Stomatal Characteristics and Their Plasticity in Response to Light Variation in Epiphytic Plant Leaves in Subtropical Forests (Postprint)

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Date: 2020-08-03T14:03:10+00:00

Abstract

Epiphytic plants are one of the biological groups with extremely high species diversity and are extremely vulnerable and sensitive in tropical and subtropical forest ecosystems. Light is considered a key factor that drove the evolution of epiphytic plants from terrestrial groups and determines their growth and distribution. However, due to limitations in approaching the canopy and standardized sampling, the relationship between epiphytic plants and light remains to be urgently elucidated. To reveal the response and adaptation strategies of epiphytic plants to changes in light intensity, this study used 6 epiphytic plant species from subtropical evergreen broad-leaved forests (canopy layer woody plants: Sorbus rhamnoides, Rhododendron moulmainense; canopy layer herbaceous plants: Coelogyne rigida, Pleione hookeriana; trunk zone herbaceous plants: Polygonatum punctatum, Cautleya gracilis) as study subjects, and conducted a comparative analysis of their leaf stomatal characteristics and plasticity under 4 light treatment gradients. The results showed that: (1) The stomatal area (SA), stomatal density (SD), potential stomatal conductance index (PCI), and epidermal cell density (ECD) of the two epiphytic small trees all responded significantly to changes in light intensity. The two epiphytic orchids had the largest SA and the smallest SD; the light response trends of SD and ECD in epiphytic tree leaves were more similar to those of terrestrial plants, while epiphytic herbs exhibited interspecific variation. (2) There were no significant differences in stomatal and epidermal cell characteristics and their phenotypic plasticity among the 6 epiphytic plants between herbaceous-woody, evergreen-deciduous plants, or canopy-trunk zone. (3) The average plasticity index of stomatal characteristics and epidermal cells in epiphytic plants was lower than that in terrestrial plants. These results indicate that epiphytic plants in subtropical evergreen broad-leaved forests have relatively weak adaptability to changes in light environment. Different epiphytic plants can adapt to high-light habitats by increasing leaf SD and ECD to varying degrees, and cope with low-light stress through dual regulation of SD and SA to increase potential photosynthetic capacity.

Full Text

Response of Stomatal Characteristics and Its Plasticity to Light Change in Leaves of Six Epiphytes in Subtropical Forests

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Abstract

Epiphytes, which grow non-parasitically upon other plants, comprise one of the most diverse and vulnerable groups in subtropical and tropical forests. Light can promote the evolutionary transition of plants from terrestrial to epiphytic life-forms and determines the growth and distribution of epiphytes. Nevertheless, research on the relationship between epiphyte growth and light stress has been plagued by technical challenges such as direct canopy access and systematic sampling. To explore the adaptation strategies and mechanisms of epiphytes to light change, we surveyed six vascular epiphytes in evergreen broad-leaved forests of the Ailao Mountains, Yunnan Province: two canopy trees (*Sorbus rhamnoides* and *Rhododendron moulmainense*), two canopy herbs (*Coelogyne punctulata* and *Pleione hookeriana*), and two trunk herbs (*Polygonatum punctatum* and *Cautleya gracilis*). We characterized stomatal traits and plasticity in leaves and their responses to light variation. The results showed that: (1) Stomatal area (SA), stomatal density (SD), potential stomatal conductance index (PCI), and epidermal cell density (ECD) of the two canopy epiphytic trees responded significantly to light change. Canopy epiphytic herbs had the largest SA and smallest SD among all studied epiphytes. The SD and ECD responses of epiphytic trees to light change were consistent with those of terrestrial plants, while epiphytic herbs showed interspecific variation. (2) Stomatal and epidermal cell characteristics and phenotypic plasticity showed no significant differences between herbs and trees, evergreen and deciduous plants, or canopy and trunk epiphytes. (3) Plasticity indexes of stomatal and epidermal cell characteristics were lower than those of terrestrial plants. Our results indicate that epiphytes have relatively weak adaptability to light change in subtropical forests. Epiphytes can adapt to high light intensity by increasing SD and ECD to varying degrees, and cope with low light stress by increasing potential photosynthetic capacity through trade-offs between SD and SA.

Keywords: Plant physioecology, Ailao Mountains, canopy, light change, epiphyte, stomatal characteristic, plasticity

Introduction

Epiphytes are organisms that grow on the surfaces of other plants without parasitizing their hosts, obtaining water and nutrients primarily from the atmosphere. They are extremely sensitive to environmental changes and serve as important bio-indicators for monitoring climate change (Song and Liu, 2011; Leao et al., 2014). Vascular epiphytes account for approximately 9% of all known vascular plant species globally (Zotz, 2013) and play crucial roles in forest water balance and nutrient cycling (Nadkarni, 1984; Coxson and Nadkarni, 1995), while providing diverse resources and ecological niches for other organisms (Nadkarni and Matelson, 1989; Montero et al., 2009; Mccracken and Forstner, 2014). China possesses the world' s largest area of subtropical evergreen broad-leaved forests, with tropical forests distributed in southwestern and southern regions, and hosts abundant epiphyte diversity (Xu and Liu, 2005). However, these subtropical evergreen broad-leaved forests have suffered severe destruction from human disturbance and expanding socioeconomic activities. Forest fragmentation is increasingly serious in tropical and high-altitude mountain forests of southwestern China, significantly affecting epiphyte groups that are exceptionally sensitive to environmental changes. Alarmingly, this environmentally-sensitive taxonomic group has received far too little attention in China. Research on the responses of forest epiphytes to environmental changes and related physiological-ecological mechanisms urgently needs strengthening.

Light is the sole and ultimate energy source for plant photosynthesis and the most fundamental factor affecting it (Ye and Yu, 2008). The morphological and physiological adaptability of epiphytes to light environment changes is a key factor influencing their distribution and growth. However, the mechanisms underlying how epiphyte physiological-ecological characteristics respond to light environment changes remain inadequately elucidated (Hietz and Briones, 1998; Zotz and Andrade, 1998; Stuntz and Zotz, 2001). Moreover, the unique characteristics of epiphytes and their habitats often result in distinctly different responses to light variation compared to terrestrial plants. For instance, studies have found that epiphytic and terrestrial groups of Bromeliaceae, Orchidaceae (Kuang and Zhang, 2015), ferns, and *Ficus* species (Hao et al., 2011) generally exhibit markedly different light response characteristics (Zhang et al., 2008; Song et al., 2013; Scarano et al., 2016). Therefore, specialized investigation and analysis of epiphyte physiological-ecological adaptation strategies and mechanisms to various light environments are urgently needed.

Notably, stomata are the primary pathway for water-gas exchange between plants and the external environment. This organ, retained through plant evolution, possesses strong stability (Caglar and Tekin, 1999; Zhu, 2013). Plant photosynthesis and transpiration—the two most fundamental physiological processes in ecosystem material cycling—are both controlled by stomatal behavior (Hetherington and Woodward, 2003; Tayloy et al., 2012). Because stomatal behavior responds sensitively to environmental changes, examining stomatal trait parameters to explore plant regulation processes in response to environmental change has become a research hotspot in recent years (Uprety et al., 2002; Wang et al., 2014; Liu et al., 2018). Therefore, this study selected six common vascular epiphytes from subtropical evergreen broad-leaved forests in the Ailao Mountains of Yunnan as research subjects. Through comparative analysis of stomatal and epidermal cell characteristics and phenotypic plasticity in epiphyte leaves under controlled light conditions, we examined differences in how light environment changes affect stomatal and epidermal traits among different life-form epiphytes. Our aim was to reveal the adaptive strategies and mechanisms of epiphyte leaf stomatal and epidermal characteristics to light intensity changes, providing a basis for understanding epiphyte adaptation to habitat light variation and theoretical reference for ecological restoration of epiphyte groups in damaged subtropical evergreen broad-leaved forests.

1.1 Experimental Site

The Ailao Mountains are located in southwestern Yunnan Plateau, in the southern section of the Hengduan Mountains, belonging to the southern branch of the Yunling Range. The region preserves China' s most intact and extensive mid-montane moist evergreen broad-leaved forest (Wu, 1983). The Xujiaba area in the Jingdong section lies on the western slope of Ailao Mountains (100°44 – 101°30 E, 23°36 –24°56 N), with a mean annual temperature of 11°C and warm-temperate to cool-temperate climate characteristics. The primary Lithocarpus xylocarpus forest (mid-montane moist evergreen broad-leaved forest) covers 85% of the vegetation area at 2200–2600 m elevation, with island-like mossy dwarf forests above 2600 m. The L. xylocarpus community reaches 25–30 m in height with distinct stratification, dominated by *Lithocarpus xylocarpus*, *Lithocarpus hancei*, and *Castanopsis wattii* in the upper canopy (Li, 2001).

We selected an open area near the Ailao Mountain Ecological Station of the Chinese Academy of Sciences. Based on natural light levels in epiphyte habitats and ensuring consistent precipitation, air humidity, temperature, and elevation, we established high-light, medium-light, and low-light treatment groups using steel frames and shade nets, with full-light (no shade net) as control. Light treatment classifications referenced local forest vertical light profiles and canopy cover data before and after the 2015 snow disaster (Li et al., 2011; Song et al., 2018). The high-light treatment corresponded to post-disaster L. xylocarpus forest and associated oak secondary forest (with few epiphytic vascular plants), medium-light to pre-disaster understory average light, and low-light to closed-canopy primary forest conditions. In each of the four experimental plots, we installed U23-001 temperature-humidity recorders (Hobo, USA) and self-recording quantum sensors (Odyseey, Newsland) to monitor air temperature, relative humidity, and photosynthetically active radiation (PAR). Substrate water content was maintained adequately through regulated irrigation frequency and volume.

Monitoring data from 2016 to 2019 showed that mean annual PAR values in the four light-controlled plots were 636.84, 143.71, 73.99, and 8.84 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ [Figure 1: see original paper]. Using full-light as control, the annual, rainy season, and dry season PAR ratios were approximately full-light:high-light:medium-light:low-light = 100:22:11:1. Mean annual temperature (13.21-15.27°C) and relative humidity (58.77%-64.18%) differed by less than $±$0.5% among plots, confirming light as the sole controlling factor.

1.2 Species Selection and Cultivation

We selected six widespread vascular epiphytes from the Ailao Mountains' moist evergreen broad-leaved forest as study subjects (Table 1). All plants were collected from fallen trees caused by the 2015 snow disaster in primary evergreen broad-leaved forest. Collections focused on intact mature individuals or perennial rhizomes. For *Rhododendron moulmainense* and *Sorbus rhamnoides*, which have large mature individuals with low survival rates, we collected individuals under 2 m tall. Collected plants were transplanted into pots (moss/humus volume ratio 1:1) in a cultivation shade house (medium light). During cultivation, all plants received consistent soil moisture, timely removal of non-target plants, but no artificial fertilization. After healthy establishment, plants were transferred to the four light treatment plots in early January 2018, with $ $20 pots per species in each plot.

1.3 Measurement Methods

In July 2019, we selected six potted samples per species from each light treatment and collected one mature leaf from current-year growth. Leaf specimens were prepared in the laboratory by cutting ~0.5 cm^2 fragments, soaking in potassium chloride-dissolved nitric acid for 12 h, then treating with 5% potassium hydroxide solution until translucent. Epidermis was peeled using forceps and dissecting needles, mesophyll removed with brushes, and epidermal tissue stained with 1% safranin before slide preparation and photography using a Leica DM1000LED microscope. Stomatal length and width were measured at 40× magnification, and stomatal and epidermal cell counts were made at 20× magnification using ImageJ software, with six fields analyzed per leaf.

Calculations: - **Stomatal index (SI)**: SI = SN/(SN + ECN), where SN = stomatal number, ECN = epidermal cell number - **Stomatal area (SA)**: SA = 1/4 × π × SL × SW, where SL = stomatal length, SW = stomatal width - **Stomatal density (SD)**: Mean of six fields - **Potential conductance index (PCI)**: PCI = SL^2 × SD × 10^{-4} - **Epidermal cell density (ECD)**: Mean of six fields - **Plasticity index**: (Maximum value - Minimum value)/Maximum value (Valladares, 2000)

1.4 Statistical Analysis

We performed one-way ANOVA on stomatal and epidermal cell parameters among light treatments using Sigmaplot 14, and used SPSS 25 for regression analysis to examine trends in stomatal and epidermal characteristics with PAR.

Results

Only leaf SA of the two canopy epiphytic trees differed significantly among light intensities [Figure 2: see original paper]A. Further analysis showed that only SA of two epiphytes correlated significantly with PAR [Figure 2: see original paper]B. *Sorbus rhamnoides* SA showed a significant cubic relationship with PAR ($R^2 = 0.864$, $P < 0.001$), with high-light treatment significantly lower than full-light ($P = 0.015$) and low-light ($P < 0.001$). *Rhododendron moulmainense* SA showed a weak negative correlation with PAR, but was significantly lower in full-light and medium-light than in high-light ($P = 0.034$) and low-light ($P = 0.001$). SA of *Pleione hookeriana* and *Coelogyne punctulata* followed binomial distributions with PAR, reaching maximum and minimum values in high-light, respectively. *Polygonatum punctatum* SA correlated positively with PAR ($R^2 = 0.206$, $P < 0.05$), while *Cautleya gracilis* SA increased slightly with decreasing PAR but not significantly. SA of the two epiphytic orchids (*P. hookeriana* and *C. punctulata*) was significantly greater than the other four epiphytes (all $P \leq 0.004$ and $P < 0.001$, respectively).

Four epiphyte species showed significant differences in leaf SD among light intensities [Figure 3: see original paper]A, and all correlated significantly with PAR [Figure 3: see original paper]B. SD of *S. rhamnoides*, *R. moulmainense*, *P. hookeriana*, and *C. gracilis* decreased significantly in low-light (all $P \leq 0.008$) and correlated significantly with PAR (all $P \leq 0.045$). *S. rhamnoides* showed a clear binomial trend.

Only SI of *P. hookeriana* was significantly lower in low-light than the other three treatments (all $P \leq 0.029$) [Figure 4: see original paper]A, showing significant binomial correlation with PAR ($R^2 = 0.593$, $P < 0.001$) [Figure 4: see original paper]B. SI of *C. punctulata* correlated linearly with PAR ($R^2 = 0.165$, $P < 0.05$).

Four epiphytes showed significant differences in leaf PCI among light intensities [Figure 5: see original paper]A, with two species showing significant PAR correlations [Figure 5: see original paper]B. *S. rhamnoides* PCI showed significant cubic correlation with PAR ($R^2 = 0.814$, $P < 0.001$), with high-light significantly lower than full-light ($P = 0.028$) and low-light ($P < 0.001$). *C. punctulata* PCI showed significant binomial correlation ($R^2 = 0.375$, $P < 0.001$), with high-light significantly lower than medium-light ($P = 0.021$) and low-light ($P = 0.003$). *R. moulmainense* PCI showed weak negative correlation with PAR, but was significantly lower in medium-light than low-light ($P = 0.006$). PCI of *P. hookeriana*, *P. punctatum*, and *C. gracilis* showed no significant PAR correlation, though *P. punctatum* PCI was significantly lower in high-light than full-light ($P = 0.039$) and medium-light ($P = 0.006$). PCI of the two epiphytic orchids was significantly greater than the other four epiphytes (all $P < 0.001$ and $P \leq 0.026$, respectively).

Four epiphytes showed significant differences in leaf ECD among light intensities [Figure 6: see original paper]A, with three species showing significant PAR correlations [Figure 6: see original paper]B. ECD of *S. rhamnoides* ($R^2 = 0.627$, $P < 0.001$) and *R. moulmainense* ($R^2 = 0.589$, $P < 0.001$) showed significant binomial correlations with PAR, with low-light significantly lower than the other three treatments (all $P \leq 0.011$). *P. hookeriana* ECD correlated linearly with PAR ($R^2 = 0.472$, $P < 0.01$), with medium-light significantly lower than full-light ($P = 0.001$). ECD of *P. punctatum* and *C. punctulata* showed weak negative correlations with PAR, though *P. punctatum* was significantly lower in medium-light than high-light and low-light. *C. gracilis* ECD showed weak positive correlation with PAR, with no significant differences among treatments.

2.2 Plasticity of Stomatal and Epidermal Cell Characteristics Under Different Light Intensities

Plasticity differed among stomatal parameters [Figure 7: see original paper]. The average plasticity index ranking for the six epiphytes was: PCI > SA > SD > SI > ECD. Phenotypic plasticity showed no significant differences between herbaceous and woody epiphytes, deciduous and evergreen plants, or canopy and trunk epiphytes.

Discussion and Conclusion

Stomata are important epidermal organs consisting of paired guard cells and the pore between them, with aperture size directly determining plant transpiration and photosynthesis (Zheng et al., 2005). External environmental factors (light intensity, water conditions, nutritional status) affect stomatal morphology and physiological characteristics, thereby influencing photosynthesis, transpiration, and respiration (Sun and Zou, 1991; Lü, 2000; Cao et al., 2002; Hetherington and Woodward, 2003). However, current research on epiphyte light response mechanisms has focused primarily on leaf morphology, chlorophyll content, photosynthesis, and respiration (Schäfer and Lüttge, 1988; Maxwell et al., 1994; Pires et al., 2012; Liu et al., 2018), with limited understanding of how light intensity affects leaf anatomical structures such as stomatal and epidermal characteristics. This study addresses this gap through light-controlled experiments examining responses of epiphyte leaf stomatal and epidermal cell characteristics to different light intensities.

3.1 Responses of Epiphyte Leaf Stomatal Area and Density to Light Environment Changes

Our study revealed substantial differences in leaf SD and SA between epiphytic trees and herbs, with epiphytic trees having higher SD and smaller SA than herbs. This aligns with Liu et al. (2018), who found that among 737 terrestrial plant species across tropical and boreal-temperate forests, SD followed the trend trees > shrubs > herbs, while stomatal size was greatest in herbs. Research indicates that maximum stomatal conductance is determined by both SD and stomatal size, with trade-offs between them (Franks et al., 2009). Generally, trees tend to increase SD to enhance maximum photosynthetic efficiency for greater water acquisition, whereas short-lived herbs preferentially increase SA to rapidly improve photosynthetic efficiency for completing their life cycle (Franks and Beerling, 2009; Lammertsma et al., 2011; Cheng, 2013). This explains the SA differences between canopy epiphytic orchids and small trees in our study.

Although epiphyte SD responses to light variation showed interspecific differences, some results were consistent with terrestrial plants. Canopy epiphytic trees (*S. rhamnoides*, *R. moulmainense*), *P. hookeriana*, and trunk-zone *P. punctatum* showed SD responses similar to terrestrial plants, decreasing significantly with reduced light intensity (He and Lü, 1995; Meng et al., 2002; Cai et al., 2004). In contrast, SD of canopy *C. punctulata* and trunk-zone *C. gracilis* showed no significant differences among light intensities, differing from most terrestrial plants (Meng et al., 2002; He et al., 2007) and indicating insensitivity of their SD characteristics to light changes.

Epiphyte SA responses to light variation also showed interspecific differences. Canopy epiphytic tree SA increased significantly with decreasing light intensity, consistent with Cai et al. (2004). However, SA increased significantly in both full-light and high-light treatments, possibly representing an adaptation strategy to high-light stress—simultaneously increasing SD and SA to enhance stomatal conductance and achieve high photosynthetic rates under strong light. The four epiphytic herbs showed no significant SD differences among light intensities, inconsistent with most terrestrial plants (Meng et al., 2002; He et al., 2007), indicating that epiphytic herb leaf SA is insensitive to light variation.

3.2 Responses of Epiphyte Leaf Stomatal Index to Light Environment Changes

Our results show that epiphyte leaf stomatal index (SI) was affected by light changes, decreasing with reduced light intensity. SI of the two epiphytic orchids correlated significantly with PAR, contrasting with early research suggesting SI is primarily water-affected rather than light-affected (Ticha, 1982). SI commonly serves as an indicator of stomatal differentiation intensity, representing stomatal frequency per unit leaf surface (Artemios and George, 2002; Masle et al., 2005). Cai et al. (2004) found that SI of three mid-story and four canopy tropical rainforest tree seedlings increased with light intensity. Five of our six epiphytes (except *P. hookeriana*) showed similar patterns, suggesting that certain plant groups in relatively water-sufficient tropical and subtropical forests may share similar adaptation mechanisms.

3.3 Responses of Epiphyte Leaf Potential Stomatal Conductance to Light Environment Changes

Potential stomatal conductance index (PCI) reflects plant potential photosynthetic capacity (Holland et al., 2009), determined by both SD and stomatal length, and can be approximated as stomatal area per unit leaf surface (Tian et al., 2016). Our results show interspecific differences in epiphyte PCI responses to light variation, mostly inconsistent with terrestrial plant studies. Except for *P. punctatum*, PCI increased with decreasing light intensity, contrasting with Zhang (1987), who found that rice leaf SD and stomatal length decreased under low light. This discrepancy may arise because epiphyte native habitats have weaker light due to canopy shading (Xu and Liu, 2005), giving epiphytes superior low-light adaptation and utilization strategies. Additionally, PCI of the two epiphytic orchids was significantly greater than the other four epiphytes, differing from Wen et al. (2018), who found no significant PCI differences among trees, shrubs, and herbs in Taibai Mountain. This suggests epiphytes may enhance potential photosynthetic capacity and reduce stomatal conductance through dual regulation of SD and SA to cope with low-light stress, showing better weak-light utilization than some terrestrial plants.

3.4 Responses of Epiphyte Leaf Epidermal Cell Density to Light Environment Changes

Our results show that epiphyte leaf epidermal cell density (ECD) responses to light changes were generally consistent with SD trends, showing interspecific differences but partially inconsistent with terrestrial plant studies. For example, leaf ECD of the two canopy epiphytic trees showed photoinhibition in full-light, while *P. hookeriana* ECD increased significantly with light intensity—both inconsistent with Lee et al. (2015), who found no significant ECD response in red leaf lettuce under different light treatments. Canopy epiphytic tree SD and ECD responses were more similar to terrestrial plants (He and Lü, 1995; Cai et al., 2004), while epiphytic herbs showed clear interspecific differences, indicating that different life-form epiphytes adapt to low-light stress by reducing leaf SD and ECD to varying degrees.

3.5 Phenotypic Plasticity of Epiphyte Leaf Stomatal and Epidermal Cell Characteristics in Response to Light Environment Changes

Phenotypic plasticity is an important way for organisms to adapt to environmental changes. High plasticity often indicates greater potential adaptability, wider ecological amplitude, and better environmental tolerance (Strauss-Debenedetti and Bazzaz, 1991; Geng et al., 2004). Our results show that epiphyte stomatal and epidermal cell plasticity differs from terrestrial plants. Average plasticity indexes were lower than those reported for terrestrial trees and herbs (Cai et al., 2004), with no significant differences between herbaceous and woody epiphytes, deciduous and evergreen plants, or canopy and trunk epiphytes. This contrasts with terrestrial plants, where upper-canopy species typically show greater phenotypic plasticity than lower-canopy species (Valladares et al., 2000; Wen et al., 2018). This suggests epiphytes have relatively weak adaptability to environmental changes, narrower ecological amplitude, and poorer environmental tolerance than terrestrial plants. This plasticity perspective helps explain why epiphytic seed plants are typically restricted to primary forests and are extremely sensitive to environmental changes.

In summary, epiphytes in subtropical forest systems can adapt to increased habitat light intensity by increasing leaf stomatal density and epidermal cell density to varying degrees, and cope with low-light stress by increasing potential photosynthetic capacity through dual regulation of SD and SA. However, different life-form epiphytes employ different mechanisms under low- or high-light stress. In our study, stomatal characteristic responses of canopy epiphytic trees and trunk epiphytic herbs were generally consistent with terrestrial plants (He and Lü, 1995; Meng et al., 2002; Cai et al., 2004; Liu et al., 2018). Different light response mechanisms in the two epiphytic orchids (Meng et al., 2002; He et al., 2007) may relate to whether they are CAM plants, requiring further investigation. Phenotypic plasticity showed no significant differences among epiphytes from different vertical zones or between upper- and lower-canopy trees (Valladares et al., 2000; Cai et al., 2004; Wen et al., 2018), and average plasticity indexes were lower than terrestrial trees and herbs (Cai et al., 2004; Liu et al., 2018), suggesting epiphytes have relatively weak adaptability and poorer tolerance to light variation. During post-2015 snow disaster recovery in the Ailao Mountain forest system (Song et al., 2017; Song et al., 2018), long-term monitoring of epiphyte community changes is needed to better protect these sensitive taxa and their species diversity.

A limitation of this study is that we only examined light intensity effects on epiphyte species distribution and individual growth through leaf stomatal characteristic changes. Notably, when fitting binomial models to *S. rhamnoides* SA and PCI against PAR, minimum values became negative—physiologically unrealistic. Using cubic models produced minimal R^2 changes, suggesting that epiphyte adaptation mechanisms across high- to low-light gradients may be more complex and variable. Future research should comprehensively investigate light response mechanisms of forest epiphytes through broader studies.

Acknowledgments

We thank the Ailaoshan Station for Subtropical Forest Ecosystem Studies, Chinese Academy of Sciences, for field experiment support, and Dr. Song Liang of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, for providing sectioning equipment.

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