprise many species of different growth forms (e.g., tree species *Cinnamomum camphora*, shrub *Broussonetia papyrifera*, and herb *Bidens pilosa*) that often coexist in the same microhabitat. How these different species achieve nutrient resource allocation through CMN is unclear. Previous isotopic tracing studies examined nitrogen transfer between ectomycorrhizal and nitrogen-fixing plants but did not consider different growth forms under the same habitat conditions.

We hypothesized that: (1) CMN transfer nutrients between plant individuals, affecting both conspecific and heterospecific individuals; (2) CMN differentially allocate nutrients between conspecific and heterospecific individuals; and (3) CMN affect growth traits and root phenotypic characteristics of different species. This study used isotopic tracing technology to construct microcosms simulating natural conditions, investigating CMN effects on nutrient transfer and plant functional traits among different species in karst soil.

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1. Experimental Apparatus

We constructed microcosms simulating natural conditions using a custom-designed apparatus [Figure 1: see original paper]. Each microcosm unit consisted of a circular polypropylene pot (11.8 cm $\times$ 14.0 cm) containing seven cylindrical compartments. One central compartment served as the donor chamber, surrounded by six receiver compartments. The donor chamber bottom had a circular opening connecting to an external isotope-labeling dish, separated by nylon mesh to allow donor plant root penetration for isotope labeling while preventing soil leakage.

From each compartment’ s bottom upward, 3–10 cm holes were drilled in the chamber walls and covered with nylon mesh on both sides. The 0.45 m mesh (Amersham Hybond, USA) allowed soil ion passage but blocked hyphae and roots, while 20 m mesh allowed hyphal penetration but blocked roots. This design enabled CMN formation between different plant individuals within the microcosm. The M+ treatment used 20 m mesh, allowing donor chamber hyphae to infect receiver plants, while the M- treatment used 0.45 m mesh, blocking hyphal connections.

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2. Experimental Materials and Treatments

The experiment was conducted in a greenhouse at Guizhou University College of Forestry (106°22 E, 29°49 N, 1120 m). Soil was collected from limestone soils in typical karst areas of Huaxi District, Guiyang, and mixed with sand at a 3:1 volume ratio as the plant growth substrate. The substrate was autoclaved at 126°C and 0.14 MPa for 2 hours. Substrate physicochemical properties were: pH 6.92, alkali-hydrolyzable nitrogen 137.43 mg/kg, available phosphorus 19.58 mg/kg, and available potassium 170 mg/kg.

Three karst-adapted plant species of different growth forms were used: tree species *Cinnamomum camphora*, shrub *Broussonetia papyrifera*, and herb

Bidens pilosa. Seeds were collected from adult plants at the soil sampling site. The AMF species *Glomus etunicatum* was purchased from the Institute of Nutrition Resources, Beijing Academy of Agriculture and Forestry Sciences, with a spore density of 19.5 spores/g. The inoculum was propagated on white clover (*Trifolium repens*) for three months before use.

Each compartment contained 2.5 kg of sterilized substrate, with gaps between compartments filled with sterilized substrate to the same height. Seeds were surface-sterilized in 10% H_2O_2 for 10 minutes, rinsed in sterile water, and sown in compartments. The donor chamber received 10 *C. camphora* seeds inoculated with 100 g of *G. etunicatum* inoculum, while receiver chambers received *B. papyrifera* and *B. pilosa* seeds without AMF inoculation. Three receiver chambers used 20 m mesh (M+), and three used 0.45 m mesh (M-).

After seedling emergence, five seedlings were retained per compartment. When seedlings grew for two months, 20 mL of ^{15}N-enriched $(NH_4)_2SO_4$ solution ($\delta^{15}N$ = 99.14%) was injected into the labeling dish to label donor plant roots. All plants were harvested after one week for analysis.

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3. Measurements and Methods

Biomass was determined by oven-drying at 70°C to constant weight. Plant nitrogen content was measured using the Kjeldahl method with a Büchi Distillation Unit B-324. Leaf $\delta^{15}N$ values were determined after drying and grinding samples in a ball mill, analyzed at the Third Institute of Oceanography, State Oceanic Administration, using a Thermo Finnigan TC/EA-IRMS Delta V Advantage.

Mycorrhizal infection rates were determined using staining and observation methods described by Kormanik et al. [19] and Brundrett et al. [20]. Root average diameter, length, surface area, and volume were measured using WinRHIZO_{Pro} LA2400 root analysis system. Leaf area was measured with a leaf area meter.

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4. Data Processing and Analysis

Data were analyzed using SPSS 13.0 software. Differences in traits between M+ and M- treatments were compared using t-tests, while differences among species were analyzed by one-way ANOVA with LSD multiple comparisons. Significance level was set at $P < 0.05$. Figures were created using Origin 8.0.

Results

1. Mycorrhizal Infection Rates of Receiver Plants Under Different Treatments No AMF infection was observed in any receiver plants under M-treatment, with no hyphal fragments or infection structures detected. Under M+ treatment, infection rates were 55.50% for *C. camphora*, 61.75% for *B. papyrifera*, and 43.50% for *B. pilosa*. Infection rates did not differ significantly between *C. camphora* and *B. papyrifera*, but both were significantly higher than *B. pilosa* ($P < 0.05$). These results confirm that 0.45 m mesh effectively blocked CMN formation, while 20 m mesh allowed hyphal penetration and root colonization.

2. Leaf δ^{15}N Values of Receiver Plants Leaf δ^{15}N values of the three receiver species in M+ treatment were significantly higher than those in M- treatment [Figure 2: see original paper]. Under M+ treatment, *C. camphora* seedlings showed δ^{15}N values significantly higher than *B. papyrifera* and *B. pilosa*, which did not differ significantly from each other. Under M- treatment, no significant differences existed among species. These results indicate that CMN transferred ^{15}N from donor *C. camphora* to receiver plants, with significantly greater transfer to conspecific *C. camphora* than to heterospecific species.

3. Effects on Nitrogen Acquisition of Different Receiver Plants Total nitrogen acquisition of *C. camphora* seedlings in M+ treatment was significantly higher than in M- treatment, while no significant differences were observed for *B. papyrifera* or *B. pilosa* between treatments [Figure 3: see original paper]. Under M+ treatment, *C. camphora* total nitrogen acquisition was significantly lower than *B. papyrifera* and *B. pilosa*, which did not differ significantly. Under M- treatment, all three species differed significantly from each other.

For aboveground nitrogen acquisition, M+ treatment significantly increased *C. camphora* compared to M- treatment, but showed no significant effects on *B. papyrifera* or *B. pilosa*. Under M+ treatment, *C. camphora* aboveground nitrogen acquisition was significantly lower than the other two species, while belowground nitrogen acquisition showed similar patterns. These results demonstrate that CMN significantly enhanced nitrogen acquisition in conspecific *C. camphora* but not in heterospecific species.

4. Effects on Biomass of Different Receiver Plants Total biomass of *C. camphora* in M+ treatment was significantly higher than in M- treatment, while no significant differences were observed for *B. papyrifera* or *B. pilosa* between treatments [Figure 4: see original paper]. Under M+ treatment, *B. papyrifera* and *B. pilosa* total biomass did not differ significantly but were both significantly higher than *C. camphora*. Under M- treatment, all three species differed significantly.

For aboveground biomass, M+ treatment significantly increased *C. camphora* and *B. pilosa* compared to M- treatment, with *C. camphora* showing extremely significant differences, while *B. papyrifera* showed no significant difference. For belowground biomass, M+ treatment significantly increased *C. camphora* but decreased *B. papyrifera* compared to M- treatment, while *B. pilosa* showed no significant difference. These results indicate that CMN effects on biomass were species-specific, with positive effects on conspecific *C. camphora* but negative effects on heterospecific *B. papyrifera*.

5. Effects on Growth Traits of Different Receiver Plants M+ treatment significantly increased *C. camphora* seedling height, ground diameter, and leaf area compared to M- treatment . *B. pilosa* height and ground diameter were significantly higher in M+ treatment, though leaf area differences were not significant. *B. papyrifera* growth traits showed no significant differences between treatments.

Under M+ treatment, *B. pilosa* showed the highest values for height and ground diameter, followed by *B. papyrifera*, with *C. camphora* being lowest. Leaf area followed a different pattern, with *B. papyrifera* > *B. pilosa* > *C. camphora*. These results demonstrate that CMN significantly promoted growth traits in *C. camphora* and *B. pilosa* but not in *B. papyrifera*.

6. Effects on Root Traits of Different Receiver Plants Root traits showed species-specific responses to CMN [Figure 5: see original paper]. M+ treatment significantly increased root average diameter, length, surface area, and volume in *C. camphora* compared to M- treatment. Conversely, M+ treatment significantly decreased these traits in *B. papyrifera*. *B. pilosa* root traits showed no significant differences between treatments.

Under M+ treatment, *C. camphora* root average diameter, surface area, and volume were significantly higher than in M- treatment, while *B. papyrifera* showed significantly lower values. These results indicate that CMN significantly promoted root growth in conspecific *C. camphora* while inhibiting root growth in heterospecific *B. papyrifera*.

Discussion and Conclusion

Our results demonstrate that CMN transferred ^{15}N from donor *C. camphora* to receiver plants, consistent with previous studies showing nitrogen transfer through mycorrhizal networks [6,21]. This transfer may occur through direct hyphal bridges connecting donor and receiver roots, or indirectly through root exudates and hyphal absorption from soil [22–24]. The transfer pathway may be bidirectional, as shown in studies between nitrogen-fixing and hemiparasitic plants [25,26], though our experiment only examined unidirectional transfer.

CMN effects on nitrogen acquisition differed significantly among species, with positive effects on conspecific *C. camphora* but no significant effects on heterospecific *B. papyrifera* and *B. pilosa*. This species-specific response may result from host plant functional selection by CMN [27–28], which can amplify size inequality and create non-balanced resource allocation among species [29–30]. The differential nitrogen acquisition among species supports the hypothesis that CMN mediate competitive interactions and nutrient partitioning in plant communities.

The observed changes in biomass allocation and root morphology indicate that CMN can alter plant functional traits to maximize nutrient acquisition in heterogeneous environments [31]. Root traits such as average diameter, surface area, and volume are critical for water and mineral uptake [32–33]. Our findings that CMN increased root growth in *C. camphora* but decreased it in *B. papyrifera* align with previous reports of species-specific mycorrhizal effects on root architecture [34–35]. These changes reflect CMN-mediated reallocation of resources that modifies original trait expressions, with effects ranging from positive to negative depending on species identity [30,36].

The non-balanced effects of CMN on different plant individuals may facilitate species coexistence in heterogeneous karst habitats [37–38]. Karst ecosystems are characterized by discontinuous soil cover and high spatial heterogeneity in soil chemical properties [39], creating uneven nutrient distribution. CMN-mediated resource redistribution may thus be a key mechanism promoting species coexistence in these environments. Our microcosm experiment demonstrates that CMN can differentially affect nutrient transfer, biomass accumulation, and phenotypic traits among coexisting species, with conspecific individuals receiving greater benefits than heterospecifics.

In conclusion, this study reveals that CMN in karst microcosms non-equally affected nitrogen acquisition and growth traits among different plant species. The network significantly enhanced nitrogen uptake, biomass accumulation, and root growth in conspecific *C. camphora* seedlings compared to heterospecific species. These findings suggest that CMN may contribute to species coexistence in heterogeneous karst habitats through differential resource allocation, though further research is needed to explore bidirectional transfer mechanisms and long-term community dynamics.

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Note: Figure translations are in progress. See original paper for figures.