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Trait acclimation of the clonal fern *Selliguea griffithiana* to forest epiphytic and terrestrial habitats

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Abstract
Although epiphytic habitats are more stressful and heterogeneous than terrestrial habitats, how facultative epiphytes acclimate to such contrasting environments has been poorly understood. Our study focused on the variation of functional traits between epiphytic and terrestrial individuals of *Selliguea griffithiana*, and provided considerable functional acclimation of this species to such contrasting environments. We sampled ramets of *S. griffithiana* from epiphytic and terrestrial habitats of a subtropical montane moist forest, SW China. Morphological and anatomical traits, photosynthesis, biomass and ramet density of *S. griffithiana* were measured and it was found that these traits differed significantly between the two habitats. Frond length, stipe length, spacer length (interramet distance), stomatal density, vein density, maximal chlorophyll fluorescence and relative chlorophyll content of fronds, and biomass per ramet were all lower in epiphytic habitat than those in terrestrial habitat, whereas frond thickness and ramet density were higher in the former. Photosynthetic light–response curves revealed a higher carbon assimilation capability of individuals in terrestrial habitat than in epiphytic habitat, whereas cumulative water loss curves showed a lower water loss rate in the latter. The findings demonstrate acclimation of *S. griffithiana* to both habitats, that is, epiphytic ramets can mitigate water scarcity at some cost of a reduced photosynthetic capacity, whereas terrestrial ramets can afford to improve the light capture to a higher photosynthetic capacity without any water stresses.

KEYWORDS
clonal growth, facultative epiphyte, functional trait, light response curve, plasticity, water loss curve

1 | INTRODUCTION

Functional trait variability allows plants to acclimate to contrasting environments (Albert et al., 2010; Kamiyama et al., 2014). In forest ecosystems, the distribution of light and water is heterogeneous in fine scale. The availability of light and water might display constant effects on morphological and physiological traits which were responsible for carbon gain and biomass accumulation of the whole plant (Manzoni, Vico, Palmroth, Porporato, & Katul, 2013; Noda, Muraoka, & Washtani, 2004). Some studies have suggested the existence of a trade-off between traits favoring rapid light-acquisition and those enhancing the ability to conserve leaf water (Niinemets & Valladares, 2006; Pérez-Ramos, Volaire, Fattet, Blanchard, & Roumet, 2013). For instance, the increase of plant hydraulic resistance of *Primula sieboldii*, *Sasa kurilensis* or *Abies koreana*, may result in the decrease of instantaneous photosynthetic rate (Je, Kim, & Woo, 2018; Noda et al., 2004; Tsunoda, Furukawa, & Mizunaga, 2017). Je et al. (2018) found that plants under high light intensity suffered greater adverse effects of drought on light absorption and utility during the photosynthetic process than those under shading conditions. Due to the vertical environmental gradients (such as light and water) along the forest canopy to understory (Lowman & Schowalter, 2012; Zotz, 2016), it is reasonable to predict some variations and trade-offs of functional traits between canopy dwelling plants (i.e., epiphytes) and terrestrial ones.

Epiphytes are an important group of plant species that occur in diverse microhabitats of the forest canopies in montane forest ecosystems (Benzing, 2004). As a key component in tropical and subtropical forest floras, epiphytes serve important ecological functions in biomass accumulation, forest hydrology and nutrient fluxes (Mondragón Chaparro & Ticktin, 2011; Ozanne et al., 2003; Umana & Wanek, 2010; Zotz, 2013). They exhibit diverse features in growth and morphology and clonal growth is very common in canopy-dwelling obligate or facultative epiphytes (Lu et al., 2015; Zotz, 2013, 2016). The clonal facultative epiphytes, which can both grow in forest canopies (i.e., epiphytic habitats) and root in the understory soil (i.e., terrestrial habitats), are thought to have a strong plasticity in functional traits, that allows them to acclimate to distinct habitats (Freitas, Scarano, & Blesboer, 2003; Lu et al., 2015). Epiphytic habitats are characterized by a limited storage capacity for water and nutrients, sporadic and dilute nutrient inputs, low physical stability, extreme fluctuations in moisture and temperature, high wind speed, and severe and variable vapor pressure deficits (Lowman & Schowalter, 2012; Song et al., 2016; Théry, 2001; Zotz, 2016). However, how clonal facultative epiphytes acclimate to such contrasting environments has been poorly understood (Lu et al., 2015).

Water shortage is the foremost abiotic stress for epiphytes in forest canopies (Freschi et al., 2010; Lowman & Schowalter, 2012; Zotz, 2016). Epiphytes may be subjected to long-term desiccation periods in the dry season and frequent short-term desiccation processes in the wet (growing) season in rain forests and cloud forests (Lu et al., 2015; Zotz, 2016). To cope with water shortage, obligate epiphytes have developed special adaptations (Benzing, 2004; Zhang et al., 2015). This may result in specific trait combinations for epiphytes (i.e., an "epiphyte syndrome" sensu; Zotz, 2016). For example, crassulacean acid metabolism is more pervasive among the epiphytes than any other ecologically defined group of plants (Benzing, 2004). Compared to terrestrial plants, leaves of obligate epiphytes often have higher leaf mass per unit area, percentages of spongy tissue, leaf thickness, epidermal thickness, saturated water content and time required to dry saturated leaves to 70% relative water content (Zhang et al., 2015). Therefore, when growing in epiphytic habitat, clonal facultative epiphytes may show morphological, physiological and anatomical acclimation to mitigate water stress and may also have a high water retention capacity.

From forest canopies to forest floors, light intensity decreases sharply, but its stability increases (Wagner, Bogusch, & Zotz, 2013). Terrestrial plants need to tolerate shady conditions and have evolved some mechanisms to acquire sunlight quickly or survive in low light conditions (Wagner et al., 2013; Zhu et al., 2016). For instance, terrestrial ferns developed an unconventional photoreceptor, a chimera of the red/far-red light receptor phytochrome and phototropin; this chimeric photoreceptor may have played a key role in the divergence and proliferation of fern species under low light conditions (Kawai et al., 2003). Terrestrial ferns have a shorter active period and a faster photosynthetic response to light flecks compared to epiphytic ferns (Zhang, Chen, Li, & Cao, 2009). Within a species, sun leaves generally have a higher light-saturated photosynthetic capacity per unit leaf area and a carbon gain, while shade leaves are more efficient in capturing light at low irradiance even though they are more vulnerable to photoinhibition (Demmig-Adams & Adams, 1992). Therefore, when growing in terrestrial habitat, clonal facultative epiphytes may show morphological, physiological and anatomical acclimation to mitigate low light stress and may also have a high carbon assimilation capability.

The montane moist evergreen broad-leaved forest widely distributed in Ailao Mountains of southwest China is an important global forest vegetation type, with about 114 epiphytic fern species occurred in the area (Li et al., 2014). Based on a previous field survey, some facultative epiphytic ferns were recorded and they construct stable populations with epiphytic and terrestrial individuals in visibly varied features. *Selliguea griffithiana* is one species with many individuals, though it is sporadically distributed in the region. We sampled plants of a typical rhizomatous facultative epiphytic fern *S. griffithiana* in both forest epiphytic and terrestrial habitats, and measured morphological, anatomical and physiological traits. Specifically, we addressed the following questions. (a) How do morphological, anatomical and physiological traits of *S. griffithiana* differ between the two contrasting habitats (i.e., epiphytic vs. terrestrial)? (b) How do these traits match with the environmental conditions of each habitat?

2 | MATERIALS AND METHODS

2.1 | Study site

Field investigations were conducted from September 15 to October 30, 2015, in a primary subtropical montane moist forest in the Xujiaba region (24° 32′ N, 101° 01′ E) of Yunnan Province, China, a core area covering 5,100 ha of the northern crest of the Ailao Mountain National Nature Reserve with a seasonal climate. In this region, the dry season spans from November to April, and the wet season from May to October (Lu et al., 2015, 2016). The mean annual precipitation was 1859 mm, with 86% occurring in the wet season and 14% in the dry season. The mean annual relative humidity (RH) was 84%, and the mean air temperature was 11.6°C (Song et al., 2016). This forest is dominated by *Lithocarpus xylocarpus*, *Castanopsis wattii*, *L. chintungensis*, *Schima noronhae*, *Machilus viridis*, and *Hartia sinensis.* Additionally, it is inhabited by a diverse community of epiphytes; more than 600 species of epiphytes occur in Ailao Mountains and epiphytic ferns account for 52–53% of vascular epiphytic biodiversity there (Ma, 2009; Xu & Liu, 2005).

At this study site, the temperature within the terrestrial habitat is much lower than outside the forest, and the maximal temperature was lower but the minimal temperature was higher in the terrestrial habitat than those outside the forest (You et al., 2013a, 2013b). Understory radiation components are greatly reduced by the forest canopy (You et al., 2013a, 2013b). On the hilltops, where *S. griffithiana* is frequent, the forest canopy is 5–7 m high and has strong effects on understory micrometeorology (Shi & Zhu, 2009; You et al., 2013a, 2013b). We measured microclimatic variables of the epiphytic and terrestrial habitats with microclimatic observation systems (Hobo U30; Onset Computer Corporation, Bourne, MA) for about 6 weeks. To this end, instrument arms of two height levels were mounted on a triangular meteorological tower within the study area. Accordingly, 1-week-measurement for humus temperature, leaf wetness (humidity of leaf surface measured with a leaf-sized rectangular sensor), and photosynthetically active radiation (PAR) on three tree trunks or ground soil points two times across the study sites one by one that were separated by at least 50 m (i.e., 1-week-measurement per tree trunk or soil point per site × 3 sites × 2 times). All measurements were recorded with a sampling interval of 30 min. The 12-month data of air temperature and RH were from Ailaoshan Station for Subtropical Forest Ecosystem Studies.

2.2 | Plant materials and sampling design

S. griffithiana (Hook.) Fraser-Jenk. (Polypodiaceae) occurs in southeast, east and south Asia (Li et al., 2012). It is an evergreen, facultative, epiphytic fern with overwintering leaves, and grows in both epiphytic and terrestrial habitats (Lu et al., 2015; Zhang, 2012). This fern can propagate via rhizomes and form vertical, perennial simple fronds (a leaf of a fern is a frond, and a frond of this clonal fern is a ramet) with adventitious roots. The size of an interconnected clone varies greatly and depends on the age of the clone and the disturbance status of the forest. A previously interconnected clone can be broken into fragments of different sizes due to violent disturbance (e.g., rodents, strong wind and storms) or aging. A clonal fragment of *S. griffithiana* can consist of a few to several hundreds of interconnected ramets and span a few centimeters to several meters (Lu et al., 2015).

In epiphytic habitats, 30 ramets were randomly sampled between 0.5 and 2.5 m above the ground on tree trunks of 30 different phorophytes (hosts of epiphytes) separated by at least 10 m; in terrestrial habitats, 30 independent ramets were located within three sites 500 m apart, with a similar slop direction. Terrestrial individuals distributed within 3 m around tree trunks of the phorophytes.

2.3 | Measurements of traits

Traits of *S. griffithiana* from both epiphytic and terrestrial habitats were measured, including morphology, anatomy, physiology and growth. The morphological traits examined were frond length (FL), frond width (FW), frond thickness (LT), spacer length (SPL, i.e., distance between adjacent interconnected ramets), stipe length (STL), rhizome diameter (RHD), specific leaf area (SLA, i.e., frond area divided by frond dry weight) and root to shoot ratio (RSR). The anatomical traits measured were stomatal density (SD), stomatal size (SS) and vein density (VD). The physiological traits measured were maximal quantum efficiency of photosystem II (F_v/F_m) and relative chlorophyll content (RCC). The growth traits examined were total biomass (B_t), aboveground biomass (B_a, i.e., frond plus stipe biomass) and belowground biomass (B_b, i.e., rhizome plus root biomass) per ramet and ramet density (RD).

From both epiphytic and terrestrial habitats, 30 mature ramets of *S. griffithiana* were randomly sampled for measuring FL, FW, LT, STL, spacer length, RHD, SLA, biomass and RSR. Fronds from 12 epiphytic and terrestrial ramets were scanned with a Li-Cor 3000 A area meter before being oven-dried at 70°C for 48 hr for assessing biomass and SLA. Biomass of other parts was measured after being oven-dried at 70°C for 48 hr.

For both habitats, F_v/F_m and RCC were determined in situ from 30 mature fronds of the same 30 ramets which were used for measuring morphology and biomass in the laboratory. Before each measurement, fronds were subjected to a dark adaptation of at least 30 min. Then, F_v/F_m values for each frond were measured using a portable chlorophyll fluorescence system (FSM-2; Hansatech, King's Lynn, UK). RCC was measured in six different parts of each mature frond with a compact chlorophyll meter (Minolta SPAD-502; Konica Minolta Sensing Inc., Osaka, Japan), and one mean value was obtained for each frond. Before each measurement, the detector was clipped down without any leaf sample in the chamber for calibration.

From both habitats, six mature fronds were randomly collected for anatomical measures. Each frond was divided along its midrib. One half of each frond was soaked for 1 hr in a 5% NaOH aqueous solution to remove mesophyll tissue for subsequently analyzing VD, while the other half was used for examining SS and density. For vein observations, after the mesophyll tissue was removed, three sections were excised from the top, middle and bottom portions of each frond, stained with 1% safranin, and mounted in glycerol to obtain VD. Samples were photographed at 10× magnification with a digital camera mounted on a Leica DM2500 microscope (Leica Microsystems GmbH, Wetzlar, Germany). Vein lengths were determined from digital images using the ImageJ program (version 1.51q) (Schneider, Rasband, & Eliceiri, 2012). Values for VD were expressed as vein length per unit area. For stomatal observations, the lower and upper epidermises were peeled from the middle portions of fresh leaves, and the images were captured under the Leica DM2500 microscope. Stomata were observed from 30 randomly selected fields, and SD was calculated as the number of stomata per unit leaf area. Stomatal size was expressed as the length of guard cells. One mean value of both SS and density was obtained for each frond.

To measure RD (ramet number per area) in epiphytic habitats, one 1 dm^2 plot per tree was located on sun-exposed tree trunk of ten different phorophytes embraced in the above measurements. For terrestrial individuals, ten same plots were set on the forest ground of different study sites. All ramets in the plots were recorded.

2.4 | Photosynthetic light–response curves

From both epiphytic and terrestrial habitats, six pieces of mats (clonal fragments mixed with soil and humus) were collected and transported to the Ailaoshan Station immediately for measuring. Previous studies indicated that transplantation or moving of "epiphytic mats" alone did not affect the viability or growth of epiphytes (Nadkarni, Schaefer, Matelson, & Solano, 2002). One ramet with an expanded and healthy mature frond from each piece was selected randomly to measure with a portable photosynthesis system (LI-6400XT; LI-COR, Lincoln, NE) with an LED red/blue light source. We measured photosynthetic light–response curves between 8:00 a.m. and 11:30 a.m. on consecutive sunny days. PAR was set at 14 specific steps, 1,200, 1,000, 800, 600, 550, 500, 450, 400, 300, 200, 100, 50, 20 and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The ambient CO_2 concentration was 380 μmol/mol. At each PAR step, ramets were exposed to the above conditions for 5–15 min to allow photosynthetic parameters to stabilize. Light–response curves were obtained by fitting the data to a rectangular hyperbola model (Ye, 2007; Ye & Yu, 2008),

$$P_n = \frac{\alpha I P_{n\max}}{\alpha I + P_{n\max}} - R_d \tag{1}$$

where P_n is the net photosynthetic rate; I is the light intensity; $P_{n\max}$ is the maximum net photosynthesis rate; R_d is the dark respiration rate; and α is a coefficient.

The light saturation point (I_{sat}, light intensity on the light curve, beyond which further increases will not increase the rate of photosynthesis; $\mu mol \cdot m^{-2} \cdot s^{-1}$) was calculated as follows,

$$P_{n\max} = \mathrm{AQE} \times I_{sat} - R_d, \tag{2}$$

where $P_{n\max}$ and R_d are as mentioned above and AQE is the apparent quantum efficiency, which is obtained by fitting the data ($I \leq 200$ $\mu mol \cdot m^{-2} \cdot s^{-1}$) to the linear model,

$$P_n = \mathrm{AQE} \times I + b, \tag{3}$$

where b is a coefficient. Using Equation (2) we can infer that

$$I_{sat} = (P_{n\max} + R_d)/\mathrm{AQE}. \tag{4}$$

The light compensation point (I_{com}, light intensity on the light curve where the rate of photosynthesis exactly matches the rate of respiration; $\mu mol \cdot m^{-2} \cdot s^{-1}$) is denoted by the x-intercept where the net photosynthetic rate is equal to zero. In other words, when

$$\begin{aligned} &I = I_{com}, P_n = 0 \text{ in } (1), \text{ so} \\ &I_{com} = (P_{n\max} + R_d)/[a \times (P_{n\max} - R_d)]. \end{aligned} \tag{5}$$

2.5 | Cumulative water loss curves

The rate of water loss after excision was measured from undamaged, mature leaves (fronds). The collected leaves were saturated overnight with distilled water. After the cut, stipes were sealed with Parafilm, fronds were placed on a lab bench under dim light (3–4 $\mu mol \cdot m^{-2} \cdot s^{-1}$), with an air temperature of approximately 25°C. Sample weights were measured periodically on an electronic balance (AL204-IC; Mettler Toledo Instruments Ltd., Shanghai, China) until there were few changes between 24-hr intervals. The measuring times were 0, 0.17, 0.67, 1, 2, 5, 14, 26, 38, 50, 62, 86, 110, 134, 158, 182, 206, 230 and 254 hr. At the end of the observation period, all samples were dried for 48 hr at 70°C to determine their dry weights. Six replicates were measured for ramets from each habitat.

2.6 | Data analysis

Initially, t-tests were used to compare environmental factors (i.e., air temperature, air moisture, humus temperature, leaf wetness and PAR), morphology, anatomy, physiology, biomass and ramet density between epiphytic and terrestrial habitats. By convention, alpha = 0.05 was used for the justification of significance level in traits between the two habitats. In order to show the relationship between traits, data were standardized using the Z-score to conduct a principle component analysis (PCA). Statistical analyses were performed in SPSS 18.0 (IBM, Armonk, NY).

3 | RESULTS

One-year data from the Ailaoshan Station for Subtropical Forest Ecosystem Studies showed that the air temperature was higher ($p < 0.001$), but air moisture was lower ($p < 0.05$) in epiphytic habitat relative to terrestrial habitat

TABLE 1 Differences in environmental factors between epiphytic and terrestrial habitats in the montane moist forest study site

	Habitat				
Factor	**Epiphytic**	**Terrestrial**	***df***	***t***	***p***
Air temperature (°C)[a]	11.8 ± 1.05	11.3 ± 1.03	11	6.859	0.000
Air moisture (%)[a]	78.7 ± 4.60	87.7 ± 3.30	11	−2.704	0.021
Humus temperature (°C)	6.9 ± 0.28	6.7 ± 0.32	5	0.286	0.787
Leaf wetness (%)	27.5 ± 8.94	36.1 ± 10.14	5	−4.074	0.010
PAR (μmol·m^{-2}·s^{-1})	19.7 ± 4.87	12.0 ± 2.09	5	2.622	0.047

Means ± *SE* are given for each parameter. PAR: photosynthetically active radiation.

[a] 12-month data from Ailaoshan Station for Subtropical Forest Ecosystem Studies.

(Table 1). The microclimatic observation systems recorded that leaf wetness in epiphytic habitat was lower ($p < 0.05$) than in terrestrial habitat whereas PAR exhibited the opposite pattern ($p < 0.05$) (Table 1). For humus temperature, no significant difference was found between the two habitats (Table 1).

Frond length of *S. griffithiana* was significantly smaller in the epiphytic than in the terrestrial habitat, while FW showed no significant difference between the two habitats (Table 2). Epiphytic ramets exhibited significantly greater LT, whereas lower SLA, STL and SPL than terrestrial ones (Table 2). Rhizome diameter and RSR did not differ significantly between epiphytic and terrestrial habitats (Table 2). With respect to anatomical traits, no significant difference was found in SS between the two habitats (Table 2), but SD and VD of epiphytic *S. griffithiana* were lower than terrestrial ones (Table 2). F_v/F_m and RCC of fronds were significantly lower in epiphytic habitat than in terrestrial habitat (Table 2). Total biomass and belowground biomass per ramet were smaller in the epiphytic than in the terrestrial habitat (Table 2), whereas ramet density was significantly higher (Table 2).

Based on the light-response curve of *S. griffithiana*, terrestrial ramets in general had a higher carbon assimilation capability than epiphytic ramets (Figure 1a). Exposed to a light gradient, terrestrial ramets exhibited higher photosynthesis rate (P_n) than epiphytic ones when PAR was no less than 100 μmol·m^{-2}·s^{-1} (Figure 1a). The maximum photosynthesis rate (P_{nmax}) was 2.33 ± 0.15 μmol CO_2·m^{-2}·s^{-1} in epiphytic habitat and 3.24 ± 0.44 μmol CO_2·m^{-2}·s^{-1} in terrestrial habitat. The light saturation point (I_{sat}) was 332.69 ± 12.49 μmol·m^{-2}·s^{-1} in epiphytic habitat and 306.91 ± 6.64 μmol·m^{-2}·s^{-1} in terrestrial habitat. The light compensation point (I_{com}) was 5.01 ± 0.96 μmol·m^{-2}·s^{-1} in epiphytic habitat and 1.8 ± 0.48 μmol·m^{-2}·s^{-1} in terrestrial habitats. These results indicated that terrestrial ramets from the shaded forest understory can intercept light and gain carbon faster than epiphytic ones from relatively brighter canopy conditions.

The water loss rate of *S. griffithiana*was was lower in epiphytic habitat than in terrestrial habitat (Figure 1b). When the water-saturating fronds of ramets were exposed to air, the water loss rate differed between epiphytic and terrestrial ramets after approximately one hour, and was lower for epiphytic ramets than terrestrial ramets. This represented that epiphytic ramets

TABLE 2 Comparison of functional traits of *Selliguea griffithiana* in forest epiphytic and terrestrial habitats

		Habitat				
Trait	**Abbreviation**	**Epiphytic**	**Terrestrial**	***df***	***t***	***p***
Frond length (cm)	FL	12.40 ± 0.64	13.50 ± 0.82	29	−2.188	0.037
Frond width (cm)	FW	3.34 ± 0.09	3.42 ± 0.11	29	−0.532	0.599
Frond thickness (mm)	LT	0.32 ± 0.03	0.29 ± 0.01	29	2.697	0.012
Specific leaf area (dm^2/g)	SLA	0.24 ± 0.01	0.28 ± 0.03	11	−2.242	0.047
Stipe length (cm)	STL	6.14 ± 0.45	7.64 ± 0.41	29	−2.370	0.025
Rhizome diameter (cm)	RHD	0.21 ± 0.05	0.22 ± 0.03	29	−0.441	0.662
Spacer length (cm)	SPL	3.95 ± 0.12	4.34 ± 0.14	29	−2.075	0.047
Ramet density (number per dm^2)	RD	4.25 ± 0.18	3.05 ± 0.05	9	4.811	0.001
Biomass (g)	B_t	0.42 ± 0.02	0.51 ± 0.03	29	−2.156	0.040
Aboveground biomass (g)	B_a	0.29 ± 0.11	0.34 ± 0.14	29	−1.820	0.079
Belowground biomass (g)	B_b	0.13 ± 0.11	0.17 ± 0.12	29	−2.119	0.043
Root to shoot ratio	RSR	0.51 ± 0.04	0.54 ± 0.05	29	−0.543	0.592
Stomatal density (number per mm^2)	SD	37.50 ± 2.25	53.64 ± 2.88	5	−4.989	0.004
Stomatal size (μm)	SS	45.52 ± 1.06	47.49 ± 1.14	5	−1.756	0.139
Vein density (mm/mm^2)	VD	1.21 ± 0.01	1.32 ± 0.05	5	−2.597	0.049
F_v/F_m	F_v/F_m	0.76 ± 0.01	0.78 ± 0.02	29	−2.208	0.035
Relative chlorophyll content	RCC	34.85 ± 0.83	38.53 ± 1.23	29	−2.239	0.033
Maximum photosynthesis rate (μmol·m^{-2}·s^{-1})	P_{nmax}	2.33 ± 0.15	3.24 ± 0.44	5	−2.601	0.048
Light saturation point (μmol·m^{-2}·s^{-1})	I_{sat}	332.69 ± 12.49	306.91 ± 6.64	5	2.399	0.062
Light compensation point (μmol·m^{-2}·s^{-1})	I_{com}	5.01 ± 0.96	1.84 ± 0.48	5	2.752	0.040

Means ± *SE* are given for each trait.

exhibited higher water retention capacity than terrestrial ones during the same time intervals (Figure 1b).

Result of PCA for functional traits showed that the first and second axes, respectively, explained 27.20 and 20.32% of the total variance (Table S1, Supporting Information; Figure 2). P_{nmax} dominated on the positive side of the first axis while ramet density, RSR and I_{sat} on the negative side; the second axis loaded VD and FW positively with just F_v/F_m on its negative part (Table S1; Figure 2). Accordingly, epiphytic and terrestrial samples were separated by the first axis, with terrestrial ones on the positive side and epiphytic conspecifics on the negative side (Figure 2).

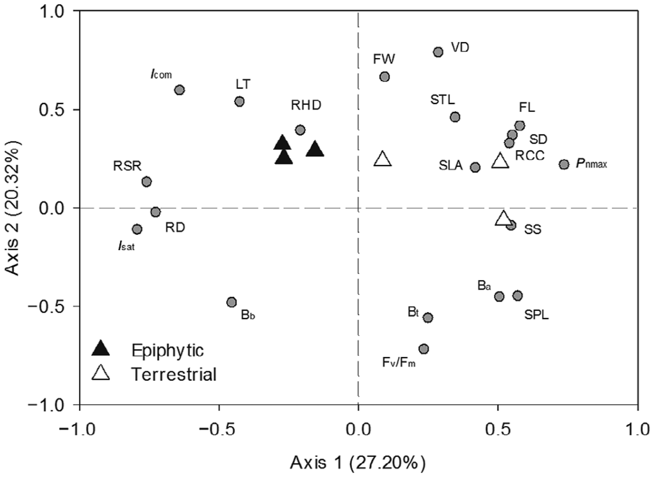

FIGURE 2 Principal component analysis (PCA) for functional traits of epiphytic and terrestrial samples of *Selliguea griffithiana*. Trait codes are defined in Table 2

4 | DISCUSSION

The study provided detailed information on the variation of functional traits of *S. griffithiana* between epiphytic and terrestrial habitats in a primary forest. Our results indicated that the photosynthetic capacity was lower in epiphytic individuals than in terrestrial conspecifics, and their water conservation efficiency was higher. By contrast, terrestrial individuals exhibited a higher photosynthetic capacity despite being exposed to lower light levels. PCA results also revealed two suites of traits related to light and water acclimation, showing different ecological strategies for *S. griffithiana* in the two contrasting habitats. Evidently, the first axis was responsible by light-related traits, and epiphytic and terrestrial samples distributed separately on its two sides. Though most of the samples distributed on the positive side of the second axis which was responsible by some water-related traits such as VD, individuals from both habitats exhibited distinct water conservative capacity. Here, we are going to elaborate trait acclimation of *S. griffithiana* to both habitats.

In the epiphytic habitat, *S. griffithiana* developed thicker and shorter fronds and relatively scarce stomata and veins (i.e., lower stomata and VD). These results were consistent with previous studies showing that obligate epiphytic ferns had smaller and thicker leaves than obligate terrestrial ferns which had larger and thinner fronds (Watkins & Cardelús, 2012; Watkins, Mack, & Mulkey, 2007). Plants in water shortage conditions commonly produce thick leaves and exhibit low water conductance to store and conserve water (Bartlett, Scoffoni, & Sack, 2012; North, Lynch, Maharaj, Phillips, & Woodside, 2013). Similarly, Zhang et al. (2015) found that epiphytic orchids exhibited traits indicative of greater drought tolerance and increased water storage capacity compared with terrestrial species. Waite and Sack (2010) showed that the leaves of branch-dwelling epiphytic mosses were smaller, composed of smaller cells with thicker cell walls and lower in quantum efficiency relative to ground-dwelling counterparts.

In terrestrial habitat, *S. griffithiana* produced longer stems (i.e., higher frond and STLs), thinner leaves (i.e., lower LT), greater SLA and higher RCC than epiphytic

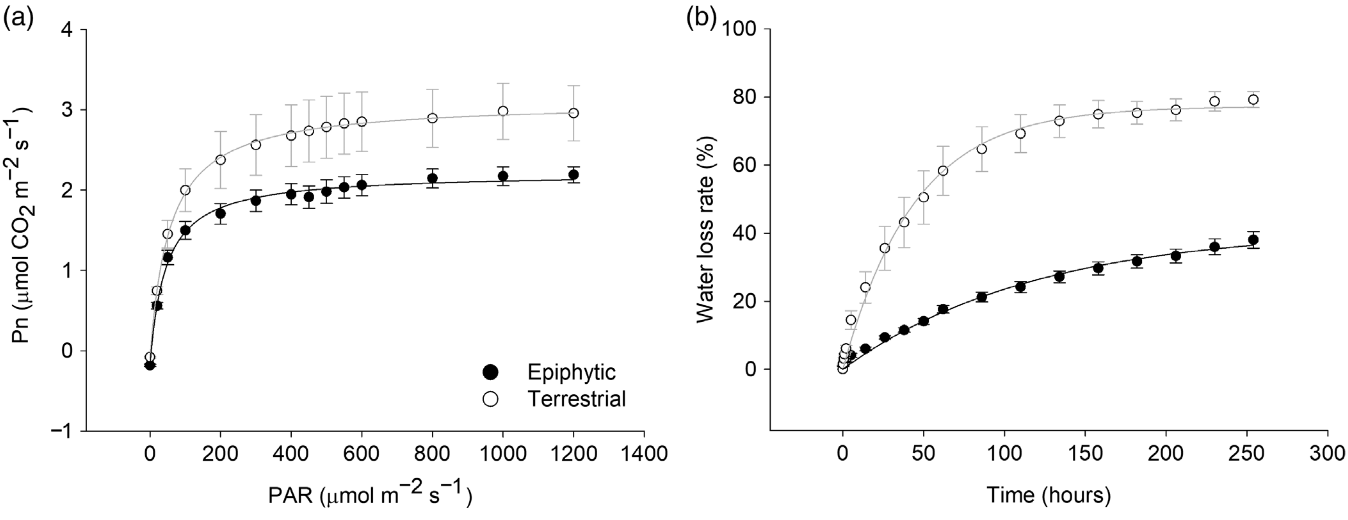

FIGURE 1 Photosynthetic light–response curve (a) and cumulative water loss curve (b) of *Selliguea griffithiana* in forest epiphytic and terrestrial habitats. Means ± *SE* ($n = 6$) are shown

ramets. Responses of these traits and the light–response curve suggested that *S. griffithiana* was better able to capture light and assimilate carbon in terrestrial habitat, which had lower light availability and more stable environments (Matelson, Nadkarni, & Longino, 1993). Longer stems increase leaf access to light and larger leaves maximize the light capture area. In addition, SLA is highly responsive to variation in light conditions, and plays an important role in the trade-off between light capture area and photosynthetic capacity per unit area (Zhu et al., 2016). Under different light conditions, species or genotypes are apt to adjust frond traits to make such acclimation (Barros et al., 2012; Vermeulen, Anten, Stuefer, & During, 2013). For example, the terrestrial fern *Blechnum chilense* (Blechnaceae) exhibited larger and thinner fronds in low-light forest understory comparing to the forest gaps with high light (Saldaña, Lusk, Gonzales, & Gianoli, 2007). In another study, three tree ferns distributed under either closed or open canopies also differed significantly in SLA, maximum electron transport rate and light saturation point (Riaño & Briones, 2013).

S. griffithiana produced shorter spacers in epiphytic habitat than in terrestrial habitat. Previous studies have shown that spacers can increase, decrease, or do not change in response to resource shortage (de Kroon & Hutchings, 1995; Gao, Xing, Jin, Nie, & Wang, 2012; Pottier & Evette, 2010; Weiser & Smyčka, 2015). The shorter spacers between adjacent ramets from epiphytic habitats may not be an active response to the shortage of water and nutrients, but a passive response as a result of the reduced growth (Cornelissen, Song, Yu, & Dong, 2014; de Kroon & Hutchings, 1995; Song et al., 2013). In support of this view, we did find that mean biomass of *S. griffithiana* was smaller in epiphytic habitat than in terrestrial habitat. On the other hand, a previous study showed that the survival and growth of the *S. griffithiana* ramets relied more on clonal integration (resource sharing) when they grew in epiphytic habitat than they grew terrestrially in understory (Lu et al., 2015). Because SPL is negatively correlated with the efficiency of resource sharing between interconnected ramets (Schmid & Bazzaz, 1987), shorter spacers in epiphytic individuals may provide an addition explanation why the effect of clonal integration was stronger in epiphytic habitat than in terrestrial habitat (Lu et al., 2015).

S. griffithiana produced smaller but more (denser) ramets in epiphytic habitat than in terrestrial habitat, suggesting a trade-off between size and number of ramets. This might benefit epiphytic individuals to explore the stressful and patchy canopy and it could be ascribed to four reasons. Firstly, the fragmentation of a clone may occur by violent disturbance frequently in epiphytic habitat. But disconnection between ramets may be fatal for this species, especially in the canopies (Lu et al., 2015, 2016). Smaller ramets may minimize the cost of the clone fragment or the whole clone in case of ramet death. Secondly, epiphytic habitat is more stressful and heterogeneous than terrestrial one. The more ramets, the more microhabitats they could inhabit. There are enough individuals to maintain epiphytic populations, although some of fronds (aboveground part) may wither and die out under adverse conditions. We did find there were lots of leafless ramets (i.e., ramets without fronds) in the canopies in the field. Thirdly, epiphytic individuals suffer from frequent overexposure to the sun. Reductions in organ size, such as leaves and ramets, is a key mechanism of photoprotection because it improves heat dissipation (Vogel, 1968; Waite & Sack, 2010). Lastly, undertaking a conservative strategy of water and resource use, limited assimilation products of epiphytic individuals cannot afford a large number of big ramets (Brodribb & Holbrook, 2004; Zhang et al., 2009).

The present study found higher maximal photosynthesis rate and chlorophyll fluorescence in the low-light terrestrial habitat. This result contrasts with other findings comparing individuals in different light environments with similar water availability. For example, in *B. chilense*, the photosynthetic capacity and dark respiration rate of individuals were lower in forest understory than those in forest gaps (Saldaña et al., 2007). Zhu et al. (2016) also found that ferns in high-light habitats captured resources and grew rapidly in the open environment (i.e., exhibited a fast-return strategy), while ferns in low-light habitats had lower carbon assimilation rates and persisted in the shaded understory (i.e., exhibited a slow-return strategy). The discrepancy may result from three aspects. Firstly, epiphytic habitat is characterized as a resource-limited (especially water-limited) and resource heterogeneous environment. Epiphytes dwelling in it are subjected to resource shortages that restrict photosynthetic capacity, resulting in a lower F_v/F_m. Actually, our PCA results revealed that maximum photosynthesis rate was positively correlated with VD, while negatively correlated with ramet density. Thus, lower VD of epiphytic rametes might also limit the photosynthesis via its influence on frond hydraulic efficiency (Brodribb, Field, & Jordan, 2007). Secondly, epiphytes have evolved a higher capacity in water conservation at the expense of a lower light use efficiency, which ultimately results in a lower growth rate (Gauslaa, Lie, Solhaug, & Ohlson, 2006). Epiphytic ferns completely close stomata when frond relative water content reaches about 70%, whereas terrestrial ferns keep partial stomata open until the relative water content reaches 45% (Zhang et al., 2009). Lastly, terrestrial ferns in the understory have evolved a special photoreceptor of the red/far-red light receptor to cope with low light conditions (Kawai et al., 2003). The ramets of terrestrial individuals can maximize the photosynthetic capacity without the shortages of water and nutrients.

5 | CONCLUSIONS

We conclude that the individuals of *S. griffithiana* from epiphytic and terrestrial habitats varied in morphological, anatomical, physiological and growth traits, where acclimated to such contrasting habitats. This intra-specific variation of functional traits may represent different strategies for facultative epiphytes to cope with different habitats. The epiphytic strategy was more costly in terms of photosynthetic capacity than the terrestrial strategy. This is because the epiphytic habitat is more water limited, and therefore, epiphytes have to reduce water losses at the expense of photosynthesis. Since among-individual variation is the substrate for natural selection, these results open interesting ecological and evolutionary questions for the future. Therefore, further studies should focus on how the epiphytic individuals, which have a lower photosynthetic capacity, are maintained in facultative epiphyte populations, whether they are frequent or rare, and whether they have a differential fitness.

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