Response of Arbuscular Mycorrhizal Fungi Colonization Rate to Slope Position and Shrub Species on Karst Slopes: Postprint

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Abstract

Clarifying the response of arbuscular mycorrhizal fungi (AMF) infection rates to slope position and species in karst slopes and their key influencing factors is a prerequisite for the rational utilization of soil AMF to promote karst vegetation restoration. Based on a comprehensive investigation of the environmental background information of typical shrub slopes in karst peak-cluster depressions, this study employed the trypan blue staining-microscopy method to detect and calculate AMF infection rate parameters such as infection frequency, infection intensity, and arbuscule abundance in the roots of typical shrubs Vitex negundo, Alchornea trewioides, and Pyracantha fortuneana. The results were as follows: (1) At the same slope position, the infection frequency, infection intensity, and arbuscule abundance of Pyracantha fortuneana were significantly lower than those of Alchornea trewioides and Vitex negundo; the infection intensity of Vitex negundo and Pyracantha fortuneana at the lower slope position was higher than that at the middle/upper slope positions, while the arbuscule abundance of Alchornea trewioides at the middle slope position was significantly higher than that at the upper/lower slope positions ($P<0.05$). (2) Species significantly affected AMF infection frequency, infection intensity, and arbuscule abundance, slope position significantly affected AMF infection intensity, and the interaction between species and slope position only had a significant effect on AMF arbuscule abundance ($P<0.05$). (3) The key soil factors affecting AMF infection rate were soil depth and total potassium content ($P<0.05$). Therefore, the rational utilization of soil AMF to promote vegetation restoration in karst areas requires consideration of topographic and species selection, and attention should be paid to balancing soil and water conservation in karst regions.

Full Text

Responses of Arbuscular Mycorrhizal Fungi Colonization Rate to Slope Position and Shrub Species in Karst Slopes

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Abstract: Understanding the response of arbuscular mycorrhizal fungi (AMF) colonization percentage to slope position and shrub species, along with identifying the key influencing factors, is a prerequisite for rationally utilizing soil AMF to promote karst vegetation restoration. Based on a comprehensive survey of environmental background information in typical shrub communities on karst slopes in a peak-cluster depression catchment, this study employed the trypan blue staining-microscopy method to detect and calculate AMF colonization parameters—including colonization frequency, colonization intensity, and arbuscular abundance—in the roots of three typical shrub species: *Vitex negundo*, *Alchornea trewioides*, and *Pyracantha fortuneana*. The results were as follows: (1) At the same slope position, the colonization frequency, intensity, and arbuscular abundance of *P. fortuneana* were significantly lower than those of *A. trewioides* and *V. negundo*. The colonization intensity of *V. negundo* and *P. fortuneana* at lower slope positions was higher than that at middle and upper slope positions, while the arbuscular abundance of *A. trewioides* at middle slope positions was significantly higher than at upper and lower slope positions ($P<0.05$). (2) Species significantly affected AMF colonization frequency, intensity, and arbuscular abundance, while slope position significantly affected AMF colonization intensity. The interaction between species and slope position only had a significant effect on AMF arbuscular abundance ($P<0.05$). (3) The key soil factors influencing AMF colonization rate were soil depth and total potassium content ($P<0.05$). Therefore, rationally utilizing soil AMF to promote vegetation restoration in karst areas requires consideration of both terrain and species selection, with attention to soil and water conservation in karst regions.

Keywords: karst, arbuscular mycorrhizal fungi, frequency, intensity, abundance

Introduction

Arbuscular mycorrhizal fungi (AMF) form symbiotic associations with approximately 80% of terrestrial plants (Smith & Smith, 2011), providing critical ecological functions such as expanding root systems, promoting nutrient uptake, and enhancing plant drought resistance (Mi et al., 2020; Kang et al., 2020; Liu et al., 2021). AMF have been widely applied in the restoration and reconstruction of degraded ecosystems (Wei et al., 2012). Southwest China' s karst region is characterized by intense karstification, shallow and discontinuous soil layers, and extremely fragile ecological conditions, representing one of the country' s most severely affected areas of soil erosion (Huang et al., 2019). The most critical task for restoring degraded ecosystems in this region is vegetation restoration (Li et al., 2003). Among karst landforms, peak-cluster depressions exhibit the fastest vegetation recovery rates (Tong et al., 2020), with slopes accounting for over 70% of the area. Constrained by geological and geomorphological backgrounds, rapid hydrological processes occur on slopes, resulting in thin, discontinuous soil layers and karst leakage that leads to poor water and fertilizer retention capacity and soil infertility (Li et al., 2008). Soil nutrient conditions often vary significantly across different slope positions (Li et al., 2003; Liang et al., 2017), substantially influencing fundamental AMF characteristics such as colonization rate (Zhang et al., 2015; Qu et al., 2021). Colonization rate is a key indicator of whether mycorrhizal fungi establish symbiotic relationships with host plants, primarily comprising parameters such as colonization frequency, colonization intensity, and arbuscular abundance (Ren et al., 2014). Previous studies have shown that AMF colonization rates are higher when soil phosphorus content is low (Wang et al., 2006).

As symbiotic fungi of plants, host plant species represent an important factor affecting AMF colonization (Yang et al., 2019). Different plants inevitably influence AMF colonization due to variations in biological characteristics and ecological habits (Liang et al., 2018). For example, the AMF colonization rates of *Castanopsis hystrix* and *Kmeria septentrionalis* roots are significantly higher than those of *Celtis biondii* (Zhang et al., 2016), and the colonization rate of *Toona sinensis* is significantly higher than that of *Delavaya toxocarpa* (Zhang et al., 2018). Shrubland is both the main vegetation type in karst peak-cluster depressions and a critical stage of karst vegetation restoration (Hu et al., 2018). In karst peak-cluster depression slopes, the AMF colonization rates in roots of dominant shrub species change with slope position, and these changes may also vary among plant species. Investigating the response of AMF colonization rates in typical karst shrub species to slope position is important for deepening our understanding of plant-AMF interactions and rationally utilizing AMF to promote vegetation restoration in this region.

This study selected three slope positions (upper, middle, and lower) and three dominant shrub species—*Vitex negundo*, *Alchornea trewioides*, and *Pyracantha fortuneana*—in a typical karst peak-cluster depression in Huanjiang, Guangxi. We measured soil physicochemical properties at different slope positions and

AMF colonization parameters including colonization frequency, colonization intensity, and arbuscular abundance in plant roots. The objectives were to determine: (1) whether an interactive effect exists between slope position and shrub species on AMF colonization rate, and (2) the main factors influencing AMF colonization rate. This research aims to provide a scientific basis for rationally utilizing the symbiotic relationship between soil AMF and plants to promote ecological restoration in karst peak-cluster depressions.

1.1 Study Area Description

The study area is located in the Mulian peak-cluster depression catchment at the Huanjiang Karst Ecosystem Observation and Research Station of the Chinese Academy of Sciences, in Huanjiang Maonan Autonomous County, Guangxi Zhuang Autonomous Region (108°18 -108°19 E, 24°43 -24°44 N). The region has a subtropical monsoon climate with an average annual temperature of 13°C and annual precipitation of 800–1,500 mm. Seasonal precipitation distribution is uneven, with rainfall concentrated in summer and drought conditions in winter. The main soil type is limestone soil, and slope vegetation is dominated by shrub communities.

1.2 Plot Setup and Vegetation Survey

Based on preliminary investigations, three transects were established on slopes with consistent aspect (all southwest-facing), similar altitude, and high vegetation community similarity. Shrub community survey plots (10 m × 10 m) were set up at upper, middle, and lower slope positions along each transect, with vertical elevation differences of 28-46 m between plots on the same transect (detailed plot information is provided in Table 1). Each plot was divided into four subplots (5 m × 5 m) using a total station. Vegetation surveys were conducted during the peak growing season (July–August). For woody plants (including lianas) with diameter at breast height (DBH) $\geq$ 1 cm, species name, DBH, height, and crown width were recorded. For tree and shrub seedlings with DBH $<$ 1 cm and herbaceous layer plants, species name, individual number, height, and coverage were briefly recorded. Species importance values were calculated as: (relative abundance + relative frequency + relative coverage)/3 (Zheng et al., 2016; Wang et al., 2021).

1.3 Target Plant Selection and Sample Collection

The dominant species *Vitex negundo*, *Alchornea trewioides*, and *Pyracantha fortuneana*, which were common across all plots, were selected as target plants. Within each plot, four healthy individuals of each species with consistent DBH ($±$0.05 cm) were selected, and plant root systems were excavated. Fine roots with diameter $<$ 2 mm (Liang et al., 2021) were selected, thoroughly mixed, and 20 g samples were placed in plastic ziplock bags and stored in a low-temperature ice box for transport to the laboratory within 24 hours. Root samples were rinsed 2-3 times with clean water to remove attached soil, then rinsed 2-3 times with distilled water and stored at 4°C (Shi et al., 2017) for AMF colonization rate determination.

Surface soil (0-20 cm) was collected using a grid method: each 10 m × 10 m plot was divided into 25 grids of 2 m × 2 m, and soil samples were taken at each grid intersection using a soil auger (36 points total) and thoroughly mixed. The quartering method was used to obtain 500 g for soil physicochemical property determination.

1.4.1 AMF Colonization Rate Determination

The trypan blue staining-microscopy method (Muthukumar & Udaiyan, 2000) was used. Following conventional procedures of clearing, acidification, staining, and destaining, 30 root segments were selected for slide preparation and microscopic examination. Each root segment was classified based on mycorrhizal colonization (categories: 0, <1%, <10%, <50%, >50%, >90%, corresponding to levels N0, N1, N2, N3, N4, N5) and vesicle abundance (categories: 0, few, many, very many, corresponding to levels A0, A1, A2, A3). Representative colonization status is shown in Figure 1 [Figure 1: see original paper]. Data were input into "MYCOCALC" software to calculate colonization parameters: colonization frequency, colonization intensity, and arbuscular abundance (Feng et al., 2003). The parameters are defined as follows:

Colonization frequency (%): Represents the proportion of root segments containing fungal structures relative to the total root system. Any root segment containing at least one entry point is counted as colonized.

$$\text{Colonization frequency} = \frac{\text{Number of colonized root segments}}{\text{Total number of root segments}} \times 100\%$$

Colonization intensity (%): Represents the intensity of AMF structure formation throughout the root system.

$$\text{Colonization intensity} = \frac{0.95 \times n_5 + 0.7 \times n_4 + 0.3 \times n_3 + 0.05 \times n_2 + 0.01 \times n_1 + 0 \times n_0}{\text{Total number of root segments}} \times 100\%$$

where n_5 represents the number of root segments with >90% colonization (N5 level), n_4 represents the number of root segments with >50% colonization (N4 level), and so forth.

Arbuscular abundance (%): Represents the abundance of arbuscule formation within mycorrhizal root segments.

$$\text{Arbuscular abundance} = \frac{(1 \times m_{A3} + 0.5 \times m_{A2} + 0.1 \times m_{A1}) \times 100\%}{0.95 \times n_5 + 0.7 \times n_4 + 0.3 \times n_3 + 0.05 \times n_2 + 0.05 \times \text{Number of colonized root segm}}$$

where m_{A3} represents the number of N5, N4, N3, N2, N1, and N0 root segments in vesicle abundance level A3; m_{A2}, m_{A1}, and m_{A0} are calculated similarly; and m represents the mycorrhizal colonization density of colonized root segments, calculated as:

$$m_{A3} = \text{Colonization intensity} \times \frac{\text{Total number of root segments}}{\text{Number of colonized root segments}}$$

1.4.2 Soil Physicochemical Property Determination

Soil physicochemical properties were determined using conventional methods (Bao et al., 2000). Soil organic matter (OM) was measured using the potassium dichromate external heating method. Total nitrogen (TN) was determined using the semi-micro Kjeldahl method. Total phosphorus (TP) and available phosphorus (AP) were measured using the molybdenum-antimony anti-colorimetric method. Total potassium (TK) and available potassium (AK) were determined by flame photometry. Available nitrogen (AN) was measured using the alkali-hydrolysis diffusion method. Soil pH was measured with a Metro320 pH meter (soil:water ratio of 2.5:1). Soil water content (WC) was determined using the drying method. Soil depth was measured with a soil probe. Surface soil gravel content was determined by weighing (gravel content).

1.5 Data Processing and Statistical Analysis

SPSS 26.0 was used to test data normality and homogeneity of variance, with data transformations applied when necessary to meet assumptions. One-way ANOVA with Duncan' s multiple comparisons was used to analyze differences in soil physicochemical properties among slope positions. Two-way ANOVA with Duncan's multiple comparisons was used to examine the effects of slope position, shrub species, and their interaction on AMF colonization parameters. Plant relative density, abundance, and frequency importance values were calculated using the vegan package in R. Canoco 5.0 software was used for redundancy analysis (RDA) to clarify the relationship between AMF colonization rates of each shrub species and environmental factors. The significance level was set at $\alpha = 0.05$. Data in figures and tables are presented as mean ± standard deviation.

Results

2.1 Differences in Soil Physicochemical Properties Among Slope Positions

Soil organic matter, total nitrogen, total phosphorus, total potassium, pH, water content, and gravel content showed no significant differences among slope positions (Table 2). However, available potassium content was significantly higher at lower slope positions compared to upper and middle positions. Available phosphorus content was significantly higher at middle and lower slope positions than at upper positions. Available nitrogen content followed the trend: lower > middle > upper slope positions. Soil depth was significantly greater at lower slope positions compared to upper positions.

2.2 AMF Colonization Status

Microscopic examination of stained plant roots revealed clear observation of AMF structures including hyphae, vesicles, and arbuscules in most samples. Some intercellular hyphae branched laterally into host plant cells, forming dichotomously branched, shrub-like arbuscules. Vesicle structures were observed in the intercellular and intracellular spaces of cortical cells in *V. negundo* and *A. trewioides* roots. Observed vesicles were elliptical, round, rectangular, and irregular in shape, with elliptical vesicles being the most common.

All three species—*V. negundo*, *A. trewioides*, and *P. fortuneana*—were colonized by AMF at upper, middle, and lower slope positions (Plate I). Compared with *P. fortuneana*, *V. negundo* (Plate I: B) and *A. trewioides* (Plate I: D, F) roots formed more distinct arbuscular mycorrhizal structures.

2.3 Characteristics of AMF Colonization Rate Variation

At the same slope position, the colonization frequency (Figure 1: A), colonization intensity (Figure 1: B), and arbuscular abundance (Figure 1: C) of *P. fortuneana* were significantly lower than those of *A. trewioides* and *V. negundo* ($P<0.05$). For the same species, no significant differences were observed among slope positions in colonization frequency for all three species, colonization intensity for *A. trewioides*, or arbuscular abundance for *P. fortuneana* and *V. negundo* ($P>0.05$). However, colonization intensity of *V. negundo* and *P. fortuneana* was significantly higher at lower slope positions compared to middle and upper positions, while arbuscular abundance of *A. trewioides* was significantly higher at middle slope positions compared to upper and lower positions ($P<0.05$).

2.4 Factors Influencing AMF Colonization Rate

Slope position had a significant effect only on AMF colonization intensity ($P<0.01$), while species significantly affected AMF colonization frequency, intensity, and arbuscular abundance ($P<0.01$). The interaction between slope position and species significantly affected AMF arbuscular abundance ($P<0.05$) (Table 3).

Redundancy analysis indicated that the first and second principal variables explained 71.99% of the variation, accounting for 42.14% and 29.85% respectively (Figure 2 [Figure 2: see original paper]). The main soil factors influencing AMF colonization rate were soil depth ($F=2.8$, $P=0.034$) and total potassium content

(F=2.7, P=0.040). Upper and lower slope positions were relatively clustered, while middle slope positions were more dispersed.

As shown in Figure 2, colonization frequency of *V. negundo* and *A. trewioides*, and colonization frequency, intensity, and arbuscular abundance of *P. fortuneana* were significantly positively correlated with soil depth and significantly negatively correlated with soil total potassium. Colonization intensity of *V. negundo* and *A. trewioides* showed the highest correlation with soil total potassium (negative correlation) and was negatively correlated with soil depth. Arbuscular abundance of *V. negundo* was highly correlated with both soil depth and total potassium.

Discussion

Karst regions exhibit unique dual soil and water loss characteristics, causing substantial differences in soil nutrients among slope positions and consequently affecting soil microbial distribution (Li et al., 2003; Feng et al., 2015). In this study, slope position significantly affected AMF colonization intensity, likely because soil organic matter and available nutrients in karst slopes are higher at lower slope positions, which benefits AMF growth and reproduction and can significantly increase colonization intensity in plant roots (Wang & Wang, 2009), ultimately resulting in significantly higher colonization intensity for *V. negundo* and *P. fortuneana* at lower slope positions.

Species significantly affected AMF colonization frequency, intensity, and arbuscular abundance, indicating that host plant species importantly influence AMF. In this study, the higher AMF colonization frequency, intensity, and arbuscular abundance in *V. negundo* and *A. trewioides* compared to *P. fortuneana* may be related to differences in biological characteristics and ecological habits among host plants (Chen et al., 2016; Che et al., 2022). In terms of leaf epidermal morphology, *V. negundo* and *A. trewioides* have greater stomatal density and more developed vascular tissue compared to *P. fortuneana*, which helps reduce water loss and promotes water transport and nutrient migration, making them better adapted to the dry conditions of karst environments (Li & Cao, 2008; Deng et al., 2010; Dong et al., 2011). Regarding root architecture, *V. negundo* and *A. trewioides* exhibit typical dichotomous branching patterns, while *P. fortuneana* shows a fish-tail branching pattern (Su et al., 2018a; Wu et al., 2022). Dichotomous root systems more easily acquire nutrients and water from surface soil and occupy larger spaces in the topsoil (Su et al., 2018a), increasing the contact area between roots and soil AMF and facilitating AMF colonization and symbiosis establishment. This ultimately results in significantly higher AMF colonization frequency, intensity, and arbuscular abundance in *V. negundo* and *A. trewioides*.

The interaction between slope position and species significantly affects soil microbial communities; for example, under different slope conditions, plant community structure jointly influences soil AMF community structure (Liang et al., 2017). However, few studies have examined the effects on AMF colonization rates. Under the high temperature and heavy rainfall climate of southwest China, soil particles migrate from upper to lower slope positions after rainfall events, resulting in nutrient content patterns of lower > middle > upper slope positions (Qiu et al., 2013; Peng et al., 2017). The unique karstification in karst areas creates countless grooves of varying sizes on rock surfaces, which accumulate on slopes and intercept water and nutrients, making spatial and temporal heterogeneity of water and nutrients among slope positions more pronounced (Li et al., 2008; Qiu et al., 2013). To adapt to such extreme spatial resource distribution, plants require well-developed root systems to expand water and nutrient absorption areas (Li et al., 2008), a strategy that better enables plant root-AMF symbiosis (Wang et al., 2008; Jiang & Wang, 2012). Therefore, the interaction between slope position and species significantly affects AMF colonization rate. In this study, the interaction between slope position and shrub species significantly affected AMF arbuscular abundance in karst slopes. Arbuscular abundance comprehensively reflects the frequency and intensity of arbuscule formation in colonized root segments, representing the richness of arbuscule structures in mycorrhizal roots (Feng, 2003). Specifically, the significantly higher arbuscular abundance of *A. trewioides* at middle slope positions compared to upper and lower positions indicates that arbuscule formation richness in mycorrhizal roots responds strongly to the combined effects of slope position and species in karst areas. When characterizing AMF colonization rate, AMF arbuscular abundance is more sensitive than colonization frequency and intensity.

Soil depth and total potassium content were significant factors affecting AMF colonization rate in karst slopes. Karst areas suffer from water shortage, thin soils, and extremely harsh site conditions (Li et al., 2008). In such resource-poor habitats, plants need to recruit AMF to expand root systems for water and nutrient acquisition, while different AMF compete for opportunities to colonize plant roots to obtain carbon sources (Zheng, 2006; Sanders & Croll, 2010; Liu et al., 2021). Small differences in soil depth may cause significant differences in total available nutrients for plants (Qiu et al., 2013), directly affecting host plant root distribution and consequently influencing root colonization rates (Su et al., 2018b). Potassium ions are the primary inorganic osmotic substances in plant cells; adequate potassium induces accumulation of soluble substances, thereby reducing osmotic potential, helping cells maintain turgor under osmotic stress, and improving plant tolerance to drought stress (Wang et al., 2013). Since potassium in natural ecosystems mainly originates from soil parent material, the rapid hydrological processes in karst soils exacerbate potassium loss (Qiu et al., 2013). Under water-deficit conditions, plant demand for potassium increases, further promoting plant-AMF symbiosis (Visentin et al., 2016; Liu et al., 2021). Therefore, total potassium content significantly affects both AMF community composition and colonization rates in roots of dominant tree species in karst areas (Zhang et al., 2016).

Conclusion

Karst AMF colonization rate is simultaneously affected by slope position and species, but these factors have different effects on AMF colonization parameters. Colonization frequency is mainly influenced by species, colonization intensity is primarily affected by nutrient conditions of slope position, while AMF arbuscular abundance reflects the combined effects of both species and slope position.

Soil depth and total potassium content are significant factors influencing AMF colonization rates of dominant shrubs on karst peak-cluster depression slopes. Vegetation restoration in karst slopes must consider not only plant species selection but also the spatial heterogeneity of water and nutrient distribution controlled by the unique geological background of karst and the supply of potassium nutrients. Future research should focus on plant macronutrient potassium studies, combined with hydrological processes and nutrient cycling, to further elucidate species selectivity for soil AMF symbiosis, quantify the ecological effects of plant-mycorrhizal symbiosis, and provide scientific guidance for the application of soil AMF resources in vegetation restoration in karst fragile habitats.

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