

Analysis of Leaf Functional Traits of Dominant Species in Karst Plateau Canyons (Postprint)

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Abstract

Elucidating the leaf functional traits of dominant species in karst plateau canyon regions and exploring the correlations between functional traits and rhizosphere soil nutrients can help reveal plant survival strategies adapted to specific habitats. This study analyzed the leaf functional traits of dominant species in karst rocky desertification plateau canyon areas, investigating seven readily measurable leaf functional traits that reflect plant survival strategies across 17 plant species, including leaf thickness, leaf area, leaf fresh weight, leaf dry weight, leaf dry matter content, specific leaf area, and leaf tissue density. Stepwise regression was employed to explore the relationships between leaf functional traits and four soil nutrients. The results demonstrated: (1) Significant interspecific variations in leaf functional traits existed among dominant species in this region, with leaf thickness ranging from 0.18–0.78 mm, leaf fresh weight from 0.07–6.51 g, leaf dry weight from 0.04–3.19 g, leaf area from 3.07–325.64 cm², leaf dry matter content from 318.61–573.22 mg · g⁻¹, specific leaf area from 60.98–236.90 cm² · g⁻¹, and leaf tissue density from 0.022–0.036 g · cm⁻³; (2) Comparative studies with other regions revealed that plants in this area adapt to high-temperature, water-deficient, and soil-scarce environments by reducing water loss and increasing nutrient storage through smaller specific leaf area and larger leaf dry matter content; (3) Extensive correlations existed among leaf functional traits, all reaching extremely significant levels. Leaf thickness exhibited promoting effects on both fresh weight and dry weight, while highly significant inhibitory effects were observed between specific leaf area and leaf dry matter content as well as leaf tissue density; (4) Leaf functional traits exhibited regular changes in response to soil nutrient variations. Soil total nitrogen, total potassium, and organic carbon exerted significant influences on leaf functional traits, with soil organic carbon having the most pronounced effect. Further analysis indicated that the dominant or constructive species for vegetation restoration and reconstruction in karst plateau canyon regions include *Cladrastis platycarpa*, *Pistacia*

weinmannifolia, and loquat; applying organic fertilizer can enhance the adaptability of economic forest tree species such as *Zanthoxylum bungeanum* and *Lonicera japonica*. These findings deepen the understanding of vegetation in karst plateau canyon regions and hold certain theoretical and practical significance for the restoration and reconstruction of degraded vegetation.

Full Text

Preamble

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Leaf Functional Traits of Dominant Species in Karst Plateau-Canyon Areas

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Abstract

Clarifying the leaf functional traits of dominant species and exploring their correlations with rhizosphere soil nutrients in karst plateau-canyon areas can reveal plant survival strategies in specific habitats. This study analyzed the leaf functional traits of 17 dominant plant species in a karst rocky desertification plateau-canyon region. Seven easily measurable leaf functional traits that reflect plant survival strategies were investigated: leaf thickness, leaf area, leaf fresh weight, leaf dry weight, leaf dry matter content, specific leaf area, and leaf tissue density. Stepwise regression was used to explore relationships between these leaf functional traits and four soil nutrients. The results showed: (1) Significant interspecific variation existed in leaf functional traits, with leaf thickness ranging from 0.18–0.78 mm, fresh weight from 0.07–6.51 g, dry weight from 0.04–3.19 g, leaf area from 3.07–325.64 cm², leaf dry matter content from 318.61–573.22 mg · g⁻¹, specific leaf area from 60.98–236.90 cm² · g⁻¹, and leaf tissue density from 0.0221–0.036 g · cm⁻³. (2) Comparative studies with other regions indicated that plants in this area reduce water loss and increase nutrient storage through smaller specific leaf area and larger leaf dry matter content to adapt to high temperatures, water scarcity, and thin soils. (3) Extensive and highly significant correlations existed among leaf functional traits. Leaf thickness showed positive effects on both fresh and dry weight, while specific leaf area exhibited highly significant negative effects on leaf dry matter content and leaf tissue density. (4) Leaf functional traits changed systematically with soil nutrient availability. Soil total nitrogen, total potassium, and organic carbon significantly influenced leaf functional traits, with organic carbon having the most pronounced effect. Further analysis identified *Cladrastis platycarpa*, *Pistacia weinmannifolia*, and *Eriobotrya japonica* as optimal dominant or constructive

species for vegetation restoration and reconstruction in karst plateau-canyon areas. Applying organic fertilizer can enhance the adaptability of economic forest species such as *Zanthoxylum bungeanum* and *Lonicera japonica*. These findings deepen understanding of vegetation in karst plateau-canyon regions and provide theoretical and practical guidance for degraded vegetation restoration and reconstruction.

Keywords: dominant species, leaf functional traits, soil nutrients, karst plateau-canyon area

Introduction

Plant functional traits have long been a focal point in botany and ecology research. Through interactions with the environment, plants develop various internal physiological and external morphological strategies to cope with adverse environmental effects while altering their contributions to ecosystem functions (Meng et al., 2007). Plant traits that respond to environmental changes and influence ecosystem functions are termed plant functional traits (Diaz et al., 2001), with leaf-related traits referred to as leaf functional traits. As the organ with the largest environmental contact area and highest sensitivity to stimuli, leaf functional traits are closely linked to plant resource utilization capacity and efficiency (Sack et al., 2013). Studying leaf functional traits can deepen understanding of resource allocation patterns and reveal different plant adaptation strategies to habitats (Sun et al., 2017), thereby informing species selection (Yang et al., 2015) and community configuration (Cao et al., 2013) in ecological restoration efforts.

Numerous studies have demonstrated strong relationships between leaf functional traits and environmental factors such as elevation, light, temperature, and water availability. At broad scales, leaf size shows significant positive correlations with mean annual temperature and precipitation, and negative correlations with elevation (Peppe et al., 2011). Leaf mass per area (LMA) decreases with increasing annual precipitation but increases with elevation (Scheepens et al., 2010). At finer scales, although soil effects on leaf traits are gradual, soil moisture, nitrogen, phosphorus, potassium, and organic carbon all participate in plant nutrient cycling and life activities, thereby influencing leaf functional traits. Li et al. (2016) found that soil nutrients significantly affect plant functional traits, with plants coordinating or combining traits to adapt to specific soil environments. Kang et al. (2017) confirmed that leaf functional trait variations are closely related to soil organic carbon, nitrogen, and phosphorus contents across individual, intraspecific, interspecific, and community scales. Currently, research on the response relationships between leaf functional traits and soil nutrients remains insufficient, and unified perspectives have yet to emerge.

The karst region of southern China represents one of the world's three major contiguous karst areas, with the largest distribution and most complete developmental types. Guizhou Province lies at the center of southern China's karst

region, featuring diverse karst landforms. Therefore, research findings from Guizhou's karst areas provide valuable references for similar regions. Karst areas face prominent human-land conflicts and land degradation manifested as rocky desertification, urgently requiring prevention, control, and coordinated ecological-economic development (Xiong et al., 2011). Restoration and optimized configuration of degraded plant communities represent key components of comprehensive rocky desertification control in karst regions (Xiong et al., 2016). Dominant species are those with strong adaptability to specific habitats. Analyzing their functional traits in karst plateau-canyon areas can reveal optimal adaptation strategies to high temperatures, drought, and scarce soil resources, providing a scientific foundation for species selection, community configuration, and sustainable forest management in vegetation restoration. This study selected 17 dominant species from the Guanling-Zhenfeng Huajiang moderate-to-severe rocky desertification control demonstration area in southern China's karst region to analyze leaf functional traits and their responses to rhizosphere soil nutrients, addressing two scientific questions: What are the characteristics of leaf functional traits of dominant species in karst plateau-canyon areas? How do these traits respond to rhizosphere soil conditions?

Study Area

The study area (105°36'30" E, 25°39'13" N) is located in the Huajiang River section of the Beipan River basin, south of Guanling County and north of Zhenfeng County in southwestern Guizhou Province. Elevation ranges from 370-1,473 m. The region has a subtropical humid monsoon climate with pronounced vertical differentiation of habitat elements, representing a typical dry-hot valley climate. Winters and springs are warm and dry, while summers and autumns are hot and humid. Light and heat resources are abundant, with mean annual temperature of 18.4°C, mean annual extreme maximum temperature of 32.4°C, mean annual extreme minimum temperature of 6.6°C, and annual accumulated temperature of 6,542.9°C. Precipitation is abundant (mean annual precipitation 1,100 mm) but unevenly distributed temporally and spatially. Combined with the region's unique "dual-layer structure" geological characteristics, seasonal droughts are severe in some areas. The exposed strata are mainly Middle and Upper Triassic formations with thick rock layers and thin cultivated soils (mostly 10-20 cm). Carbonate rocks account for over 95% of the area, and soils are primarily clayey limestone soils lacking granular structure.

Although classified as moderate-to-severe rocky desertification, the study area has abundant water and heat resources with relatively high soil nutrient content (Sheng et al., 2015). Implementation of rocky desertification comprehensive control projects from the Ninth to Thirteenth Five-Year Plan periods, focusing on vegetation restoration and soil and water conservation, has significantly increased species diversity. At 500-800 m elevation, large-scale characteristic economic forests of *Zanthoxylum bungeanum* and *Juglans regia* have formed, while enclosed forest areas have developed evergreen forests dominated by *Lin-*

dera pulcherrima and *Pistacia weinmannifolia* and deciduous forests dominated by *Toona sinensis* and *Mallotus barbatus*. At 800-1,000 m, besides large-scale plantings of *Broussonetia papyrifera*, *Eriobotrya japonica*, and *Lonicera japonica*, enclosed forest areas have developed deciduous broad-leaved forests dominated by *Cladrastis platycarpa*. Above 1,000 m in enclosed forest areas, three types of secondary forests dominate: evergreen broad-leaved forests with *Buddleja officinalis* and *Itea yunnanensis*, evergreen shrub forests with *Viburnum foetidum* and *Pyracantha fortuneana*, and coniferous-broadleaf mixed forests with *Cupressus funebris* and *Eucalyptus robusta*.

Methods

Sampling Design

During July–August 2017, multiple surveys were conducted using transect methods. Three to five stable, strongly zonal plant communities were selected in each elevation range (<700 m, 700–800 m, 800–900 m, >900 m; communities in <700 m and >900 m zones were relatively simple). Typical 20 m × 20 m plots were established with three replicates per stand for community surveys. Species name, individual count, plant height, crown width, and DBH/basal diameter were recorded for trees and shrubs. Important values were calculated and ranked for each species. Dominant species in secondary forests were selected based on the highest important value or top two values (when differences were small), totaling 17 species (Table 1). Economic forest dominant species were those locally planted for over 30 years forming stable communities, considered primary species for rocky desertification ecological restoration. In each plot, three dominant trees with minimal mutual interference were selected for simultaneous leaf and rhizosphere soil collection. Leaf collection involved harvesting 10 fully expanded, healthy, unshaded leaves from outer crowns in all directions. Rhizosphere soil was collected within 1.0 m of the selected tree's root and at least 1.5 m from other species' roots. After removing the humus layer, physical soil samples were collected using a ring knife method. Due to thin soils and high gravel content below 10 cm, only 0–10 cm soil layers were sampled as physical samples, weighed fresh in the field, and stored in sealed bags. Chemical soil samples were collected from 0–20 cm layers at the same locations, mixed uniformly, and 1.5 kg was brought to the laboratory.

Leaf Functional Trait Measurement and Calculation

Leaf thickness, fresh weight, dry weight, and leaf area elucidate plants' self-regulation mechanisms in response to water and temperature changes, while leaf dry matter content, specific leaf area, and leaf tissue density indicate differences in resource allocation and utilization efficiency. These metrics can reveal how dominant species in karst plateau-canyon areas respond and adapt to environmental changes.

After collection, leaf surfaces were wiped clean of dust. Leaf thickness (LT) was

immediately measured using a digital caliper (precision 0.02 mm) at the front, middle, and end of each leaf, avoiding veins, with the mean value recorded. Fresh weight (FW) was measured using an electronic balance (precision 0.01 g). Each leaf was measured five times, and the three closest values with coefficient of variation within 5% were selected, with the median used as the final value. All dry and fresh weight measurements were performed by the same person to minimize operational error. Leaf area was determined using the paper method: a 10 cm × 10 cm filter paper was weighed (M), the leaf outline was drawn and cut out, and the cut paper was weighed (m) following the same measurement standards. Leaf area s (cm²) = 100 × m/M.

Leaves were oven-dried at 120°C for 30 minutes, then at 75°C for 48 hours to constant weight before measuring dry weight (DW). Specific leaf area (SLA), leaf tissue density (LTD), and leaf dry matter content (LDMC) were calculated using the following formulas:

$$\text{Specific leaf area (SLA, cm}^2 \cdot \text{g}^{-1}) = \text{Leaf area} / \text{Leaf dry weight} \quad (1)$$

$$\text{Leaf tissue density (LTD, g} \cdot \text{cm}^{-3}) = \text{Leaf dry weight} / (\text{Leaf area} \times \text{Leaf thickness}) \quad (2)$$

$$\text{Leaf dry matter content (LDMC, mg} \cdot \text{g}^{-1}) = \text{Leaf dry weight} / \text{Leaf fresh weight} \quad (3)$$

Soil Analysis

Chemical soil samples were processed by removing visible plant and animal residues and gravel, then air-dried and ground through 2 mm and 0.15 mm sieves. Soil bulk density (BD), total nitrogen (TN), total phosphorus (TP), total potassium (TK), and organic carbon (OC) were measured. Bulk density was determined using the ring knife method. Total nitrogen was measured by semi-micro Kjeldahl digestion. Total phosphorus was determined by NaOH fusion-molybdenum antimony colorimetry. Total potassium was measured by NaOH fusion-flame photometry. Organic carbon was determined by potassium dichromate volumetry with external heating (Bao, 2008).

Data Processing and Analysis

Data were preliminarily processed using Microsoft Excel 2010, plotted with OriginPro 2017, and statistically analyzed using SPSS 22.0. One-way ANOVA was used to test differences in leaf functional traits among dominant species. Spearman correlation analysis examined trait relationships, and stepwise regression analysis identified relationships between leaf functional traits and soil nutrients.

Results

Variation in Leaf Functional Traits Among Dominant Species

Leaf traits of the 17 dominant species showed considerable variation (Table 2). Leaf thickness ranged from 0.18-0.78 mm (coefficient of variation [CV] =

50.02%). Fresh weight varied from 0.07–6.51 g (CV = 116.07%), and dry weight from 0.04–3.19 g (CV = 124.03%). Leaf area ranged from 3.07–325.64 cm² (CV = 101.48%). Leaf dry matter content was highest in *Pistacia weinmannifolia* (573.22 mg·g⁻¹) and lowest in *Buddleja officinalis* (318.61 mg·g⁻¹; CV = 20.51%). Specific leaf area was highest in *Rhus chinensis* (236.90 cm²·g⁻¹) and lowest in *Eriobotrya japonica* (60.98 cm²·g⁻¹; CV = 31.96%). Leaf tissue density was highest in *Eriobotrya japonica* (0.036 g·cm⁻³) and lowest in *Buddleja officinalis* (0.008 g·cm⁻³; CV = 37.55%). Based on Tables 1 and 2, shrubs had slightly higher specific leaf area than trees, evergreen species had slightly higher specific leaf area than deciduous species, and economic forest species had slightly lower specific leaf area than secondary forest species. Additionally, leaf functional traits varied significantly among elevations, though no clear patterns emerged.

Comparison of Leaf Functional Traits Across Regions

Comparative studies with other regions (Table 3) revealed that leaf thickness in Guizhou was slightly greater than in Guangxi. Leaf area ranked as: this study > Guangxi Daming Mountain > Eastern Guangdong > Northwestern Guizhou > Guilin Yaoshan. Leaf dry matter content ranked as: this study > Northwestern Guizhou > Guangxi Daming Mountain > Guilin Yaoshan > Horqin Sandy Land > Eastern Guangdong. Specific leaf area ranked as: Eastern Guangdong > Guangxi Daming Mountain > Guilin Yaoshan > Horqin Sandy Land > this study > Northwestern Guizhou.

Relationships Among Leaf Functional Traits

Correlation analysis of the 17 dominant species showed that leaf thickness was highly significantly positively correlated with leaf fresh weight, dry weight, and leaf area ($P < 0.01$). Fresh weight was highly significantly positively correlated with dry weight and leaf area. Dry weight was highly significantly positively correlated with leaf area. Leaf thickness, fresh weight, dry weight, and leaf area were all highly significantly negatively correlated with specific leaf area, leaf dry matter content, and leaf tissue density. Specific leaf area was highly significantly negatively correlated with leaf tissue density and leaf dry matter content. Leaf tissue density was highly significantly positively correlated with leaf dry matter content (Table 4).

Associations Between Leaf Functional Traits and Soil Properties

Rhizosphere soil physicochemical properties varied considerably among dominant species (Figure 1 [Figure 1: see original paper]). Secondary forests generally had lower soil bulk density (*Alchornea trewioides* 0.73 g·cm⁻³, *Pistacia weinmannifolia* 0.75 g·cm⁻³, *Viburnum foetidum* 0.95 g·cm⁻³, *Pyracantha fortuneana* 0.87 g·cm⁻³) than economic forests (*Juglans regia* 1.14 g·cm⁻³, *Zanthoxylum bungeanum* 1.07 g·cm⁻³, *Eriobotrya japonica* 1.24 g·cm⁻³, *Broussonetia papyrifera* 1.12 g·cm⁻³). Secondary forests also had higher specific leaf area (*Alchornea trewioides* 218.88 cm²·g⁻¹, *Rhus chinensis* 236.90 cm²·g⁻¹, *Lindera*

pulcherrima 207.85 $\text{cm}^2 \cdot \text{g}^{-1}$, *Mallotus barbatus* 226.52 $\text{cm}^2 \cdot \text{g}^{-1}$) than economic forests (*Juglans regia* 100.38 $\text{cm}^2 \cdot \text{g}^{-1}$, *Zanthoxylum bungeanum* 190.19 $\text{cm}^2 \cdot \text{g}^{-1}$, *Eriobotrya japonica* 60.89 $\text{cm}^2 \cdot \text{g}^{-1}$, *Broussonetia papyrifera* 173.81 $\text{cm}^2 \cdot \text{g}^{-1}$). Economic forest rhizosphere soils generally had lower total nitrogen, total phosphorus, and organic matter but higher total potassium compared to secondary forest soils. Stepwise regression revealed that soil total nitrogen, total potassium, and organic carbon significantly influenced leaf functional traits in the karst plateau-canyon region (Table 5). Leaf thickness was significantly negatively correlated with soil total nitrogen. Leaf fresh and dry weights were significantly positively correlated with soil total potassium. Leaf area, specific leaf area, leaf tissue density, and leaf dry matter content all showed significant relationships with soil organic carbon. In the specific leaf area regression equation, the standardized coefficient for soil bulk density (-0.758) had greater absolute value than that for organic carbon (-0.426), indicating that bulk density was the primary factor affecting specific leaf area, followed by organic carbon content.

Discussion and Conclusions

Regional Differences in Leaf Functional Traits of Dominant Species

At global scales, leaf functional traits vary greatly among climate types (Wright et al., 2004), and within the same climate zone, traits vary with specific terrain and elevation (Feng et al., 2008). In karst plateau-canyon areas, high temperatures, seasonal drought, and soil scarcity are the main stress factors that local species must adapt to, resulting in distinct leaf functional trait combinations that differ from other regions. These trait differences reflect both inherent genetic characteristics and adaptive strategies (Liu and Ma, 2015). Significant differences in leaf area among regions showed no clear pattern, likely because genetic characteristics influence leaf area more strongly than environment.

Specific leaf area is an important indicator of plant resource use efficiency (Ven-dramini et al., 2002). Eastern Guangdong plants had the largest specific leaf area, while this study's values were relatively low, only higher than northwestern Guizhou plateau-mountain areas. Eastern Guangdong's climate and soil resources provide abundant available resources, resulting in larger specific leaf area, stronger light capture capacity, higher photosynthetic efficiency, faster resource turnover, and consequently higher relative growth rates to maintain competitive advantages. In contrast, rocky desertification in this study area and northwestern Guizhou results in scarce water and soil resources that constrain plant growth. Smaller specific leaf area indicates less area per unit dry weight, greater leaf dry matter density, lower photosynthetic efficiency, and slower nutrient cycling. Combined with low total soil nutrients, plants invest more nutrients in basic physiological activities, leading to "stunted tree" growth and relatively low resource use efficiency.

Leaf dry matter content reflects nutrient accumulation capacity (Qi et al., 2008). Higher values in both Guizhou study areas indicate greater investment in leaf

construction, stronger tolerance, and greater nutrient accumulation capacity. Lower values in Eastern Guangdong suggest less leaf construction investment, lower tissue density, more active leaf processes, and greater nutrient consumption due to intensified competition for growth resources, resulting in lower nutrient accumulation capacity. Horqin Sandy Land plants had leaf dry matter content only higher than Eastern Guangdong but lower than Guizhou and Guangxi regions. Although Horqin experiences seasonal water shortage, its thick, loose soil layers facilitate deep root water uptake, with absorbed nutrients largely invested in root development (Wang et al., 2014), leaving less for leaf construction. In contrast, Guizhou and Guangxi have thin soil layers, especially in northwestern Guizhou and this study's karst plateau-canyon area where root growth is restricted, causing plants to allocate more absorbed nutrients to leaf construction, increase aboveground biomass, accelerate growth rates, and store more nutrients to adapt to poor soil conditions.

Trait Coordination in Karst Plateau-Canyon Dominant Species

Multiple associations exist among leaf functional traits, with trait combinations acting simultaneously to achieve environmental adaptation (Shi et al., 2011), reflecting convergent adaptation strategies. In the resource-poor karst plateau-canyon environment, plants employ obvious functional balance strategies. Specific leaf area was highly significantly negatively correlated with both leaf dry matter content and leaf tissue density, consistent with Yang et al. (2014). Greater tissue density and dry matter content reflect more dry matter investment in leaf construction, increased mesophyll density, and reduced leaf water content, which increases the distance or resistance for internal water diffusion to leaf surfaces (Wang et al., 2016). Consequently, specific leaf area is smaller, reducing water loss and enhancing drought resistance. Although specific leaf area is the ratio of leaf area to dry weight, it showed weak relationships with leaf area but significant correlations with other indices, likely because high solar radiation, atmospheric temperature, and variable leaf temperatures among species with different canopy layers, light capture abilities, orientations, and leaf angles cause substantial fluctuations in leaf water content.

Leaf Functional Trait Responses to Soil Factors in Karst Plateau-Canyon Areas

Leaf functional traits respond to soil nutrient resources, with soil fertility determining plant resource use strategies (Liu and Ma, 2012). Changes in soil nitrogen, phosphorus, and organic carbon significantly affect functional traits (Bai et al., 2014). In karst plateau-canyon areas, soil bulk density and nutrient contents (total nitrogen, total potassium, organic carbon) significantly influence leaf functional traits and strongly regulate environmental adaptation strategies.

High temperature and drought are primary environmental characteristics. Photosynthetic capacity is significantly constrained by stomatal closure controlled by leaf defense systems. Potassium can enhance photosynthesis by promot-

ing chlorophyll synthesis and thylakoid membrane stability (Terry et al., 1983), strengthening stomatal regulation and nutrient accumulation for higher biomass. Thus, within a certain range, higher soil total potassium content leads to greater leaf fresh and dry weights.

In this region, leaf area and specific leaf area decrease with increasing soil organic carbon content, while leaf tissue density and dry matter content show the opposite trend. Typically, soil erosion in karst secondary forests results in thin soil layers, while exposed rock surfaces create nutrient accumulation effects with relatively high nutrient content. Additionally, minimal human disturbance allows intense soil fauna and microbial activity and thorough litter decomposition, resulting in relatively high soil organic carbon content. Secondary forest dominant species such as *Pistacia weinmannifolia*, *Itea yunnanensis*, *Pyracantha fortuneana*, and *Viburnum foetidum* develop smaller leaf area and specific leaf area to reduce water evaporation under water- and soil-scarce conditions. However, favorable soil nutrient conditions provide adequate resources for leaf dry matter synthesis, enabling greater nutrient storage to cope with harsh environments, thus maintaining high tissue density and dry matter content.

Species Selection and Management Based on Leaf Functional Traits

Greater leaf dry matter content and smaller specific leaf area represent the primary adaptation strategies of karst plateau-canyon plants. Based on these criteria, species with strong adaptability to drought and high temperatures include *Cladrastis platycarpa*, *Pistacia weinmannifolia*, *Pyracantha fortuneana*, *Juglans regia*, and *Eriobotrya japonica*, which can serve as dominant or constructive species for vegetation restoration and optimized configuration.

Stepwise analysis of leaf functional traits and soil nutrients revealed that soil organic carbon significantly affects specific leaf area and leaf dry matter content, with specific leaf area decreasing and dry matter content increasing as organic carbon content rises. This suggests that lower organic carbon content may explain the lower dry matter content and higher specific leaf area observed in economic forest species such as *Zanthoxylum bungeanum*, *Broussonetia papyrifera*, and *Lonicera japonica*, while stronger adaptability of secondary forest species relates to abundant and rapidly cycling organic carbon. Therefore, appropriate organic fertilizer application can enhance economic species' adaptability to high temperature, water, and soil scarcity, achieving greater ecological and economic benefits. For natural secondary forests, cultivating coniferous-broadleaf mixed forests to increase litter quantity and accelerate organic matter decomposition and cycling represents an important pathway for improving forest ecosystem adaptability.

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