Effects of Soil Nutrients on Functional Traits of Juglans sigillata in Karst Rocky Desertification Areas: Postprint

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Abstract

Investigating plant leaf functional traits and their influencing factors in karst rocky desertification areas can reveal the adaptation mechanisms to desertification environments. This study takes Juglans sigillata in the karst plateau canyon region of southern China as the research object to reveal the effects of soil nutrients on leaf structural and photosynthetic traits. The results show that: (1) With increasing rocky desertification grade, the leaf functional traits of Juglans sigillata exhibit the following patterns: leaf area decreases, specific leaf area increases, leaf dry matter content and leaf tissue density first decrease and then increase, transpiration rate, intercellular CO2 concentration, stomatal conductance, and light use efficiency first decrease and then increase, while other traits show no significant trends. (2) Redundancy analysis indicates that soil nutrients can explain 37.4% of the variation in photosynthetic traits and 53.4% of the variation in structural traits, with total phosphorus and dissolved organic carbon having the greatest influence on photosynthetic traits; the most significant factors affecting structural traits are alkali-hydrolyzable nitrogen and available phosphorus. (3) Specific leaf area is extremely significantly negatively correlated with leaf dry matter content and extremely significantly positively correlated with net photosynthetic rate; leaf thickness is extremely significantly negatively correlated with leaf tissue density; transpiration rate is extremely significantly positively correlated with intercellular CO2 concentration and stomatal conductance; water use rate is extremely significantly negatively correlated with transpiration rate, intercellular CO2 concentration, and stomatal conductance; light use efficiency is significantly positively correlated with net photosynthetic rate. The research results indicate that to adapt to the special habitat of karst rocky desertification, Juglans sigillata adopts an exploitative growth strategy that enhances growth functional traits while improving resource acquisition capacity, thereby increasing its resistance and adaptation to environmental stress.

Full Text

Effects of Soil Nutrients on Functional Traits of *Juglans sigillata* in Karst Rocky Desertification Areas

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Abstract

Exploring leaf functional traits and their influencing factors in karst rocky desertification areas can reveal plant adaptation mechanisms to such environments. This study investigated the effects of soil nutrients on leaf structural and photosynthetic traits of *Juglans sigillata* in the karst plateau canyon region of southern China. The results showed: (1) With increasing rocky desertification grade, leaf area decreased while specific leaf area increased; leaf dry matter content and leaf tissue density first decreased then increased; transpiration rate, intercellular CO_2 concentration, stomatal conductance, and light energy utilization efficiency first decreased then increased; other traits showed no significant trends. (2) Redundancy analysis indicated that soil nutrients explained 37.4% of photosynthetic trait variation and 53.4% of structural trait variation, with total phosphorus and dissolved organic carbon having the greatest influence on photosynthetic traits, while alkaline hydrolyzed nitrogen and available phosphorus most significantly affected structural traits. (3) Specific leaf area was extremely significantly negatively correlated with leaf dry matter content and extremely significantly positively correlated with net photosynthetic rate; leaf thickness was extremely significantly negatively correlated with leaf tissue density; transpiration rate was extremely significantly positively correlated with intercellular CO_2 concentration and stomatal conductance; water use efficiency was extremely significantly negatively correlated with transpiration rate, intercellular CO_2 concentration, and stomatal conductance; light energy utilization efficiency was significantly positively correlated with net photosynthetic rate. These findings demonstrate that *J. sigillata* adopts an pioneering growth strategy in karst rocky desertification habitats by enhancing growth functional traits while improving resource acquisition capacity to increase resistance and adaptation to environmental stress.

Keywords: *Juglans sigillata*, photosynthetic characteristics, structural traits, soil nutrients, rocky desertification, karst

Introduction

Plant functional traits are widely used to detect and interpret adaptive characteristics of plants in various environments, encompassing both external morphology and internal physiology [?]. As exposed and sensitive organs to external environmental changes, leaves represent important functional traits [?]. Physiological traits reflect the physiological characteristics of leaf growth and metabolism, with photosynthesis serving as a crucial source of material and energy for plant growth and development [?]. Structural traits represent relatively stable biological morphological structures under specific environmental conditions [?]. Numerous studies at different scales have investigated relationships between plant functional traits and environmental factors, demonstrating that precipitation, topography, and soil nutrients are important shaping factors. At small scales, topographic factors such as slope, aspect, and position influence light, precipitation, temperature, and soil nutrients [?, ?]. [?] analyzed plant traits across six primary forest sites along an alpine vertical zone on the eastern slope of Gongga Mountain, finding that leaf lifespan and leaf nitrogen content increased with elevation. [?] reported that specific leaf area was greater on shady slopes than sunny slopes, while wood density showed the opposite pattern. [?] demonstrated that island plant functional traits were primarily constrained by topographic factors (slope and position) and soil factors (organic matter and total nitrogen). Across individual, species, and community scales, variation in leaf functional traits is closely related to soil organic carbon [?] and nitrogen and phosphorus contents [?]. [?] found that surface soil water content was significantly negatively correlated with leaf net photosynthetic rate and transpiration rate during community succession, while [?] showed that soil water content was a primary driver of soil nutrient variation, suggesting that soil nutrients also influence plant photosynthetic physiological characteristics.

Juglans sigillata, a woody oil plant with strong adaptability, can increase vegetation cover in karst areas while providing both economic and environmental benefits, making it an effective species for comprehensive rocky desertification control. Rich in unsaturated fatty acids and protein, *J. sigillata* contains various amino acids, mineral elements, and vitamins beneficial to human health, offering therapeutic and health benefits for cardiovascular and cerebrovascular diseases. As one of the four major dried nuts, walnuts are distributed across many regions in China, with *J. sigillata* being predominant in southwestern China [?]. Studies examining relationships between soil nutrients and plant photosynthetic physiological traits have shown that high phosphorus stress significantly inhibits walnut seedling growth and photosynthesis [?], while appropriate phosphorus supply can significantly improve net photosynthetic rate, transpiration rate, and water use efficiency in apple seedlings [?]. [?] found that nitrogen effects on walnut seedling xylem development could alter water transport capacity, thereby influencing photosynthetic capacity.

Karst habitats exhibit high spatial heterogeneity, characterized by thin and discontinuous soil layers and high bedrock exposure rates [?]. Soil physicochemical properties vary across different rocky desertification grades [?], with soil factors representing important components influencing plant functional traits [?]. Currently, few studies have examined relationships between leaf structural traits, photosynthetic physiological traits, and soil nutrients in karst habitats [?, ?], and research on the influence mechanisms of soil nutrients on functional traits of economic forests such as *J. sigillata* is particularly lacking. Therefore, this study selected *J. sigillata* from karst rocky desertification control orchards as the research object, investigating differences in leaf physiological traits, structural traits, and soil nutrients across rocky desertification gradients to explore the influence mechanisms of soil nutrients on *J. sigillata* functional traits. This research is significant for understanding adaptation characteristics of *J. sigillata* to rocky desertification environments and provides references for ecological restoration and scientific management of *J. sigillata* economic forests in rocky desertification areas.

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1. Materials and Methods

1.1 Study Area The study area is located in Cha' eryan Village, Beipanjiang Town, Zhenfeng County, southwestern Guizhou Province (105°38 48 E, 25°39 35 N). This region features a dry-hot valley climate with an average annual rainfall of 1,100 mm, uneven seasonal distribution, and severe droughts in winter-spring and summer periods. The average annual temperature is 18.4 °C, with average extreme high and low temperatures of 32.4 °C and 6.6 °C, respectively, and accumulated annual temperature of 6,542.9 °C, indicating abundant water and heat resources. The area has a valley topography with deeply incised valleys, deeply buried groundwater, steep slopes, and elevations ranging from 530 to 1,473 m (vertical difference of approximately 940 m). Rocky desertification is well-developed, with bedrock exposure rates between 50% and 80%, primarily representing moderate to intense rocky desertification. Carbonate rocks account for 78.45% of the geology, and soils are primarily limestone-derived with thin, discontinuous distribution, poor water retention, and drought resistance, creating an extremely fragile ecological environment [?]. Main economic forest species include *Zanthoxylum armatum*, *Juglans sigillata*, *Eriobotrya japonica*, and *Lonicera japonica*.

1.2 Experimental Design and Sampling Between July and August 2020, extensive field surveys were conducted in the Huajiang Cha' eryan area (105°38 48 E, 25°39 35 N). Based on the karst rocky desertification intensity classification standard [?] and field survey conditions, twelve 20 m × 20 m standard plots were established in *Juglans sigillata* forests of the same variety and stand age, with distances >20 m between plots. The plots included four gradients: potential rocky desertification (PRD), slight rocky desertification (SRD), moderate rocky desertification (MRD), and intense rocky desertification (IRD), with three replicates per gradient. Basic information including elevation, longitude, latitude, slope, aspect, and slope position was recorded for each plot (Table 1).

Within each standard plot, three healthy, vigorous trees were selected. Within the projected canopy area and avoiding fertilizer trenches (pits), five surface soil samples (0–20 cm) were collected using a "plum blossom" pattern after removing litter and surface vegetation. Samples were mixed, and 1 kg was bagged and transported to the laboratory. Soils were air-dried in a ventilated, contamination-free environment, impurities were removed, and samples were ground and sieved through 1 mm and 0.25 mm meshes for chemical property determination. Soil dissolved organic carbon (DOC) was measured using the potassium dichromate external heating oxidation method [?]. Total nitrogen (TN) was determined by the Kjeldahl method, ammonium nitrogen (NH_4^+-N) by continuous flow analyzer, alkali-hydrolyzed nitrogen (AN) by the alkali diffusion method, total phosphorus (TP) by $HClO_4$ digestion-molybdenum antimony colorimetry, available phosphorus (AP) by sodium bicarbonate extraction with molybdenum antimony colorimetric determination, and pH by potentiometry [?].

1.2.2 Leaf Photosynthetic Physiological Parameter Measurement Physiological trait measurements were conducted in August 2020 during three consecutive sunny days between 9:00–11:00 using a photosynthesis system (LI-6800, LI-COR Inc, USA) with a broadleaf chamber. Measurements were taken on healthy, mature, fully expanded sun-exposed leaves, with ambient values controlling leaf chamber air relative humidity and temperature. CO_2 concentration was set at 400 $\mu mol \cdot mol^{-1}$ with a flow rate of 600 $\mu mol \cdot s^{-1}$. Parameters measured included net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), and intercellular CO_2 concentration (Ci). Instantaneous water use efficiency (WUE) was calculated as Pn/Tr, and light use efficiency (LUE) as Pn/photosynthetically active radiation (PAR).

1.2.3 Leaf Structural Index Measurement Within each standard plot, three healthy, vigorous trees were selected. Fully expanded, pest-free mature leaves were collected before 11:00 AM, bagged, and stored in a cooler for structural trait determination. Fresh leaf weight (FLW) was measured, and leaf area (LA) was scanned using a scanner and measured with a portable leaf area meter (YMJ-D). Leaf thickness (LT) was measured at the leaf tip, middle, and base using a digital caliper (Guanglu, 111N-101-10), with the mean value used. Dry leaf weight (DLW) was determined by constant temperature drying. Leaf dry matter content (LDMC) was calculated as DLW (g)/FLW (g), specific leaf area (SLA) as LA/DLW, leaf moisture content (LMC) as (FLW-DLW)/FLW, and leaf tissue density (LTD) as DLW/(LA×LT). Leaf trait measurement methods primarily followed [?].

1.3 Data Processing Microsoft Excel 2010 was used for preliminary data organization. SPSS 22.0 statistical software was employed for analysis, with one-way ANOVA used for difference testing of photosynthetic physiological parameters, structural functional traits, and soil nutrient indicators among rocky desertification grades. Pearson correlation analysis explored relationships between leaf structural functional traits and photosynthetic physiological parameters. Redundancy analysis (RDA) investigated correlations between plant functional traits and soil nutrients. RDA constrained ordination analysis requires two matrices (species data and environmental data), with all parameters of different dimensions standardized before ordination. In the resulting ordination diagram, arrow length represents the magnitude of the eigenvector, interpreted as the explanatory power of environmental factors on functional traits. The angle between arrows indicates correlation between plant functional traits and environmental factors: 0°–90° indicates positive correlation, 90°–180° indicates negative correlation, and 90° indicates no significant correlation. Data are expressed as mean ± standard deviation, with significance level set at P=0.05 and extremely significant level at P=0.01. Origin 8.6 and Canoco 5.0 were used for figure preparation.

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2. Results

2.1.1 Leaf Structural Traits *Juglans sigillata* DLW, LSFW, and LA all decreased significantly with increasing rocky desertification grade ($P<0.05$). SLA, LDMC, and LTD showed a trend of first decreasing then increasing; LT and LMC showed the opposite trend, first increasing then decreasing. FLW, DLW, LSFW, LA, LDMC, and LTD reached maximum values in potential rocky desertification, while SLA peaked in intense rocky desertification and FLW, DLW, LSFW, LA, and LT reached minimum values (Figure 1 [Figure 1: see original paper]).

2.1.2 Leaf Photosynthetic Physiological Trait Characteristics As shown in Table 2 , Tr, Ci, Gs, and LUE showed a decreasing then increasing trend with intensifying rocky desertification, with significant differences between intense rocky desertification and other grades for Tr, Ci, and Gs. WUE generally showed an increasing then decreasing trend with rocky desertification grade, with significant differences between intense desertification and other grades. Pn reached its maximum in potential rocky desertification and minimum in slight rocky desertification, with significant differences among all grades. Tr, Ci, and Gs peaked in intense rocky desertification where WUE was lowest, while Tr, Ci, Pn, and LUE reached minimum values in slight rocky desertification where WUE was highest.

2.1.3 Correlation Analysis Between Leaf Physiological and Structural Traits As shown in Table 3 , LT was extremely significantly negatively correlated with LTD ($P<0.01$) and significantly positively correlated with Ci. DLW was extremely significantly positively correlated with LSFW, LDMC, and LTD, and extremely significantly negatively correlated with LMC. SLA was extremely significantly negatively correlated with LDMC, LTD, and DLW, and extremely significantly positively correlated with Pn. LTD was extremely significantly positively correlated with LDMC and significantly negatively correlated with Ci. Tr was extremely significantly positively correlated with Ci and Gs, and extremely significantly negatively correlated with WUE. Pn was significantly negatively correlated with WUE and extremely significantly positively correlated with LUE. Ci was extremely significantly positively correlated with Gs. WUE was extremely significantly negatively correlated with Tr, Ci, and Gs.

2.2 Soil Nutrient Characteristics As shown in Table 4 , NO_3^--N, AN, pH, and DOC first decreased then increased with rocky desertification intensity, reaching minimum values in intense rocky desertification. AP and TP showed negative correlations with rocky desertification grade, gradually decreasing with increasing desertification. All soils were acidic (pH 6.03–6.82). DOC and AN varied substantially across rocky desertification grades, ranging from 17.03–36.80 $mg \cdot kg^{-1}$ and 150.50–259 $mg \cdot kg^{-1}$, respectively. NH_4^+-N and TN showed no clear trends, with values of 0.91–1.72 $mg \cdot kg^{-1}$ and 1.48–4.31 $mg \cdot kg^{-1}$, respectively.

2.3 Correlation Analysis Between Leaf Functional Traits and Soil Nutrients RDA ordination analysis showed that soil nutrients explained 37.4% of photosynthetic trait variation (influence order: TP>DOC>TN>AN) (Figure 2 [Figure 2: see original paper]a) and 53.4% of structural trait variation (AN had the greatest influence, followed by AP, TN, DOC, and NO_3^--N) (Figure 2b). Relationships between functional traits and soil nutrients showed that Tr, Ci, and Gs were positively correlated with TN and negatively correlated with TP, AN, and DOC. Pn and LUE increased with TP and TN but decreased with DOC. WUE was positively correlated with AN, TP, and DOC but negatively correlated with TN. SLA was positively correlated with AP and NO_3^--N but negatively correlated with DOC, AN, and TN. LDMC and LTD decreased with increasing AP but increased with AN, DOC, and TN. LA was positively correlated with TN and negatively correlated with NO_3^--N.

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3. Discussion

3.1 Analysis of *Juglans sigillata* Leaf Functional Traits Across Rocky Desertification Grades Plant adaptation to environments is often manifested through trait changes [?]. This study showed that FLW, DLW, LSFW, and LA decreased with intensifying rocky desertification, consistent with [?], indicating that rocky desertification stress affects *J. sigillata* structural trait development and inhibits leaf expansion. This may result from reduced surface soil moisture and increased temperature associated with rocky desertification development, creating more stressful microhabitats where plants adopt protective strategies to reduce water loss by decreasing LA. Smaller LA under stress benefits plants by reducing transpiration and respiration, thereby decreasing water loss and maintaining water balance, consistent with [?] on dominant species in different rocky desertification areas.

Higher LDMC enhances plant capacity to tolerate nutrient deficiency and drought while improving nutrient storage [?]. In this study, LDMC first decreased then increased with rocky desertification intensity. Due to the presence of "pile-nest soil" in rocky desertification areas with high spatial heterogeneity in water and nutrient distribution and frequent intermittent precipitation, plants exhibit strong hydrotropism to obtain necessary nutrients and moisture for growth and survival. Complex environmental variation leads to complex trait changes, and LDMC primarily reflects plant nutrient absorption rates. The irregular change pattern suggests complex soil nutrient variation across rocky desertification grades, resulting in abnormal LDMC changes [?]. SLA reflects plant capacity to acquire light resources and self-protect under intense light, with larger SLA indicating stronger light acquisition capacity and faster plant growth rates and nutrient cycling [?]. This study showed that *J. sigillata* SLA increased with rocky desertification intensity, indicating enhanced light acquisition capacity and adoption of higher growth rate strategies with stronger self-protection under intense light. This differs from [?] and [?] on dominant species in karst areas, possibly due to different study subjects. Karst area dominant species are mostly evergreen, adopting low-growth-rate conservative strategies to acquire and conserve resources [?], while *J. sigillata* is deciduous, tending toward high SLA but shortened lifespan, accelerating growth through enhanced photosynthesis to increase dry matter storage [?], while adopting leaf shedding during dry seasons to reduce water transpiration and adapt to the environment. Alternatively, higher rocky desertification grades create more fragile habitats where plants improve resource use efficiency to resist habitat stress.

In this study, Pn showed a decreasing-increasing-decreasing trend with rocky desertification intensity, reaching its minimum in slight rocky desertification. Generally, Pn variation results from interactions between internal physiology and external environmental factors [?]. The rocky desertification environment has complex effects on *J. sigillata* Pn. In slight rocky desertification areas, minimum Pn values coincided with low Tr, Ci, and Gs values. Due to stomatal limitation factors and transpiration rate effects in *J. sigillata*, lower Tr slowed internal substance transport, while lower Gs limited CO_2 entry, causing Pn to decrease with reductions in Tr and Gs. This may represent an adaptive strategy derived in response to the variable rocky desertification environment characterized by drought and thin soil. Water use efficiency reflects the relationship between plant water consumption and productivity [?]. Under water deficit, plants adapt to adverse environments by regulating water use efficiency. This study showed that WUE first increased then decreased with rocky desertification grade, peaking in slight rocky desertification. This was related to Tr decreasing less than Pn, directly causing WUE elevation. Competition for water between transpiration deficit and photosynthetic carbon assimilation led to increased WUE under slight drought stress [?]. From slight rocky desertification onward, WUE gradually decreased, possibly because intensifying rocky desertification stress disrupted leaf physiological dynamic balance, decreasing overall function and water use efficiency, consistent with drought stress research conclusions [?]. This reflects different response types of plant functional traits to the variable environment of rocky desertification areas characterized by drought, thin soil, and high temperature [?].

3.2 Relationship Between *Juglans sigillata* Leaf Functional Traits and Soil Nutrients The unique aboveground-underground "binary three-dimensional" structure of karst [?] leads to severe soil nutrient loss, rock exposure, and uneven thin soil distribution [?], with substantial nutrient variation affecting plant growth [?]. RDA ordination analysis showed that soil nutrients explained 37.4% of photosynthetic trait variation (TP having the greatest influence, followed by DOC, TN, and AN) and 53.4% of structural trait variation (influence order: AN>AP>TN>DOC). These results are similar to other studies where soil organic matter and TN were primary environmental factors affecting stem and leaf functional traits of island plants [?], and soil organic matter was the main factor constraining stem diameter and leaf thickness in different-aged *Robinia pseudoacacia* forests [?]. [?] found that soil organic matter, TP, and available potassium were primary influencing factors for leaf functional traits of different life-form plants. TP, AN, and DOC, as important components of ecosystem carbon-nitrogen-phosphorus cycling, substantially influence plant functional trait variation. This study showed that Tr, Ci, and Gs were significantly positively correlated with TN, while Pn and LUE increased with TP and TN. This may occur because P participates in energy metabolism of adenosine triphosphate (ATP) and is an important component of membrane lipids and nucleotides, playing vital physiological roles in plant photosynthesis and respiration [?]. Research indicates that nutrient element P substantially affects photosynthesis [?], and Pn is significantly positively correlated with LUE, consistent with [?] on relationships between photosynthetic characteristics of shrubs in arid regions and environmental factors. P affects LUE by influencing Pn. N significantly affects leaf chlorophyll, photosynthetic rate, and photorespiration intensity, directly or indirectly acting on plant photosynthesis [?]. Generally, plant respiration is affected by Tr, Gs, and Ci, causing these parameters to vary with TN. [?] demonstrated that appropriate N application increases leaf N levels, enhances N assimilation, and consequently improves photosynthetic rate.

SLA was significantly negatively correlated with DOC, AN, and TN, similar to [?] on dominant populations of *Cyclobalanopsis glauca* in karst hills of Guilin, but differing from [?] and [?] on relationships between soil nutrients and plant functional traits on different slopes. Generally, SLA is greater in high-nutrient habitats than in nutrient-poor and dry habitats, contrary to our results. This discrepancy may result from the complex microhabitats in the karst plateau canyon region and the strong adaptability and drought tolerance of *J. sigillata*, indicating that SLA variation is not only environment-dependent but also influenced by other factors such as genetic characteristics [?]. LDMC and LTD were significantly positively correlated with AN, DOC, and TN, similar to [?] on environmental factors and plant functional traits on islands. Higher LDMC and LTD content leads to more organic matter entering the soil through litter. Additionally, under conditions of high soil AN, DOC, and TN, plants enhance resource conservation capacity by increasing LDMC and LTD to effectively resist hazards from drought and high temperature. Carbon-nitrogen cycling is an important component of ecosystem nutrient cycling and plays a significant role in LDMC and structural composition [?]. Karst rocky desertification areas have more complex and fragile environmental changes, with sparse soil cover prone to loss, making habitat recovery difficult once destroyed. *Juglans sigillata* is an effective species for rocky desertification control. To adapt to this special environment, it adopts corresponding survival strategies, coordinating photosynthetic physiological traits and structural functional traits. TP and AN are the primary soil factors affecting *J. sigillata* photosynthetic physiological traits and structural functional traits. Overall, *J. sigillata* in this region adopts a pioneering growth strategy of enhancing growth functional traits and improving resource acquisition capacity to increase resistance and adaptation to environmental stress.

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