Responses of Plant Functional Traits in Guilin Karst Rocky Mountain Plant Communities to Environmental Factors on Different Slope Aspects: Postprint

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Abstract

Investigating the variation patterns of plant functional traits at the community level along slope aspect gradients is of great significance for understanding the formation of plant communities on different slope aspects and their mechanisms for coping with environmental changes. This study took plant communities on different slope aspects in the karst hills of Guilin as research subjects, and explored the variation patterns of plant functional traits (specific leaf area (SLA), leaf total chlorophyll content (CC), wood density (WD)) and environmental factors along slope aspects. The results showed that: specific leaf area and chlorophyll content exhibited the trend of shady slope > semi-shady slope > sunny slope, with significant differences between shady slope and sunny slope, and between semi-shady slope and sunny slope; wood density exhibited the trend of shady slope < semi-shady slope < sunny slope, with significant differences between shady slope and sunny slope, and between semi-shady slope and sunny slope. Soil organic matter content was higher on shady slopes than on sunny slopes, with significant differences between shady and sunny slopes; soil total phosphorus and available phosphorus both showed the highest content on sunny slopes, with significant differences between shady and sunny slopes; soil available potassium and total potassium showed the highest content on shady slopes and semi-shady slopes respectively, with soil total potassium content showing significant differences among all slope aspects, while soil available potassium showed significant differences between shady and sunny slopes, and between semi-shady and sunny slopes. Regression analysis indicated that: community-level specific leaf area was significantly negatively correlated with soil organic matter content on shady and semi-shady slopes; community-level chlorophyll content was significantly positively correlated with soil total phosphorus content and soil available potassium content on shady slopes; community-level wood density showed no correlation with environmental factors across slope aspect gradients. The variation patterns of plant functional traits at the community level along slope aspects reflect the environmental filtering effects on functional traits during the assembly process of plant communities in karst hills. The research results have certain practical significance for species selection and vegetation layout planning in vegetation restoration and reconstruction in this region.

Full Text

Response of Plant Functional Traits to Soil Environmental Factors Along Slope Aspects in Karst Hills of Guilin, South China

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Abstract

Understanding how plant functional traits at the community level vary along slope aspect gradients is crucial for elucidating community formation mechanisms and plant adaptation strategies to environmental changes. This study investigated plant functional traits (specific leaf area, SLA; leaf total chlorophyll content, CC; wood density, WD) and environmental factors across different slope aspects in karst hills of Guilin. Results showed that SLA and CC followed the pattern of shady slope > semi-shady slope > sunny slope, with significant differences between both shady and semi-shady slopes compared to sunny slopes. WD showed the opposite trend: shady slope < semi-shady slope < sunny slope, with significant differences between shady and sunny slopes as well as between semi-shady and sunny slopes. Soil organic matter content was significantly higher on shady slopes than on sunny slopes. Total phosphorus and available phosphorus contents were highest on sunny slopes, with significant differences between shady and sunny slopes. Total potassium and available potassium contents were highest on shady and semi-shady slopes, respectively; total potassium differed significantly among all slope aspects, while available potassium showed significant differences between shady/semi-shady slopes and sunny slopes. Regression analysis revealed that community-level SLA was significantly negatively correlated with soil organic matter on shady and semi-shady slopes. Community-level CC was significantly positively correlated with total phosphorus and available potassium on shady slopes. No correlations were found between community-level WD and environmental factors across slope aspects. The variation in community-level plant functional traits along slope aspects reflects environmental filtering effects during community assembly in karst hills. These findings provide practical guidance for species selection and vegetation layout planning in vegetation restoration efforts in this region.

Keywords: plant communities, functional traits, slope aspect, environmental factors, karst hills

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Introduction

Plant functional traits refer to the morphological and physiological characteristics that plants adjust in response to environmental changes, primarily manifested in differences in leaves, roots, seeds, and other organs. These traits represent the outcome of long-term evolutionary adaptation strategies and reflect plants' ecological indicator roles in ecosystem functioning, leading to species composition changes along local and regional environmental gradients. Slope aspect variation redistributes temperature, precipitation, and light, creating spatial heterogeneity in climatic conditions that influences plant functional traits. Previous studies have found significant differences in leaf phosphorus content and specific leaf area between shady and sunny slopes in the Loess Hilly Region, with higher values on shady slopes. Research on alpine meadows revealed significant positive correlations between soil moisture and chlorophyll content from shady to sunny slopes. Furthermore, dominant environmental factors affecting plant traits differ across slope aspects. Studies in karst hills of Guilin showed that on shady slopes, soil available nitrogen significantly influenced specific leaf area, while on sunny slopes, soil moisture and pH were key factors. Other research found specific leaf area was positively correlated with soil moisture on shady slopes, negatively correlated with soil pH on semi-shady slopes, and positively correlated with soil organic matter on sunny slopes. Investigating these relationships between plant functional traits and soil environmental factors along slope aspects can reveal plant adaptation strategies and provide a basis for ecological restoration in topographically complex areas.

Karst habitats represent one of China' s most fragile and complex ecosystems, characterized by fragmented terrain, discontinuous soil cover, thin soil layers, and scarce surface water. The mosaic of exposed bedrock and shallow soil creates highly heterogeneous microhabitats and spatial differentiation of soil ecological functions, increasing the difficulty of vegetation restoration. Vegetation plays a crucial role in maintaining ecosystem stability, regulating regional carbon balance, and conserving biodiversity in degraded karst ecosystems. The peak-cluster karst landform exhibits significant slope aspect variations, with clear differences in soil moisture and temperature among slopes, leading to redistribution of soil nutrients. This study focused on dominant communities for vegetation restoration in karst hills—primarily *Cyclobalanopsis glauca* forests and secondary shrub communities (*Alchornea trewioides*, *Loropetalum chinense*, etc.)—to examine variations in key functional traits (SLA, CC, WD) and environmental factors across shady, semi-shady, and sunny slopes. We aimed to reveal how environmental filtering shapes plant community spatial patterns and provide theoretical guidance and scientific basis for vegetation restoration and forest management in degraded karst ecosystems.

1.1 Study Area Description

The study area is located in the karst hill region of Guilin, northeastern Guangxi Zhuang Autonomous Region, China (110°19 -110°25 E, 22°47 -25°50 N). The landform consists of typical peak-cluster depressions at elevations of 100–500 m. The climate is mid-subtropical humid monsoon, with abundant rainfall, mild temperatures, an annual mean temperature of 19°C, annual sunshine of 1,465 hours, mean temperature of 28°C in the hottest month (August) and 8°C in the coldest month (January), a frost-free period of 309 days, annual precipitation of 1,856.7 mm (unevenly distributed with dry autumns and winters), and annual evaporation of 1,458.4 mm. Rock exposure is severe, with significantly higher exposure rates on sunny slopes than shady slopes. Adapted plants exhibit calciphilic, drought-resistant, and lithophytic characteristics. Dominant species include *Cyclobalanopsis glauca*, *Alchornea trewioides*, *Alchornea davidii*, *Pittosporum planilobum*, *Radermachera sinica*, *Fordia cauliflora*, *Celtis sinensis*, *Mallotus philippensis*, and *Elaeagnus pungens*.

1.3.1 Functional Trait Sampling and Measurement

Community-level SLA and CC measurement: For trees with diameter at breast height (DBH) 1 cm and shrubs with stem base diameter (SBD) 1 cm, 3–5 fully expanded, healthy, mature sun leaves were collected from each individual. Leaves were sealed in plastic bags to maintain moisture content and transported to the laboratory. Leaf area (LA) and chlorophyll content (CC) were measured using a leaf area meter (Yaxin-1241) and a chlorophyll meter (SPAD-502), respectively. Fresh weight was measured with an electronic balance (precision 0.001 g). Leaves were then oven-dried at 80°C for 72 hours and weighed for dry mass. Specific leaf area (cm^2 · g ^{1}) was calculated as leaf area divided by leaf dry mass. **Wood density measurement:** Simultaneously, three ~10 cm branches (1 cm DBH 2 cm) were collected from each plant. Bark, phloem, and pith were removed, fresh volume was measured by water displacement, and dry mass was determined after oven-drying at 80°C for 72 hours. Branch density (g · cm ^{3}) was calculated as dry mass divided by volume. Based on a significant linear regression between branch density and wood density passing through the origin ($P < 0.001$), branch density was used as a proxy for wood density.

1.3.2 Soil Environmental Factor Sampling and Measurement

Each 20 m × 20 m plot was divided into four 10 m × 10 m subplots. Soil samples (0–15 cm depth) were collected at the four corners and center of each subplot using a soil auger and mixed. Each soil sample was analyzed in triplicate. Measured parameters included soil organic matter (SOM, $g \cdot kg^{1}$), total phosphorus (TP, $g \cdot kg^{1}$), total potassium (TK, $g \cdot kg^{1}$), available phosphorus (AP, $mg \cdot kg^{1}$), and available potassium (AK, $mg \cdot kg^{1}$). SOM was determined by potassium dichromate volumetric method; TP by molybdenum-antimony colorimetry; TK by alkali fusion-flame photometry; AP by sodium bicarbonate extraction-molybdenum-antimony colorimetry; and AK by ammonium acetate extraction-flame photometry.

1.4 Data Processing

Importance value (IV) quantifies species relative importance in communities. Tree species IV was calculated as (relative density + relative frequency + relative dominance)/3, and shrub species IV as (relative density + relative frequency + relative coverage)/3. Community-level functional traits were calculated as abundance-weighted means based on IV. One-way ANOVAs were used to test differences in community-level traits and environmental factors across slope aspects, followed by Tukey-Kramer HSD tests for multiple comparisons. Simple regression models were used to identify soil factors significantly affecting community-level traits, with five soil factors as independent variables and three functional traits as dependent variables. Regression relationships were evaluated based on R^2 and P-values, and visualized in scatter plots. All statistical analyses were performed in R.

2.1 Comparison of Community-Level Functional Traits Across Slope Aspects

Community-level SLA and CC showed consistent patterns across slope aspects: shady > semi-shady > sunny slopes, with significant differences between shady/semi-shady and sunny slopes ($P < 0.05$) [Figure 1: see original paper]A–B. Community-level WD showed the opposite trend: shady < semi-shady < sunny slopes, with significant differences between shady and sunny slopes and between semi-shady and sunny slopes ($P < 0.05$) [Figure 1: see original paper]C.

2.2 Comparison of Soil Environmental Factors Across Slope Aspects

Soil organic matter content was significantly higher on shady slopes than sunny slopes ($P < 0.05$). Total phosphorus and total potassium differed significantly among all slope aspects ($P < 0.05$). Available phosphorus was lower on shady and semi-shady slopes than sunny slopes, with significant differences ($P < 0.05$). Available potassium was higher on shady and semi-shady slopes than sunny slopes, with significant differences ($P < 0.05$) [Figure 2: see original paper].

2.3 Regression Analysis Between Community-Level Functional Traits and Soil Environmental Factors

SLA was significantly negatively correlated with soil organic matter on both shady and semi-shady slopes ($P < 0.05$, $R^2 = 0.851$ and 0.799, respectively) [Figure 3: see original paper]A–B. Chlorophyll content was significantly positively correlated with total phosphorus and available potassium on shady slopes ($P < 0.05$, $R^2 = 0.798$ and 0.721, respectively) [Figure 3: see original paper]A. No significant correlations were found between WD and environmental factors across slope aspects.

3.1 Response of Community-Level Functional Traits to Different Slope Aspects

The peak-cluster karst landform creates highly heterogeneous microhabitats with distinct slope aspect variations. SLA and CC were higher on shady and semi-shady slopes than sunny slopes [Figure 1: see original paper]A–B. Under low light conditions on shady slopes, increased leaf area and reduced leaf dry mass (high SLA) enhance light capture and increase the ratio of assimilatory to conductive and structural tissues. Higher SLA and CC on shady/semi-shady slopes represent adaptive strategies to low-light environments. On sunny slopes with abundant light, high SLA is unnecessary due to sufficient photosynthetic photon flux; plants reduce SLA and CC to minimize photodamage, adapting to high-light conditions. Additionally, high SLA on shady slopes may result from allocation of photosynthates to vertical growth and leaf area expansion to acquire more carbohydrates under light limitation. Thus, our results confirm different ecological strategies for SLA across slope aspects. Higher WD on sunny slopes likely reflects slower growth due to strong solar radiation and limited soil nutrients (as confirmed by lower nutrient contents on sunny slopes), requiring long-term biomass accumulation. Differences in SLA, CC, and WD across slope aspects reflect distinct ecological strategies: high SLA and CC indicate resource-acquisitive strategies, while high WD indicates conservative strategies.

3.2 Response of Soil Environmental Factors to Different Slope Aspects

Soil organic matter originates mainly from litter decomposition, influenced by litter quality and microbial activity. Higher SOM on shady slopes [Figure 2: see original paper]A likely results from moderate solar radiation and suitable soil temperatures that promote microbial decomposition of litter and humus. Phosphorus is essential for plant growth, derived from litter mineralization and weathering of mineral particles. The lowest TP and AP on semi-shady slopes may result from severe soil weathering and lower pH at the transition between slope aspects. Our findings of lower phosphorus on shady slopes align with previous research. The distribution of total and available potassium may relate to soil leaching characteristics, as potassium is highly mobile and susceptible to loss. Higher solar radiation on sunny slopes accelerates soil weathering, reducing potassium release from parent material and causing nutrient loss through leaching, resulting in lower potassium contents compared to shady slopes.

3.3 Relationship Between Community-Level Functional Traits and Soil Environmental Factors

SLA is closely linked to plant growth and survival strategies, reflecting adaptation to different habitats. Our results show that community-level SLA and CC responded distinctly to shady and semi-shady slopes. The significant negative correlation between SLA and soil organic matter on shady/semi-shady slopes contrasts with some previous studies showing positive correlations. This discrepancy may relate to our focus on *Cyclobalanopsis glauca*, a dominant species adapted to nutrient-poor, drought-prone habitats. Thus, factors influencing SLA are complex, including not only soil nutrients but also species' biological characteristics. Chlorophyll content was significantly positively correlated with total phosphorus and available potassium on shady slopes [Figure 3: see original paper]A. Phosphorus is a major limiting factor in many forests, particularly in China' s tropical and subtropical regions. Phosphorus deficiency reduces photosynthetic rate and leaf growth by affecting nitrogen allocation to Rubisco, energy transduction in thylakoid membranes, and activity of key Calvin cycle enzymes. Increased phosphorus availability thus enhances chlorophyll content and photosynthesis. Potassium is also essential for photosynthesis; potassium deficiency accelerates leaf senescence and reduces chlorophyll content. Therefore, our findings of positive correlations between chlorophyll content and both total phosphorus and available potassium are well-supported.

Conclusion

From shady to sunny slopes, community-level SLA and CC decreased while WD increased. Soil TP and AP were highest on sunny slopes, whereas SOM, TK, and AK were highest on shady slopes. Regression analysis revealed significant negative correlations between SLA and soil organic matter on shady

and semi-shady slopes, and significant positive correlations between chlorophyll content and both total phosphorus and available potassium on shady slopes. These results demonstrate clear environmental filtering effects during plant community assembly in Guilin' s karst hills, where surviving species possess distinct trait combinations adapted to specific microhabitats. Understanding these vegetation-environment adaptation mechanisms provides important guidance for vegetation restoration and reconstruction in this region.

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