


Divergent Strategies of Epiphytic Pteridophytes and Angiosperms Responding to Dry and Wet Seasons in a Tropical Cloud Forest

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Abstract

Epiphyte is a unique component of forest diversity vulnerable to changing environments. Characterizing variations in functional traits of epiphytes across dry and wet seasons can enhance our understanding their strategies to environments. We measured and assessed variations of 14 leaf functional traits responding to water conditions for epiphytic pteridophytes (EP) and epiphytic angiosperms (EA) across dry and wet seasons in a tropical cloud forest. Results showed that leaf dry weight (LDW) and stomatal length (SL) of EP were significantly higher than EA, while leaf water content (LWC) of EA was significantly higher than EP. The SL, stomatal density (SD), upper epidermis thickness (UET), lower epidermis thickness (LET), palisade tissue thickness (PT), spongy tissue thickness (ST), and leaf thickness (LT) of EP and EA were significantly higher in wet season than dry season. The variance of stomatal and anatomical traits explained by season types (0.24–0.78) was higher than plant groups (0.0–0.25), while the variance of LDW and LWC explained by plant groups (0.12–0.40) was higher than season types (0.0–0.29). Principal component analysis and correlation analyses showed that SL, stomatal index, UET, ST, LET, and LT were the key traits reflecting epiphyte adaptation to dry season, as well as that LWC and leaf density were the key traits in wet season. Our results suggest that the different taxonomic groups exhibit divergent strategies responding to water differences. Great variations in leaf traits to dry seasons are predicted that vascular epiphytes, especially pteridophytes, are prone to disappear with drought events.

Keywords

dry and wet season, epiphytic angiosperms, epiphytic pteridophytes, functional traits, tropical cloud forest

Plant functional traits, which reflect components of plant life history strategies (Ackerly, 2003; Violle et al., 2007), are often used to explore plant adaptation to external environmental stimuli (Klich, 2000) and predict the effects of environmental changes on plant communities (Suding et al., 2008). For example, leaf morphological traits have been demonstrated to predict vegetation distributions (Cornelissen et al., 2003) and play an important role in maintaining water balances in epiphytes (Zhang et al., 2015). It is generally believed that drought-tolerant plants have small and thick leaves. Small leaves often minimize evaporation, while thicker leaves have a larger water-storage capacity to pass through arid environments (Bartlett et al., 2012). Although co-occurring taxa have been observed divergent adaptive performances in response to water

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availability, the underlying physiological and morphological mechanisms by epiphyte species coping with water stress, however, remain poorly understood (Cach-Pérez et al., 2018; Gotsch et al., 2015, 2018; Zhang et al., 2016; Zotz & Bader, 2009).

There are more than 20,000 vascular epiphyte species in the world usually growing in environments with high precipitation, high humidity, and frequent cloudy weather and play an important ecological role in hydrologic and nutrient cycling in forest ecosystems (Benzing, 1990; Gotsch et al., 2018; Zotz & Bader, 2009). Orchidaceae, Araceae, and Bromeliaceae have been observed to be the major groups of epiphytes (Zotz & Bader, 2009). Due to the lack of buffering by forest floor and soil, epiphytes are highly vulnerable to changing external environmental conditions such as temperature, water, and atmospheric nutrient input (Benzing, 1998; Foster, 2001). For example, water availability has been proved to be a key factor determining epiphytes' survival, because water supply is limited due to their low substrate use efficiency (Kreft et al., 2004; Laube & Zotz, 2003; Rada & Jaimez, 1992; Song et al., 2015; Zotz et al., 2001). Vascular epiphytes exhibit a variety of traits such as thick leaves, cuticles, and large tuber-like storage structures to resist water loss, that are likely adaptations to withstand dry periods by aiding in the maintenance of positive water balance and drought resistance (Benzing, 1990; Darby et al., 2016; Gotsch et al., 2015; Wu et al., 2018; Zotz & Winter, 1994). In water-rich habitats, however, epiphytes may still face the stress of short-term drought (Sinclair, 1983). Since the increase of global fog line and changing environments have been demonstrated to threaten the survival of high-altitude forest plants (Lenoir et al., 2008), further studies, therefore, is urgent to improve the knowledge of conservations.

Tropical cloud forests are characterized by strong winds, low air temperature, frequent cloud cover, saturated soil, and large numbers of endangered and endemic species (Bubb et al., 2004). Trees in tropical cloud forest with an average small leaf surface area and specific leaf area (SLA) are found to undergo low temperature and vapor pressure deficit environments and experience a long period of low water evaporation (Long et al., 2011b). Vascular epiphytes are important components of tropical cloud forest (Wang et al., 2016) and are often grouped into epiphytic pteridophytes (EP) and epiphytic angiosperms (EA). It is likely that these two groups with different evolutionary relationships exhibit divergent functional traits responding to water difference environments. For example, EP often exhibit bird's nest structure that absorb and retain water (John & Hasenstein, 2017); while epiphytic orchids form pseudobulbs that are important organs for storage of water (Ng & Hew, 2000). Also, it is likely that epiphyte species show differing ecological strategies to dry

and wet seasons in tropical cloud forests. But still little is known about how these high-altitude forest plants survive through the changing environments. In this study, we measured both physiologic and anatomical traits of EP and EA species that reflect plants' water utilization strategy across both dry and wet seasons, and tested whether the two plant groups exhibited divergent adaptation strategies to water conditions. We hypothesized that (a) vascular epiphytes would take different ecological water use strategies between dry and wet seasons in tropical cloud forests and (b) EP species and EA species would show different leaf functional traits responding to either dry or wet seasons in tropical cloud forests.

Methods

Study Sites

The study was conducted in tropical cloud forests in Bawangling National Nature Reserve (BNR; 109°05'-109°25'E, 18°50'-19°05'N) in Hainan Island, South China. There were 21 tropical cloud forest plots (20 × 20 m) randomly established in 2011 in BNR, in which there were a total of 139 tree species (trees ≥ 1 cm diameter at breast height), with an average tree height of 4.79 ± 2.80 m, a diameter at breast height of 9.38 ± 3.22 cm, and a density of 9633 stems ha⁻¹. The dominant species are *Distylium racemosum*, *Symplocos poilanei*, *Syzygium buxifolium*, *Cinnamomum tsoi*, *Engelhardtia roxburghiana*, and *Rhododendron moullainense*. Tropical cloud forests in BNR are primary old growth forests and are mainly distributed on the mountaintops at elevations over 1200 m, with an eastern slope ranging from 36° to 45° (Long et al., 2015). It is tropical monsoon climate, with a distinct wet seasons from May to October and dry season from November to April of the next year (Long et al., 2011a). There are about 300 days of fog per year. The mean daily relative humidity in the wet season ranges from 87.88% to 100%, and the mean daily air temperature ranges from 17.6°C to 24.8°C. The mean daily relative humidity in the dry season ranges from 57.68% to 100%, and the mean daily air temperature ranges from 15.2°C to 22.6°C. Soils in cloud forest are montane meadow soils developed from sandstone.

Measurement of Leaf Functional Traits

Functional traits that reflect plant water physiology and resistance to environmental stress were selected (Table 1). There were 30 epiphytic vascular plant species in the plots including 11 EP species and 19 EA species (Table S1). Trees in these forests are frequently malformed and efin, which makes us easily survey the epiphytes. Leaf traits were measured in the February 20th

Table 1. Selected Functional Traits of Vascular Epiphytic Plants and Their Ecological Significance.

Functional traits	Ecological significance
Leaf dry weight (LDW)	Indicates plant photosynthesis and its responses to water scarcity.
Leaf water content (LWC)	Indicates plant water status and adaptability to environment; is related to leaf energy balance.
Specific leaf area (SLA)	Indicates plant's ability to capture resources and adapt to environmental changes; is related to photosynthesis.
Chlorophyll content (CHL)	Is directly related to photosynthetic capacity, reflecting carbohydrate synthesis in plant.
Stomatal length (SL)	Allows for gas and moisture exchange, directly affecting plant transpiration and photosynthesis.
Stomatal density (SD)	Directly affects plant transpiration and photosynthesis, and is related to plant stress resistance.
Stomatal index (SI)	Indicates the ability of plant leaves to regulate water transport, photosynthetic rate, and transpiration rate through stomata.
Upper epidermis thickness (UET)	Reflects plant water retention, protects plants, and is associated with plant stress tolerance.
Palisade tissue thickness (PT)	Reflects plant water status, regulates transpiration efficiency, and affects photosynthesis.
Spongy tissue thickness (ST)	Reflects plant drought resistance, affects photosynthesis.
Lower epidermis thickness (LET)	Reflects plant water status.
Leaf thickness (LT)	Reflects plant's response to environment and resistance to stress, and prevents water evaporation.
Leaf density (LD)	Reflects plant water and nutrient availability.
Palisade tissue/spongy tissue (P/S)	Indicates plant photosynthesis and transpiration.

to 25th of dry season and in the July 10th to 15th of wet season in 2019. Epiphyte species were often found to be segregated in the host tree, sampling height and orientation thus may affect functional traits. A total of three to six host trees were selected for each epiphyte species, and three to six recently and fully expanded south-oriented leaves (current year's growth) from ground to the 2 m of the host tree stems were sampled for each individual host (thus there were at least nine sampled leaves for each epiphyte species). The samples across both dry and wet seasons were collected from the same host tree, to avoid the variation in functional traits of epiphytes due to different host tree environments (e.g., tree barks).

The chlorophyll content (CHL, SPAD) was measured using a portable chlorophyll meter (SPAD-502 Plus, Konica Minolta, Japan). Leaves were dried to a constant weight at 70°C for at least 3 days and then weighted to the nearest 0.01 g, and leaf dry weight (LDW, g) was obtained. Leaf water content (LWC, %) was calculated by the ratio of difference between fresh weight (FW, g) and LDW to FW. The leaf area (cm²) was measured using a scanner (Epson Perfection V800 Photo). Specific leaf area (SLA, cm²·g⁻²) and leaf mass per area (g·cm⁻²) values were calculated from the ratio of LDW to leaf area. After the cross section of each sampled leaf was prepared, the sample was examined with a 20× optical microscope (LEICA DM3000 LED), and the upper epidermis thickness (UET, μm), lower epidermis thickness (LET, μm), palisade tissue thickness (PT, μm), spongy tissue thickness (ST, μm), and leaf thickness (LT, μm) were measured using an Image J software. Then, leaf density (LD, g·mm⁻³) was calculated by ratio of leaf mass per area to LT. The leaf stomatal traits of a half leaf were measured using a nail polish blotting method. After a sample with leaf surface film was prepared, the sample was examined and assessed under a 40× objective of an optical microscope (LEICA DM3000 LED); 10 images were randomly taken and the stomatal structure and stomatal guard cell length were analyzed with Image J software. Stomatal length (SL, μm), number of pores per unit area, and stomatal density (SD, number·mm⁻²) were calculated according to the measurements. Stomatal index (SI, %) was obtained by multiplying the SD with square of the SL.

Data Analysis

Variations in functional traits of epiphytes across plant groups (pteridophytes and angiosperms) and season types (dry and wet seasons) were assessed using two-way analysis of variance. To normalize the data, functional trait values were transformed using a standard log (base 10) transformation before data analysis. The variance of plant functional traits explained by plant groups and season types was decomposed using a generalized linear model and *varcomp* function. For instance, when LDW was measured, the functional traits were obtained by replacing LDW:

```
varcomp.LDW<-varcomp(lme(log(LDW)~1,random=~1|season|type,data=d,na.action=na.omit),1)
```

Correlations among leaf functional traits were analyzed using Pearson's correlations. After principal component analysis (PCA), the effect values of different functional traits were assessed according to the loadings

of each variable. All statistical analyses and data mapping were performed using R software version 3.5.2.

Results

Variations in Functional Traits Across Plant Groups and Season Types

There were no significant differences in SLA and CHL between the two plant groups and across dry and wet seasons ($p > .05$). LDW and LWC, however, showed significant differences between plant groups ($p < .001$), with the LDW of EP significantly higher than EA, while LWC of EA significantly higher than EP. SD, PT, ST, LET, and LT were significantly lower in dry season than wet season ($p < .01$). SL, SI, UET, and LD were significantly affected by both plant groups and season types ($p < .05$; Table 1), with SL, SI, UET, and LD not only significantly lower in dry season than wet season but also significantly higher in EP than EA except UET.

Variance of Functional Traits Explained by Plant Groups and Season Types

The explained variance of LD (0.11) was similar for both plant groups and season types (Figure 1). The variance

of SL, SD, SI, UET, PT, ST, LET, and LT, however, explained by season types (0.24–0.78) was higher than plant groups (0.0–0.25). But the variance of LDW and LWC explained by plant groups (0.12–0.4) was higher than season types (0.0–0.29).

Correlation Analysis of Vascular Epiphytes

Stomatal traits (SL, SD, SI) and leaf anatomical structure, as well as LDW, LWC, SLA, and LD, were strongly correlated not only for all epiphyte species but also for species of EA across the dry and wet seasons (Figure 2A and B). Nevertheless, LDW, LWC, and SLA were significantly correlated with LD, but SD and leaf anatomical structure showed nonsignificant correlation with EP (Figure 2C).

PCA of Vascular Epiphytes

When all the species of EP and EA were mixed, species were not obviously grouped according to variation in leaf traits across dry and wet season using a PCA (Figure 3A and Table S2). But when the EP and EA were separately PCA analyzed, epiphyte species were grouped along Axis 1 according to variation in leaf traits across dry and wet season (Figure 3). For example, for EA species SI, UET, PT, and LET with loadings

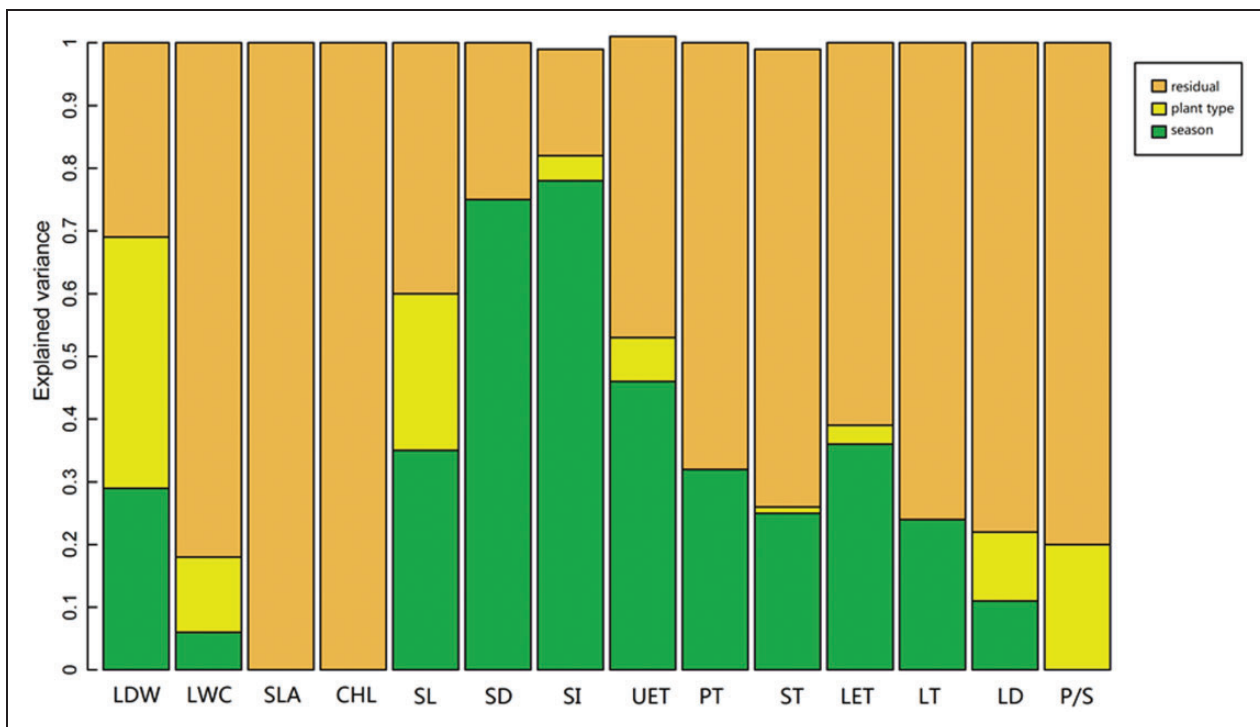


Figure 1. Variance Decomposition of the 14 Functional Traits With Changes in Plant Population and Season Type. LDW = leaf dry weight; LWC = leaf water content; SLA = specific leaf area; CHL = chlorophyll content; SL = stomatal length; SD = stomatal density; SI = stomatal index; UET = upper epidermis thickness; PT = palisade tissue thickness; ST = spongy tissue thickness; LET = lower epidermis thickness; LT = leaf thickness; LD = leaf density; P/S = Palisade tissue/spongy tissue.

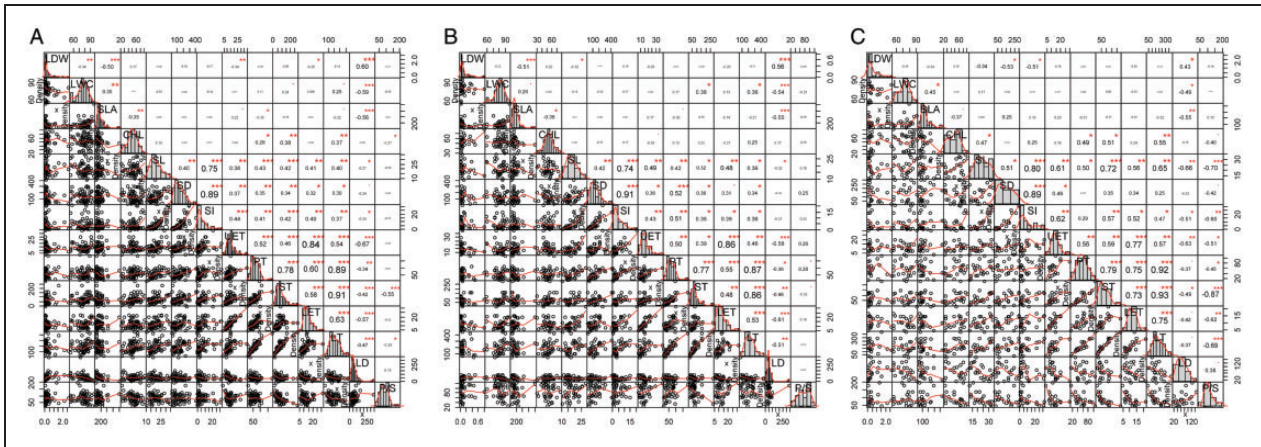


Figure 2. Correlation Analysis Among Functional Traits Among in Dry Season and Wet Season for all Species, and Separately for Epiphytic Pteridophytes Species and Epiphytic Angiosperms Species. LDW = leaf dry weight; LWC = leaf water content; SLA = specific leaf area; CHL = chlorophyll content; SL = stomatal length; SD = stomatal density; SI = stomatal index; UET = upper epidermis thickness; PT = palisade tissue thickness; ST = spongy tissue thickness; LET = lower epidermis thickness; LT = leaf thickness; LD = leaf density; P/S = Palisade tissue/spongy tissue.

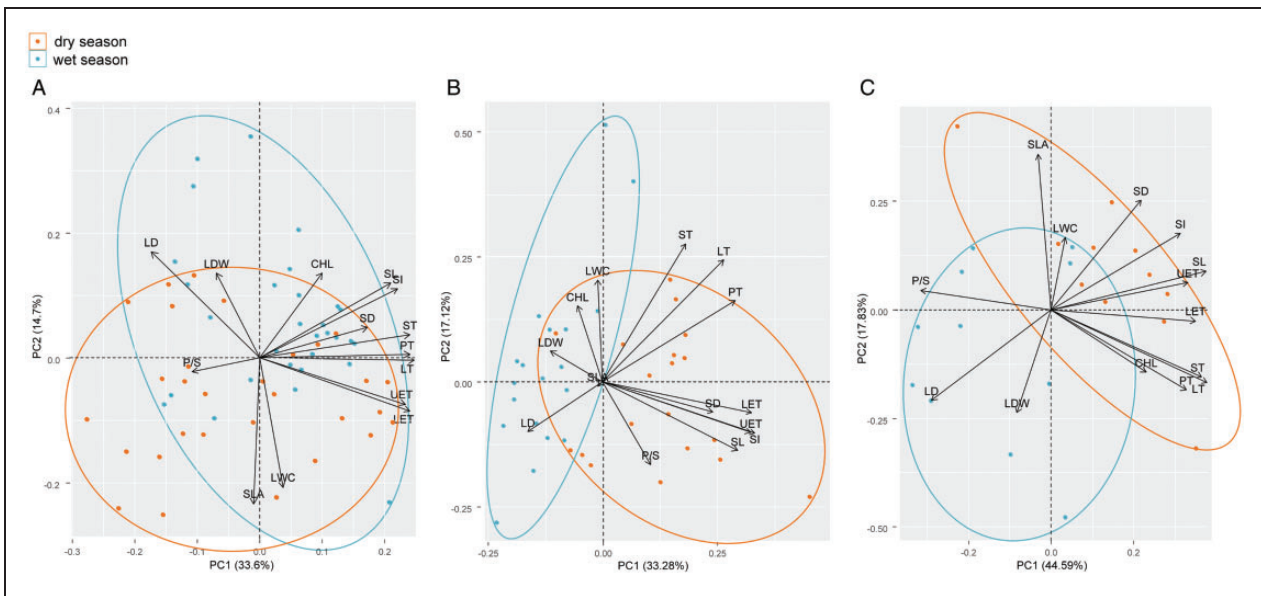


Figure 3. Principal Component Analysis for Dry Season and Wet Season for all Species, and Separately for Epiphytic Pteridophytes Species and Epiphytic Angiosperms Species. LDW = leaf dry weight; LWC = leaf water content; SLA = specific leaf area; CHL = chlorophyll content; SL = stomatal length; SD = stomatal density; SI = stomatal index; UET = upper epidermis thickness; PT = palisade tissue thickness; ST = spongy tissue thickness; LET = lower epidermis thickness; LT = leaf thickness; LD = leaf density; P/S = Palisade tissue/spongy tissue.

exceeding 0.75 were positively related to PCA Axis 1 (explained variance 33.28%); while LWC and LD were negatively related to PCA Axis 2 (17.12% explained variance, Figure 3B and Table S2). For the functional traits of EP species, when the first and second principal components accounted for 44.59% and 17.83% of total variance, SL, ST, LET, and LT with loadings exceeding 0.8 were positively related to PCA Axis 1. But LDW and LD were negatively related to PCA Axis 2 (Figure 3C and Table S2).

Discussion

Vascular Epiphytes Adaptation Strategies Across Dry and Wet Seasons

As hypothesized, the water use strategies of vascular epiphytes differed across dry and wet seasons (Figures 1 to 3 and Table S2). Consistent with previous results (He et al., 2018; Lin et al., 2017), we find that leaf functional traits including SL, SD, SI, UET, LET, PT,

ST, and LT in dry season were significantly lower than wet season. The significant differences in stomatal and anatomical traits result from the facts that the rainfall, temperature, and relative humidity in dry seasons were lower than wet seasons (Wenxing Long, 2018), as well as that the fog in dry season largely eliminates the atmospheric vapor pressure deficit (Sso & Dawson, 2010), and effectively suppressed the transpiration of plants during dry season. The low values in the traits in dry seasons may help trees reduce transpiration and maintained the water, since the stomata primarily regulate water loss and CO₂ uptake, and conserve water during drought (Wang et al., 2013). Chen et al. (2019) also found that epiphytes showed morphological, physiological, and anatomical acclimation to mitigate water stress, and had a higher water retention capacity, which is consistent with our findings that the reduction of stomatal and anatomical traits of vascular epiphytes is an important strategy to adapt to the dry season in tropical cloud forests.

Interestingly, we found both SL and SD in dry season were significantly lower than wet season (Table 2). This indicates that vascular epiphytes reduce stomatal density and length to adapt to environments by preventing water loss through transpiration (Rada & Jaimez, 1992). A recent study by Hamanishi et al. (2012) suggested that drought stress leads stomata become small. In contrast, high SD and SL are helpful for vascular epiphytes to obtain high transpiration and growth rate in wet season.

PCA showed that LD shows adaptation strategies of vascular epiphyte in wet seasons in tropical cloud forests (Figures 1 to 3 and Table S2). This may result from the fact that this plant character changes greatly due to strong photosynthesis and rapid growth in wet seasons.

For example, vascular epiphytes often increase water storage capacity by developing PT, ST, and LT in wet seasons (He et al., 2018), which enhance the photosynthesis rate and increase the organic matters. On the other hand, plants tend to invest great carbon amounts in the sclerophyllous structures of the rather sturdy foliage to increase LD in the wet seasons to resist strong winds.

In addition, differences in solar irradiance along tree height have been demonstrated to be associated with the changes in plant functional traits (He et al., 2018; Long et al., 2011c). For example, percentage reduction of photosynthetic photon flux density was related to variation in maximum species height distribution in tropical cloud forest (Long et al., 2015). But in tropical areas such as tropical cloud forests in Hainan Island, solar irradiance might not differ between the dry and wet seasons. Furthermore, tropical cloud forests in our study site is located at the top of the mountain, and the mean tree height is low (i.e., less than 5 m). The amount of light at the sampling areas of host trees (e.g., from ground to the 2 m of the host tree stems) is predicted to be relative consistent between the dry and wet seasons, and thus may not lead to differences in leaf functional traits across the two seasons.

Effects of Plant Groups on Variations in Functional Traits

We found the two plant groups, EP and EA, showed different functional traits in tropical cloud forests (i.e., SL and LDW of EP were higher than EA, while LWC of EA was higher than EP; Table 2; Figure 3A and B). Our results thus support the hypothesis that EP and EA species take different strategies responding to dry and wet seasons. High SL of Pteridophytes species often have

Table 2. Two-Way Analysis of Variance of Functional Traits of Vascular Epiphytic Plants.

Functional traits	Season		Plant type		Season: Plant type	
	F	P	F	P	F	P
Leaf dry weight (LDW)	1.22	.27	21.69	<.001***	1.01	.32
Leaf water content (LWC)	0.49	.49	11.36	.001***	0.78	.38
Specific leaf area (SLA)	0.18	.68	1.35	.25	0.54	.47
Chlorophyll content (CHL)	0.02	.89	0.07	.79	0.58	.45
Stomatal length (SL)	32.53	<.001***	17.95	<.001***	1.62	.21
Stomatal density (SD)	91.9	<.001***	0.62	.43	1.27	.26
Stomatal index (SI)	131.57	<.001***	5.74	.02*	3.13	.08
Upper epidermis thickness (UET)	30.57	<.001***	5.5	.02*	0.52	.47
Palisade tissue thickness (PT)	18.39	<.001***	2.68	.11	0.77	.38
Spongy tissue thickness (ST)	14.84	<.001***	0.13	.72	0.99	.32
Lower epidermis thickness (LET)	11.1	.002**	0.73	.4	2.08	.15
Leaf thickness (LT)	10.31	.002**	1.67	.2	0.37	.54
Leaf density (LD)	6.27	.02*	5.1	.03*	0.98	.33
Palisade tissue/spongy tissue (P/S)	0.14	.71	0.75	.39	11.91	.001***

* $p < .05$. ** $p < .01$. *** $p < .001$.

large stomata (Carlquist & Schneider, 2001). Large stomata of EP on the tropical cloud forest tree stems may help epiphytes increase transpiration and make water easily loss from the leaf surface, leading a low LWC (Zobayed et al., 2000). On the other hand, large stomata of EP probably help plants increase the uptake rate of CO₂, leading a high LDW. Finally, EP leaves with high LDW may also tend to be relatively tough, and help the plants be resistant to strong winds in the tropical cloud forests (Poorter et al., 2009). Thus, EP species in tropical cloud forests tend to take a quick water utilization strategy.

Epiphytic angiosperms species with small stomata typically respond quickly to environmental stimuli, resulting in a relatively low loss in internal water content (Zotz & Andrade, 1998). Also, these species often have pseudobulbs for growth, survival, and storage of water (Ng & Hew, 2000). These characteristics allow EA leaves to achieve high diffusion conductivity and maintain a high LWC during the drought in tropical cloud forests (Drake et al., 2018; Krööt et al., 2001; Niinemets et al., 1999). Thus, we find that EA species tend to take a conservative strategy in water utilizations. Our findings provide evidence that EP and EA independently evolved a variety of different morphological and physiological characteristics (Benzing, 1990). Such differences between taxonomic might affect the response of leaf functional traits to water difference conditions across the dry and wet seasons (Petter et al., 2016).

Implications for Conservation

As hypothesized, we found that both EP and EA showed lower leaf functional traits in SL, SD, SI, UET, LET, PT, ST, and LT in dry seasons than wet season. This indicates the epiphyte species take differing water use strategies across dry and wet seasons in the tropical cloud forests. That is, epiphytes tend to conserve water by regulating water loss to pass through the dry seasons, while these plants probably increase water storage capacity and carbon production rate to gain rapid growth in wet seasons. Thus, our findings suggest that drought environments be critical to the growth of epiphyte. Compared with EA, EP species have a higher SL and LDW but lower LWC. This indicates that EP species in tropical cloud forests take a quick water utilization strategy, while EA species tend to take a conservative water utilization strategy. Thus, it can be concluded that EP species are more vulnerable to water shortage than EA, which help us predict that epiphytes in tropical cloud forest, especially EP (though EP species often take unique ways adapting to dry environments; John & Hasenstein, 2017; Zotz & Bader, 2009), are easily disappear if the fog water reduction and extreme drought events happened. Our results also add evidence

that taxonomic groups independently evolved a variety of different morphological characteristics to respond to water difference conditions.

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Supplemental Material

Supplemental material for this article is available online.

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