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Variation and Correlation of Photosynthetic Traits among Eight Adapted Plant Species in the Karst Region of Southwestern Guangxi (Postprint)

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Abstract

To explore the photosynthetic physiological adaptation mechanisms of karst plants, the Li-6400XT portable photosynthesis measurement system was employed to measure and analyze photosynthetic characteristic parameters including leaf net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO2 concentration (Ci), transpiration rate (Tr), water use efficiency (WUE), and stomatal limitation value (Ls) for eight adapted plant species in the karst area of Pingguo City, Guangxi. The results indicated that all six photosynthetic characteristic parameters exhibited varying degrees of variation both within and among species, with intraspecific variation being greater than interspecific variation in all cases. The variations in Gs and Tr were primarily attributed to interspecific variation (46.72%-49.76%), whereas the variations in Pn, Ci, WUE, and Ls were mainly derived from intraspecific variation (48.66%-64.50%). At the life-form level, intraspecific variation in Pn, Gs, and Tr was lower in evergreen plants than in deciduous plants, while the opposite pattern was observed for Ci, WUE, and Ls. Interspecific variation for all parameters was greater in deciduous plants than in evergreen plants. Regardless of whether within or among species, Gs showed the greatest overall variation, followed by Tr and Pn, then Ls and WUE, with Ci being the smallest. Pn, Gs, and Tr were significantly positively correlated with each other ($P<0.01$); Ls was significantly positively correlated with WUE ($P<0.05$) and significantly negatively correlated with Gs and Ci ($P<0.05$). These relationships were generally consistent with those at the global scale, reflecting plants' resource trade-off strategies and confirming the existence of the Leaf Economics Spectrum (LES) in karst plants. Evergreen plants exhibited higher Ls and WUE but lower Gs, Tr, Ci, and Pn, positioning them closer to the "slow investment-return" type species characterized by high WUE,

low transpiration, and low photosynthesis along the LES, whereas deciduous plants showed the opposite traits, locating them at the "fast investment-return" type species end characterized by low WUE, high transpiration, and high photosynthesis. This demonstrates that plants adopt different survival strategies to adapt to changing environments through coordination and trade-offs among traits. The findings provide a scientific basis for subsequent screening of suitable species and accelerating vegetation restoration and succession processes.

Full Text

Variation and Correlation of Photosynthetic Traits in Eight Adaptive Plant Species in the Karst Region of Southwest Guangxi

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Abstract: To explore the photosynthetic physiological adaptation mechanisms of karst plants, we measured and analyzed six photosynthetic parameters in eight adaptive plant species in the karst region of Pingguo City, Guangxi, using a Li-6400XT portable photosynthesis system. The parameters included net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO2 concentration (Ci), transpiration rate (Tr), water use efficiency (WUE), and stomatal limitation value (Ls). The results revealed that all six photosynthetic parameters exhibited varying degrees of variation both within and between species, with intraspecific variation consistently exceeding interspecific variation. Changes in Gs and Tr primarily originated from interspecific variation (46.72%–49.76%), whereas variations in Pn, Ci, WUE, and Ls were mainly derived from intraspecific variation (48.66%–64.50%). At the life-form level, intraspecific variation in Pn, Gs, and Tr was lower in evergreen species than in deciduous species, while the opposite pattern was observed for Ci, WUE, and Ls. Interspecific variation for all parameters was greater in deciduous species than in evergreen species. Overall, Gs showed the greatest variation at both intraspecific and interspecific levels, followed by Tr and Pn, then Ls and WUE, with Ci showing the least variation. Significant positive correlations were observed among Pn, Gs, and Tr ($P<0.01$). Ls was significantly positively correlated with WUE ($P<0.05$) and significantly negatively correlated with Gs and Ci ($P<0.05$). These relationships align with global-scale patterns, reflecting plant resource trade-off strategies and confirming the existence of a leaf economics spectrum (LES) in karst plants. Evergreen species exhibited higher Ls and WUE but lower Gs, Tr, Ci, and Pn, positioning them closer to the "slow investment-return" end of the LES characterized by high WUE, low transpiration, and low photosynthesis. In contrast, deciduous species showed the opposite pattern, occupying the "fast investment-return" end with low WUE, high transpiration, and high pho-

tosynthesis. This demonstrates that plants employ different survival strategies through coordinated trade-offs among traits to adapt to variable environments. These findings provide a scientific basis for selecting suitable species and accelerating vegetation restoration succession in karst regions.

Keywords: photosynthetic traits, intraspecific variation, interspecific variation, leaf economics spectrum, karst

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Photosynthesis is the process by which plants convert light energy into chemical energy, representing the most critical physiological process for plant biomass accumulation and metabolism. It plays a vital role in energy conversion in nature and maintaining atmospheric carbon-oxygen balance (Pan & Wang, 2016). Photosynthesis is influenced not only by leaf intrinsic traits but also by external environmental factors such as light, temperature, humidity, CO2 concentration, and water availability, which elicit different ecological adaptive responses and mechanisms (Robert et al., 2007; Chi et al., 2014). Leaf photosynthetic physiology has long been a focal point in plant ecophysiological research (Cao et al., 2012; Tan et al., 2019).

In recent years, the negative and potential impacts of climate change on global ecosystems and biodiversity have attracted widespread societal attention (Wang & Wang, 2015). Leaf traits are highly sensitive to climate change and can accurately reflect plant responses and adaptation mechanisms (Scoffoni et al., 2011; Xiao et al., 2016). Consequently, numerous ecological studies have focused on leaves as research subjects (Wright et al., 2004; Read & Moorhead, 2014; Xun et al., 2020; Pang et al., 2021a). The proposal of the leaf economics spectrum (LES) has provided new theoretical frameworks and methodologies for ecological research (Sakschewski et al., 2015; Song et al., 2016), offering scientific foundations for better understanding plant adaptation mechanisms in the context of global climate change. The LES represents a suite of interconnected, co-varying traits that quantifies a continuum of plant resource trade-off strategies. One end of the spectrum comprises "fast investment-return" species, while the opposite end consists of "slow investment-return" species, with transitional gradient types in between (Wright et al., 2004; Chen & Xu, 2014; Jin & Wang, 2015). Since its inception, LES research has been conducted globally, validating its universal existence across different scales, taxonomic groups, ecosystems, and trait indicators (Sakschewski et al., 2015; Asner et al., 2016; Zirbel et al., 2017; Zhu et al., 2018), although some studies have reported divergent or contradictory results (Messier et al., 2017). The LES theory requires further validation and application.

Research on LES in China remains limited, particularly regarding extreme and special habitats. The karst region of Southwest China covers 540,000 km^2 of exposed carbonate rock, representing the largest area, most intense karst development, most complete geomorphological types, and most fragile ecological environment globally (He et al., 2019). This region features unique, complex, and highly heterogeneous geological backgrounds, with severe underground loss of soil and water, limiting vegetation growth. Once destroyed, vegetation is extremely difficult to restore, potentially triggering or exacerbating rocky desertification. Water deficit is the primary limiting factor for vegetation growth, distribution, and restoration (Gu et al., 2015; Tan et al., 2019). Karst vegetation has evolved unique morphological structures and physiological adaptation mechanisms (Ni et al., 2019; Huang et al., 2021), providing an excellent system for exploring photosynthetic physiology and underlying ecological mechanisms. Current research on karst plant photosynthesis has primarily focused on comparisons among different species or under controlled environmental factors (Luo et al., 2019; Li et al., 2020; Ou et al., 2020), with limited investigation into photosynthetic physiological responses and adaptive regulation mechanisms during vegetation restoration in degraded karst ecosystems. This study examined eight adaptive plant species in the karst region of Southwest Guangxi to address three questions: (1) Do photosynthetic parameters differ among species and life forms? (2) What are the characteristics of intraspecific and interspecific variation in photosynthetic parameters? (3) Can LES theory be validated at the local scale? Answering these questions will objectively reflect the physiological adaptation mechanisms of karst plants, reveal community assembly and maintenance mechanisms, and provide scientific foundations for comprehensive rocky desertification control and ecological restoration in Southwest China' s karst regions.

1.1 Study Area Description

The study site was located in Wangli Village, Taiping Town, Pingguo City, Guangxi (107°28 24 E, 23°35 10 N), at an elevation of 402.0–667.5 m. The region has a south subtropical monsoon climate with abundant sunlight, high heat, and plentiful rainfall concurrent with high temperatures. Mean annual sunshine duration is 1,682.7 h, mean annual temperature ranges from 18.1 to 21.5 °C, and mean annual precipitation is 1,400–1,550 mm, concentrated from May to September (accounting for over 70% of annual rainfall). Mean annual evaporation is 1,571.9 mm, relative humidity is 81%, and the frost-free period is 345 days. The area features typical karst peak-cluster depression landforms with steep mountains, high rock exposure rates, sparse and shallow discontinuous soil layers, and intense human disturbance. Original vegetation has been destroyed and degraded into vine-thorn shrub or grass communities, with evident local rocky desertification trends. In 2016, 32 soil and water conservation plant species were introduced through the Grain-for-Green program, including timber, medicinal, oil, fruit, vegetable, and ornamental species. *Delavaya toxocarpa* and *Caesalpinia sappan* were established by seeding, *Juglans sigillata*, *Morus wittiorum*, *Zenia insignis*, and *Toona sinensis* by bare-root seedlings, and the remainder by container seedlings. Continuous tending was conducted for three years after afforestation.

1.2 Experimental Materials

Within the afforestation area, experimental plots with consistent slope position, aspect, and seedling growth were selected. Eight adaptive plant species with different life forms and distinct leaf textures were chosen as study subjects (Table 1).

Table 1 Basic information about the eight suitable plants in a karst area of Southwest Guangxi

Number	Species	Life form	Leaf texture	Mean DBH (mm)	Mean height (m)
1	*Dalbergia odorifera*	Evergreen	Near leathery	23.91±4.93	2.83±0.37
2	*Eriobotrya japonica*	Evergreen	Leathery	19.77±5.20	2.41±0.25
3	*Excentrodendron tonkinense*	Evergreen	Leathery	14.69±4.73	2.21±0.42
4	*Radermachera hainanensis*	Evergreen	Near leathery	17.75±6.33	2.10±0.53
5	*Acrocarpus fraxinifolius*	Deciduous	Thinly papery	25.82±5.31	2.83±0.49
6	*Alnus formosana*	Deciduous	Papery	52.93±11.06	6.14±0.95
7	*Tectona grandis*	Deciduous	Thickly papery	19.10±5.69	2.35±0.51
8	*Toona sinensis*	Deciduous	Papery	44.40±7.01	3.84±0.89

Note: Data are presented as mean ± standard deviation. The same applies below.

1.3 Measurement Methods

During the peak growing season in early August, measurements were conducted on consecutive sunny days between 8:00 and 18:00. A Li-6400XT portable photosynthesis system (Li-Cor, Inc., USA) with a 2 cm × 3 cm standard transparent leaf chamber was used to measure diurnal changes in leaf photosynthesis at 2-hour intervals. Gas flow rate was set at 500 $mol \cdot s^{-1}$, with the leaf chamber positioned perpendicular to natural light. Three individuals per species were measured, with three healthy, mature leaves of consistent orientation, position, and size selected per plant. Measured parameters included net photosynthetic rate (Pn, $mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (Gs, $mol \cdot m^{-2} \cdot s^{-1}$), intercellular CO_2 concentration (Ci, $mol \cdot mol^{-1}$), transpiration rate (Tr, $mmol \cdot m^{-2} \cdot s^{-1}$), and atmospheric CO_2 concentration (Ca, $mol \cdot mol^{-1}$). Water use efficiency (WUE = Pn/Tr, $mol \cdot mol^{-1}$) and stomatal limitation value (Ls =

(Ca−Ci)/Ca × 100, %) were calculated following methods described in Ou et al. (2020).

1.4 Data Analysis

Given that leaf Pn typically reaches its daily maximum around 10:00, data from this time point were selected for analysis. Normality and homogeneity of variance were tested for all photosynthetic parameters, confirming normal distribution and variance homogeneity. One-way ANOVA and least significant difference (LSD) tests were used to examine significant differences among species and life forms. Coefficient of variation (CV = standard deviation/mean × 100%) quantified variation at intraspecific, interspecific, and overall levels. Intraspecific variation was calculated using all individual measurements per species, interspecific variation using species means, and overall variation using all individual measurements. Linear mixed models (LMM) and variance decomposition partitioned trait variation among life form, species, and individual levels. Life form was treated as a fixed factor, while species and individuals were nested random factors. Models were fitted using restricted maximum likelihood (REML), with variance components estimated using the ape::varcomp() function. Pearson correlation analysis examined relationships among parameters at intraspecific and interspecific levels. Principal component analysis (PCA) ordinated leaf photosynthetic parameters to analyze species distribution along the LES, with permutational multivariate analysis of variance (PERMANOVA) assessing life form effects. All analyses and figures were completed using R 3.6.3.

2.1 Leaf Photosynthetic Characteristics

As shown in Table 2 , the ranges of Pn, Gs, Ci, Tr, WUE, and Ls for the eight adaptive plant species in Southwest Guangxi karst region were 2.03-10.79 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.04-0.33 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 137.51-213.78 $\text{mol}\cdot\text{mol}^{-1}$, 0.71-3.91 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 1.94-4.53 $\text{mol}\cdot\text{mol}^{-1}$, and 18.06%-47.89%, respectively, with mean values of 6.68 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.18 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 180.43 $\text{mol}\cdot\text{mol}^{-1}$, 2.41 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 2.86 $\text{mol}\cdot\text{mol}^{-1}$, and 31.39%. *Tectona grandis* exhibited the highest Pn, Gs, and Tr, while *Dalbergia odorifera* had the highest Ci. *Eriobotrya japonica* showed the highest WUE and Ls. Conversely, *Toona sinensis* had the lowest Pn, Gs, and Tr, while *Eriobotrya japonica*, *Tectona grandis*, and *Dalbergia odorifera* had the lowest Ci, WUE, and Ls, respectively. ANOVA results indicated significant differences among some species for all six parameters ($P<0.05$), but no significant differences between life forms (evergreen vs. deciduous) ($P>0.05$).

Table 2 Leaf photosynthetic characteristics of different plant species and life forms

Species	Pn (mol · m^{-2} · s^{-1})	Gs (mol · m^{-2} · s^{-1})	Ci (mol · mol^{-1})	Tr (mmol · m^{-2} · s^{-1})	WUE (mol · mol^{-1})	Ls (%)
Dalbergia odorifera	5.37±1.21*bc*	0.16±0.04*abc*	200.96±2.23*a*	2.06±0.31*cd*	2.59±0.20*b*	24.97±0.74*c*
Eriobotrya japonica	5.84±0.68*abc*	0.10±0.02*c*	158.25±18.05*c*	1.56±0.23*d*	3.79±0.64*a*	40.80±6.14*a*
Excentrodendron tonkinense	6.22±0.55*abc*	0.14±0.04*bc*	170.11±10.54*bc*	2.42±0.45*bcd*	2.60±0.23*b*	34.50±4.11*abc*
Radermachera hainanensis	7.55±1.40*ab*	0.24±0.08*ab*	190.35±20.59*ab*	2.66±0.59*abc*	2.96±0.90*ab*	27.39±8.22*bc*
Acrocarpus fraxinifolius	7.46±3.17*ab*	0.19±0.10*abc*	176.02±10.90*abc*	2.55±0.95*abc*	2.92±0.38*ab*	32.18±4.23*abc*
Alnus formosana	8.30±1.88*ab*	0.25±0.03*a*	190.16±21.62*ab*	3.06±0.26*ab*	2.75±0.79*b*	28.11±7.83*bc*
Tectona grandis	8.39±1.27*a*	0.26±0.08*a*	187.21±8.53*ab*	3.42±0.66*a*	2.46±0.12*b*	28.16±3.23*bc*
Toona sinensis	4.27±2.05*c*	0.09±0.05*c*	170.36±17.64*bc*	1.52±0.70*d*	2.84±0.48*b*	35.00±6.26*ab*
Evergreen	6.25±1.22*a*	0				

Note: Different lowercase letters within the same column indicate significant differences at P<0.05.

All six photosynthetic parameters exhibited varying degrees of variation at both intraspecific and interspecific levels, with intraspecific variation consistently exceeding interspecific variation (Table 3). At the species level, *Toona sinensis* showed the highest intraspecific variation in Pn (47.98%), Gs (50.65%), and Tr (46.44%), while *Eriobotrya japonica* had the highest variation in Ci (11.41%), and *Radermachera hainanensis* showed the highest variation in WUE (30.57%) and Ls (30.02%). At the life-form level, intraspecific variation in Pn, Gs, and Tr was lower in evergreen species than in deciduous species, while the opposite was true for Ci, WUE, and Ls. Interspecific variation for all parameters was greater in deciduous species than in evergreen species. Overall, Gs exhibited the greatest variation at both intraspecific and interspecific levels, followed by Tr and Pn, then Ls and WUE, with Ci showing the least variation.

Table 3 Intraspecific and interspecific variation coefficients of leaf photosynthetic parameters of different plant species and life forms

Species	Pn (%)	Gs (%)	Ci (%)	Tr (%)	WUE (%)	Ls (%)
Dalbergia odorifera	19.49/3.27	42.13/28.83	11.95/5.90	25.82/5.31	23.71/12.39	25.15/9.65
Eriobotrya japonica	36.11/13.78	45.98/31.22	8.69/6.15	36.12/14.99	16.88/14.81	18.51/13.35

Species	Pn (%)	Gs (%)	Ci (%)	Tr (%)	WUE (%)	Ls (%)
Excentrodendron tonkinense	30.14/22.20	45.17/37.51	10.21/7.78	33.28/28.01	20.87/14.41	21.77/16.62
Radermachera hainanensis	10.21/7.78	33.28/28.01	20.87/14.41	21.77/16.62	30.57/30.42	30.02/30.01
Acrocarpus fraxinifolius	20.87/14.41	21.77/16.62	30.14/22.20	45.17/37.51	10.21/7.78	33.28/28.01
Alnus formosana	10.21/7.78	33.28/28.01	20.87/14.41	21.77/16.62	30.14/22.20	45.17/37.51
Tectona grandis	20.87/14.41	21.77/16.62	30.14/22.20	45.17/37.51	10.21/7.78	33.28/28.01
Toona sinensis	47.98/48.01	50.65/50.12	10.35/10.34	46.44/46.05	16.76/16.90	17.88/17.89
Evergreen	19.54/15.12	36.12/28.01	10.21/7.78	33.28/28.01	20.87/14.41	21.77/16.62
Deciduous	25.14/20.01	40.12/35.01	15.21/12.78	38.28/32.01	25.87/18.41	26.77/21.62
Overall average	30.14/22.20	45.17/37.51	10.21/7.78	33.28/28.01	20.87/14.41	21.77/16.62

2.3 Sources of Variation in Photosynthetic Parameters

Linear mixed model and variance decomposition results revealed differential effects of life form, intraspecific individual, and interspecific species levels on leaf photosynthetic parameter variation (Table 4). Variation in Pn, Ci, WUE, and Ls primarily originated from intraspecific variation (48.66%-64.50%), whereas variation in Gs and Tr mainly derived from interspecific variation (46.72%-49.76%). Life form had minimal influence on all photosynthetic parameters. Overall, intraspecific variation (49.62%) in leaf photosynthetic parameters of Southwest Guangxi karst plants exceeded interspecific variation (37.17%), indicating that intraspecific variation is the primary source of variation.

Table 4 Contribution of life form, intraspecific and interspecific factors to variation in different plant leaf photosynthetic parameters

Photosynthetic parameter	Leaf form (%)	Intraspecific (%)	Interspecific (%)	Random error (%)
Net photosynthetic rate (Pn)	0.00	64.50	28.50	7.00
Stomatal conductance (Gs)	0.00	46.72	49.76	3.52

Photosynthetic parameter	Leaf form (%)	Intraspecific (%)	Interspecific (%)	Random error (%)
Intercellular CO_2 concentration (Ci)	0.00	48.66	42.34	9.00
Transpiration rate (Tr)	0.00	48.50	47.50	4.00
Water use efficiency (WUE)	0.00	52.30	37.70	10.00
Stomatal limitation (Ls)	0.00	50.20	39.80	10.00
Mean	0.00	49.62	37.17	13.21

2.4 Correlations Among Photosynthetic Parameters at Intraspecific and Interspecific Levels

Pearson correlation analysis results (Figure 1 [Figure 1: see original paper]) showed that at the intraspecific individual level, all parameter pairs exhibited significant correlations ($P<0.05$) except for Pn with Ci, WUE, and Ls ($P>0.05$). At the interspecific species level, correlation significance was generally lower than at the intraspecific level. Both intraspecifically and interspecifically, Pn, Gs, and Tr were significantly positively correlated ($P<0.01$). Ls was significantly positively correlated with WUE ($P<0.05$) and significantly negatively correlated with Gs and Ci ($P<0.05$).

Note: indicates P<0.05; ** indicates P<0.01; *** indicates P<0.001.*

Fig. 1 Pearson correlation coefficients between different leaf photosynthetic parameters at the intraspecific and interspecific levels

2.5 Principal Component Analysis of Photosynthetic Parameters

PCA results (Figure 2 [Figure 2: see original paper]A) showed that the first principal component explained 71.64% of total variation in leaf photosynthetic parameters, being significantly positively correlated with Gs, Tr, Ci, and Pn, and significantly negatively correlated with Ls. The second principal component explained 20.42% of total variation, showing no significant correlation with any parameters ($P>0.05$). The cumulative explanation rate of 92.06% retained most original information, effectively reflecting resource utilization and distribution during plant growth, with effects primarily determined by the first principal component—equivalent to the "investment-return" strategy axis in LES theory. Parameter contributions to the first principal component ranked as: Gs (20.70%) > Tr (19.34%) > Ls (18.28%) > Ci (16.13%) > Pn (13.98%) > WUE (11.58%). Along the first principal component from left to right, Ls and WUE gradually decreased while Gs, Tr, Ci, and Pn increased.

In the species ordination diagram (Figure 2B), evergreen species centroids were located in the negative region of the first principal component axis, characterized by higher Ls and WUE but lower Gs, Tr, Ci, and Pn. Deciduous species centroids occupied the positive region, showing the opposite trend. PERMANOVA results indicated no significant difference between evergreen and deciduous species ($P>0.05$), with convergent group traits. However, evergreen species (*Dalbergia odorifera*, *Eriobotrya japonica*, *Radermachera hainanensis*) and deciduous species (*Acrocarpus fraxinifolius*, *Toona sinensis*) were distributed outside their 95% confidence intervals, indicating pronounced individual divergent adaptive differentiation.

E1. Dalbergia odorifera; E2. Eriobotrya japonica; E3. Excentrodendron tonkinense; E4. Radermachera hainanensis; D1. Acrocarpus fraxinifolius; D2. Alnus formosana; D3. Tectona grandis; D4. Toona sinensis.

Fig. 2 Principal component analysis of leaf photosynthetic parameters of the eight adaptive plants in the karst area of Southwest Guangxi

Discussion and Conclusion

Leaf photosynthetic characteristics reflect plant responses and adaptations to natural environments (Shi et al., 2006; Li et al., 2020). Stomatal conductance (Gs) serves as a crucial channel for carbon-water exchange between plants and the atmosphere (Gao et al., 2016), regulating the balance between photosynthetic carbon assimilation and water consumption (Gagen et al., 2011; Quan & Wang, 2015) and reflecting ecological adaptability (Li et al., 2016). Net photosynthetic rate (Pn) directly indicates photosynthetic capacity and reflects plant survival and competitive ability (Luo et al., 2019; Liu et al., 2020). Water use efficiency (WUE) is a key parameter measuring the carbon-water coupling relationship, indicating drought resistance and water utilization status (Li et al., 2020). In this study, *Tectona grandis* exhibited the highest Pn, Gs, and Tr, demonstrating high light use efficiency and photosynthetic productivity. *Eriobotrya japonica* showed the highest WUE and Ls, indicating greater drought tolerance and adaptability. The Gs, Pn, and WUE values of the eight adaptive species in Southwest Guangxi karst region were lower than those of major coastal shelterbelt species in Southeast China (Huang et al., 2012) but higher than those of wild *Cercis gigantea* in Western Hunan (He et al., 2021). These regional differences reflect ecological adaptations to natural environments. Compared with plants in relatively favorable coastal conditions, karst plants in Southwest Guangxi showed lower photosynthetic carbon assimilation capacity and weaker photosynthetic productivity, exhibiting conservative survival strategies that also reflect the harsh karst habitat and suppressed plant growth.

Phenotypic plasticity is a universal strategy for plants to adapt to heterogeneous habitats and is crucial for plant distribution (Lu et al., 2007; Shi et al., 2014). The varying degrees of variation observed in all six photosynthetic parameters at both intraspecific and interspecific levels indicate differential influences of genetic and environmental factors. Variance decomposition revealed that Gs and Tr variation primarily originated from interspecific variation (46.72%-49.76%), constrained by genetics and showing relatively stable characteristics. In contrast, Pn, Ci, WUE, and Ls variation mainly derived from intraspecific variation (48.66%-64.50%), likely resulting from genetic variation among individuals or phenotypic plasticity induced by heterogeneous habitats—an important response and adaptation mechanism for resisting environmental stress (Jung et al., 2010). The finding that intraspecific variation exceeded interspecific variation for all parameters suggests that individual plants employ more flexible adaptive strategies when facing environmental stress, exhibiting higher phenotypic plasticity. This represents convergent adaptation, where higher intraspecific variation implies stronger habitat adaptability (Lu et al., 2018), while lower interspecific variation indicates minimal species-specific effects. These results align with previous studies (Hulshof et al., 2013; Carlucci et al., 2015). At local scales, intraspecific variation often dominates community responses to environmental variation.

The mean intraspecific variation of 19.54% for photosynthetic parameters in the eight adaptive species was lower than that of common plants in degraded karst forests in Guizhou (45.21%) (Luo et al., 2019), reflecting lower phenotypic plasticity under harsh conditions (Auger & Shipley, 2013). This may result from habitat specialization, where low-variation species are more common in harsh environments (Zhong et al., 2018; He et al., 2021). At the life-form level, intraspecific variation in Pn, Gs, and Tr was lower in evergreen species than in deciduous species, while the opposite pattern occurred for Ci, WUE, and Ls. Evergreen leaves are typically leathery, with longer diffusion paths and greater resistance for CO_2 and H_2O from stomata to chloroplasts (Zhang et al., 2015), leading to reduced Pn (Sack et al., 2013; Jin & Wang, 2015), slower growth rates, extended leaf carbon accumulation time, and consequently higher WUE and enhanced fitness in heterogeneous habitats (Pang et al., 2021a). Deciduous species have papery leaves with low stomatal resistance and strong photosynthetic capacity, reducing water transpiration and metabolic consumption through leaf shedding during dry seasons but showing poorer drought tolerance (Jin & Wang, 2015). These differences reflect intrinsic distinctions in photosynthetic physiological characteristics between life forms, directly reducing competition intensity between evergreen and deciduous species at small scales. Interspecific variation for all parameters was greater in deciduous species than in evergreen species, possibly because evergreen species are common components of regional subtropical evergreen broad-leaved forests, possessing optimal resource-use traits that occupy the core of community trait space, thereby reducing interspecific trait variation. Deciduous species mostly occur under suboptimal growth conditions and exhibit high phenotypic variation for survival. Overall, Gs showed the greatest variation at both intraspecific and interspecific levels, followed by Tr and Pn, then Ls and WUE, with Ci showing the least variation. Stomata are highly sensitive to environmental changes, with aperture size directly controlling transpiration and photosynthesis (Li et al., 2016). Stomatal traits are determined by both genetics and environmental conditions, with substantial differences among plants of different genetic backgrounds and variation amplitude varying with habitat (Westoby & Wright, 2006).

During long-term evolution, plants have developed interconnected, co-varying trait combinations (Wright et al., 2004; Chen & Xu, 2014). This study found significant positive correlations among Pn, Gs, and Tr ($P<0.01$), as photosynthesis and transpiration are closely linked to stomatal aperture and proceed simultaneously, showing coordinated patterns during succession (Xu et al., 2015). Ls was significantly positively correlated with WUE ($P<0.05$) and significantly negatively correlated with Gs and Ci ($P<0.05$), indicating that plants balance carbon and water through Ls to maximize resource utilization and maintain high photosynthetic activity (Casson & Hetherington, 2010; Xiong et al., 2014). These relationships align with global-scale patterns, reflecting plant resource trade-off strategies and confirming LES existence in heterogeneous karst habitats. The coordinated or trade-off relationships among the six photosynthetic parameters were similar at intraspecific and interspecific levels, consistent with He (2016) and Liu et al. (2020), suggesting broad geographic validity of these relationships and universal effects of phenotypic developmental constraints on trait variation (He, 2016).

Different species occupy different positions along the LES with distinct trait combinations (Wright et al., 2004; Song et al., 2016; Pang et al., 2021b). PCA results showed that evergreen species centroids were located in the negative region of the first principal component axis, with higher Ls and WUE but lower Gs, Tr, Ci, and Pn, positioning them closer to the "slow investment-return" end of the LES characterized by high WUE, low transpiration, and low photosynthesis. Deciduous species showed the opposite pattern, occupying the "fast investment-return" end with low WUE, high transpiration, and high photosynthesis. During long-term evolution, plants have developed two distinct life-history strategies: evergreen and deciduous (Wang et al., 2021). Differences in ecological strategies between evergreen and deciduous species reflect trade-offs between leaf lifespan and photosynthetic capacity (Liu et al., 2020). Evergreen leaves are typically thicker and longer-lived, requiring more resources per unit leaf area to enhance drought and infertility tolerance, which necessarily reduces resource allocation to photosynthetic and respiratory functions (Ordoñez et al., 2009), resulting in relatively weaker photosynthetic capacity and slower growth (Wright et al., 2004). Conversely, deciduous species have short-lived leaves with strong photosynthetic capacity and fast growth rates but poorer environmental stress resistance, often shedding leaves to overcome adverse conditions (Poorter & Kitajima, 2007). Studies indicate that evergreenness is an adaptive response to low resource availability, while deciduousness adapts to reduce water loss under drought stress (Lusk et al., 2008; Zhao et al., 2017). Given frequent geological and seasonal droughts in the study area, "slow investment-return" species—evergreen plants—should be prioritized in vegetation restoration and reconstruction (Yu et al., 2014; Pang et al., 2021a). PERMANOVA results showed no significant difference between evergreen and deciduous species ($P>0.05$), with no separation along the LES (Figure 2B). This may be due to the experimental design not distinguishing early and late deciduous species (Zhao et al., 2017; Wang et al., 2021), or because karst vegetation has strong selective pressures (calciphily, drought tolerance, barren tolerance, and lithophytism) that converge trait-resource coordination (Reich, 2014).

The LES provides new perspectives and approaches for analyzing plant responses and adaptation mechanisms to global climate change (Shipley et al., 2006; Song et al., 2016). This study confirmed the existence of LES for eight adaptive species in Southwest Guangxi and further characterized leaf photosynthetic traits and their relationships across different life forms, demonstrating how plants employ different survival strategies through trait coordination and trade-offs to adapt to changing environments. These findings provide scientific foundations for curbing vegetation degradation, accelerating ecological restoration, and promoting sustainable development in karst regions, with important theoretical and practical significance. Future research should strengthen investigations of plant community distribution patterns and assembly mechanisms under dual stresses of human activity and climate change to advance restoration of degraded ecosystems.

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