Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Photosynthetic Characteristics of 13 Liana Species in a Karst Rocky Mountain Area:A Comparative Study of Woody and Herbaceous Growth Forms

Ningxin Li

1240040756@qq.com

Guangxi Institute of Botany https://orcid.org/0009-0005-4018-761X

Ting Chen

Guangxi Institute of Botany

Xin Li

Guilin University of Technology

Fuzhao Huang

Guangxi Institute of Botany

Shujun Wen

Guangxi Institute of Botany

Xuehan Liu

Guilin University of Technology

Chongyuan Qin

Guangxi Institute of Botany

Xiankun Li

Guangxi Institute of Botany

Shuhua Lu

Guangxi Institute of Botany https://orcid.org/0000-0002-2721-1727

Research Article

Keywords: lianas, karst ecosystem, photosynthetic traits, light response, functional strategy, gas exchange

Posted Date: November 10th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10838075/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations:

Figure 8 is not available with this version

Photosynthetic Characteristics of 13 Liana Species in a Karst Rocky Mountain Area:A Comparative Study of Woody and Herbaceous Growth Forms

Ningxin Li[1†], Ting Chen[1†], Xin Li[2†], Fuzhao Huang[1], Shujun Wen[1], Xuehan Liu[2], Chongyuan Qin[1], Xiankun Li[1], Shuhua Lu[1*]

[1] Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Chinese Academy of Sciences, Guangxi Zhuang Autonomous Region, Guilin 541006, China

[2] College of Tourism & Landscape Architecture, Guilin University of Technology, Guilin 541006, China

† These authors contributed equally to this work and should be considered co-first authors.

* Correspondence Email: lushuhua13@163.com.

Abstract

Lianas are important components of tropical and subtropical ecosystems, yet their photosynthetic adaptation and resource-use strategies under stressful karst environments remain poorly understood. In particular, whether woody and herbaceous lianas exhibit distinct photosynthetic strategies remains largely unknown. This study investigated the the photosynthetic characteristics and resource-use strategies of 13 dominant liana species (nine woody and four herbaceous) from karst rocky mountain area in northern Guangxi, China. Photosynthetic parameters were derived using the non-rectangular hyperbola model. Growth form differences were assessed via t-tests and Mann-Whitney U tests. Relationships among traits were explored using Pearson correlation and principal component analysis (PCA). Results showed considerable interspecific variation: A_{max} ranged from 4.00 to 13.39 μmol m^{-2} s^{-1} (mean 8.01), AQY from 0.028 to 0.095 (mean 0.070), LSP from 804 to 1538 μmol m^{-2} s^{-1} (mean 1098), and LCP from 14.0 to 38.1 μmol m^{-2} s^{-1} (mean 25.3). No significant differences were found between woody and herbaceous lianas for any parameter (Mann-Whitney U, all $p > 0.05$). PCA resolved two principal axes—resource acquisition-conservation and light-use-water economy—accounting for 64.3% of trait variation, but no clear separation by growth form was observed. Hierarchical clustering identified three clusters not strictly corresponding to growth form. Our findings demonstrate that photosynthetic differentiation in karst lianas is primarily associated with ecological strategies rather than growth-form differences. This suggests that selective pressures of the karst

environment may override morphological differences between growth forms. This study provides valuable baseline data on liana photosynthetic physiology in karst ecosystems.

Keywords: lianas; karst ecosystem; photosynthetic traits; light response; functional strategy; gas exchange

Introduction

Lianas are functionally important in forest ecosystems worldwide, and contributing significantly to forest biomass, carbon sequestration, nutrient cycling, and food web dynamics (Schnitzer 2002; Schnitzer 2005).Unlike self-supporting trees, lianas allocate less biomass to structural support and more to leaf production and canopy expansion, enabling rapid ascent to the canopy and effective competition for light (Chen el al. 2015). Previous studies have consistently shown that lianas maintain higher photosynthetic rates per unit leaf area than co-occurring trees, a pattern attributed to their lower allocation to stem support and higher allocation to leaf production (Avalos and Mulkey 2014; Slot and Winter 2017). Within climbing plants, woody lianas develop persistent, secondary-thickened stems, while herbaceous vines have non-woody, usually annual stems (Allen 2016). This distinction is ecologically important because woody and herbaceous species may differ in their resource allocation strategies, life history patterns, and responses to environmental stress (Allen 2016; Luo el al. 2026). Understanding these differences is essential for predicting the functional diversity of climbing plant communities and their responses to environmental change. Moreover, increasing evidence suggests that lianas are becoming more abundant in many tropical and subtropical forests under global environmental change, potentially altering forest dynamics, carbon cycling, and species interactions. Understanding their physiological strategies is therefore increasingly important for predicting forest responses to environmental change (Medina el al. 2022; Rueda el al. 2024; Schnitzer 2018).

Karst landscapes cover approximately 15% of the Earth's land surface and are particularly extensive in southwestern China (Liao el al. 2018; Li el al. 2021). This ecosystem is characterized by shallow, discontinuous limestone-derived soils with high calcium content, low water-holding capacity, and pronounced seasonal drought (Liu el al. 2021; Zhang el al. 2023). These factors create challenging conditions for plant growth, imposing strong selective pressures on the physiological traits of resident species (Xu and Zhang 2021). Karst landscapes are characterized

by high habitat heterogeneity, with sharp transitions between exposed rock surfaces, shallow soil patches, and deeper soil accumulations in fissures and depressions (Wang el al. 2019). The high environmental heterogeneity characteristic of karst landscapes creates a mosaic of microhabitats with contrasting resource availability, thereby promoting functional differentiation and diverse ecological strategies among plant species (Qiao el al. 2021; Valladares el al. 2007). Therefore, the karst ecosystem in southwestern China provides an ideal natural laboratory for studying the physiological adaptability and ecological strategies of plants under environmental stress.

Photosynthetic light-response curves provide an effective framework for evaluating plant carbon assimilation, light-use efficiency, and physiological adaptation to heterogeneous environments (Dusenge el al. 2019; Ye el al. 2013). The derived parameters, including apparent quantum yield (AQY), maximum net photosynthetic rate (A_{max}), light saturation point (LSP), light compensation point (LCP), and dark respiration rate (R_d), collectively characterize species-specific strategies of light capture, carbon gain, and resource use (Mejdová el al. 2021). Combined with gas-exchange traits, such as stomatal conductance (Cond), intercellular CO_2 concentration (C_i), transpiration rate (Trmmol), and water-use efficiency (WUE), these measurements provide mechanistic insights into plant responses to environmental stress (Flexas el al. 2014; Lemonnier and Lawson 2024). Because photosynthetic performance is strongly influenced by environmental conditions, light-response analysis has become a widely used tool for evaluating plant physiological adaptation to resource limitation and environmental stress (Herrmann el al. 2020). At present, numerous studies have been conducted on the photosynthetic characteristics of plants in karst regions. The photosynthetic characteristics of *Cladrastis platycarpa* (Maxim.) Makino (Jiang el al. 2017), *Zanthoxylum bungeanum* (Liu el al. 2021), *Coriaria nepalensis* Wall (Qin el al. 2022), and *Pueraria lobata* (P. lobata) (Li el al. 2025) were studied in karst regions. Furthermore, a previous study have shown that evergreen and deciduous tree species adopt contrasting photosynthetic strategies in response to karst environmental conditions (Jiang el al. 2025). However, previous studies have mainly focused on the photosynthetic traits of mature woody and herbaceous plants in karst forests, whereas those of lianas remain poorly understood (Jiang el al. 2025; Schnitzer and Bongers 2011). In particular, whether woody and herbaceous lianas differ significantly in their photosynthetic light-response

characteristics under resource-limited karst conditions remains unclear (Mejdová el al. 2021). To address this knowledge gap, this study aimed to (1) characterize the photosynthetic performance and resource-use strategies of karst lianas; (2) identify the physiological trade-offs and functional dimensions driving interspecific differentiation in photosynthetic strategies; and (3) compare photosynthetic strategies between woody and herbaceous lianas. The findings will improve our understanding of the adaptive mechanisms of karst lianas and provide a scientific basis for selecting suitable species for vegetation restoration in environmentally heterogeneous karst habitats.

Materials and Methods

Study Site and species selection

The study was conducted in a typical karst rocky mountain area in Gongcheng Yao Autonomous County (24.8-25.1 N, 110.3-110.6 E), Guangxi Zhuang Autonomous Region, southwestern China. The region is characterized by a typical subtropical karst mountainous landscape dominated by limestone hills. The climate is subtropical monsoon, with a mean annual temperature of 20.0 °C and an average annual precipitation of 1517.5 mm. Karst habitats are characterized by shallow discontinuous soils, extensive rock exposure, high calcium availability, and pronounced environmental heterogeneity, leading to frequent seasonal water limitation (Guo el al. 2022). The vegetation is dominated by secondary shrublands and commercial plum orchards, with only scattered secondary evergreen-deciduous broadleaf forests, but supports abundant liana communities.

In 2024, based on the investigation of the original sample plots in the study region,the importance values of all liana species were calculated, and 13 dominant species were selected for analysis, including nine woody lianas and four herbaceous lianas (Table 1). Species identification followed the Flora of China and was confirmed by local botanical experts. One representative individual per species with healthy mature leaves was selected for measurement.

Table 1. List of the 13 studied liana species.

No.	Species	Family	Genus	Growth Form
1	*Causonis japonica*	*Vitaceae*	*Causonis*	Herbaceous
2	*Phanera championii*	*Fabaceae*	*Phanera*	Woody
3	*Trichosanthes kirilowii*	*Cucurbitaceae*	*Trichosanthes*	Herbaceous
4	*Parthenocissus dalzielii*	*Vitaceae*	*Parthenocissus*	Woody
5	*Smilax glaucochina*	*Smilacaceae*	*Smilax*	Woody
6	*Trachelospermum jasminoides*	*Apocynaceae*	*Trachelospermum*	Woody
7	*Kadsura heteroclita*	*Schisandraceae*	*Kadsura*	Woody
8	*Dioscorea polystachya*	*Dioscoreaceae*	*Dioscorea*	Herbaceous
9	*Ipomoea obscura*	*Convolvulaceae*	*Ipomoea*	Herbaceous
10	*Akebia trifoliata*	*Lardizabalaceae*	*Akebia*	Woody
11	*Lonicera japonica*	*Caprifoliaceae*	*Lonicera*	Woody
12	*Vitis amurensis*	*Vitaceae*	*Vitis*	Woody
13	*Mallotus repandus*	*Euphorbiaceae*	*Mallotus*	Woody

Light Response Curve Measurements

Photosynthetic light-response curves were measured using a LI-6400XT portable photosynthesis system (LI-COR Biosciences, Lincoln, NE, USA) during the peak growing season (July–August 2024). Measurements were conducted between 08:00 and 11:30 on clear days using fully expanded mature leaves or leaflets. Photosynthetically active radiation (PAR) was sequentially decreased from 1800 to 0 μmol m^{-2} s^{-1} at 12 irradiance levels (1800, 1500, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, and 0 μmol m^{-2} s^{-1}). Chamber CO_2 concentration was maintained at 400 μmol m^{-2} s^{-1}, leaf temperature at 26 ± 2℃, and relative humidity at 50–70%. Before measurements, leaves were acclimated under saturating light (1000–1200 μmol m^{-2} s^{-1}) until photosynthetic rates stabilized (Okamoto el al. 2022). Three healthy individuals were selected for each species, and one fully expanded leaf was measured per individual. Each measurement was repeated three times, and the mean value was used for subsequent analyses.

Curve Fitting

Light-response curves were fitted using the non-rectangular hyperbola model, which is widely used to describe plant photosynthetic responses under different irradiance conditions (Ye el al. 2013). By incorporating a curvature parameter (θ), this model provides a biologically

realistic representation of the transition from light limitation to light saturation and allows the estimation of key photosynthetic parameters, including AQY, A_{max}, R_d, LCP, and LSP (Ye el al. 2013; Yang el al. 2025).The non-rectangular hyperbola model is expressed as follow:

$$P_n = \frac{\alpha PAR + A_{\max} - \sqrt{(\alpha PAR + A_{\max})^2 - 4\theta\alpha A_{\max} PAR}}{2\theta} - R_d$$

where α represents AQY and θ represents the curvature parameter, which was fixed at 0.8 according to previous studies. LSP was defined as the PAR value corresponding to 95% of A_{max}, whereas LCP was determined as the PAR value at which net photosynthesis equals zero. Model parameters were estimated using nonlinear least-squares regression implemented in Python 3.14(SciPy).

Gas Exchange and Chlorophyll

Steady-state gas exchange measurements were conducted using the LI-6400XT system under saturating light conditions (PAR = 1200 μmol m^{-2} s^{-1}). Measurements were recorded after photosynthetic parameters stabilized, with coefficients of variation for net photosynthetic rate (Pn), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) maintained below 0.5% for at least 30 s before data logging. Leaf temperature was maintained at 26 ± 2℃, and leaf-to-air vapor pressure deficit (VPD) was maintained below 2.0 kPa to minimize stomatal limitation (Liu el al. 2025).Gas exchange parameters including Pn, g_s, C_i, and transpiration rate (E) were recorded. Water-use efficiency (WUE) was calculated as Pn/E. Leaf chlorophyll content was measured using a SPAD-502 Plus meter (Konica Minolta, Japan), with five readings averaged per leaf.

Statistical Analysis

All statistical analyses were performed using Python with relevant statistical and visualization packages. Descriptive statistics, including mean, standard deviation, and coefficient of variation, were calculated for each photosynthetic trait. Normality and homogeneity of variance were assessed using the Shapiro–Wilk and Levene tests, respectively. Differences in photosynthetic traits between woody and herbaceous lianas were evaluated using the Mann–Whitney U test due to the small and unequal sample sizes between growth forms. Pearson correlation analysis was conducted to examine relationships among photosynthetic parameters.

Principal component analysis (PCA) was performed using standardized variables (zero mean and unit variance) to identify major axes of variation in photosynthetic strategies. The number of retained components was determined based on eigenvalues >1 (Kaiser criterion) and further evaluated using scree plots. Hierarchical clustering was conducted using Ward's minimum variance method with Euclidean distance, and cluster separation was assessed using silhouette coefficients. All statistical tests were two-tailed with a significance threshold of $P < 0.05$.

Results

Light Response Characteristics and Interspecific Variation

The fitted light-response curves (Figure 1) revealed a typical photosynthetic response pattern among the karst lianas, characterized by a rapid increase in net photosynthetic rate under low irradiance followed by gradual saturation at higher light levels. However, considerable interspecific differences were observed across the entire irradiance gradient. Vitis amurensis exhibited the highest photosynthetic performance, with the highest curve plateau and maximum net photosynthetic rate, whereas Trachelospermum jasminoides and Dioscorea polystachya maintained relatively lower photosynthetic rates throughout the light gradient.

The significant variation in photosynthetic parameters among the 13 liana species (Figure 2) further indicates diverse photosynthetic strategies and adaptive mechanisms in response to heterogeneous karst environments. Among the woody lianas, *Vitis amurensis* (A_{max} = 13.39 μmol m^{-2} s^{-1}) and *Akebia trifoliata* (A_{max} = 11.25 μmol m^{-2} s^{-1}) exhibited the highest photosynthetic capacities, indicating adaptation to high-light environments such as bare rock, forest edges and canopy gaps. These species also showed high Rd values (2.18 and 1.76 μmol m^{-2} s^{-1} respectively), suggesting substantial metabolic investment in photosynthetic machinery. In contrast, *Trachelospermum jasminoides* (A_{max} = 4.26 μmol m^{-2} s^{-1}) and *Mallotus repandus* (A_{max} = 5.87 μmol m^{-2} s^{-1}) showed the lowest A_{max} values among woody lianas, consistent with a shade-tolerant strategy. Among herbaceous lianas, *Causonis japonica* (A_{max} = 10.60 μmol m^{-2} s^{-1}) and *Ipomoea obscura* (A_{max} = 10.55 μmol m^{-2} s^{-1}) showed relatively high photosynthetic capacities, comparable to the high-performing woody species, while *Dioscorea polystachya* showed the lowest A_{max} of

all 13 species (3.99 μmol m^{-2} s^{-1}). The range of AQY values (0.028-0.095 μmol m^{-2} s^{-1}) spans most of the expected range for C_3 plants, with the exceptionally low AQY of *T. jasminoides* (0.028) suggesting possible photosynthetic down-regulation under the low-light conditions of its typical karst habitat.

Photosynthetic light-response parameters differed markedly among the 13 dominant liana species (Figure 2). Mean A_{max} was 8.01 ± 2.80 μmol m^{-2} s^{-1}, ranging from 3.99 μmol m^{-2} s^{-1} in *Dioscorea polystachya* to 13.39 μmol m^{-2} s^{-1} in *Vitis amurensis*. Among all parameters, A_{max} showed the greatest interspecific variation (CV = 34.9%), whereas LSP was the least variable (CV = 15.6%). AQY, LCP, and R_d also exhibited considerable interspecific variation (CV = 27.2–28.6%).

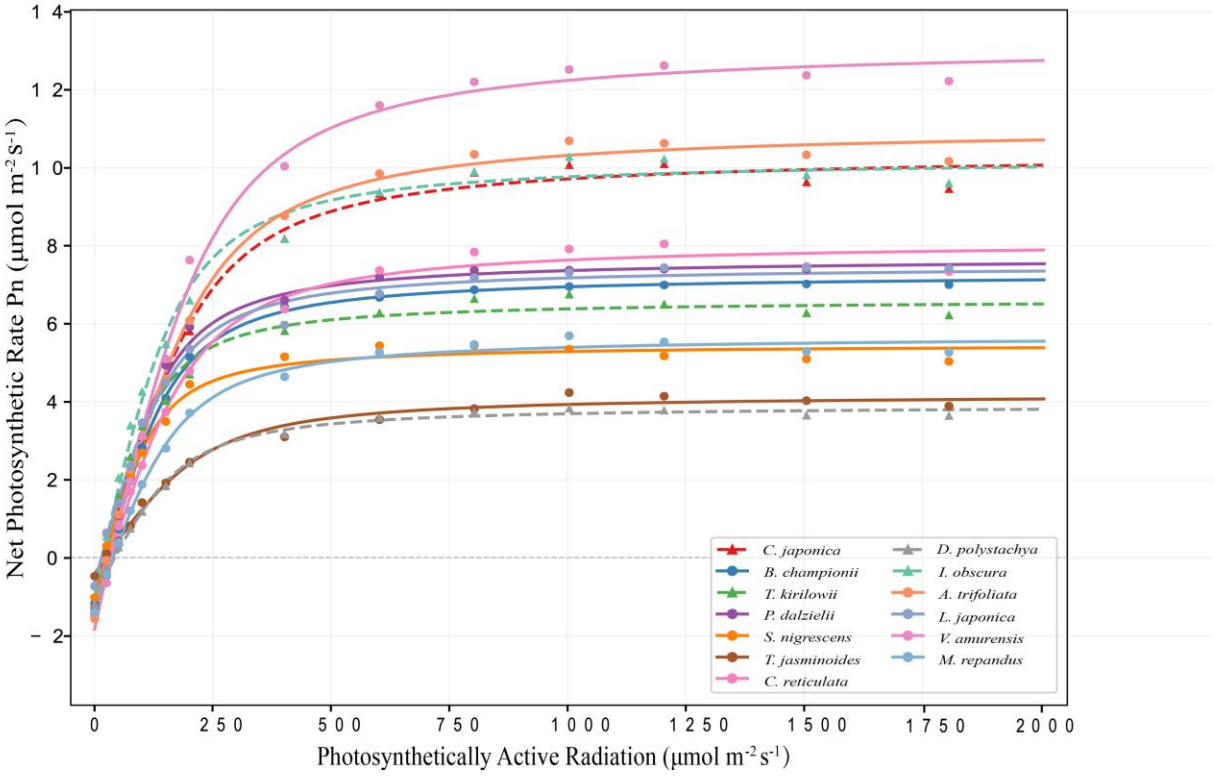


Figure 1. Light response curves of 13 liana species fitted with the non-rectangular hyperbola model.

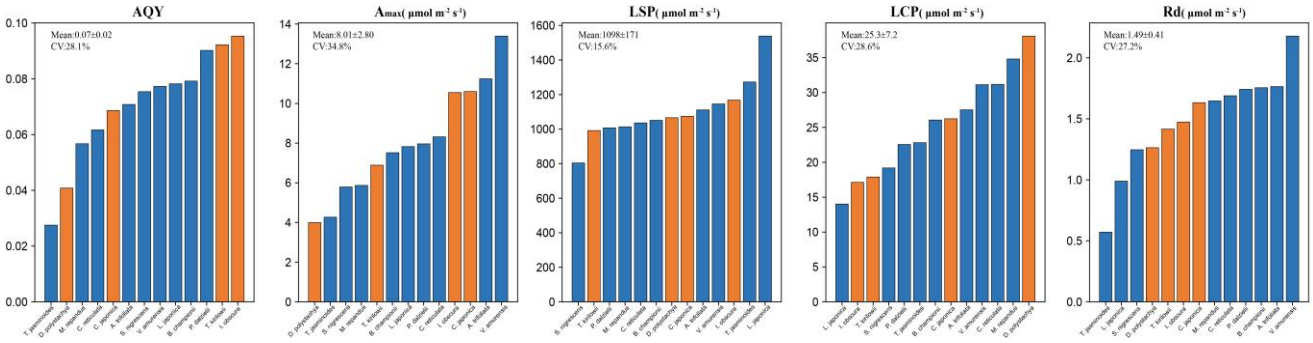


Figure 2. Variation in photosynthetic light-response parameters among 13 liana species.

Note: CV represents the coefficient of variation between species.

Comparison Between Growth Forms

No statistically significant differences were found between woody and herbaceous lianas for any of the 11 measured parameters based on Mann–Whitney U tests (all $P > 0.05$; Table 2). P-values ranged from 0.260 (for C_i) to 1.000 (for LSP). Woody lianas exhibited slightly higher mean values for LSP , R_d and WUE , whereas herbaceous lianas had marginally higher means for AQY, Cond and C_i.

The boxplot comparisons (Figure 3) and mean light-response curves with 95% bootstrap confidence intervals (Figure 4) visually confirm the extensive overlap between the two growth forms. Notably,woody lianas slightly greater interspecific variation than herbaceous lianas, with higher coefficients of variation for most measured traits, particularly LSP and R_d. Overall, within-group variation among species exceeded the differences between growth forms, indicating that photosynthetic trait variation was not clearly separated by woody versus herbaceous growth habits. This pattern was further supported by the largely overlapping light-response curves between the two growth forms (Figure 4).

Table 2. Descriptive statistics and Mann-Whitney U test results.

Parameter	Woody Mean ± SD	Woody CV	Herb Mean ± SD	Herb CV	U	p
AQY	0.069 ± 0.018	26.68%	0.074 ± 0.025	34.05%	14.0	0.604
A_{max}	8.02 ± 2.81	35.10%	8.01 ± 3.19	39.83%	19.0	0.940
LSP	1108.6 ± 204.3	18.43%	1074.9 ± 72.1	6.71%	18.0	1.000
LCP	25.47 ± 6.54	25.68%	24.84 ± 9.74	39.23%	20.0	0.825
R_d	1.51 ± 0.49	32.24%	1.45 ± 0.15	10.54%	24.0	0.414

Photo	7.77 ± 2.75	35.45%	7.73 ± 3.11	40.21%	19.0	0.940
Cond	0.211 ± 0.066	35.88%	0.232 ± 0.097	41.91%	15.0	0.711
C_i	239.6 ± 15.5	6.47%	249.3 ± 17.0	6.81%	10.0	0.260
Trmmol	3.76 ± 1.43	38.00%	4.08 ± 1.40	34.24%	15.0	0.711
WUE	2.22 ± 0.64	28.42%	1.90 ± 0.43	22.33%	24.0	0.414
Chl	26.98 ± 7.76	28.77%	25.25 ± 2.67	10.56%	19.0	0.940
Mean	-	28.27%	-	26.02%	-	-

213 *Note: All p-values from Mann-Whitney U tests. None significant at alpha = 0.05.*

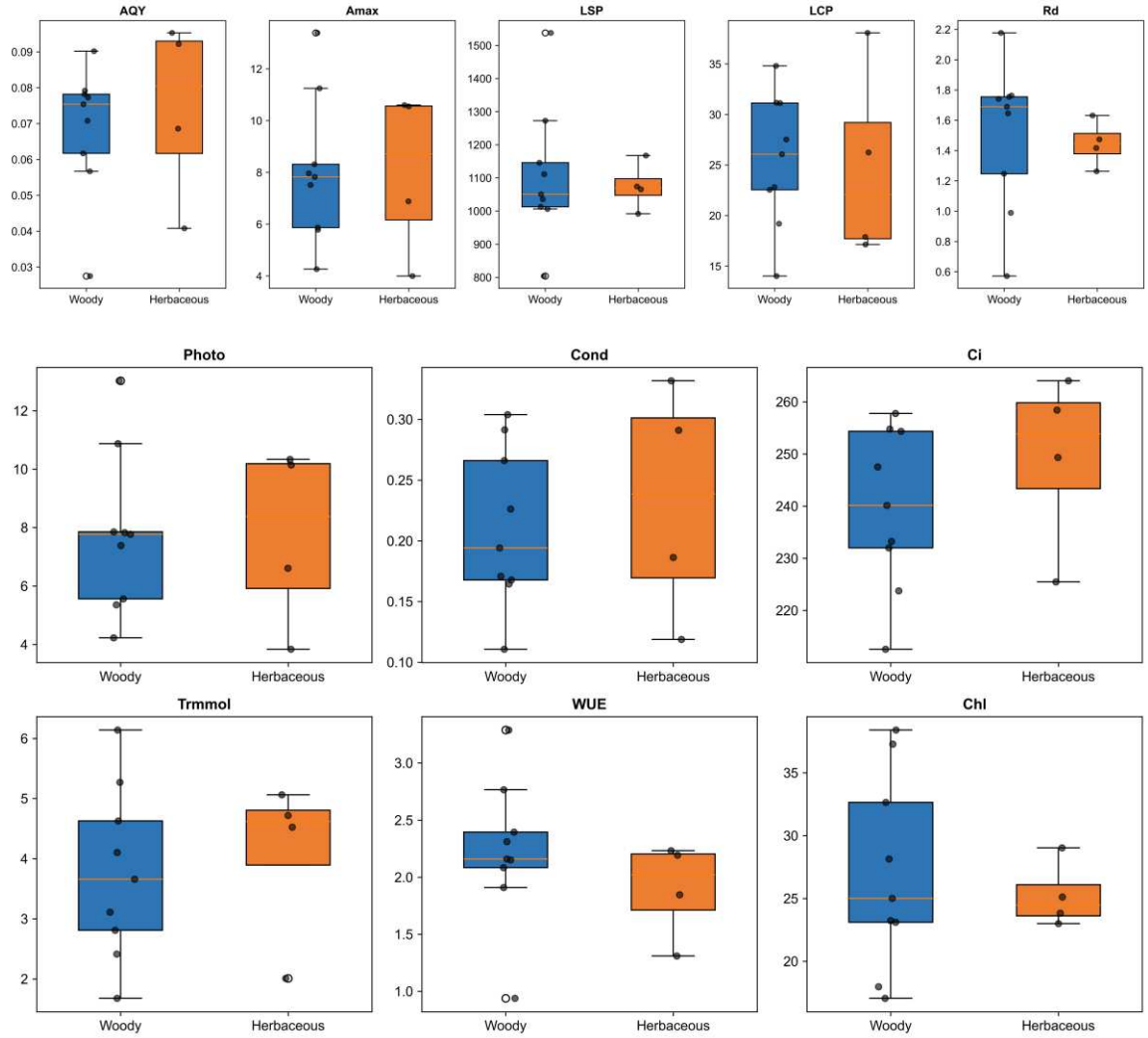


Figure 3. The boxplot comparison of photosynthetic parameters between woody and herbaceous lianas.

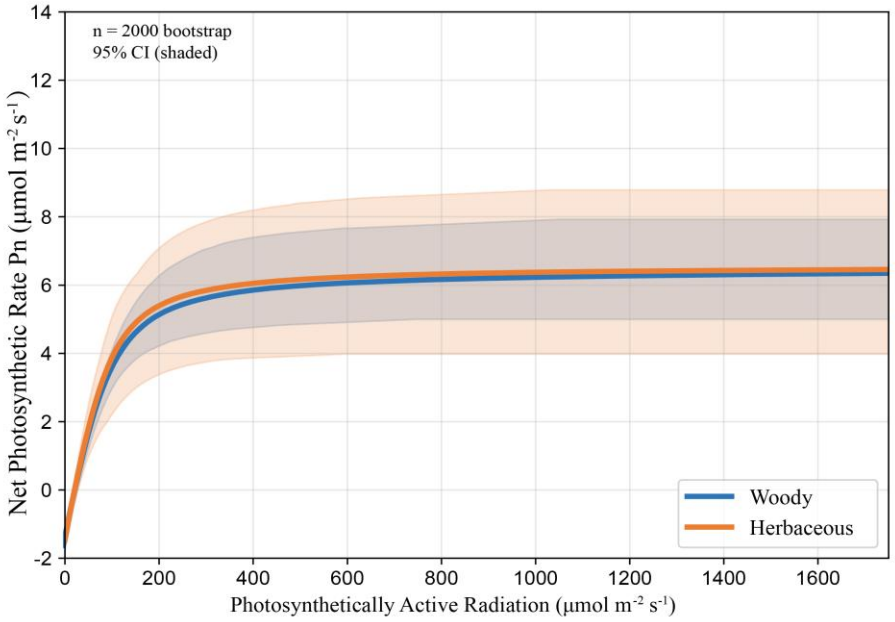


Figure 4. Mean light response curves with 95% bootstrap confidence intervals for woody and herbaceous lianas.

Correlation Analysis

Pearson correlation analysis revealed several significant relationships among photosynthetic traits (Figure 5). The strong positive correlation between A_{max} and R_d is a well-documented relationship in plant physiology, reflecting the metabolic cost of maintaining photosynthetic capacity. A_{max} was positively correlated with R_d and Trmmol, indicating that higher photosynthetic capacity is associated with higher maintenance respiration and transpiration rates. Stomatal conductance (Cond) showed strong positive correlations with C_i, Trmmol, and Photo, highlighting the central role of stomatal regulation in coupling CO_2 supply, water loss and carbon gain. AQY was positively correlated with A_{max} and negatively with LCP, suggesting that species with higher quantum efficiency tend to have higher photosynthetic capacity and lower light compensation points, consistent with adaptation to low-light environments. WUE exhibited negative correlations with C_i and Cond, though these were not statistically significant, reflecting the expected trade-off between carbon gain and water conservation. Chlorophyll showed generally weak correlations with other parameters.

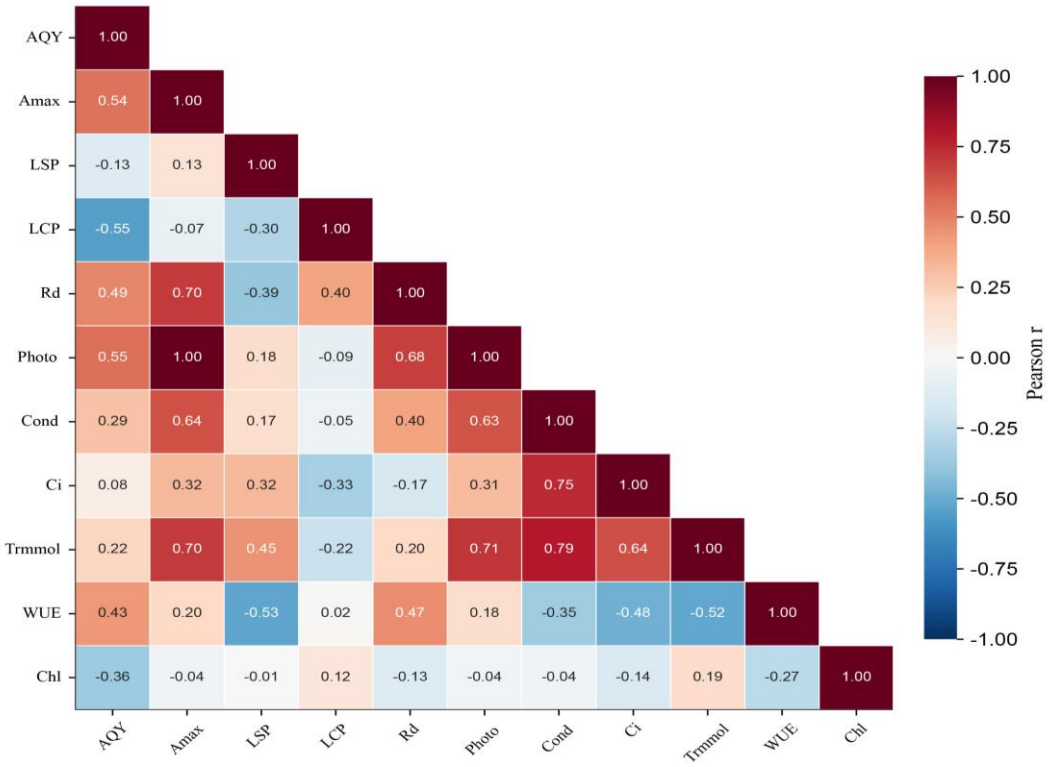


Figure 5. Pearson correlation matrix of photosynthetic parameters.

Principal Component Analysis

Principal component analysis (PCA) was performed on the 11 standardized photosynthetic parameters (Figure 6). The first two principal components had eigenvalues > 1.0 and cumulatively explained 64.3% of the total variance (PC1: 38.6%, PC2: 25.7%). PC1 was mainly associated with A_{max}, Photo, R_d, Trmmol and Cond, representing an axis of overall photosynthetic capacity and gas exchange activity. PC2 was primarily related to variation in AQY, LCP, and WUE, reflecting differences in light-use efficiency and water-use characteristics.

The PCA biplot showed a continuous distribution of the 13 liana species along the two functional axes, with extensive overlap between woody and herbaceous lianas and no clear separation by growth form. Species with high PC1 scores, such as *Vitis amurensis* and *Adenia trifoliata*, were associated with greater photosynthetic capacity and gas exchange activity, whereas species with low PC1 scores, such as *Trachelospermum jasminoides* and *Dioscorea polystachya*, exhibited relatively lower photosynthetic performance. *Ipomoea obscura* was

positioned at the positive end of PC2, consistent with its high AQY and efficient light utilization capacity. The result revealed continuous variation in photosynthetic trait combinations among karst lianas, suggesting diverse ecological strategies rather than distinct functional separation between woody and herbaceous growth forms.

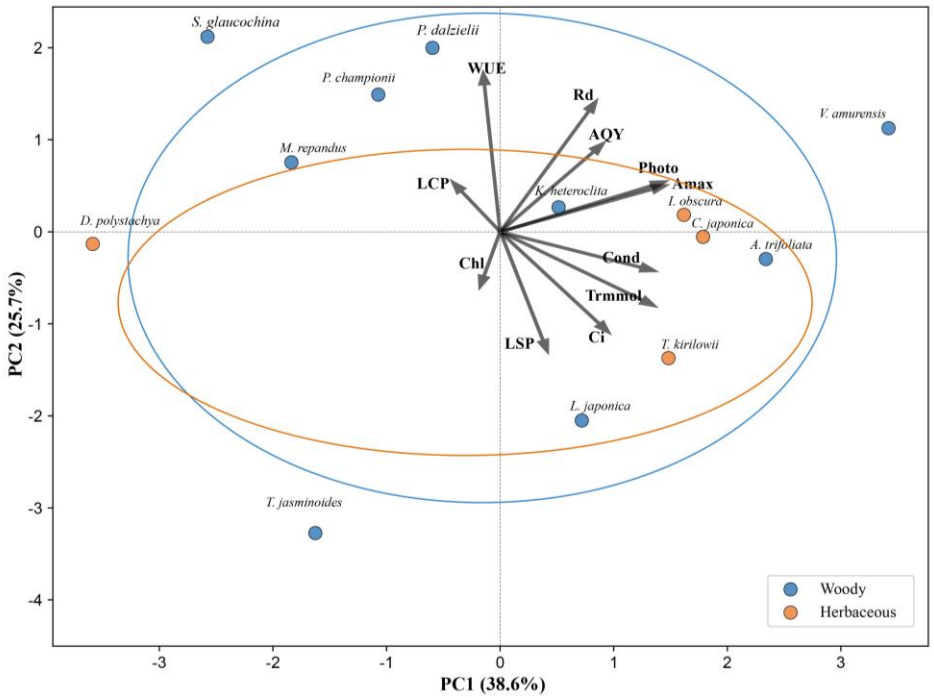


Figure 6. PCA biplot of photosynthetic parameters for 13 liana species.

Note:Ellipses represent 95% confidence intervals for woody and herbaceous lianas.

Clustering Analysis

Hierarchical clustering based on Ward's method and Euclidean distance classified the 13 liana species into three clusters according to their photosynthetic trait profiles (Figure 8).The cophenetic correlation coefficient of the three-cluster solution was 0.85, indicating a good fit between the clustering structure and the original distance matrix.

Ward clustering grouped the 13 species into three clusters. Cluster 1 contained four woody and three herbaceous species, and showed intermediate values for most photosynthetic traits. Cluster 2 included four woody and one herbaceous species, and was characterized by relatively higher photosynthetic capacity and gas-exchange parameters. Cluster 3 contained only *T.*

jasminoides, which exhibited the lowest AQY, low A_{max} and R_d, but relatively high chlorophyll content. The three clusters contained species from both woody and herbaceous growth forms, showing no clear correspondence with growth-form classification.

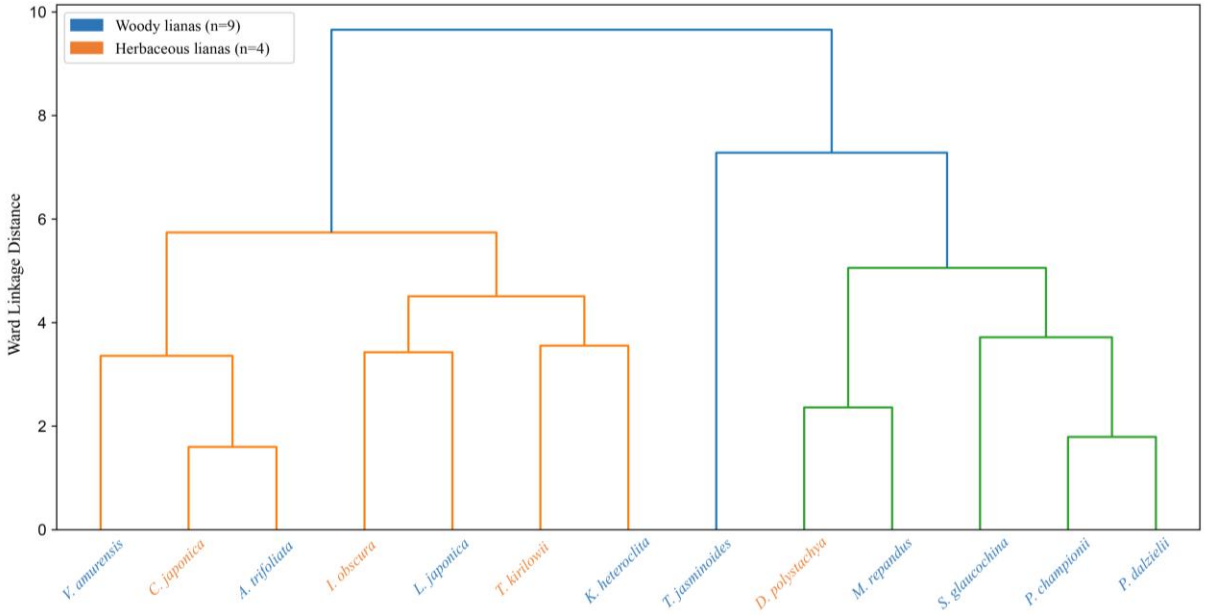


Figure 7. Cluster Analysis of 13 liana Species based on photosynthetic traits.

Discussion

Photosynthetic Characteristics and Strategies of Karst Lianas

The mean maximum net photosynthetic rate (A_{max}) of karst lianas was 8.01 μmol m^{-2} s^{-1}, which was comparable to values reported for lianas in other tropical and subtropical forests. Chen et al. reported A_{max} of 5-10 μmol m^{-2} s^{-1} for lianas in Xishuangbanna (Chen el al. 2015), while Slot and Winter reported comparable A_{max} values for tropical lianas in lowland rainforest environments (Slot el al. 2024). This comparability with more mesic environments is notable given the additional edaphic constraints of the karst habitat-shallow discontinuous soils, high $CaCO_3$ content, alkaline pH and pronounced seasonal drought (Li el al. 2021; Liu el al. 2021; Zhang el al. 2023), and confirms that lianas maintain competitive carbon gain across diverse conditions, consistent with their strategy of prioritizing leaf production over stem structural investment (Avalos and Mulkey 2014; Rueda 2024). The mean apparent quantum yield (AQY) of

0.070 μmol umol^{-1} falls within the typical C_3 plant range of 0.04-0.09 (Yang el al. 2025) and is comparable to values reported for tropical lianas (Chen el al. 2015). The relatively high LSP(1098 μmol m^{-2} s^{-1}) and low LCP(25.3 μmol m^{-2} s^{-1}) suggest that karst lianas possess broad light adaptability, allowing efficient carbon gain across contrasting light environments and promoting their persistence in heterogeneous karst landscapes (Yan el al. 2025; Zhang el al. 2020). The mean R_d of 1.49 μmol m^{-2} s^{-1} is comparable to tropical liana values (Santiago and Wright 2007). Notably, the mean WUE of karst lianas (2.12 μmol mol^{-1}) was lower than values reported for tropical lianas and woody plants, suggesting a relatively less conservative water-use strategy characterized by greater investment in carbon gain rather than strict water conservation (Slot el al. 2024). This may be associated with frequent agricultural activities (fertilization and irrigation). On one hand, adequate water supply maintains high stomatal conductance and transpiration, reducing instantaneous WUE; on the other hand, agricultural practices alter soil properties and promote vegetative growth and leaf expansion, further exacerbating transpirational water loss (Liu el al. 2026; White el al. 2016).

Species-level variation revealed divergent photosynthetic strategies among karst lianas. *Vitis amurensis* exhibited a high carbon-acquisition strategy, characterized by greater photosynthetic capacity and respiratory investment, consistent with the fast end of the plant economics spectrum, while *Trachelospermum jasminoides* (A_{max} = 4.23) and *Dioscorea polystachya* (A_{max} = 3.99) adopt strategies that prioritize light capture efficiency over maximum photosynthetic rate (Givnish 2015; Reich 2014). *Lonicera japonica* displays the highest LSP (1538 μmol m^{-2} s^{-1}) and LCP (14.0 μmol m^{-2} s^{-1}), suggesting broad ecological amplitude with tolerance of both shaded and high-light microsites. This diversity of photosynthetic strategies within a single growth form community is consistent with niche differentiation along light gradients as a mechanism for species coexistence (Kraft el al. 2015). Particularly in karst landscapes, heterogeneous light environments may promote the coexistence of liana species exhibiting divergent photosynthetic strategies (Valladares el al. 2007). Notably, the relatively high coefficients of variation among photosynthetic parameters across the 13 liana species (CV = 15.6%–34.9%) reveal pronounced interspecific differentiation in photosynthetic traits. Similar patterns have been reported for karst

297 adapted plants, where functional trait variation reflects diverse strategies for coping with
298 heterogeneous and resource-limited environments (Pang el al. 2023). These variations suggest
299 that karst lianas occupy different positions along a photosynthetic strategy continuum, ranging
300 from rapid carbon acquisition to conservative resource-use strategies (Reich 2014). Such
301 differentiation may enhance species coexistence by allowing lianas to exploit distinct
302 microhabitats within the heterogeneous karst landscape (Medina el al. 2021).

303 **Photosynthetic Trait Coordination and Strategy Differentiation**

304 Photosynthetic traits are often coordinated rather than independently regulated, and their
305 covariation reflects fundamental trade-offs underlying plant resource-use strategies (Onoda el al.
306 2017). In this study, the significant positive correlation between A_{max} and R_d indicates a
307 physiological trade-off between carbon gain and metabolic maintenance costs, and consistent
308 with the global leaf economics spectrum (Reich 2014). The positive relationship between A_{max}
309 and transpiration rate (Trmmol) reflects the coupling between carbon gain and water loss, as
310 higher photosynthetic capacity usually requires greater stomatal opening and transpirational
311 investment (Anderegg el al. 2018). The negative correlation between AQY and LCP indicates a
312 trade-off between low-light carbon acquisition efficiency and light requirements (Flexas el al.
313 2004). Similarly, the significant correlations between stomatal conductance and gas exchange
314 traits (Cond–C_i and Cond–Trmmol) demonstrate the central role of stomatal regulation in
315 coordinating CO_2 uptake and water loss (Buckley 2019). However, the negative relationships
316 between WUE and C_i and between WUE and Cond indicate that enhanced carbon assimilation is
317 accompanied by increased water consumption (Xiong el al. 2017). Such carbon–water trade-offs
318 are particularly important for karst lianas, where shallow soils and low water retention capacity
319 impose seasonal drought constraints, promoting diverse strategies from rapid carbon acquisition
320 to conservative water use (Ding el al. 2021; Wu el al. 2021).

321 The two strategy axes identified by PCA correspond well with established plant functional
322 frameworks, representing gradients of resource acquisition–conservation and light–use–water
323 economy (Díaz el al. 2016). Similar multidimensional strategy spaces have been reported in

other liana studies. For instance, Liu et al. identified three functional spectra among tropical lianas, including tissue toughness, water use, and nutrient–carbon acquisition, which correspond well with the metabolic capacity and light–water economy axes observed in our study (Liu el al. 2021). Zhang et al. further demonstrated that PCA clearly separated savanna lianas from tropical rainforest lianas along a resource acquisition–conservation axis, with savanna species exhibiting more conservative strategies (Zhang el al. 2022). In karst environments specifically, PCA based studies have also classified plants into quick-gain (herb and liana), slow-gain (arbor), and transitional (shrub) types (Zhang el al. 2020). Consistently, our hierarchical clustering further identified three ecological function groups among karst lianas, including intermediate, acquisitive, and shade-adapted types. This further demonstrates that liana communities also exhibit comparable differentiation in resource-use strategies.

Functional Convergence between Growth Forms and Ecological Implications

However, unlike the clear functional divergence often observed between herbaceous and woody plants(Lou el al. 2026), woody and herbaceous lianas in this study showed no distinct separation in PCA space, with extensive overlap between the two groups. This pattern was further supported by the largely overlapping light-response curves of the two growth forms, which exhibited comparable photosynthetic responses across the irradiance gradient, indicating convergence in leaf-level photosynthetic strategies. This suggests that growth form differences were not the primary determinant of photosynthetic strategies in karst lianas (Díaz el al. 2016; Kunstler el al. 2016). Under strong environmental filtering imposed by shallow soils, seasonal drought, and high irradiance, both woody and herbaceous lianas may converge toward similar leaf-level physiological solutions to maintain carbon balance (Kraft el al. 2015; Laughlin el al. 2014; Liu el al. 2024). Moreover, because both growth forms share a climbing strategy that reduces structural investment and enhances leaf carbon acquisition, stem morphological differences may exert weaker effects on leaf-level photosynthetic differentiation than environmental constraints (Givnish 2015). The lack of strict correspondence between functional clusters and growth forms further suggests that (Figure7), under the strong environmental constraints of karst habitats, environment factors such as heterogeneous light availability, shallow

soils, and seasonal water limitation may exert stronger influences than stem morphology in shaping photosynthetic differentiation and leaf trait variation (Wyka el al. 2013; Zhang el al. 2020).

Together, these analyses indicate that photosynthetic variation in karst lianas reflects ecological strategy differentiation along a resource acquisition and light-use continuum rather than growth form divergence. Such functional diversity may be maintained by the heterogeneous light, soil, and water conditions characteristic of karst habitats, which create diverse ecological niches for species with contrasting resource-use strategies (Wu el al. 2021). The coexistence of high carbon-acquisition and conservative strategies within the liana community may facilitate species coexistence by enabling different species to exploit contrasting light and water conditions in karst habitats (Liu el al. 2021; Zhou el al. 2022). In highly heterogeneous karst habitat, this functional differentiation may contribute to community stability by buffering environmental fluctuations and increasing ecosystem resilience under recurrent drought and resource limitations (Liu el al. 2021; Zhou el al. 2022). Therefore, the maintenance of diverse photosynthetic strategies among karst lianas represents an important mechanism supporting species coexistence and vegetation persistence in stressful karst ecosystems.

Conclusions

This study examined the photosynthetic traits and ecological strategies of 13 liana species from in a karst region of northern Guangxi. Despite shallow alkaline soils and seasonal drought, these lianas maintained effective carbon assimilation, with trait trade-offs evident between carbon gain, metabolic cost, light use, and water regulation. Woody and herbaceous lianas showed convergent photosynthetic responses, indicating that strong environmental filtering overrides growth-form differences at the leaf level. Conversely, substantial interspecific variation positioned species along a continuous resource-use spectrum—from acquisitive to conservative—likely reflecting niche partitioning driven by heterogeneous light, soil, and moisture conditions. Overall, our findings demonstrate that both environmental filtering and habitat heterogeneity jointly shape functional adaptation and diversity in karst liana communities. Future work

integrating seasonal dynamics, intraspecific trait plasticity, and additional functional traits will further advance our understanding of liana adaptation and support vegetation management in these ecologically fragile karst landscapes.

Author contribution statement This work was designed by XL and SL. NL, TC and XL performed the experiments and collected the data.Technical support was provided by SW and FH. NL, XL and CQ analysed the data. NL, TC and XL developed the figures and prepared the manuscript. SL reviewed and edited the manuscript. All authors participated in data interpretation and manuscript revision.

Acknowledgements This study was supported by Guangxi Key Research and Development Programme Project (Gui Ke AB24010024, Gui Ke FN2600640371).

Conflict of interest statement The authors have no conflicts of interest to declare that are relevant to the contents of this article.

References

Allen BP (2016) Patterns of Liana Abundance, Diversity and Distribution in Temperate Forests. In: Parthasarathy, N. Biodiversity of Lianas. Sustainable Development and Biodiversity. vol 5. Cham: Springer. https://doi.org/10.1007/978-3-319-14592-12

Anderegg WRL, Konings AG, Trugman AT, Yu K, Bowling DR, Gabbitas R, Karp DS, Pacala S, Sperry JS, Sulman BN, Zenes N (2018) Hydraulic diversity of forests regulates ecosystem resilience during drought. Nature 561:538–541. https://doi.org/10.1038/s41586-018-0535-7

Avalos G, Mulkey SS (2014) Photosynthetic and morphological acclimation of seedlings of tropical lianas to changes in the light environment. American Journal of Botany 101:2088–2096. https://doi.org/10.3732/ajb.1400127

Buckley TN (2019) How do stomata respond to water status? New Phytologist 224:21–36. https://doi.org/10.1111/nph.15899

Chen YJ, Cao KF, Schnitzer SA, Fan ZX, Zhang JL, Bongers F (2015) Water-use advantage for lianas over trees in tropical seasonal forests. New Phytologist 205:128–136. https://doi.org/10.1111/nph.13036.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Zanne AE, Chave J, Gorné LD (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Ding Y, Nie Y, Chen H, Wang K, Querejeta JI (2021) Water uptake depth is coordinated with leaf water potential, water-use efficiency and drought vulnerability in karst vegetation. New Phytologist 229:1339–1353. https://doi.org/10.1111/nph.16971

Dusenge ME, Duarte AG, Way DA (2019) Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. New Phytologist 221:32–49. https://doi.org/10.1111/nph.15283

Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004) Diffusive and Metabolic Limitations to Photosynthesis under Drought and Salinity in C_3 Plants. Plant Biology 6:269–279. https://doi.org/10.1055/s-2004-820867

Flexas J, Carriquí M, Coopman RE, Gago J, Galmés J, Martorell S, Morales F, Diaz-Espejo A (2014) Stomatal and mesophyll conductances to CO2 in different plant groups: Underrated factors for predicting leaf photosynthesis responses to climate change? Plant Science 226:41–48. https://doi.org/10.1016/j.plantsci.2014.06.011

Givnish TJ (2015) Adaptation to sun and shade: A whole-plant perspective. Annual Review of Ecology, Evolution, and Systematics 46:233–257. https://doi.org/10.1146/annurev-ecolsys-112414-054241

Guo YL, Li YF, Li JX, Li JQ, Wen SJ, Huang FZ, He W, Wang B, Lu SH, Li DX, Xiang WS, Li XK(2022) Comparison of Aboveground Vegetation and Soil Seed Bank Composition among Three Typical Vegetation Types in the Karst Regions of Southwest China. Agronomy 12(8): 1871. https://doi.org/10.3390/agronomy12081871

Herrmann HA, Schwartz JM, Johnson GN (2020) From empirical to theoretical models of light response curves – linking photosynthetic and metabolic acclimation. Photosynthesis Research 145:5–14. https://doi.org/10.1007/s11120-019-00681-2

Jiang X, Su C, Wu S, Zhang X (2017) Photosynthetic and physiological characteristics of Cladrastis platycarpa (Maxim.) Makino in spring in dolomite rocky hills of karst region. Guangdong

Agricultural Sciences 44:41–47. https://doi.org/10.16768/j.issn.1004-874X.2017.09.007
Jiang X, Zhou H, Zhao W, Cui Y, Hou Y, Zhou T, Hu F, Wu P (2025) The Impact of Microhabitat and Microtopography on the Photosynthetic Characteristics of Typical Karst Forest Plants in Guizhou, China. Forests 16(3):532. https://doi.org/10.3390/f16030532
Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29(5):592–599. https://doi.org/10.1111/1365-2435.12345
Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ, Aiba M, Westoby M (2016) Plant functional traits have globally consistent effects on competition. Nature 529:204–207 https://doi.org/10.1038/nature16476
Laughlin DC (2014) The intrinsic dimensionality of plant traits and its relevance to community assembly. Journal of Ecology 102:186–193. https://doi.org/10.1111/1365-2745.12187
Lemonnier P, Lawson T (2024) Calvin cycle and guard cell metabolism impact stomatal function. Seminars in Cell & Developmental Biology 155:59–70. https://doi.org/10.1016/j.semcdb.2023.03.001.
Li SL, Liu CQ, Chen JA, Wang SJ (2021) Karst ecosystem and environment: Characteristics, evolution processes, and sustainable development. Agriculture, Ecosystems & Environment 203:107173. https://doi.org/10.1016/j.agee.2020.107173
Li X, Wei Y, Liu J, Ma J, Luo Q, Huang F (2025) Photosynthetic Responses of Two Plant Species on Karst Highway Slopes During Drought in Guangxi, China. Polish Journal of Environmental Studies 34(4):4189–4200. https://doi.org/10.15244/pjoes/188453
Liao CJ, Yue YM, Wang KL, Fensholt R, Tong XW, Brandt M (2018) Ecological restoration enhances ecosystem health in the karst regions of southwest China. Ecological Indicators 90:416–425. https://doi.org/10.1016/j.ecolind.2018.03.036
Liu CN, Huang Y, Wu F, Liu WJ, Ning YQ, Huang ZR, Tang SQ, Liang Y (2021) Plant adaptability in karst regions. Journal of Plant Research 134:889–906. https://doi.org/10.1007/s10265-021-01330-3
Liu H, Yu Y, Xiong K, Zhang S, Yang S (2021) Response characteristics of photosynthesis to light intensity of three non-wood forests tree species in karst habitat. Journal of Southern Agriculture 52:2507–2515. https://d.wanfangdata.com.cn/periodical/gxnykx202109021
Liu Q, Jin W, Huang L, Wang D, Xu K, Wei Y (2025) Photosynthetic Induction Characteristics in Saplings of Four Sun-Demanding Trees and Shrubs. Plants 14(1):144. https://doi.org/10.3390/plants14010144
Liu Q, Sterck FJ, Zhang JL, Scheire A, Konings E, Cao M, Sha LQ, Poorter L (2021) Traits, strategies, and niches of liana species in a tropical seasonal rainforest. Oecologia 196:499–514. https://doi.org/10.1007/s00442-021-04937-4
Liu X, Liao P, Li X, Hou Z, Compson ZG, Song Q, Luan F, Fang X, Huang D, Yang Q, Liu J (2026) Lianas and trees exhibit distinct hydraulic and functional traits in a subtropical forest. Functional Ecology 40:280–293. https://doi.org/10.1111/1365-2435.70226
Liu Y, Tao J, He Y, Yu L, Yan L, Du Y, Liu J (2024) Soil depth drives community assembly and functional traits of karst shrubland. Basic and Applied Ecology 80:40–48. https://doi.org/10.1016/j.baae.2024.09.005.
Luo JL, Li JL, Sun Y, Degen AA, Wang XT, Xiong JL, Aqeel M, Xie SB, Tang D, Li F, Hu WG, Dong LW, Peng J, Hou QQ, Deng Y, Ran JZ, Deng JM (2026) Differential resource acquisition strategies of herbaceous and woody plants in temperate forests. BMC Plant Biology 26:196. https://doi.org/10.1186/s12870-025-08026-z

Medina-Vega JA, Bongers F, Poorter L, Schnitzer SA, Sterck FJ (2021) Lianas have more acquisitive traits than trees in a dry but not in a wet forest. Journal of Ecology 109:2367–2384. https://doi.org/10.1111/1365-2745.13644

Medina-Vega JA, Wright SJ, Bongers F, Schnitzer SA, Sterck FJ (2022) Vegetative phenologies of lianas and trees in two Neotropical forests with contrasting rainfall regimes. New Phytologist 235:457–471. https://doi.org/10.1111/nph.18150

Mejdová M, Dušek J, Foltýnová L, Macálková L, Čížková H (2021) Photosynthetic parameters of a sedge-grass marsh as a big-leaf: effect of plant species composition. Scientific Reports 11:3723. https://doi.org/10.1038/s41598-021-82382-2

Okamoto A, Koyama K, Bhusal N (2022) Diurnal Change of the Photosynthetic Light-Response Curve of Buckbean (Menyanthes trifoliata), an Emergent Aquatic Plant. Plants 11(2):174.https://doi.org/10.3390/plants11020174

Onoda Y, Wright IJ, Evans JR, Hikosaka K, Kitajima K, Niinemets Ü, Poorter H, Tosens T, Westoby M (2017) Physiological and structural tradeoffs underlying the leaf economics spectrum. New Phytologist 214:1447–1463. https://doi.org/10.1111/nph.14496

Pang S, Ou Z, Ye S, Wu Z, Shen W, He F, Lu G (2023) Variation and correlation of photosynthetic traits of eight adaptive plants in karst region of Southwest Guangxi. Guihaia 43(3):536–546. https://www.sciengine.com/doi/10.11931/guihaia.gxzw202203099.

Qiao Y, Jiang Y, Zhang C (2021) Contribution of karst ecological restoration engineering to vegetation greening in southwest China during recent decade. Ecological Indicators 121:107081. https://doi.org/10.1016/j.ecolind.2020.107081

Qin X, Xing D, Wu Y, Wang W, Li M, Solangi K (2022) Diurnal Variation in Transport and Use of Intracellular Leaf Water and Related Photosynthesis in Three Karst Plants. Agronomy 12(11):2758. https://doi.org/10.3390/agronomy12112758

Reich PB (2014) The world-wide "fast–slow" plant economics spectrum: A traits manifesto. Journal of Ecology 102(2):275–301. https://doi.org/10.1111/1365-2745.12211

Rueda-Trujillo MA, Veldhuis MP, van Bodegom PM, Deurwaerder HPT, Visser M (2024) Global increase of lianas in tropical forests. Global Change Biology 30:e17485. https://doi.org/10.1111/gcb.17485

Santiago LS, Wright SJ (2007) Leaf functional traits of tropical forest plants in relation to growth form. Biotropica 39(3):306–317. https://doi.org/10.1111/j.1744-7429.2007.00271.x

Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166(2):262–276. https://doi.org/10.1086/431250

Schnitzer SA (2018) Testing ecological theory with lianas. New Phytologist 220:366–380. https://doi.org/10.1111/nph.15431

Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends in Ecology and Evolution 17(5):223–230. https://doi.org/10.1111/j.1461-0248.2011.01590.x

Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecology Letters 14:397–406. https://doi.org/10.1016/S0169-5347(02)02491-6

Slot M, Rifai SW, Eze CE, Winter K (2024) The stomatal response to vapor pressure deficit drives the apparent temperature response of photosynthesis in tropical forests. New Phytologist 244:1238–1249. https://doi.org/10.1111/nph.19806

Slot M, Winter K (2017) In situ temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall regimes. New

Phytologist 214:1103–1117. https://doi.org/10.1111/nph.14469
Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New Phytologist 176:749–763. https://doi.org/10.1111/j.1469-8137.2007.02275.x
Wang KL, Zhang CH, Chen HS, Yue YM, Zhang W, Zhang MY, Qi XK, Fu ZY (2019) Karst landscapes of China: patterns, ecosystem processes and services. Landscape Ecology 34:2743–2763. https://doi.org/10.1007/s10980-019-00912-w
White DA, Beadle CL, Worledge D, Honeysett JL (2016) Wood production per evapotranspiration was increased by irrigation in plantations of Eucalyptus globulus and E. nitens. New Forests 47(2):303–317. https://doi.org/10.1007/s11056-015-9516-2
Wu Z, Behzad HM, He Q, Wu C, Bai Y, Jiang Y (2021) Seasonal transpiration dynamics of evergreen Ligustrum lucidum linked with water source and water-use strategy in a limestone karst area, southwest China. Journal of Hydrology 597:126199. https://doi.org/10.1016/j.jhydrol.2021.126199
Wyka TP, Oleksyn J, Karolewski P, Schnitzer SA (2013) Phenotypic correlates of the lianescent growth form: a review. Annals of Botany 112(9):1667–1681. https://doi.org/10.1093/aob/mct236
Xiong D, Flexas J, Yu T, Peng S, Huang J (2017) Leaf anatomy mediates coordination of leaf hydraulic conductance and mesophyll conductance to CO2 in Oryza. New Phytologist 213:572–583. https://doi.org/10.1111/nph.14186
Xu E, Zhang H (2021) Human–desertification coupling relationship in a karst region of China. Land Degradation & Development 32:4988–5003. https://doi.org/10.1002/ldr.4085
Yan Y, Li B, Dechant B, Xu M, Luo X, Qu S, Miao G, Leng J, Shang R, Shu L, Jiang C, Wang H, Jeong S, Ryu Y, Chen JM (2025) Plant traits shape global spatiotemporal variations in photosynthetic efficiency. Nature Plants 11:924–934. https://doi.org/10.1038/s41477-025-01958-2.
Yang XL, An T, Ye ZWY, Kang HJ, Robakowski P, Ye ZP, Wang FB, Zhou SX (2025) Modeling light response of effective quantum efficiency of photosystem II for C3 and C4 crops. Frontiers in Plant Science 16:1478346. https://doi.org/10.3389/fpls.2025.1478346
Ye ZP, Suggett DJ, Robakowski P, Kang HJ (2013) A mechanistic model for the photosynthesis–light response based on the photosynthetic electron transport of photosystem II in C3 and C4 species. New Phytologist 199:110–120. https://doi.org/10.1111/nph.12242
Zhang H, Zhang W (2023) Plant–Soil Interactions in Karst Regions. Forests 14:922. https://doi.org/10.3390/f14050922
Zhang SH, Zhang Y, Xiong KN, Yu YH, Min XY (2020) Changes of leaf functional traits in karst rocky desertification ecological environment and the driving factors. Global Ecology and Conservation 24:e01381. https://doi.org/10.1016/j.gecco.2020.e01381.
Zhang YB, Yang D, Zhang KY, Bai XL, Wang YSD, Wu HD, Ding LZ, Zhang YJ, Zhang JL (2022) Higher water and nutrient use efficiencies in savanna than in rainforest lianas result in no difference in photosynthesis. Tree Physiology 42(1):145–159. https://doi.org/10.1093/treephys/tpab099
ZZhou H, Xu X, Jiang X, Ding B, Wu P, Ding F (2022) Plant Functional Trait Responses to Dolomite and Limestone Karst Forests in Southwest China. Forests 13(12):2187. https://doi.org/10.3390/f13122187