

Leaf Micromorphology, Photosynthetic Physiological Characteristics, and Ecological Adaptation of Dominant Tree Species in Karst Seasonal Rainforest: Postprint

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Abstract

To investigate the adaptation strategies of dominant tree species in karst seasonal rainforests to heterogeneous habitat conditions, we studied seven dominant tree species in primary forests of Nonggang, Guangxi, measuring leaf micromorphological traits of adult individuals and photosynthetic physiological characteristics during the growing season, and explored the response patterns of leaf structural and functional traits to heterogeneous habitats in karst peak-cluster mountains. The results showed that: (1) Along the habitat gradient from depression to mid-slope to summit in karst landform positions, nine micromorphological traits including leaf compactness, palisade tissue thickness, cuticle thickness, and upper epidermis thickness exhibited significant increasing trends, while leaf looseness showed a significant decreasing trend; (2) Along the depression-mid-slope-summit habitat gradient, light compensation point, dark respiration efficiency, and maximum transpiration rate of trees showed significant increasing trends, whereas maximum water use efficiency, maximum intercellular CO₂ concentration, and apparent quantum efficiency displayed significant decreasing trends; (3) Leaf compactness showed significant positive correlations with photosynthetic capacity, transpiration capacity, and related indicators, while leaf looseness exhibited significant negative correlations with these two categories of indicators. In summary, leaf functional traits of dominant tree species in karst seasonal rainforests exhibit a trade-off between photosynthetic efficiency and drought tolerance; trees growing in depressions have prominent low-light adaptation characteristics, those on mid-slopes demonstrate a relatively broad habitat adaptation range, and species distributed on summits, constrained by high light intensity, high temperature, and bare rock, show strong drought adaptation characteristics and a conservative ecological adaptation strategy.

Full Text

Leaf Micromorphological and Photosynthetic Physiological Characteristics and Their Ecological Adaptability of Dominant Tree Species in a Karst Seasonal Rain Forest in Guangxi, China

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Abstract: To investigate the adaptive strategies of dominant tree species in karst seasonal rain forests to heterogeneous habitat conditions, we examined seven dominant species in a primary forest in Nonggang, Guangxi. Leaf micromorphological indices of adult individuals and photosynthetic physiological characteristics during the growing season were measured to explore how leaf structural and functional traits respond to heterogeneous habitats in karst peak-cluster depressions. The results showed that: (1) Along the habitat gradient from depression to midslope to hilltop, nine micromorphological indices—including leaf compactness, palisade tissue thickness, cuticle thickness, and upper epidermis thickness—increased significantly, while leaf looseness decreased significantly. (2) Along the same gradient, the light compensation point, dark respiration rate, and maximum transpiration rate increased significantly, whereas maximum water use efficiency, maximum intercellular CO₂ concentration, and apparent quantum efficiency decreased significantly. (3) Leaf compactness was significantly positively correlated with photosynthetic and transpiration capacity indices, while leaf looseness was significantly negatively correlated with these indices. These findings demonstrate a trade-off between photosynthetic efficiency and drought tolerance in leaf functional traits of dominant tree species. Trees in depressions exhibited clear shade-adaptation characteristics, those on midslopes showed broad habitat adaptability, and hilltop species—constrained by intense light, high temperature, and exposed rock—displayed strong drought-adaptation features and conservative ecological strategies.

Keywords: karst seasonal rain forest, habitat heterogeneity, leaf micromorphology, photosynthetic characteristics, ecological adaptation

Introduction

Plant functional traits represent core attributes that respond to environmental changes and influence ecological functions. Widespread trade-offs among these traits, often termed ecological strategies, reflect adaptation to specific habitat conditions. In arid environments, one key ecological strategy involves the trade-off between maintaining photosynthetic efficiency and ensuring hydraulic transport safety. The former relates to light resource competition and carbon fixation capacity, while the latter concerns drought resistance and stress tolerance.

Leaves are vital organs for photosynthesis and water transport. Leaf anatomical structural traits are closely linked to photosynthetic efficiency. The epidermis provides a window for light entry into mesophyll tissue, palisade tissue contains abundant chloroplasts to maximize light energy absorption, and spongy tissue with large intercellular spaces facilitates gas transport. Leaf hydraulic safety traits are critical for drought tolerance. When water supply cannot meet transpiration demand, leaf water transport channels may collapse, causing embolism and threatening hydraulic safety. These traits involve leaf mechanical strength and vein conduit resistance to collapse, correlating with leaf hardness, cell wall thickness, cell arrangement compactness, and leaf mass per area. Additionally, stomatal traits—including size, density, and aperture—are closely associated with habitat adaptation strategies.

Plants employ key functional trait variations to cope with environmental changes, achieving trade-offs between photosynthetic efficiency and water transport safety. In humid regions, plants may prioritize photosynthetic efficiency to accumulate biomass and enhance competitive ability, with traits such as specific leaf area, canopy height, photosynthetic capacity, and stomatal conductance showing positive correlations with rainfall. In arid regions, plants may emphasize hydraulic safety, developing drought-resistant traits to maintain survival capacity. Drought-tolerant species typically exhibit greater leaf hardness, cuticle thickness, mesophyll tissue compactness, palisade tissue proportion, stomatal density, leaf nitrogen and phosphorus content, and dark respiration rate.

Karst seasonal rain forests represent unique vegetation developed under tropical karst geological conditions, characterized by strong habitat heterogeneity, diverse community types, and abundant endemic species. The Nonggang National Nature Reserve in Guangxi preserves typical primary karst seasonal rain forest in a classic peak-cluster depression landscape featuring a “peak-depression-peak” structure. Environmental factors such as light, water, soil conditions, and rock exposure rate change dramatically from depressions to hilltops, creating strong heterogeneity across different landform positions. To adapt to these heterogeneous habitats, plants adopt different survival strategies, forming niche differentiation along the peak-cluster depression gradient, with different species aggregating in specific karst landform positions and exhibiting rich community

types at local scales.

Previous studies have explored this niche distribution pattern from various perspectives. Zhang et al. (2021) found that branch and leaf hydraulic structural characteristics help explain plant niche differentiation patterns in karst peak-cluster depressions. Huang et al. (2019) discovered that leaf water use efficiency, measured using stable isotope techniques, differs among representative tree species in different karst habitats. However, it remains unclear how leaf structural and functional traits of dominant tree species in karst seasonal rain forests co-vary to achieve trade-offs between photosynthetic efficiency and hydraulic transport safety in response to drought gradients across different landform positions. Community-dominant species in different habitat types likely maintain a balance between resource competitiveness and drought tolerance to adapt to karst heterogeneity. Therefore, this study examined upper-canopy dominant tree species in Nonggang' s primary forest, measuring leaf micromorphology and photosynthetic physiological characteristics along with surrounding environmental factors to explore dominant species' survival strategies and their responses to karst habitat heterogeneity.

1.1 Study Area

This study focused on typical dominant tree species in the primary karst seasonal rain forest of Nonggang, Guangxi. The research site is located within the Nonggang National Nature Reserve (106°42' 28" -107°04' 54" E, 22°13' 56" -22°33' 09" N), which has a tropical monsoon climate with an annual mean temperature of 22°C, minimum and maximum temperatures of 13°C and 39°C, respectively, and annual precipitation of 1,150-1,550 mm. The rainy season extends from May to September, while the dry season lasts from November to February, creating distinct seasonal alternation.

Based on soil and vegetation distribution patterns, the forest habitats are classified into three types: (1) **Depressions** feature continuously distributed hydromorphic brown limestone soil (>60 cm depth), high canopy closure, short daily light duration, uneven rock distribution, year-round moisture, and potential waterlogging during seasonal rains. Dominant species include *Saraca dives*, *Horsfieldia kingii*, and *Ficus hispida*. (2) **Midslopes** have patchily distributed brown limestone soil (30-60 cm depth), adequate light, ~70% rock exposure, and moderate humidity. Dominant species include *Excentrodendron tonkinense*, *Garcinia paucinervis*, *Cephalomappa sinensis*, and *Diplodiscus trichospermus*. (3) **Hilltops** exhibit >90% rock exposure with black limestone soil in rock crevices (<30 cm depth), all-day direct sunlight, and summer surface temperatures reaching 60°C. Dominant species include *Sinosideroxylon pedunculatum*, *Boniodendron minus*, and *Pistacia weinmanniifolia*.

In 2011, we established a 15 ha dynamics monitoring plot in Nonggang' s karst seasonal rain forest, which contains a small hill and a complete depression, representing a "depression-midslope-hilltop" habitat gradient ranging from 184-

374 m in elevation (mean: 262.7 m), with an average slope of 41.7° and rock exposure of 68.8%. The plot contains 68,101 woody individuals with DBH \geq 1 cm, belonging to 223 species, 157 genera, and 56 families. Each tree has detailed records including ID, species, DBH, spatial coordinates, growth dynamics, and topographic factors, with vegetation comprising eight community types.

Table 1 Topographic factors (mean \pm standard deviation) around 90 sample trees of seven dominant species in the Nonggang plot

Species	Habitat	Elevation (m)	Slope (°)	Rock bareness rate (%)	Topographic wetness index	Altitude above channel (m)	
<i>Ficus hispida</i>	Depression	185.4 \pm 1.1	13.4 \pm 4.4	33.3 \pm 29.3	12.8 \pm 1.3	—	
		0.5 \pm 0.8	—	—	—	—	
		<i>Saraca dives</i> *					
		Depression	210.3 \pm 7.3	32.0 \pm 4.8	69.1 \pm 21.1	7.7 \pm 0.7	—
		0.7 \pm 2.2	—	—	—	—	
		<i>Garcinia paucinervis</i> *					
		Depression	212.0 \pm 4.4	35.2 \pm 3.2	83.4 \pm 14.9	7.5 \pm 0.5	—
<i>Diplodiscus trichospermus</i>		0.5 \pm 1.3	—	—	—	—	
		<i>Diplodiscus trichospermus</i> *					
		Midslope	262.5 \pm 25.3	46.9 \pm 8.7	65.7 \pm 17.8	6.5 \pm 0.7	3.7 \pm 6.9
		<i>Garcinia paucinervis</i> *					
		Midslope	268.2 \pm 21.0	43.5 \pm 8.5	76.0 \pm 10.8	7.3 \pm 0.6	—
		0.7 \pm 1.4	—	—	—	—	
		<i>Excentrodendron tonkinense</i> *					
<i>Boniodendron minus</i>		Midslope	293.6 \pm 44.0	38.3 \pm 11.2	70.8 \pm 29.8	6.7 \pm 1.3	0.2 \pm 2.4
		<i>Garcinia paucinervis</i> *					
		Hilltop	345.4 \pm 5.7	52.3 \pm 3.6	68.0 \pm 16.5	5.6 \pm 0.4	1.7 \pm 1.6
		<i>Boniodendron minus</i> *					
		Hilltop	352.3 \pm 3.6	50.5 \pm 5.7	91.5 \pm 6.1	5.2 \pm 0.2	9.2 \pm 3.9
		<i>Sinosideroxylon pedunculatum</i> *					
		Hilltop	353.4 \pm 7.4	59.3 \pm 11.0	96.8 \pm 3.0	5.0 \pm 0.3	10.5 \pm 5.1

Note: Higher drought index values indicate drier conditions; higher wetness index values indicate more humid conditions.

1.2.1 Leaf Sample Collection

Along the “depression-midslope-hilltop” gradient within the 15 ha plot, we selected three upper-canopy dominant species from each habitat type. For each species, we sampled 10 mature trees, collecting five mature leaves per tree. The selected species were: depression dominants (*Ficus hispida*, *Saraca dives*, *Garcinia paucinervis* from depression); midslope dominants (*Diplodiscus trichospermus*, *Garcinia paucinervis* from midslope, *Excentrodendron tonkinense*);

and hilltop dominants (*Garcinia paucinervis* from hilltop, *Boniodendron minus*, *Sinosideroxylon pedunculatum*).

Sampling procedures involved selecting mature individuals with DBH >10 cm. Using a pole pruner, we collected healthy canopy branches from four different directions, then removed mature functional leaves from the middle sections of branches. From each tree, we excised 5 leaf sections (0.5 cm × 0.5 cm) from the middle region between the midrib and leaf margin, avoiding main veins. Samples were immediately fixed in 2.5% glutaraldehyde solution, then transported to the laboratory for ethanol gradient dehydration, critical point drying, gold sputtering, and observation under a scanning electron microscope (ZEISS EVO18).

Using AxioVision SE64 Rel. 4.9.1 software, we measured leaf thickness (Lt), cuticle thickness (Ct), upper epidermis thickness (Et), lower epidermis thickness (Ht), palisade tissue thickness (Pt), spongy tissue thickness (St), stomatal length, stomatal width, and stomatal number. We calculated palisade/spongy ratio (Pt/St), leaf compactness (Pt/Lt), leaf looseness (St/Lt), stomatal aperture (SA), and stomatal density (SD). Each leaf was sectioned into multiple pieces for micromorphological trait measurement, with 5 random replicates per leaf. This yielded 2,250 data points per trait (3 habitats × 3 species × 10 trees × 5 leaves × 5 replicates).

We recorded each tree's ID in the 15 ha plot to extract surrounding topographic factor data (Table 1). The drought index and wetness index were used to characterize habitat conditions, with higher values indicating drier or more humid conditions, respectively.

1.2.2 Photosynthetic Physiological Measurements

During the growing season (late September to early October 2021), we measured photosynthetic parameters on clear days between 9:00–12:00. After 0.5–1 h of natural light induction, we used a LI-6400XT portable photosynthesis system for detached leaf measurements. CO₂ concentration was controlled at (400 ± 2) μmol·mol⁻¹, with photosynthetically active radiation gradient set at 2,000, 1,800, 1,500, 1,200, 1,000, 800, 500, 300, 200, 150 μmol·m⁻²·s⁻¹. Temperature was maintained at 25°C.

For each species, we measured 3–5 trees for net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO₂ concentration (Ci), and stomatal limitation coefficient (Ls). Light response curves were fitted using a modified rectangular hyperbola model to obtain apparent quantum efficiency (AQE), light saturation point (LSP), maximum net photosynthetic rate (Pn·max), light compensation point (LCP), dark respiration rate (Rd), maximum transpiration rate (Tr·max), and water use efficiency (WUE). Air temperature was recorded for subsequent analysis of habitat temperature effects on photosynthesis.

The light response curve was fitted using the modified rectangular hyperbola model:

$$\text{WUE} = \frac{P_n}{\text{Tr}}$$

where P_n is net photosynthetic rate and Tr is transpiration rate. The stomatal limitation value was calculated as $L_s = 1 - \frac{C_i}{C_a}$, where C_i is intercellular CO_2 concentration and C_a is atmospheric CO_2 concentration, reflecting stomatal limitations on photosynthesis.

1.3 Statistical Analysis

We used Photosynthesis Calculation Software 4.1.1 to fit light response curves and parameters, and R 4.2.0 for statistical analysis and plotting. Univariate linear regression analyzed relationships between leaf micromorphological/photosynthetic traits and elevation. Pearson correlation analysis examined relationships between leaf micromorphological and photosynthetic traits. In box plots, the four lines from bottom to top represent the 2.5th, 25th, 50th, 75th, and 97.5th percentiles, with circles indicating outliers beyond this range.

2.1 Leaf Micromorphology Across Habitats

All seven dominant species exhibited dorsiventral leaves with distinct palisade and spongy tissue differentiation (Fig. 1 [Figure 1: see original paper]). Leaf anatomical parameters varied among species (Fig. 2 [Figure 2: see original paper]). Among hilltop dominants, *Sinosideroxylon pedunculatum* showed the most drought-resistant structure, with maximum values for leaf thickness ($219.11 \pm 26.55 \mu\text{m}$), cuticle thickness ($7.27 \pm 1.12 \mu\text{m}$), and upper epidermis thickness ($44.01 \pm 7.25 \mu\text{m}$). *Boniiodendron minus* showed the second-highest drought tolerance. Among midslope dominants, *Excentrodendron* exhibited strong drought resistance with maximum lower epidermis thickness ($17.71 \pm 2.82 \mu\text{m}$), palisade tissue thickness ($17.71 \pm 2.82 \mu\text{m}$), while *Garcinia paucinervis* ranked second.

Depression dominants showed shade-adapted structures. *Saraca dives* had minimum values for palisade tissue thickness ($25.88 \pm 5.08 \mu\text{m}$), leaf compactness (0.26 ± 0.04), and stomatal aperture (0.26 ± 0.04). *Ficus hispida* had minimum cuticle thickness ($1.98 \pm 0.32 \mu\text{m}$), lower epidermis thickness ($9.27 \pm 1.67 \mu\text{m}$), and stomatal density ($787.9 \pm 117.3 \text{mm}^{-2}$), while *S. dives* had minimum stomatal density ($295.5 \pm 53.7 \text{mm}^{-2}$).

The widespread species *Garcinia paucinervis* exhibited plasticity across habitats. Depression individuals had maximum lower epidermis thickness and stomatal aperture; midslope individuals had maximum stomatal density, cuticle thickness, palisade tissue thickness, palisade/spongy ratio, and leaf compactness; hilltop individuals had maximum leaf thickness, spongy tissue thickness, upper epidermis thickness, and leaf looseness. This suggests midslope *G. paucinervis* had the strongest drought-resistant structure, followed by hilltop and depression populations, possibly related to decreasing rock exposure from depression to hilltop (Table 1).

Leaf micromorphological traits correlated with elevation (Fig. 3 [Figure 3: see original paper]). Nine indices—including palisade tissue thickness, leaf thickness, cuticle thickness, upper epidermis thickness, leaf compactness, palisade/spongy ratio, lower epidermis thickness, stomatal aperture, and spongy tissue thickness—increased significantly along the depression-midslope-hilltop gradient ($P < 0.05$), with palisade tissue thickness showing the strongest trend. Leaf looseness decreased significantly ($P < 0.05$). Stomatal density showed no significant change with elevation. These results indicate increasing xeromorphic structure with habitat gradient elevation: thicker leaves, cuticles, and palisade tissues, with decreasing spongy tissue proportion.

2.2 Photosynthetic Characteristics Across Habitats

Photosynthetic parameters varied among species (Fig. 4 [Figure 4: see original paper]). Among hilltop dominants, *Sinosideroxylon pedunculatum* had low WUE but maximum $Tr \cdot \max (5.0 \pm 0.9 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$, while *Boni dendron minus* showed broad light adaptation with maximum LCP ($19.1 \pm 2.5 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), $G_s \cdot \max (0.3 \pm 0.1 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$, and LSP ($2,427.6 \pm 13.6 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Among midslope dominants, *Diplodiscus trichospermus* showed high photosynthetic accumulation and consumption with maximum $P_n \cdot \max (13.4 \pm 1.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$ and $R_d (1.2 \pm 0.1 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$. Among depression dominants, *Sarcadives* had maximum $C_i \cdot \max (458.7 \pm 30.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1})$, while *Ficus hispida* had maximum AQE ($0.08 \pm 0.02 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Overall photosynthetic capacity ranked: midslope > depression > hilltop, with hilltop species showing clear limitations.

Garcinia paucinervis showed physiological plasticity across habitats. Depression individuals had maximum $P_n \cdot \max$, $G_s \cdot \max$, LSP, and AQE; midslope individuals had maximum WUE and $L_s \cdot \max$; hilltop individuals had maximum $Tr \cdot \max$, LCP, R_d , and $C_i \cdot \max$. This indicates highest photosynthetic efficiency in depressions, reduced efficiency due to stomatal and water limitations on midslopes, and increased transpiration and dark respiration costs under high temperatures on hilltops.

Photosynthetic traits correlated significantly with elevation (Fig. 5 [Figure 5: see original paper]). LCP, $Tr \cdot \max$, and R_d increased significantly with elevation ($P < 0.05$), indicating rising water loss and respiratory consumption. Conversely, WUE_{\max} , $C_i \cdot \max$, and AQE decreased significantly ($P < 0.05$), suggesting photosynthetic limitations at higher elevations. The decline in WUE_{\max} along the gradient resulted from disproportionately increasing $Tr \cdot \max$.

2.3 Correlation Between Leaf Micromorphology and Photosynthesis

Strong correlations existed between leaf micromorphology and photosynthetic traits (Fig. 6 [Figure 6: see original paper]). Palisade/spongy ratio was significantly positively correlated with LSP, R_d , $G_s \cdot \max$, and $P_n \cdot \max$ ($P < 0.01$), and with LCP and $Tr \cdot \max$ ($P < 0.05$), but negatively correlated with $L_s \cdot \max$

($P < 0.05$). Leaf compactness showed similar patterns, indicating that increased palisade tissue proportion enhanced tissue density, stomatal conductance, photosynthetic efficiency, and dark respiration while also correlating with drought resistance.

Leaf looseness was significantly negatively correlated with $Pn \cdot \max$ and LSP ($P < 0.01$), and with $Tr \cdot \max$, LCP, Rd , and $Gs \cdot \max$ ($P < 0.05$), but positively correlated with $Ls \cdot \max$ ($P < 0.05$). Increased leaf looseness reflects higher spongy tissue proportion and lower palisade proportion, showing opposite patterns to leaf compactness.

Upper epidermis thickness was significantly positively correlated with $Tr \cdot \max$ ($P < 0.05$). Thickened upper epidermis represents a xeromorphic trait that can limit water loss, while transpiration tends to increase under intense light and drought. Stomatal density was significantly positively correlated with stomatal conductance ($P < 0.05$) and marginally with Rd ($P < 0.1$), suggesting that denser stomatal structures facilitate gas exchange and may increase respiratory costs.

3 Discussion and Conclusion

The elevation gradient in this study reflects slope position changes in karst peak-cluster depressions, representing a comprehensive gradient of water and thermal conditions. Hilltops experience intense light, water deficit, large diurnal temperature ranges, high rock exposure, and thin soils; conditions are intermediate on midslopes and opposite in depressions. The seven dominant species showed widespread habitat associations in leaf micromorphology and photosynthetic traits, with trade-offs between photosynthetic efficiency and drought tolerance representing ecological strategies for coping with karst habitat heterogeneity.

3.1 Leaf Micromorphological Traits in Heterogeneous Habitats Leaf morphological changes reflect plant adaptation to heterogeneous habitats under selective pressure. Within a 200 m elevation range, we found increasing drought-resistant structure with habitat aridity. Plants tended to increase leaf compactness, thickness, cuticle thickness, upper epidermis thickness, palisade tissue thickness, and spongy tissue thickness. These anatomical enhancements likely improve leaf hydraulic safety and drought resistance. Overall, hilltop species showed the strongest drought tolerance, followed by midslope species, with depression species being least tolerant. The drought adaptation ranking was: *Boniodendron minus* > *Sinosideroxylon pedunculatum* > *Garcinia paucinervis* > *Excentrodendron tonkinense* > *Diplodiscus trichospermus* > *Saraca dives* > *Ficus hispida*, positively correlated with mean elevation and topographic drought index.

3.2 Photosynthetic Characteristics in Heterogeneous Habitats Photosynthetic traits are sensitive indicators of environmental adaptation, with evolution generally favoring enhanced photosynthetic capacity. Higher $Pn \cdot \max$ in-

icates greater photosynthetic potential, while high AQE and low LCP suggest strong weak-light utilization and shade tolerance. Under drought stress, stomatal limitation is a key factor reducing $P_n \cdot \max$. Depression species showed strong adaptation to weak light and humid conditions, consistent with their faster growth rates. Midslope species employed active drought-tolerance strategies, achieving highest WUE and photosynthetic potential, indicating highest habitat fitness. Hilltop species had higher LSP for strong-light adaptation but lowest average WUE due to disproportionate increases in transpiration and dark respiration relative to photosynthesis. This suggests hilltop species face combined stomatal and non-stomatal limitations, adopting conservative strategies for high temperature, intense light, and exposed rock.

Huang et al. (2019) used $\delta^{13}\text{C}$ isotopes to measure long-term WUE, finding it increased from depression to hilltop. Other studies show WUE increases under mild/moderate drought but decreases under severe drought. Our instantaneous WUE measurements from the rainy season (September–October, 9:00–12:00) showed a hump-shaped pattern along the gradient, with the decline caused by rising $\text{Tr} \cdot \max$. This temporal variability suggests hilltop plants may adopt “profligate” water-use strategies during the rainy season with high stomatal conductance and transpiration, but shift to more “conservative” strategies during the dry season (November–February) by reducing stomatal conductance and transpiration while increasing WUE to avoid carbon starvation. Dry-season experiments are needed to verify this.

3.3 Correlations Between Leaf Micromorphology and Photosynthesis

Mesophyll is the primary photosynthetic tissue, so changes in palisade/spongy tissue thickness and ratios inevitably affect photosynthetic efficiency. Leaf anatomy correlates closely with photosynthetic capacity, with light intensity differences across habitats driving anatomical changes that influence growth. Reduced leaf thickness, developed epidermal structures, and loose spongy tissue represent adaptations to weak light and ample water supply. Our results demonstrate that increased palisade proportion (higher leaf compactness and palisade/spongy ratio) significantly enhances photosynthetic capacity and strong-light utilization. Conversely, increased spongy proportion (higher leaf looseness) improves growth rate and weak-light utilization. These findings indicate that leaf functional traits are simultaneously driven by the dual demands of enhancing photosynthetic efficiency and drought tolerance, exhibiting clear trade-off strategies.

3.4 Limitations and Future Research This study has several limitations to address in future work. First, our focus on upper-canopy dominants from three typical habitats provides representative but not universally applicable results; broader species sampling is needed. Second, leaf micromorphological indices did not include vein structural traits, limiting assessment of leaf hydraulic safety. Third, trait trade-off strategies may be influenced by evolutionary history, requiring phylogenetic analysis. Fourth, survival strategy analysis

should incorporate community biotic environments, growth dynamics, and competitive abilities. Finally, photosynthetic processes vary temporally, and our instantaneous measurements during morning hours of the growing season have limitations; longer-term experiments are needed.

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Plate 1 Leaf stomata of seven dominant species (500-fold magnification, scale 20 μ m)

1: *Boniiodendron minus*; 2: *Sinosideroxylon pedunculatum*; 3: *Garcinia paucinerervis* (Hilltop); 4: *Diplodiscus trichospermus*; 5: *Excentrodendron tonkinense*; 6: *Garcinia paucinerervis* (Midslope); 7: *Ficus hispida*; 8: *Saraca dives*; 9: *Garcinia paucinerervis* (Depression).

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

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