Variations and Correlations in Leaf Functional Traits of Woody Plants among Different Microhabitats in Shenmu Tiankeng Postprint

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Abstract

To analyze the variation characteristics of leaf functional traits of woody plants in tiankengs and the influence of microhabitats on leaf functional traits of woody plants, this study took woody plants in different microhabitats (bottom, mid-slope, and edge) of Shenmu Tiankeng as the research subject, selected 10 leaf functional trait indicators including leaf thickness, leaf tissue density, leaf area, etc., and employed methods such as one-way ANOVA and correlation analysis. The results showed that: (1) Among the 10 leaf functional traits of woody plants in Shenmu Tiankeng, leaf area had the largest coefficient of variation (113.9%), while leaf carbon content had the smallest coefficient of variation (10.5%). (2) The leaf tissue density of trees at the tiankeng edge and mid-slope was significantly higher than that at the bottom ($P<0.05$), the leaf potassium content of trees and shrubs at the tiankeng bottom was significantly higher than that at the edge ($P<0.05$), and no significant differences were observed for lianas among the three microhabitats ($P>0.05$). (3) There were certain differences in the correlations among leaf functional traits across different microhabitats; as the microhabitat changed from bottom to edge, leaf thickness and leaf area gradually showed an extremely significant positive correlation; principal component analysis indicated that leaf tissue density (-0.833), leaf potassium content (0.782), and leaf dry matter content (-0.647) contributed substantially and were the main indicators of leaf functional traits of woody plants in different microhabitats of Shenmu Tiankeng. In summary, these results indicate that leaf functional traits are generally interrelated, and tiankeng woody plants adapt to different microhabitats through trade-offs among leaf functional traits. This study can provide theoretical guidance for understanding plant adaptation mechanisms to special habitats and for the conservation of tiankeng vegetation.

Full Text

Differences and Correlations in Leaf Functional Traits of Woody Plants Across Various Microhabitats in Shenmu Tiankeng

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Abstract: To analyze the variation characteristics of leaf functional traits of woody plants in tiankengs and the influence of microhabitat on these traits, we selected woody plants from different microhabitats (bottom, waist, and edge) in Shenmu Tiankeng and measured ten leaf functional trait indicators including leaf thickness, leaf tissue density, and leaf area. Single-factor analysis of variance and correlation analysis were employed to investigate trait patterns. The results showed that: (1) Among the ten leaf functional traits of woody plants in Shenmu Tiankeng, leaf area exhibited the highest coefficient of variation (113.9%), while leaf carbon content showed the lowest (10.5%). (2) Leaf tissue density of trees at the edge and waist of the tiankeng was significantly higher than at the bottom ($P<0.05$), while leaf potassium content of trees and shrubs at the bottom was significantly higher than at the edge ($P<0.05$). No significant differences were observed for woody lianas across the three microhabitats ($P>0.05$). (3) Correlations among leaf functional traits varied across microhabitats, with leaf thickness and leaf area becoming increasingly positively correlated from bottom to edge. Principal component analysis revealed that leaf tissue density (-0.833), leaf potassium content (0.782), and leaf dry matter content (-0.647) contributed substantially as key indicators of leaf functional traits across different microhabitats in Shenmu Tiankeng. These findings demonstrate that leaf functional traits are generally interrelated, and that tiankeng woody plants adapt to different microhabitats through trade-offs among these traits. This study provides theoretical guidance for understanding plant adaptation mechanisms to special habitats and for tiankeng vegetation conservation.

Keywords: leaf functional traits; woody plants; tiankeng; trait differences; correlation

Introduction

Plant functional traits reflect plant adaptations and responses to climatic and environmental changes to a certain extent, representing a hot topic in ecological research (Yang & Luo, 2015). Plant functional traits refer to any measurable morphological, physiological, or phenological characteristics at the individual plant level that indirectly affect fitness through their influence on growth, reproduction, and survival (Violle et al., 2007). Leaves are the primary sites for photosynthesis and transpiration and are sensitive organs in response to environmental stress (Gong et al., 2011; Li et al., 2017). Leaf functional traits can reflect plant nutrient dynamics and adaptation strategies to living environments (Hu et al., 2014). In-depth studies on leaf functional traits across different habitats help reveal plant growth strategies and resource allocation patterns, providing scientific basis for predicting plant responses to global warming (He et al., 2019).

Karst ecosystems can be interpreted as ecosystems constrained by karst environments, encompassing both the impact of karst environments on life and the feedback of life on karst environments (Yuan, 2001). Recent years have witnessed numerous studies on leaf functional trait variation and adaptation strategies in karst regions. In the karst area of Puding, Guizhou, woody lianas showed the highest coefficient of variation in leaf area, closely related to species genetic diversity (Wang et al., 2021). Woody plants in this region adopt smaller specific leaf area and larger leaf tissue density to adapt to arid and infertile habitats (Zhong et al., 2018). Similarly, dominant species in karst plateau-canyon areas of Guizhou employ comparable leaf functional trait strategies to survive in high-temperature, water- and soil-scarce environments (Cheng et al., 2019).

Tiankengs, fully termed karst tiankengs, refer to large pit-shaped negative landforms (Zhu et al., 2003) with unique ecological environments and comprehensive attributes of biodiversity (Zhu & Chen, 2006), serving as refugia for native flora (Su et al., 2017). Scientific expeditions to tiankengs have become more frequent, with numerous scholars conducting in-depth research on tiankeng evolution and vegetation ecosystems (Pu et al., 2021). From bottom to top edge, tiankengs exhibit zonal species distribution patterns with substantial microhabitat heterogeneity (Huang et al., 2021). The bottom receives more water and nutrients, with higher soil organic matter, total nitrogen, and calcium content (Pu et al., 2019). Tiankeng communities show obvious stratification, with uniform distribution of dominant species in tree and shrub layers (Yu et al., 2021). However, as a special karst habitat, few studies have examined leaf functional traits in tiankeng forests. Only one study investigated functional traits of a single family across different slope positions in degraded tiankengs (Feng et al., 2021), while reports on relationships among leaf functional traits across different tiankeng microhabitats remain scarce.

Given this research gap, we selected woody plants from different microhabitats (bottom, waist, and edge) in Shenmu Tiankeng and measured ten relatively stable structural traits: leaf thickness, leaf tissue density, leaf area, specific leaf area, leaf dry matter content, leaf carbon content, leaf nitrogen content, leaf phosphorus content, leaf potassium content, and leaf nitrogen-phosphorus ratio. Using single-factor analysis of variance, correlation analysis, and principal component analysis, we aimed to address: (1) What are the variation characteristics of leaf functional traits of tiankeng woody plants? (2) What differences exist in leaf functional traits among the three microhabitats? (3) How are leaf functional traits correlated? By analyzing these questions, this study provides theoretical foundations for understanding survival strategies of woody plants in tiankeng habitats and offers further references for tiankeng plant conservation.

1.1 Study Area Overview

Shenmu Tiankeng belongs to the Dashiwei Tiankeng Group in Guangxi, located in Leye County, Baise City, Guangxi Zhuang Autonomous Region (106°10 - 106°51 E, 24°03 -24°30 N). The region has a subtropical monsoon climate with an average annual precipitation of 1,400 mm and average annual temperature of 16.6°C, featuring concurrent rainfall and heat (Huang et al., 2004). Shenmu Tiankeng consists of two opposing peaks and a col, with a polygonal bottom measuring 370 m long and 340 m wide, an average depth of 186 m, maximum depth of 234 m, and a crater area of 70,860 m^2. Common plant species in the study area include *Machilus glaucifolia*, *Acer tonkinense*, *Handeliodendron bodinieri*, *Metapanax davidii*, *Celtis biondii*, *Elatostema brachyodontum*, and *Pilea glaberrima*.

[Figure 1: see original paper] Sketch map of Shenmu Tiankeng and sampling location

1.2 Sample Plot Setup and Survey

Three 20 m × 20 m sample plots were established in each of three microhabitats (bottom, waist, and edge) in Shenmu Tiankeng [Figure 1: see original paper]. All woody plants with diameter at breast height (DBH) ≥ 1 cm were surveyed, recording species name, abundance, DBH, height, and crown width, along with environmental indicators including relative humidity, altitude, and canopy density. A total of 52 woody plant species were collected, comprising 20 tree species, 18 shrub species, and 14 woody liana species. Detailed plot information and dominant species across different growth forms in various microhabitats are presented in .

Shenmu Tiankeng microhabitat information and dominating species of several growth types

1.3 Data Collection

From July to October 2019, leaves of dominant woody plants were collected from sample plots based on survey data. Mature, healthy individuals were selected (five individuals each for trees and shrubs per species; all individuals for woody lianas), with 20-40 mature, healthy leaves collected per individual. Leaf functional trait measurement methods followed Cornelissen et al. (2003). Leaf thickness was determined by stacking 10 leaves, measuring thickness at three points along the main vein using a digital vernier caliper (precision 0.01 mm) at approximately 0.25 cm from the main vein. The average of three points was divided by 10 to obtain average leaf thickness per group, with eight groups measured per species and the final species value calculated as the average of these groups. Leaf area was determined by scanning leaves using a Canon scanner (CanoScan LIDE400, Canon China Co., Ltd.) and calculating area via ImageJ software, with 10 leaves per group and eight groups per species. Leaf fresh weight was measured after soaking leaves and storing them in darkness at approximately 5°C for 12 hours, then blotting surface moisture and weighing saturated fresh weight using a 1/1000 electronic balance. Leaf dry weight was measured after oven-drying fresh leaves at 70°C for 24–48 hours. Dried leaves were ground, crushed, and passed through a 60 mm sieve for nutrient content measurement. Leaf carbon and nitrogen contents were determined using a C/N elemental analyzer (vario MICRO cube, Elementar, Germany). Leaf phosphorus content was measured using the molybdenum-antimony anti-colorimetric method (Bao, 2005), and leaf potassium content was determined by flame atomic absorption spectrometry (Bao, 2005). Leaf tissue density, specific leaf area, leaf dry matter content, and leaf nitrogen-phosphorus ratio were calculated as follows:

Leaf tissue density = Leaf area / Leaf thickness
Leaf dry matter content =

1.4 Data Processing

Species-level leaf functional trait values were calculated as the mean of sampled individuals. Coefficient of variation = (standard deviation / mean) × 100%. Data were initially processed using Microsoft Excel 2010. Normality was tested using the Shapiro-Wilk test in SPSS software. For data passing normality tests with significant variance, post-hoc comparisons were conducted using Duncan' s method for homogeneous variance or Games-Howell method for heterogeneous variance. Data failing normality tests were transformed using square root or logarithmic conversion; if still non-normal, non-parametric Kruskal-Wallis tests were applied for comparisons across microhabitats and growth forms. Spearman correlation analysis in Origin 2021 was used to examine correlations among leaf functional traits, and principal component analysis (PCA) was performed to identify key leaf functional traits. All figures were generated using Origin software.

Results

2.1 Overall Characteristics of Leaf Functional Traits

Leaf functional trait characteristics of woody plants in Shenmu Tiankeng are presented in . Leaf area showed the highest coefficient of variation (113.9%), while leaf carbon content exhibited the lowest (10.5%). Coefficients of variation for leaf thickness, leaf tissue density, specific leaf area, leaf dry matter content, leaf nitrogen content, leaf phosphorus content, leaf potassium content, and leaf nitrogen-phosphorus ratio ranged from 23.5% to 85.0%. These results indicate that leaf area is strongly influenced by species and environmental factors, whereas leaf carbon content remains relatively stable.

Characteristics of leaf functional traits of woody plants in Shenmu Tiankeng

2.2 Leaf Functional Trait Characteristics Across Different Microhabitats

Comparisons of leaf functional traits across microhabitats [Figure 2: see original paper] revealed significant differences ($P<0.05$) among growth forms in Shenmu Tiankeng. Leaf tissue density of trees at the edge and waist was significantly higher than at the bottom, while leaf potassium content of trees and shrubs was significantly higher at the bottom than at the edge. No significant differences were detected for woody lianas across microhabitats ($P>0.05$), although leaf potassium content of lianas was significantly higher than that of trees at the edge. These results suggest that trees and shrubs exhibit similar leaf functional trait patterns across the three microhabitats, whereas woody lianas show insensitivity to microhabitat variation but adopt different trait strategies to compete with trees and shrubs.

[Figure 2: see original paper] Difference comparison of leaf functional traits of woody plants in Shenmu Tiankeng

2.3 Correlation Analysis Among Leaf Functional Traits

Correlations among leaf functional traits varied across microhabitats [Figure 3: see original paper]. From bottom to edge, the correlation between leaf thickness and leaf area gradually strengthened, shifting from non-significant ($P>0.05$) to extremely significant positive correlation ($P<0.001$), indicating that the promoting effect between leaf area and thickness intensified with microhabitat variation. At the bottom, specific leaf area and leaf dry matter content showed significant positive correlation, whereas at the waist and edge they exhibited extremely significant negative correlation, demonstrating that habitat differences can influence the relationship between these traits. At the edge, leaf tissue density and leaf dry matter content showed significant or extremely significant negative correlations with leaf potassium content, leaf thickness, leaf area, and specific leaf area.

[Figure 3: see original paper] Correlation analysis of leaf functional traits in Shenmu Tiankeng

Principal component analysis of leaf functional traits , [Figure 4: see original paper] indicated that the first four ordination axes had eigenvalues greater than 1. The first principal component explained 29.50% of variance, with major contributions from leaf tissue density (-0.833), leaf potassium content (0.782), and leaf dry matter content (-0.647). The second principal component explained 18.00% of variance, with major contributions from leaf thickness (0.670) and leaf phosphorus content (-0.664). The cumulative contribution of the first four axes reached 74.53%. Leaf tissue density, leaf potassium content, and leaf dry matter content, which contributed most to the first principal component, can be considered key indicators of leaf functional traits across different microhabitats in Shenmu Tiankeng.

Load matrix and interpreted variance of leaf functional traits in Shenmu Tiankeng

[Figure 4: see original paper] Biplot of principal component analysis of leaf functional traits in Shenmu Tiankeng

Discussion

3.1 Variation Characteristics of Leaf Functional Traits

The coefficient of variation in plant traits reflects the degree of functional trait variation, which is jointly determined by environment and species (Campetella et al., 2020). Most variation in leaf area can be explained by the interaction of plant taxa, individual height, and life form (Chen et al., 2016). The coefficient of variation for leaf area in tiankeng woody plants was 113.9%, higher than the 24.3% reported for dominant woody economic plants in karst regions (Pang et al., 2021). This discrepancy may be attributed to two factors: first, the number of species examined differed substantially—our study included 52 woody species compared to five in the economic plant study, with greater species richness leading to higher variation; second, tiankeng microhabitats exhibit high heterogeneity, with substantial environmental differences among bottom, waist, and edge. Relative humidity decreases rapidly while light availability increases from bottom to edge, causing distinct species and community type distributions—shade-loving species dominate inside the tiankeng while sun-loving species occupy the edge, resulting in greater leaf area variation. Leaf carbon content showed the smallest coefficient of variation, primarily because carbon, as an essential macronutrient constituting plant skeleton, possesses inherent homeostasis. Additionally, carbon accumulation is consistent among woody plants (Zheng et al., 2007), resulting in low variation and relative stability. These findings indicate that leaf functional trait variation in tiankeng woody plants is characterized by high variation in leaf area and low variation in leaf carbon content.

3.2 Response of Woody Plant Leaf Functional Traits to Microhabitats

Plant growth form is an important indicator for describing community physiognomy and vertical structure, reflecting environmental conditions under which plants grow and representing convergent adaptation (Galmán et al., 2017). Shenmu Tiankeng features diverse microhabitats, with different growth forms developing distinct leaf functional trait strategies. Leaf tissue density is associated with plant stress and disturbance resistance, representing water and nutrient utilization and conservation capacity (Wei et al., 2020). Plants with high leaf tissue density typically exhibit slower growth rates (Zhang et al., 2018). The tiankeng edge connects with external karst forests and experiences greater human disturbance; trees in this microhabitat increase leaf tissue density to resist external interference. For example, *Handeliodendron bodinieri* shows highest leaf tissue density at the disturbed edge (0.76 $g \cdot cm^{-3}$) and lowest at the less-disturbed bottom (0.17 $g \cdot cm^{-3}$). Furthermore, woody plants inside the tiankeng predominantly adopt resource-acquisitive strategies, where lower leaf tissue density facilitates higher growth rates, whereas edge plants allocate more nutrients to storage, indicating slower growth. Studies have shown that leaf potassium content increases with shading, potentially enhancing photosynthetic rate (Zhi et al., 2020). In our study, trees and shrubs exhibited highest leaf potassium content at the tiankeng bottom, likely because the bottom' s negative topography and lowest position receive minimal light intensity, prompting plants to increase leaf potassium content to improve light utilization efficiency. Additionally, potassium is highly mobile and susceptible to leaching by rainwater (Han et al., 2004); soil at the edge is prone to water erosion, with potassium being washed down and accumulating inside the tiankeng, increasing potassium availability for bottom plants. Woody lianas showed no significant differences in leaf functional traits across microhabitats, but their trait strategies may provide competitive advantages over trees and shrubs. Leaf nitrogen-phosphorus ratio serves as an indicator of nutrient limitation, with ratios >16 indicating phosphorus limitation (Koerselman & Meuleman, 1996). Nitrogen-phosphorus ratios in all three tiankeng microhabitats exceeded 16, suggesting that tiankeng woody plants are prone to phosphorus limitation. These findings demonstrate that plants employ different adaptation strategies across microhabitats—resource-acquisitive strategies at the bottom and resource-conservative strategies at the edge—adapting to diverse tiankeng microhabitats through trade-offs among leaf functional traits.

3.3 Associations Among Leaf Functional Traits

Relationships among leaf functional traits characterize plant response mechanisms during habitat adaptation (Xie et al., 2019). Our results show that from bottom to edge, the correlation between leaf thickness and leaf area gradually became extremely significant, contrasting with findings from degraded tiankengs in Zhanyi, Yunnan (Feng et al., 2021) but aligning with studies in central Guizhou karst regions (Zhong et al., 2018), suggesting that this correlation may vary with species and environment. At the tiankeng edge, the coupling of leaf area and thickness shows promoting effects; for example, the relationship in liana *Smilax china* facilitates survival in forest gaps, consistent with *Populus euphratica* increasing photosynthetic area and efficiency alongside leaf thickness in arid environments (Huang et al., 2010). At the edge, leaf tissue density was negatively correlated with specific leaf area, consistent with findings from karst plant studies (Cheng et al., 2019; Zhong et al., 2018). Both traits indicate drought tolerance; decreased specific leaf area (smaller leaf volume) leads to increased leaf tissue density (Zheng et al., 2015). Edge woody plants increase leaf tissue density to reduce water loss, adapting to the arid, infertile edge habitat. At the bottom, however, relatively abundant water resources resulted in different correlation patterns between these traits.

Leaf tissue density, leaf potassium content, and leaf dry matter content contributed most to the first principal component. Leaf tissue density represents defense strategy, leaf potassium content is closely related to photosynthesis, and leaf dry matter content indicates nutrient retention capacity—these three traits can serve as key indicators of leaf functional traits across tiankeng microhabitats. Tiankeng woody plant leaf functional traits show both universal and unique characteristics compared to other karst regions, primarily because edge microhabitats resemble other karst areas, whereas internal microhabitats differ significantly. The edge receives ample light but is relatively dry and infertile, while the internal negative topography and underground rivers provide relatively abundant nutrients and moisture but limited light, causing trait differences across microhabitats. Tiankeng topography is a major factor influencing woody plant leaf functional traits. Our analysis of structural traits helps understand plant adaptation and response to tiankeng environments. However, given the complexity of factors influencing leaf functional traits, future studies should integrate specific environmental factors to comprehensively reveal adaptation mechanisms.

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