




## Article

# Fog Water Is Important in Maintaining the Water Budgets of Vascular Epiphytes in an Asian Tropical Karst Forests during the Dry Season

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**Abstract:** Fog may be an important source of water for forest vascular epiphytes on trees, because they lack direct access to sources of soil water, but little is known about the water use proportions from various sources and potential water uptake pathways in epiphytes. Here, we analyzed leaf carbon isotope ratios as a measure of water use efficiency (WUE), proportions of fog, rain, and soil water use, and foliar water uptake (FWU) in species of epiphyte and their host trees in a tropical karst dwarf forest in China during the dry season. We found that the WUE, as represented by leaf  $\delta^{13}\text{C}$ , was generally enriched in the epiphyte species compared to their host trees. Epiphytes used substantial proportions of fog water, whereas water use in the host trees was dominated by soil water. The leaves of epiphytes and host trees absorbed water following immersion in water for 3 h and FWU possibly related to foliar epicuticular structures, such as fungal endophytes. Our results show a divergence of water use strategies between epiphytes and their hosts and highlight the importance of fog water for epiphytes during the dry season and under a climate change scenario with a reduced occurrence of fog events.

**Keywords:** fog; stable isotope; water use efficiency; foliar water uptake; climate change

## 1. Introduction

Occult precipitation, such as mist and fog, may be a primary source of water for canopy plants in forest ecosystems that are affected by periods of low rainfall [1]. Modeling has indicated that the interception of cloud water (fog) contributes between ca. 5% and 75% of the total precipitation in tropical montane rainforests [2]. Fog water has been shown to be important for plants in forests subjected to seasonal droughts mediated by monsoons and canopy epiphytes that have no direct access to ground level water resources [3–5]. Indeed, fog mitigates drought stress in epiphytes by preventing desiccation and lengthening the photosynthetic period, and it has been suggested that epiphyte growth benefits from the interception of fog water [6–8]. However, the proportional use of fog water and water uptake pathways in epiphytes remain unclear [9,10].

Epiphytes are frequently drought stressed and use water more efficiently, as indicated by enriched  $\delta^{13}\text{C}$  signatures compared to ground-rooted plants [11]. Whole-plant water use efficiency (WUE) may be estimated using  $\delta^{13}\text{C}$ , which may also be used to identify the mode of photosynthesis [12,13]. Crassulacean acid metabolism (CAM), which is indicated when the  $\delta^{13}\text{C}$  ranges from  $-22\text{‰}$  to

–12‰ [14,15], facilitates the exploitation of the canopy habitat for epiphytes [16,17], however,  $\delta^{13}\text{C}$  is not always enriched in epiphytes relative to host trees, suggesting that fog affects WUE [18].

Differences in the stable hydrogen and/or oxygen isotope composition of meteoric water (snow or rain) may be used to identify the types and relative proportions of the water sources used by plant species [19]. A number of studies using stable isotope techniques have shown that understory plants [20], seedlings [21], and lianas rely on moisture from fog to a greater extent than canopy trees [22], and that the use of fog water may vary according to the plant growth stage. For example, 76% of water use in the epiphytic stage of *Didymopanax pittieri* Marchal (Araliaceae) in tropical cloud forests derived from fog, whereas the arborescent life stage only used recently deposited rain water [23].

Foliar water uptake (FWU) is the process by which water is absorbed into the leaves, resulting in a net increase in leaf water mass [24]. FWU provides an important water rehydration subsidy that reduces transpiration and alleviates foliar water stress during periods of little or no rainfall [25,26]. The film of water that accumulates on leaves in fog conditions is critical to maintaining the water budget in epiphytes [1,27]. The diffusion of fog water intercepted by the leaves in a number of species is mediated by fungal hyphae [19], absorbent trichomes [28], and properties of the cuticle and leaf awn [29,30], but the mechanisms and pathways for FWU in epiphytes remain unknown [10].

In forest ecosystems that experience periods of reduced rainfall, water stress in plants that are not directly rooted in the soil may be expected. It has been suggested that fog acts as a supplemental source of water and plays an important role in the water relations of plants during rainless dry periods [22,31], where it has been shown to compensate for periods of insufficient precipitation, sustain tropical rainforest vegetation [3], and support greater epiphyte richness [32]. However, there is evidence that changes in land use (deforestation) over the last 50 years have resulted in reduced radiation fog frequency and duration in an area of tropical rainforest affected by periods of drought [33,34]. It has been suggested that reductions in fog water inputs are especially critical at the northern latitudinal limit of tropical rainforest during the dry season when rainfall is minimal and fog water could be an available source of moisture [35]. Therefore, it is important to determine fog water use in epiphytes to understand potential impacts of ongoing climate change on this group of plants. Here, we quantified fog water use in epiphytes in a tropical karst forest in Xishuangbanna, testing the hypotheses that: (1) the WUE of epiphytes represented by leaf  $\delta^{13}\text{C}$  are enriched compared to those of their hosts; (2) epiphytes use a higher proportion of fog water than their host tree during periods of little or no rainfall; and, (3) the capacity for FWU in epiphytes is greater than their hosts and may relate to distinct foliar characteristics.

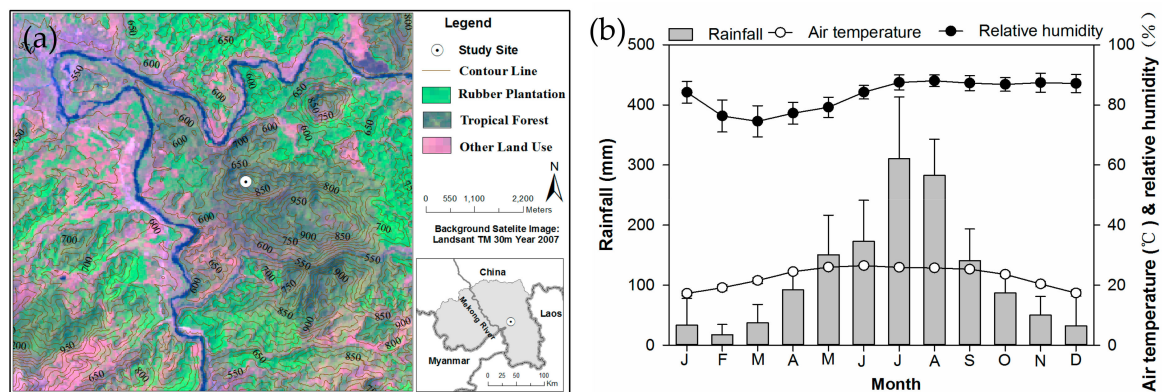
## 2. Materials and Methods

### 2.1. Study Site and Species

Xishuangbanna, in southwest China, marks the northern latitudinal limit of the Asian tropics and contains the largest area of tropical rainforest in China, with a mean annual precipitation (<1500 mm), which is considerably lower than rain forests in other parts of the world [31,36]. The climate of Xishuangbanna is dominated by the Asian monsoon, where 13% of the annual rainfall occurs outside of the rainy season, in pronounced periods of annual drought [3], however the annual throughfall and interception of fog water of up to 340 mm represents 16% of the annual hydrological input [37].

The study was conducted in a tropical karst dwarf forest c. (circa) 3 km from Xishuangbanna Tropical Botanical Garden (XTBG) (21°55'39" N, 101°15'46" E, 700 m a.s.l.) in the Indo-Burma biodiversity hotspot [38], where the forest type is one of several distinct vegetation types that have formed “islands within islands” and function as biodiversity arks [39]. This type of dwarf forest occurs on hill tops with a single tree layer and a canopy height of c. 7–15 m [40,41]. Due to the spatial heterogeneity of rock outcrops and a wide range of micro-habitats, the soil depth varied from site to site in the karst forest [42]. At our study site, the soil is very shallow, discontinuous and rocky. The mean soil depth was about 40 cm (range 20 to 70 cm) [43], but a depth of 140 m could be reached

in a few micro-habitats with carefully choice. The soil is derived from a limestone substrate and is classified as Lithic Leptosol [21]. The mean annual air temperature is 21.7 °C and the mean monthly relative humidity is 87% [3] (Figure 1); the dry season includes a foggy sub-season from November to February when the highest frequency of radiation fog occurrence is during the night and morning, and a hot sub-season from March to April characterized by hot, dry weather during the afternoon and dense radiation fog during the morning [21]. Radiation fog occurs almost daily from November to April and is heaviest when the contrast between day and night temperatures is greatest, such as in March, at the peak of the dry season.



**Figure 1.** The location of the study site in Yunnan Province, Southwest China (a). Average monthly rainfall, air temperature, and relative humidity (2003–2017) recorded at a weather station ca. 4 km from the study site (b). Vertical crossed bar represents  $\pm$  standard deviations.

Tree species at the study site were dominated by *Cleistanthus sumatranus* (Miquel) Müller Argoviensis (Euphorbiaceae) and *Pistacia weinmanniifolia* J. Poisson ex Franche (Anacardiaceae) and vascular epiphytes were abundant on the trees. We selected *Bulbophyllum ambrosia* (Hance) Schlechter (Orchidaceae), *B. delitescens* Hance (Orchidaceae), *Coelogyne viscosa* H. G. Reichenbach (Orchidaceae), and *Hoya pottsii* Traill (Asclepiadaceae) as study species, and *C. sumatranus* and *P. weinmanniifolia* as reference host trees due to their abundance and contrasting water use strategies. The orchids and *Hoya* can store atmospheric water in the pseudobulb and succulent leaves, respectively, whereas the host trees can directly access soil water via roots. A previous study of the area found that orchids were the most abundant taxa of the epiphytes (293 species from 69 genera) and with 48 species, *Bulbophyllum* was one of the dominant genera [32], while *Hoya* was found to be a frequently occurring epiphyte in the karst forest [41].

## 2.2. Sampling

We assumed that xylem water was a combination of soil water derived from rain and intercepted fog drip from the canopy, the foliar uptake of fog water, as well as the bidirectional exchange of fog water with leaf water [24]. The sampling dates for the fog, soil and xylem samples were from 19 to 27 March 2017. On the sampling dates (in the morning), xylem water samples from the host trees were collected from small cylinders of wood that were taken using a 5.15 mm inner diameter increment borer at breast height, and samples from the epiphytes were collected from the non-photosynthetic basal culm tissue. Each xylem sample was sampled from one host tree and four replicates were collected for each host species. From each host tree, 10–20 stems/rhizomes of the epiphytes were combined into a single sample and four replicates for each epiphytic species were collected. The epiphytes were sampled from neighboring trees if there were insufficient individuals on the sampled host trees. All plant samples were placed in 10 mL screw-capped and gas-tight glass vials (Yifan Instruments, Haimen, China) that were sealed with parafilm and stored in a cooler bag immediately.

Fog water samples were collected using an injection syringe fitted with a filter from a glass wall of the platform at the hill top, during a heavy fog event early in the morning prior to isotope fractionation from re-evaporation. Rainwater samples were collected from a rain gauge at a nearby weather station immediately after a rainfall event or early in the morning following overnight rainfall. Three rain water samples were collected during this period (2 February, 9 March, and 27 March). In total, five fog and three rain water samples were obtained and stored immediately in 2 mL screw-cap plastic vials, sealed with parafilm, and stored at  $-20\text{ }^{\circ}\text{C}$ . Concurrent with the xylem sampling, four replicates of c. 20 g soil samples were collected from three depths (0–10 cm, 40–50 cm, and 90–100 cm) using a 5 cm diameter soil auger at two sites located within 2 m of the base of the host trees [22]. Both of the soil and xylem water samples were stored in 10 mL screw-cap glass vials sealed with parafilm and frozen prior to water extraction using a cryogenic vacuum distillation system [44]. The extraction times were set to  $>120\text{ min}$ , and the extraction temperature was  $80\text{ }^{\circ}\text{C}$  with a 3.9 Pa extraction pressure based on the soil type (i.e., Lithic Leptosol). Additionally, during the cryogenic distillation procedure, the bottleneck of the soil sample vials were filled with glass cotton to prevent the soil particles from migrating to the collection tube and polluting the extraction water.

Mature and sun-exposed leaves from each epiphyte and host tree that was sampled were collected at xylem sampling for the determination of carbon isotope ratios. Leaves were dried at  $70\text{ }^{\circ}\text{C}$  to a constant mass, homogenized, and sieved to a fine powder (80-mesh sieve). In total, we collected 10 leaf samples for each plant species, except *B. delitescens*, for which six samples were collected.

### 2.3. Stable Isotope Analysis

The determination of the  $\delta\text{D}$  and  $\delta^{18}\text{O}$  of the water samples and  $\delta^{13}\text{C}$  of the leaf samples was carried out using a stable isotope ratio mass spectrometer (IsoPrime100; Isoprime, Stockport, UK). Isotope ratios were expressed in parts per thousand (‰) where the ratios of hydrogen and oxygen were of the heavy to light stable isotopes in the sample relative to Vienna-Standard Mean Ocean Water (V-SMOW) and those of carbon were relative to the Pee Dee Belemnite standard. The precision ( $\pm\text{SE}$ ) of the isotope measurements was less than 2‰, 0.3‰, and 0.5‰ for  $\delta\text{D}$ ,  $\delta^{18}\text{O}$ , and  $\delta^{13}\text{C}$ , respectively.

### 2.4. Foliar Water Uptake

We used gravimetric approaches to measure the FWU in the plant species [25], where one fully mature leaf of 10 individuals of each species was sampled in post-sunset darkness and the petioles were sealed immediately with petroleum jelly to prevent water loss. The leaf fresh weight ( $W_1$ ) and area ( $A_{\text{leaf}}$ ) were measured using a precision balance to the nearest 0.001 g and leaf area meter (Yaxin-1242, Yaxinliyi technology limited company, Beijing, China), respectively. Petioles were wrapped with parafilm and the leaves were submerged in water for 3 h to allow the absorption of water by foliar uptake. Afterwards, the leaves were dried using paper towels and weighed to record the saturated weight ( $W_2$ ) and following air-drying for 5 min, the leaves were weighed ( $W_3$ ), re-submerged in water for 1 s, re-dried and re-weighed ( $W_4$ ). The amount of residual water on the leaf surface was determined by calculating the difference between  $W_4$  and  $W_3$ . Finally, the leaves were dried to a constant mass in an oven at  $70\text{ }^{\circ}\text{C}$ , and weighed ( $W_d$ ).

FWU was calculated as (Equation (1)):

$$\text{FWU} = ((W_2 - W_1) - (W_4 - W_3)) / A_{\text{leaf}} \quad (1)$$

The increase in leaf water content (%LWC) was calculated as (Equation (2)):

$$\% \text{LWC} = ((W_2 - W_1) - (W_4 - W_3)) / (W_1 - W_d) * 100\% \quad (2)$$

Leaf succulence degree (LSD) was calculated as (Equation (3)):

$$\text{LSD} = (W_1 - W_d) / A_{\text{leaf}} \quad (3)$$

As an adjunct to FWU experiments, the surface structures of the tree and epiphytes leaves were assessed using scanning electron microscopy (SEM) to investigate the potential structures related to FWU. The detached leaves from each species were air-dried and sliced into c. 1 cm<sup>2</sup> sections that were mounted on aluminum stubs. The stubs were coated with gold–palladium using a sputter coater (Q150R sputter, Quorum, UK) and the coated specimens were examined using SEM (ZEISS EVO LS10, Carl Zeiss Microscopy GmbH, Jena, Germany) with an accelerating voltage of 10 kV [45].

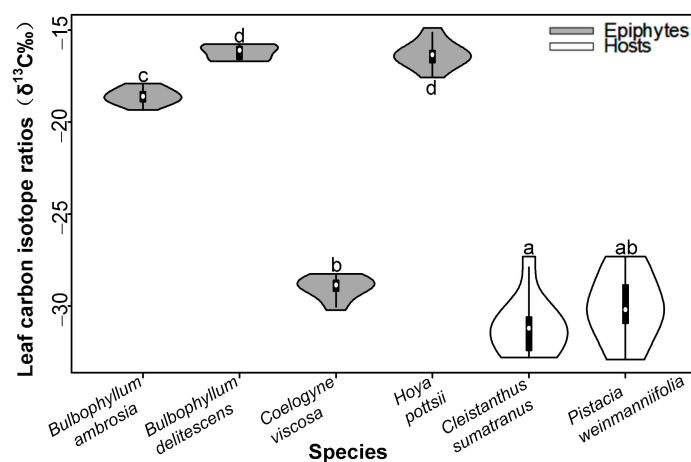
## 2.5. Statistical Analyses

The differences in the leaf  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$  of the water samples and FWU, %LWC and LSD among the species were tested using Kruskal–Wallis and Wilcoxon rank sum tests, due to a lack of homogeneity of variances and normality. Differences in water absorption were tested using a one sample *t*-test and correlations between the FWU, %LWC and LSD were tested using Pearson's correlation coefficient. We used a Bayesian stable isotope mixing model, MixSIAR package, to determine the proportions of each water source (fog, rain, and soil water) used by the epiphytes and host trees [46]. Before running mixsiar\_gui, which creates the GUI version of MixSIAR, JAGS and GTK+ were installed. Here, dual isotope ratios ( $\delta\text{D}$  and  $\delta^{18}\text{O}$ ) with zero discrimination were used and the Markov chain Monte Carlo run length was set as 'long' (i.e., 'Chains' = 3, 'Chain Length' = 300,000, 'Burn-in' = 200,000, 'Thin' = 100 and 'calcDIC' = TRUE). The error structure was set as 'Resid \* Process' and the specify prior was set as 'uninformative' / Generalist. This model incorporates recent advances in Bayesian mixing model theory since the introduction of MixSIR and SIAR and combines uncertainty in the source means and variances, and the ranges of solutions may be interpreted as probabilities [46]. All calculations and statistical analyses were performed in R 3.4.2 [47] (The R Foundation for Statistical Computing, Vienna, Austria).

## 3. Results

### 3.1. Water Use Efficiency

The mean leaf carbon isotope ratios ranged from  $-16.2 \pm 1.8\text{‰}$  (*B. delitescens*) to  $-31.1 \pm 0.4\text{‰}$  (*C. sumatranus*) and there were differences in ratios among the plants ( $p < 0.01$ ). With the exception of the difference between *C. viscosa* and *P. weinmanniifolia* ( $p = 0.5$ ), leaf  $\delta^{13}\text{C}$  of epiphytes were generally enriched compared to those of the host trees ( $p < 0.05$ ; Figure 2). There were no differences in the leaf carbon isotope ratios between the two host tree species ( $p = 0.5$ ) or between the epiphytes, *H. pottsii* and *B. delitescens* ( $p = 0.6$ ).

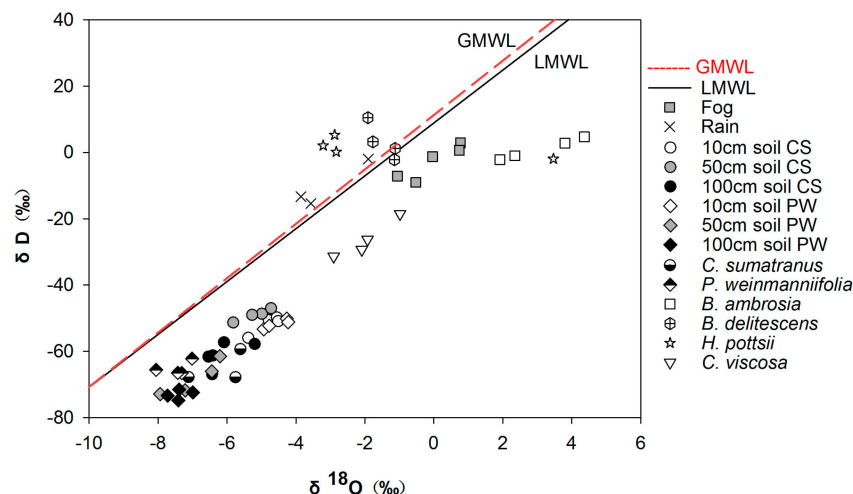


**Figure 2.** Carbon isotope ratios ( $\delta^{13}\text{C}$ ) of mature leaves collected from epiphytes and host tree species during the dry season. Lines within boxes are means, bars are  $\pm$  SE.  $n = 10$ , except for *B. delitescens* ( $n = 6$ ). Letters represent significant differences at  $p < 0.05$ .



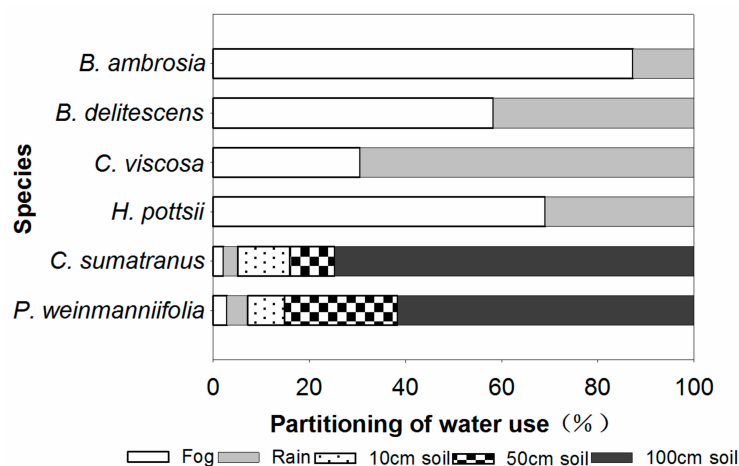
### 3.2. Partitioning of Water Use

There were differences in  $\delta^{18}\text{O}$  among the three types of water source ( $p < 0.01$ ), where the isotope ratios for fog were consistently enriched than for rain and soil water ( $p < 0.05$ ). The  $\delta^{18}\text{O}$  for soil water were lower than fog and rain ( $p < 0.05$ ) and we found that the soil water isotope ratios decreased with increasing soil depth, where the  $\delta^{18}\text{O}$  of the upper soil layer was enriched compared to the deeper layers (Figure 3). The  $\delta^{18}\text{O}$  was enriched in the epiphytes compared to the host trees ( $p < 0.05$ ). In general, the epiphyte xylem water isotope ratios were closer to the fog and rain isotope ratios, whereas those for the host trees were closer to the soil water isotope ratios (Figure 3).



**Figure 3.** Hydrogen ( $\delta\text{D}$ ) and oxygen ( $\delta^{18}\text{O}$ ) stable isotope composition of fog ( $n = 5$ ), rain ( $n = 3$ ), plant xylem ( $n = 24$ ), and soil water ( $n = 24$ ) samples. The reference line is the local meteoric water line (LMWL) (adapted from Liu et al. [48]) and global meteoric water line (GMWL).

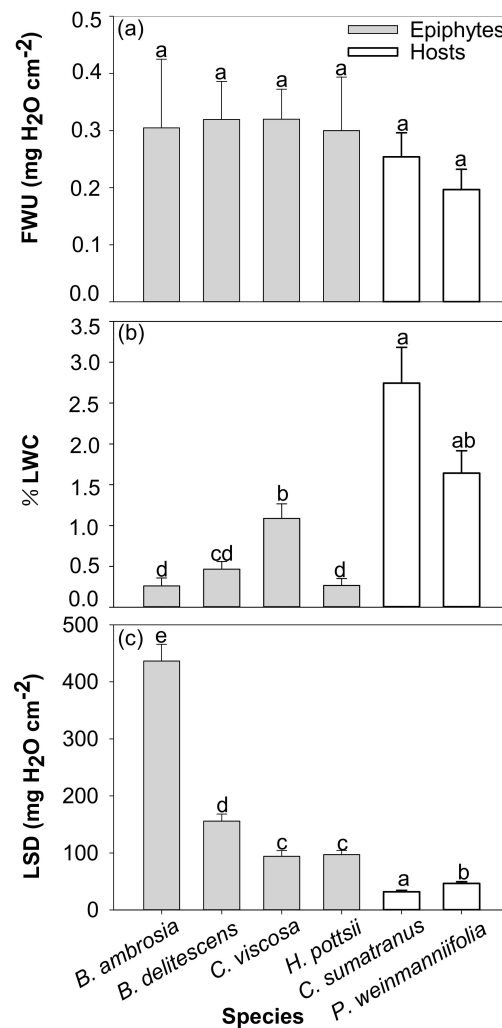
The MixSIAR mixing modeling showed that the epiphytes used large proportions of fog (Figure 4), on average ranging from  $30.5 \pm 18.2\%$  (*C. viscosa*) to  $87.3 \pm 13.9\%$  (*B. ambrosia*), whereas the host trees used negligible amounts of fog water (on average range:  $2.1 \pm 2.1$ – $2.9 \pm 2.3\%$ ). In contrast, the host trees used substantial amounts of soil water; on average  $74.8 \pm 14.8\%$  of *C. sumatranus* xylem water was derived from the deepest soil layer, whereas the upper ( $7.6 \pm 6.5\%$ ) and middle layers ( $23.5 \pm 18.2\%$ ) provided almost one third of the water for *P. weinmanniifolia* (Figure 4, Table S1).



**Figure 4.** Partitioning of potential water sources for epiphytes and their host tree species in a tropical karst dwarf forest in the peak dry season, March 2017. Means derived from the MixSIAR mixing model (Table S1).

### 3.3. Foliar Water Uptake

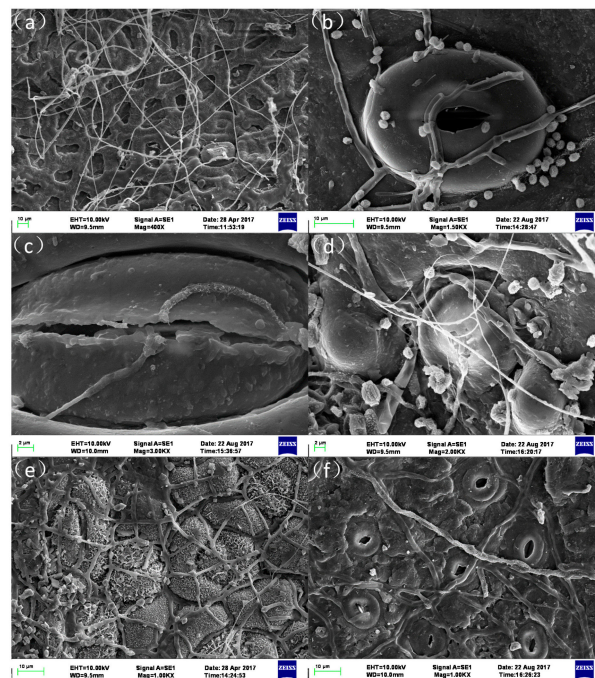
Although the mean FWU tended to be higher in the epiphytes than the host trees, this difference was not significant ( $p = 0.5$ ) (Figure 5a). The %LWC of all six plant species increased following immersion in deionized water for 3 h ( $p < 0.05$ ) and, with the exception of *C. viscosa* and *P. weinmanniifolia*, we found it was generally significantly lower in the epiphytes than in the host trees ( $p < 0.05$ ). Among the epiphytes, the %LWC was highest in *C. viscosa* ( $P < 0.01$ ) (Figure 5b). The LSD was higher in the epiphytes than the host trees ( $p < 0.01$ ), where it was highest in *B. ambrosia* and lowest in *C. sumatranus* (Figure 5c). While there was a positive correlation between the %LWC and FWU ( $r = 0.31$ ,  $p < 0.05$ ), there was a negative correlation between the %LWC and LSD ( $r = -0.39$ ,  $p < 0.01$ ).



**Figure 5.** Foliar water uptake in epiphytes and their host trees. (a) Foliar water uptake capacity per unit area (cm<sup>2</sup>) ( $n = 10$ ); (b) percent increase in leaf water content following immersion in water for 3 h (%LWC) ( $n = 10$ ); (c) leaf succulence degree (LSD) ( $n = 10$ ). Bars are means  $\pm$  SE and letters represent significant differences at  $p < 0.05$ .

The scanning electron micrographs of the *B. ambrosia* and *B. delitescens* abaxial leaf surface showed tangled fungal hyphae covering the stomata (Figure 6a,b), while an unidentified leaf fungal endophyte penetrated the stomatal pores of *C. viscosa* and *H. pottsii* leaves (Figure 6c,d). The leaves of the host tree species *C. sumatranus* had a cuticle and each stomatal pore was capped by an epicuticular wax plug that was covered with a dense mat of crystalline, wax protuberances (Figure 6e), while the leaves of *P. weinmanniifolia* had a cuticle but no wax plug (Figure 6f). Fungal hyphae grew across the

epicuticular wax plug of the *C. sumatranus* leaves and around the protruding Florin rings in the stoma of *P. weinmanniifolia*.



**Figure 6.** Scanning electron micrographs of abaxial leaf surface of epiphytes and their host trees. Fungal hyphae covering the stoma of *B. ambrosia* (a) and *B. delitescens* (b); an unidentified fungal endophyte penetrating a single stoma of *C. viscosa* (c) and *H. pottsii* (d); capping of the stomatal pore by an epicuticular wax plug in *C. sumatranus* (e); and, lack of wax plug in *P. weinmanniifolia* (f).

## 4. Discussion

### 4.1. Water Use Efficiency

The CAM represents a metabolic adaptation to drought stress that facilitates plants to conserve water by nocturnal CO<sub>2</sub> uptake as well as increasing the WUE in water-limited epiphytic habitats [49,50]. We found  $\delta^{13}\text{C}$ -values typical for CAM in the epiphytes *B. ambrosia*, *B. delitescens*, and *H. pottsii*, whereas host trees had  $\delta^{13}\text{C}$ -values typical for C3 and these results are consistent with other studies of epiphytes that frequently had more enriched  $\delta^{13}\text{C}$  compared with ground-rooted plants [11,18]. Our data support our prediction that the WUE of epiphytes, as represented by leaf  $\delta^{13}\text{C}$ , would be more enriched than their host trees in periods of little or no rainfall, indicating that more frequent drought stress and water limitation occurs in the canopy of this tropical karst forest. However, there was an anomaly in our study, because we found  $\delta^{13}\text{C}$ -values typical for C3 ( $-29.9\text{‰}$ ) in *C. viscosa*, indicating lower levels of water stress. While water stress is the most common interpretation of leaf  $\delta^{13}\text{C}$  variation, other factors may also influence the isotope composition. For example, it is possible that the pseudobulb facilitates a slow reduction in leaf water content, thus playing an important role in maintaining the leaf water balance of leaves [51]. It is also possible that the large number of long, narrow leaves in *C. viscosa* acted as nebulophytes that have been identified as functional and evolutionary approach adaptations to fog-harvesting [52], and the fungal hyphae in stomatal pores may have been considered to facilitate fog water uptake [19] (Figure 6c,d).

### 4.2. Partitioning of Water Use

We found differences in the isotope ratios among the epiphytes and their host tree species that may be attributed to the sources of available water. For example, the epiphytes were largely disassociated



from ground-level soil resources, hence fog and rain, characterized by enriched isotope ratios, were the principal sources of water. In contrast, the host trees, with direct access to the soil via the root system, utilized large amounts of soil water, as indicated by the lower isotope ratios.

The MixSIAR mixing model supported our initial hypothesis that epiphytes used a higher proportion of fog water than their host trees during periods of little or no rainfall. These results are similar to previous reports of water source use by *D. pittieri* at epiphytic, transitional, and terrestrial growth phases in a cloud forest [23], and by the epiphytic *Ficus tinctoria* in a forest close to our study site [53]. We found that fog water use in the herbaceous epiphytes ranged from 30.5–87.3% and in the epiphytic stage of *D. pittieri* it was 76%, whereas this was much lower in *F. tinctoria*, at 11%. Liu et al. [53] suggested the low amount of fog water use in *F. tinctoria* may be attributed to the windless weather conditions during fog events and the low content of liquid water that is characteristic of radiation fog [54].

The partitioning of water use varied among the epiphytes in our study (Figure 4) and may be a result of vertical stratification of the species in the canopy [55]. Indeed, we observed that *B. ambrosia* was mostly present in the upper canopy, *H. pottsii* usually occupied the mid-canopy, and *B. delitescens* and *C. viscosa* were common at the lower levels (Figure S1). Fog tends to be present above the forest floor and around the canopy [3], allowing fog water to be intercepted by the canopy; it is likely that the amount of throughfall of fog water decreases with the canopy height. In addition to this apparent spatial niche differentiation in fog water use in the epiphytes, we found that water use in the host trees reflected the growing conditions. For example, *C. sumatranus* has a high density of roots in the soil layer that allows the exploitation of water in the deeper bedrock [21], whereas *P. weinmanniifolia* was found to depend on water in the upper layers of the soil. This partitioning in water source use among species may facilitate coexistence, either for the epiphyte species in the canopy with an intermittent water supply, or for trees growing on thin soils that have periods of little or no rainfall.

However, it must be pointed out that there is a problem with the cryogenic extraction technique [56], since the soil type and cryogenic extraction conditions (extraction time, temperature, vacuum threshold) can influence the extracted water isotopic signatures [56,57]. Soil properties and/or extraction conditions should be reported to ensure the transparency of the obtained results and to make potential soil property effects known [56].

#### 4.3. Foliar Water Uptake

FWU has been shown to affect plant water dynamics in more than 70 species in forest ecosystems with fog conditions, where the capacity of FWU varies among plant communities and species [25,58]. In this study, the leaves of all the plant species absorbed significant amounts of deionized water following immersion, suggesting that both epiphytes and host tree species possess an ability to absorb liquid water during leaf wetting events, such as under fog immersion conditions. Our results support previous findings from a related experiment in the same forest [22].

FWU may play a key role in epiphyte drought tolerance and previous work has shown physiological differences between terrestrial and epiphytic *Cymbidium* species [59]. In our study, however, there were no differences in FWU among the epiphytes and their host trees (Figure 5a) and this may be attributed to the high water content of water storage organs, such as pseudobulbs in the orchids and succulent leaves in *Hoya* [51,60]. The rates of water uptake decrease as the epiphyte water content increases [54], indicating that moderate plant drought stress increases the potential for FWU [25]. When a leaf has negative water potential, saturating atmospheric water vapor drives leaf water absorption [24,58]. We found that the %LWC in the epiphytes was less than in their host trees, and this was probably caused by the higher LSD recorded in the epiphytes. Moreover, the epiphytes tend to have leaf structure that prevent their leaf water loss, while such a structure would also reduce the FWU for the epiphytes.

Leaf epicuticular organs and structures have been shown to affect FWU [61], and we observed stomata covered with tangled fungal hyphae and the penetration of a stoma by an unidentified

fungal endophyte in *C. viscosa* and *H. pottsii* leaves (Figure 6c,d). Pariyar et al. [62], found that water condensation on the exposed leaf surface of *Chamaecyparis obtusa* was initiated along linear lines formed by fungal hyphae that may act as wicking, for the transport of water past the epicuticular waxes [19]. That hyphae are involved in the leaf surface movement of water was supported by the highest levels of %LWC and FWU in the epiphytes being recorded for *C. viscosa*, however, further research is required to elucidate the role of fungal hyphae in FWU and the importance of FWU for the total water budget in plants.

#### 4.4. Ecological Implications

Our experiments demonstrated the greater reliance on fog by epiphytes than their host trees in the dry season. Deforestation in the lowland tropics has been shown to reduce fog formation, increase cloud-base height in adjacent mountains [63,64], extend the dry season, and enhance the regional vulnerability to drought [65]. This decline in the frequency of fog immersion of forest epiphytes is likely to increase the vulnerability of epiphytes under projected climate and land use change scenarios. Previous studies have showed decreased growth rates and increased mortality in epiphytes transplanted from high to low fog immersion conditions [66–68]. In this study region, the decreasing trend in the number of foggy days per year and hours of fog per day has been linked to increases in the area of monoculture rubber plantations that act as water pumps [33,69–71]. Hence, the reduction in incidence of fog is combined with the 1.2 °C increase in mean annual temperature (1961–2004) [72], it is likely that dry seasons in the future will probably increase the drought stress and mortality of epiphytes.

## 5. Conclusions

In summary, our results showed that, during the dry season, the proportion of fog water used by epiphytes was greater than that of the host trees, whereas the trees used greater proportions of soil water. The FWU may relate to foliar structures, such as the presence of fungal endophytes. The distinct physiological and morphological traits of the epiphytes facilitated adaptation to the intermittent drought stress conditions associated with the canopy. Our study highlights the importance of fog water for epiphytes during the dry season, but further research is required to determine the responses of epiphytes to changes in the amount and duration of fog immersion, and to quantify the proportion of fog uptake by roots and FWU. We suggest that epiphytes may be vulnerable to changes in the occurrence of fog events.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1999-4907/9/5/260/s1>. Figure S1: vertical stratification of vascular epiphytes at present study site. Table S1: Mean, standard deviation and probability distributions of water use proportions of vascular epiphytes and their hosts in a tropical karst forest during the dry season in March 2017.

**Author Contributions:** Y.W. and W.L. conceived and designed the experiments; L.S., S.L. and P.F. conducted the sampling and stable isotope analysis; W.L. and Y.S. prepared some figures and tables; J.W. and P.W. performed cryogenic vacuum distillation and Bayesian stable isotope mixing model; Q.C. and H.L. conducted the FWU and collected data; Y.W. wrote the first draft of the manuscript; W.L., W.L. and Y.S. contributed to revisions.

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