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# Habitat moisture is an important driver of patterns of sap flow and water balance in tropical montane cloud forest epiphytes

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**Abstract** Microclimate in the tropical montane cloud forest (TMCF) is variable on both spatial and temporal scales and can lead to large fluctuations in both leaf-level transpiration and whole plant water use. While variation in transpiration has been found in TMCFs, the influence of different microclimatic drivers on plant water relations in this ecosystem has been relatively understudied. Within the TMCF, epiphytes may be particularly affected by natural variation in microclimate due to their partial or complete disassociation from soil resources. In this study, we examined the effects of seasonal microclimate on whole plant water balance in epiphytes in both an observational and a manipulative experiment. We also evaluated the effects of different microclimatic drivers using three hierarchical linear (mixed) models. On average, 31 % of total positive sap flow was recovered via foliar water uptake (FWU) over the course of the study. We found that precipitation was the greatest driver of foliar water uptake and nighttime sap flow in our study species and that both VPD and precipitation

were important drivers to daytime sap flow. We also found that despite adaptations to withstand seasonal drought, an extended dry period caused severe desiccation in most plants despite a large reduction in leaf-level and whole plant transpiration. Our results indicate that the epiphytes studied rely on FWU to maintain positive water balance in the dry season and that increases in dry periods in the TMCF may be detrimental to these common members of the epiphyte community.

**Keywords** Water relations · Hemi-epiphytes · Foliar water uptake · Drought tolerance · Water balance · Microclimatic drivers

## Introduction

On the most fundamental level, plant success depends on a trade-off between carbon gain and water loss. Water movement in plants has traditionally been considered a unidirectional process, where water moves through the soil–root–stem–leaf pathway and out into the atmosphere. There is growing evidence that water can also move in the opposite direction via foliar water uptake (FWU) through the leaf surface (Burgess and Dawson 2004; Oliveira et al. 2005; Goldsmith et al. 2013; Gotsch et al. 2014a, b; Eller et al. 2015; Gotsch et al. 2015). While FWU has been documented to improve plant water status, the importance of this process in plant water balance across seasons is unclear (Simonin et al. 2009; Berry et al. 2014; Gotsch et al. 2014a; Goldsmith et al. 2013).

The direction and amount of water movement into and out of the leaf are influenced both by properties of the plant as well as features of the surrounding microclimate. Plant properties that influence water balance include leaf surface anatomy (i.e., cuticle and stomates) and xylem architecture (i.e., leaf venation patterns and vessel size). In turn, environmental

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This work is the first to describe the importance of different microclimatic drivers on patterns of sap flow in epiphytes. In addition, the manipulative experiment provides important information regarding the vulnerability of this important plant community to long periods of drought. Our results highlight the importance of habitat moisture in driving sap flow in this community as well as the reliance of these species on cloud water interception for positive water balance.

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supply and demand govern plant water balance. On the supply side, water movement is influenced by soil water availability and plant capacitance. On the demand side, water balance is influenced by a combination of factors including air temperature, relative humidity, solar radiation, canopy wetness, and wind speed. While it is clear that, individually, each of these parameters can influence transpiration, the relative importance of each of these factors and their interactions is less clear, especially in ecosystems that experience a large degree of variability in microclimate in both space and time.

Seasonal rainfall and low-lying clouds create a strong dichotomy between periods of high evaporative demand and frequent leaf wetting events (Holwerda et al. 2010; Rosado et al. 2010; Bruijnzeel et al. 2011; Jarvis and Mulligan 2011). These differences are often the result of the presence or absence of low-lying clouds in direct contact with vegetation. Despite variation in microclimate in the TMCF, this ecosystem experiences consistent annual input of water via rainfall and cloud immersion, which can reduce transpiration and promote FWU (Alvarado-Barrientos et al. 2014; Gotsch et al. 2014a). In other cloud-affected ecosystems, the presence of low-lying clouds has been shown to reduce evapotranspiration (Burgess and Dawson 2004), contribute to canopy soil water levels through occult precipitation (Dawson 1998) and to directly improve plant water balance through FWU (Simonin et al. 2009; Berry and Smith 2012).

Persistent contact between low-lying clouds and vegetation is projected to change as land use and climate patterns change. Changes in land use (i.e., deforestation) and climate have already caused a 25–75 m rise in orographic cloud base heights and are predicted to cause an even greater upward shift in the future, resulting in longer periods of time without cloud immersion (Ray et al. 2006; Pounds et al. 1999; Stull 1999; Pounds *pers. comm.*). While all members of the TMCF community are likely to be affected by such changes in climate, epiphytes may be disproportionately impacted since these plants are largely dependent on atmospheric inputs of water and nutrients.

A reduction in epiphyte biomass or a change in epiphyte community structure may lead to widespread impacts in the TMCF. Epiphyte biomass is exceedingly high in the TMCF and this community contributes substantial nutrient inputs to the forest floor (Nadkarni 1984; Nadkarni et al. 2004; Gotsch et al. 2015). Furthermore, canopy soils and epiphytes have a high water storage capacity, which may be important for ecosystem cloud water interception and infiltration (Pocs 1980; Holscher et al. 2004; Koehler et al. 2007; Gotsch et al. 2015). Because of these important ecosystem services provided by epiphytes, understanding how this component of the TMCF will be impacted by changes in climate is needed to determine how ecosystem processes such as nutrient and water cycling may be affected by projected changes.

In this study, we examined the effect of seasonal microclimate on the water balance of common vascular epiphytes

and hemi-epiphytes in the TMCF of Monteverde, Costa Rica. We utilized external sap flow gauges in both an observational and a manipulative experiment to address the following questions:

1. How important is FWU to epiphyte and hemi-epiphyte water balance in the dry season?
2. How responsive are epiphytes and hemi-epiphytes to temporal variation in microclimate?
3. How do epiphytes respond to an extended period of drought?
4. What are the microclimatic drivers of sap flow in epiphytes and hemi-epiphytes?

We hypothesized that transpiration would be somewhat buffered from fluctuations in microclimate due to leaf water storage, and that FWU would make up a large portion of the dry season water balance. We also hypothesized that vapor pressure deficit would be the largest driver of dry season transpiration. Despite adaptations for water storage in canopy plants, we hypothesized that an imposed 3-week drought would lead to a reduction in transpiration and high mortality in our study species.

## Methods

### Study site description

This research was conducted from January to June of 2014 on the Pacific slope of the Cordillera de Tilarán in the Monteverde Cloud Forest Reserve (10°18'N, 84°48'W; 1480–1550 m in elevation). The average daily temperature is relatively consistent throughout the year (22 °C) with diurnal changes surpassing yearly ranges (Nadkarni 1994). The site is characterized by persistent cloud-laden trade winds that deliver almost daily mist between November and May (Nadkarni 1994). Climatic patterns have shifted during the last two decades; an increase in the altitude of the cloud base has increased the number of days with little or no mist (Pounds et al. 1999). The site consists of primary forest 20–30 m high with emergent trees reaching 35 m tall and a poorly developed herbaceous layer (Nadkarni and Matelson 1991). A number of common epiphytes (including two hemi-epiphytes) within the canopy of a single mature strangler fig tree, *Ficus tuerckheimii*, were the focus of this work. This host tree was chosen because of its prevalence and large size, allowing for abundant and diverse epiphytic communities. All mature trees hold thick mats (>25 cm thick) of epiphytes and hemi-epiphytes (Nadkarni 1985). The larger individuals and thicker mats are concentrated in the center of the canopy, particularly where branches intersect, and the individuals on the outer branches are limited

mainly to bromeliads, ferns and bryophytes (Nadkarni 1985; Koehler et al. 2007).

### Study species

The study species included in the observational experiment are epiphytes and hemi-epiphytes that were present on multiple branches within the study crown (Table 1; Fig. 1). The height of shrub epiphytes and hemi-epiphytes ranged from 100 to 150 cm while the height of the other study species ranged from 30 to 45 cm. Many canopy epiphytes reproduce clonally through rhizomes and, as a result, unique stems may belong to the same individual (S. Gotsch *pers. obs.*). Individuals were chosen on different host tree branches to maximize the likelihood that we were sampling distinct individuals. Previous studies in the Monteverde reserve have quantified the biomass of different components of the TCMF canopy; the life-form of the different groups in this study comprises between 10 and 45 % of the biomass of the TCMF canopy plant community (Koehler et al. 2007; Hager and Dohrenbusch 2011). While ferns and bromeliads are two of the most common vascular plant groups in the TCMF canopy, these species are not suitable for sap flow measurements and were, therefore, excluded in the observational experiment. In the greenhouse experiment, additional species such as bromeliads and ferns were included to take advantage of material that had been removed from the canopy and to extend the number of functional groups being studied (Table 2).

### Meteorological data

A microclimate station was positioned in the canopy of the study tree and another was installed on a meteorological

**Table 1** Focal species for sap flow measured over a six-month period (10 January 2014–28 June 2014)

Species	Family	Life-form	<i>n</i>
<i>Cavendishia capitulata</i>	Ericaceae	Shrub epiphyte	2, 1
<i>Chlorogyne ensiformis</i>	Cyclantaceae	Herbaceous monocot	2, 2
<i>Clusia palmana</i>	Clusiaceae	Hemi-epiphyte	2, 0
<i>Cosmibuena valerii</i>	Rubiaceae	Hemi-epiphyte	2, 0
<i>Neomirandea croatii</i>	Asteraceae	Woody Epiphyte	2, 2
<i>Notopleura piticobia</i>	Rubiaceae	Woody Epiphyte	2, 0
<i>Oreopanax vestitus</i>	Areliaceae	Hemi-epiphyte	2, 2
<i>Schefflera rodrigueziana</i>	Areliaceae	Hemi-epiphyte	2, 1

The first number in column *n* indicates the number of individuals measured per species while the second number indicates the individuals included in the water balance calculations. Physical sensor damage and sensor failure due to moisture limited other individuals from having a complete sap flow record for the entire time period and were, therefore, excluded from calculations of total water balance



**Fig. 1** Line drawing of species instrumented with sap flow sensors in the observational study. Back row (L to R) *Cavendishia capitulata*, *Oreopanax vestitus*, *Schefflera rodrigueziana*. Front left *Chlorogyne ensiformis*, Front middle *Neomirandea croatii*. Illustration by Erica Hample

**Table 2** Species information for the manipulative drought experiment

Species/group	Family	Life-form	<i>n</i>
Bromeliad (multiple genera)	Bromeliaceae	Tank bromeliad	5, 0
<i>Cavendishia capitulata</i>	Ericaceae	Shrub epiphyte	6, 3
<i>Chlorogyne ensiformis</i>	Cyclantaceae	Herbaceous monocot	6, 2
<i>Clusia</i> sp.	Clusiaceae	Hemi-epiphyte	10, 0
<i>Elaphoglossum</i> sp.	Dryopteridaceae	Strap fern	5, 0
<i>Neomirandea</i> sp.	Asteraceae	Woody epiphyte	6, 2
<i>Notopleura</i> sp.	Rubiaceae	Woody epiphyte	3, 1
<i>Maianthemum monteverdense</i>	Asparagaceae	Herbaceous monocot	4, 2
<i>Satyria meiantha</i>	Ericaceae	Shrub epiphyte	2, 1
<i>Sobralia</i> sp.	Orchidaceae	Orchid	3, 0

Entire epiphyte mats were harvested for this experiment so species were used opportunistically. Many of the species were only known to the genus level and in one case (Bromeliad) the sample may have consisted of plants in multiple genera. The first number in the *n* column refers to the sample size for stomatal conductance and leaf thickness measurements while the second number refers to the sample size for sap flow measurements

tower located approximately 1 km away. The station mounted in the study tree contained two data loggers that measured air temperature and relative humidity (HOBO U23 Pro v2 External U23-002, Onset Corporation, Cape Cod, Mass., USA) and an Em50 data logger (Decagon Devices, Pullman, WA, USA) which collected data from a Davis cup anemometer, a soil moisture probe, a soil

temperature probe, and a leaf wetness sensor (Decagon Devices, Pullman, WA, USA). Soil probes were placed on a 45-degree angle into the epiphyte mat to a depth of 10–15 cm, which is approximately the middle of the mat. Calibration of the canopy soil moisture sensor was needed to obtain meaningful data since the lowest values in the soil moisture dataset were negative. Calibration was performed by choosing a value that mostly closely approximated dry soil, which was the last day of a 2-month dry period. This value was considered the “true zero” value; the rest of the dataset was adjusted up so that the minimum value was zero. During this period, the canopy mats appeared completely dry and many plants became partially desiccated.

The station in the meteorological tower contained a high-resolution rain gauge, a solar radiation sensor, a Davis cup anemometer, and a leaf wetness sensor, which were all connected to an Em50 data logger. The tower station also included an air temperature and relative humidity data logger (HOBO) and a visibility sensor (Optical Sensors, MiniOFS, Gothenburg, Sweden) which was connected to a CR-1000 Campbell Scientific data logger (Campbell Scientific, Logan, UT, USA). The visibility sensor measures the meters of clear sky extending from the sensor (maximum visibility is 4000 m, visibility of <1000 m is considered fog or low-lying clouds, Glickman 2000). Low visibility indicates the presence of low-lying clouds or foggy conditions which have been shown to influence plant water use by reducing transpiration and increasing leaf water potential (Simonin et al. 2009; Berry et al. 2014; Gotsch et al. 2014a; Goldsmith et al. 2013).

### Sap flow

Sap flow was measured on 16 individuals from 8 common species from 10 January 2014 to 28 June 2014 (Table 1). January is a month of transition between the wet and dry seasons while February–May are generally the driest months of the year and June is the beginning of the rainy season. This time period was chosen to determine the responsiveness of epiphytes to a variety of microclimatic conditions.

External heat ratio method probes were constructed at Franklin and Marshall College following the methods of Clearwater et al. (2009). These sensors contain a heater, flanked by two thermocouples, which were mounted in a silicon gel mold. The presence of a thermocouple on both sides of the heater allowed for the measurement of flow both upstream and downstream of the heater. A 12 V battery powered the sensors and data were taken every 10 min and were then stored in a CR-1000 data logger connected to an AM 16/32 multiplexer (Campbell Scientific, Logan UT, USA). Sensors were placed on the exterior of small

branches or main stems (4–6 mm in diameter) and were then wrapped heavily with Parafilm for thermal isolation and protection from water damage. Water balance calculations were performed using the eight sensors that remained functional throughout the entire 6-month study period (Table 1).

Sap flow was determined by differences in up and downstream temperatures measured with copper–constantan thermocouples. Every 10 min, a baseline temperature measurement was taken followed by a 6-s heat pulse. A 20-s ‘soak’ period allowed for thermal diffusion and movement within the xylem after which the average temperature at the two thermocouples was recorded again over a 40-s period. Heat pulse velocity,  $V_h$  (cm/hr), was calculated using the equation

$$V_h = \frac{k}{x} \ln \left( \frac{\delta T_1}{\delta T_2} \right) \quad (1)$$

where  $x$  represents the distance between the heater and the thermocouple (0.5 cm),  $\delta T_1$  and  $\delta T_2$  are the downstream and upstream temperature changes (°C), and  $k$  represents the thermal diffusivity constant estimated from

$$k = \frac{x^2}{4t_m} \text{ cm}^2 \text{ s}^{-1} \quad (2)$$

where  $t_m$  is the time between the heat pulse and the maximum temperature measured,  $x$  distance above and below the heater (Clearwater et al. 2009). This allowed for the determination of sap flow velocity,  $V_s$ , from

$$V_s = \frac{V_h \rho_b (c_w + m_c c_s)}{\rho_s c_s} \quad (3)$$

where  $\rho_b$  is the stem density,  $c_w$  is the specific heat capacity of the wood matrix (1200 J kg<sup>-1</sup> °C<sup>-1</sup> at 20 °C),  $c_s$  is the specific heat capacity of water (4182 J kg<sup>-1</sup> °C<sup>-1</sup> at 20 °C),  $m_c$  is the water content of the xylem and  $\rho_s$  is the density of water (Burgess et al. 2001).

The heat pulse velocity was then screened to remove values that were the result of electrical errors in the sensors. These errors varied by orders of magnitude from the surrounding values. Removed data were then filled using the average of surrounding values. Variation in sensor construction manifested as baseline values that were slightly above or below zero. To correct baseline values, the average sap flow rate was calculated for each sensor during a period when no transpiration would be expected, i.e., a night with a low vapor pressure deficit during a period when the leaf surfaces were dry (Ambrose et al. 2009; Ambrose et al. 2010). These values were considered the ‘true’ baseline for the sensor. The data for each sensor were then adjusted by adding or subtracting this value from the rest of the dataset. Previous studies have found agreement between this approach and zeroing the sensors by severing

**Table 3** Dry season water balance for eight epiphytes representing five species in an observational experiment (10 January 2014–28 June 2014)

Species	FWU (ml)	$\sigma$ FWU	FWU (ml cm <sup>-2</sup> )	% Time FWU	% FWU	NT (ml)	$\sigma$ NT	NT (ml cm <sup>-2</sup> )	% NT	% Time NT
<i>C. capitulata</i>	208.55	8.34	0.33	37.13	66.79	5.97	2.04	0.08	16.32	26.83
<i>C. ensiformis</i>	10.40	0.31	0.07	27.27	26.48	13.75	0.41	0.10	35.02	34.64
<i>C. ensiformis</i>	7.68	0.23	0.05	32.85	44.29	8.28	0.25	0.06	47.73	35.63
<i>N. croatii</i>	61.87	4.95	0.38	33.07	39.82	59.44	4.75	0.37	38.26	31.10
<i>N. croatii</i>	23.63	1.89	0.06	16.55	12.17	85.22	6.82	0.23	43.89	43.23
<i>O. vestitus</i>	77.58	5.43	0.27	33.44	35.86	64.78	4.53	0.23	29.95	30.42
<i>O. vestitus</i>	48.38	3.39	0.15	20.95	11.62	148.21	10.37	0.45	35.59	38.11
<i>S. rodrigueziana</i>	81.03	2.43	0.06	23.28	12.39	199.20	5.98	0.14	30.46	34.57
Avg	64.89	3.37	0.17	28.07	31.18	78.73	4.39	0.21	34.65	34.32

FWU is the total amount of water in milliliters that was recovered over the course of the study season.  $\sigma$  FWU (ml) is the error term associated with FWU. FWU (ml cm<sup>-2</sup>) is the negative sap flow per unit of leaf area over the course of the experiment. % Time FWU is the percent of hours where sap flow was negative out of all hours in the study season. % FWU is the total negative flow (ml) divided by the total positive flow for the study season. NF is the total amount of positive flow (ml) that transpired at night (18:00–6:00) throughout the study season.  $\sigma$  NF (L) is the error term associated with NF. NT (ml cm<sup>-2</sup>) is the night time positive sap flow per unit of leaf area over the course of the experiment. % NF is the percent of total positive flow at night out of total positive flow for the study season. % Time NF is the amount of hours when positive flow was occurring at night out of all nighttime hours. For the purposes of the % time calculations five percent of the data closest to zero was omitted from the calculation

the xylem (Ambrose et al. 2010; Gotsch et al. 2014a). This method was also employed since these individuals are undergoing continued observation and xylem severing would require killing of plants. These corrected values were then scaled up to the volumetric flow by multiplying the velocity data by the diameter of the stem where the sensor was placed. Leaf area and wood density were estimated using average species data collected previously (Gotsch et al. 2015). While leaf area was calculated in the previous wet season, these species exhibit slow growth rates and leaf turnover (Gotsch *pers. obs.*), which causes the leaf area of the study species to be relatively consistent throughout the year. Once sap flow was expressed on a volumetric basis we divided these values by the leaf area upstream of the sensor to express sap flow on a per leaf area basis.

In performing scaling calculations, a number of errors may have been introduced to the dataset. In particular, errors associated with data screening, zero correction, gap filling, and estimation of stem diameter and leaf area should be accounted for as flow rates are scaled. Because so few data points were removed in screening procedures (<0.1 %), this source of error is excluded from our analysis. Zero-flow calculations and sapwood estimation also resulted in very low variation in sap flow rates (<1 %) and were excluded from the error analysis. In contrast, we consider the estimation of the total leaf area to represent the largest source of error in this study. While leaves were counted precisely on each individual, the total leaf area for each plant was determined by multiplying this number by the average leaf area of the individual (Gotsch et al. 2015). We accounted for this error both in the calculation of the water moving in the direction of the soil (i.e.,

FWU) as well as the nighttime sap flow (i.e., NF). The error in FWU was determined with the equation (Stull 1999)

$$\sigma \text{FWU} = \text{FWU} * \frac{\sigma \text{LA}}{\text{LA}} \quad (4)$$

where LA is the leaf area of the individual. Error for nighttime flow rates was likewise calculated via

$$\sigma \text{NF} = \text{NF} * \frac{\sigma \text{LA}}{\text{LA}} \quad (5)$$

and error was then converted into ml using the percentage of the total volume (Table 3).

### Drought experiment

Entire mats (appx. 60 cm long) containing a number of common epiphyte species were removed from branch surfaces of large *Ficus* sp. canopies in the Monteverde reserve and were placed in a greenhouse. Mats (including a bryophyte later, canopy soil and roots) were placed on greenhouse benches made of wood to mimic their natural substrate. Such removal has been shown to have negligible effects on plant health (Nadkarni et al. 2004). After three and a half weeks of acclimation with twice daily watering, initial stomatal conductance, and leaf thickness were measured on 10 epiphyte species ( $n = 2$  through 10 per species depending on availability in the mats, Table 2) and the total number of leaves on each plant was counted. These measures served as control values. Air temperature and relative humidity were monitored both in the greenhouse and in a study crown throughout the experiment to detect

differences in microclimate in the experimental setting that may have affected the physiological parameters measured.

Following the acclimation period, water was withheld for 3 weeks and stomatal conductance and leaf thickness measurements were taken on the same plants every 3 days over the next 3 weeks. Stomatal conductance measurements were taken using an AP4 porometer (Delta T devices, Burwell, Cambridge, UK) while leaf thickness was measured using a digital thickness gauge (Mitutoyo, Chicago, IL, USA). Sap flow sensors were installed on 16 different individuals (Table 3) using the same methods described above. A meteorological station was also installed in the center of the greenhouse, which contained an air temperature and relative humidity data logger and an EM50 data logger (Decagon) with two soil moisture sensors and a leaf wetness sensor (same sensors as above).

## Data analysis

### *Sap flow patterns and water balance*

A series of repeated measures ANOVAs were performed following the observational study to determine the number of days before decreases in average daily sap velocity became statistically significant ( $P \leq 0.5$ ) after a decrease in precipitation (reported results represent the minimum number of days required to achieve significance). A one-way ANOVA was performed to determine the effect of "Condition" (control, dry or fog conditions) on the average sap velocity. In the drought experiment, a Friedman test was performed to examine the decrease in sap velocity since these data did not exhibit a normal distribution and transformation of the data did little to improve the distribution. A Friedman test was also used to examine the effect of drought on stomatal conductance. The effect of drought on leaf thickness was determined using a paired sample  $t$  test. Analyses were completed using SPSS V. 22 (IBM, Armonk, NY, USA).

### *Statistical modeling*

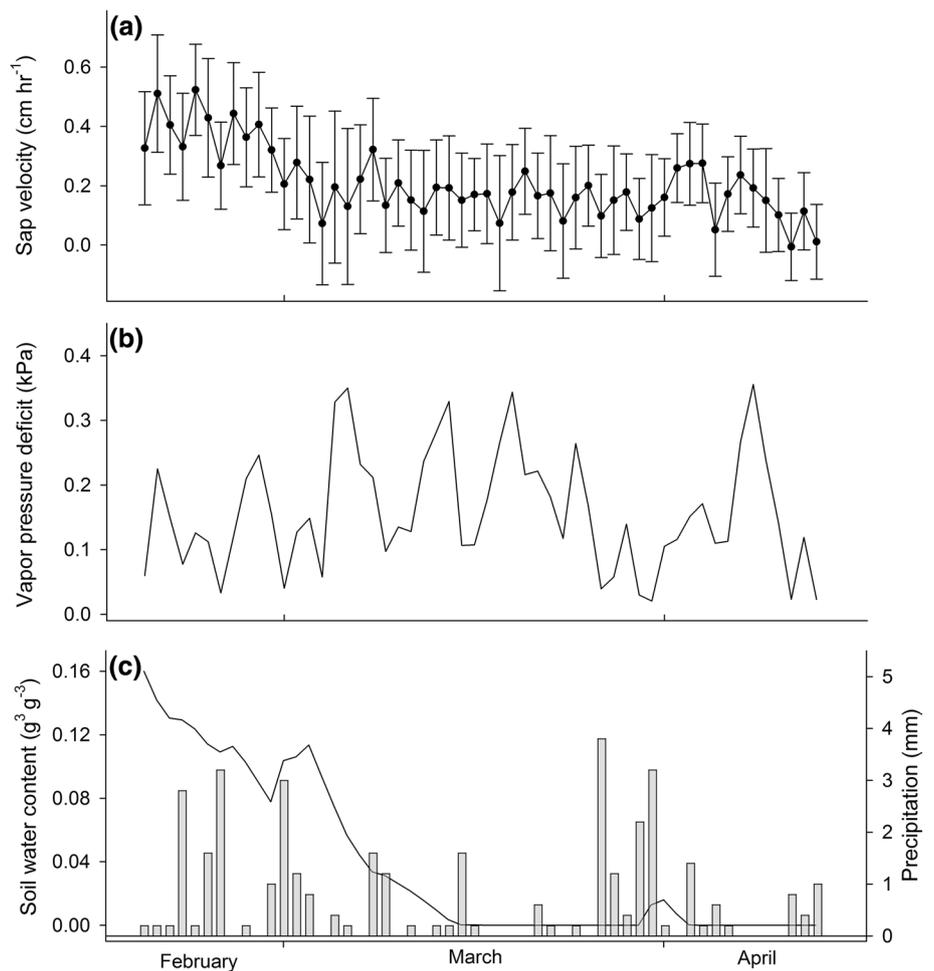
Three separate analyses were performed to determine the environmental drivers of sap flow patterns in epiphytes. The first analysis was completed on positive daytime sap flow values. The second analysis was completed on negative sap flow values to determine the environmental drivers of foliar water uptake. The third analysis was completed on positive sap flow values at night to determine the environmental drivers of nighttime sap flow. Based on solar radiation data, the nighttime period was defined from 6 pm to 5 am. For all analyses, the appropriate daily (or nightly) averages of sap flow and microclimate data were used for the analysis.

The same individuals that were included in the water balance calculations were used for statistical modeling. A hierarchical linear (mixed) model was fitted to account for the presence of different species and individuals within species. The initial model contained the random effect for plant nested within species and the fixed effects considered were for air temperature, vapor pressure deficit (VPD), wind, soil moisture, visibility, precipitation, leaf wetness (LWS), and solar radiation. The fixed effects contained all main and quadratic effects and all two-way interactions. The higher order interactions were assumed to be negligible. All parameters were estimated via maximum likelihood estimation. To eliminate the effects deemed insignificant and to construct a parsimonious model we performed a backward selection. The backward selection was performed by fitting the model and eliminating the fixed term with the highest  $p$  value. An exception to this rule was made to accommodate the *effect hierarchy* in our model, i.e., if an interaction effect was in the model then so were the two main effects that comprised that interaction. If one of the main effects, which was involved in a two-way interaction still in the model, was identified for elimination, then this main effect was held in the model and the term with next highest  $p$  value was chosen. The same exception was applied to the main effects whose quadratic effect was significant in the model.

To assess the adequacy of the term elimination, the likelihood ratio test (LRT) was performed comparing the fit of the model with the fixed term associated with the highest  $p$  value and the model without this term. If the LRT failed to reject the hypothesis that likelihood of observing the data under each model is not statistically significant at  $\alpha = 0.05$ , the elimination was accepted and the process was repeated. If the LRT rejected at  $\alpha = 0.05$ , the elimination was rejected, the procedure was stopped, and the final model was identified. To improve the assumptions of normality and homogeneity of variance, the analyses were carried out on the log-transformed values. For the second analysis, the responses were multiplied by  $-1$  before log transformation. The mixed modeling and LRTs analyses were completed using R version 3.1.1.

To examine the effect of lack of rain on the sap velocity we carried out the following analysis. Each day of data was classified either as relatively dry or wet by considering the average leaf wetness (LWS) value for that day. Each day that had an average LWS below the 20th quantile of all average LWS values was designated as a dry day. Otherwise, the day was designated as a wet day. We chose the 20th quantile of the distribution of the average LWS values as a cutoff because this point exhibited a natural break in the data distribution. Once each day was classified as dry or wet, we constructed a variable *days post-last rain* (dplr) whose values were 0 (rainy day), 1 (first dry day), 2

**Fig. 2** Average sap velocity ( $\text{cm h}^{-1}$ ) during the dry period (12 February 2014–7 April 2014) across eight common species of epiphytes (a). Error bars represent the standard error of the mean. Average daily vapor pressure deficit (kPa) during the dry period (b). Relative soil water content ( $\text{g}^3 \text{g}^{-3}$ , line) and precipitation mm, (bars) during the dry period (c)



(second consecutive dry day), 3 (third consecutive dry day), etc. To measure the effect of an increase in the number of consecutive dry days on the distribution of sap velocity, we modeled quantiles (specifically 2.5th, 50th (median), and 97.5th) of the distribution of sap flow as a function of dplr using quantile regression analysis. Similar to linear regression, quantile regression models  $Q_Y(p)$ , the  $p$ th quantile of the distribution of a random variable  $Y$  (here sap flow in  $\text{ml h}^{-1}$ ), via  $Q_Y(p) = \beta_0 + \beta_1 x$  where  $\beta_0$  represents the value of  $Q_Y(p)$  when  $x$  (here dplr) equals to 0, i.e., the day is rainy.  $\beta_1$  represents the change in the quantile value for each additional dry day.

## Results

### Observational study: microclimate and water balance

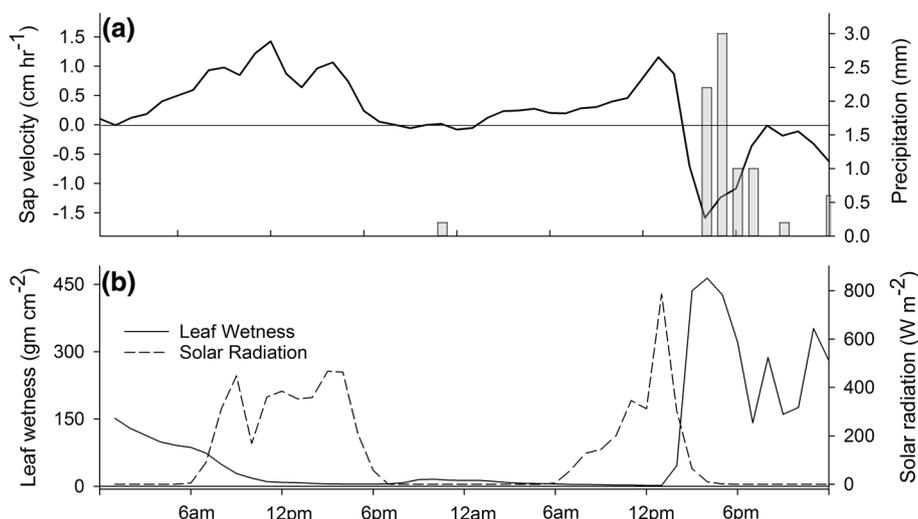
While vapor pressure deficit fluctuated throughout the study period, average values were generally  $<0.4$  kPa (Fig. 2b). In contrast, relative volumetric soil moisture exhibited a steady decrease punctuated by increases coinciding with

precipitation events (notably at the end of February and March, Fig. 2c). Precipitation inputs occurred throughout the study period but generally consisted of small ( $<3$  mm) rain events.

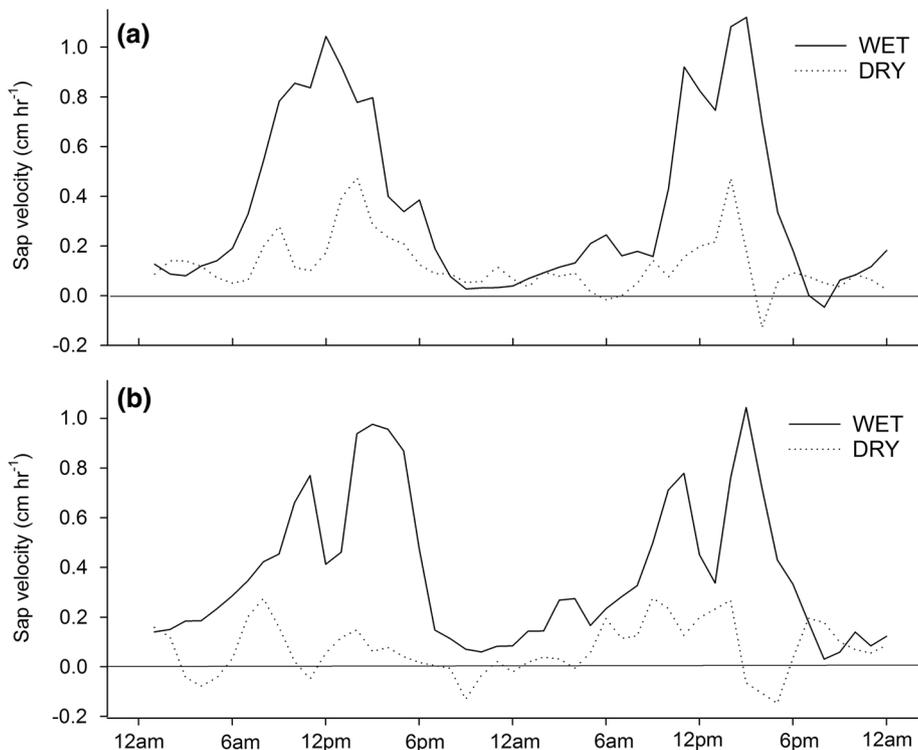
While sap velocity varied greatly across individuals and the study period, average sap velocity exhibited a decrease throughout the dry season (Fig. 2a). Periods of rainfall quickly reduced transpiration as well, and wet conditions led to periods of FWU (Fig. 3). As soil moisture decreased throughout the dry season, clear depressions were seen in overall and midday sap velocity (Fig. 4). Reductions in sap velocity as a result of drought, and fog (in the absence of rain) were statistically significant (Fig. 5, ANOVA,  $P < 0.0001$ ,  $df = 2$ ,  $F = 34.05$ ). Sap velocity decreased 82 % from the beginning to the end of the dry period and foggy conditions led to an 81 % reduction in sap velocity (Fig. 5).

Individuals recovered an average of 31.2 % of the total volume of water transpired throughout the study (Table 3). This recovery rate ranged from 11.6 % in *Oreopanax vestitus* to 66.8 % in *Cavendishia capitulata*. To account for variation in flow rates due to plant size, sap flow was

**Fig. 3** Precipitation and sap velocity of *Cavendishia capitulata* during June 1 and 2 of 2014 (a). Leaf wetness (solid line) and solar radiation (dashed line) for the same time period (b). This period was during the transition between the dry and wet seasons when conditions were relatively moist. Sap flow increases throughout the day but very quickly decreases and falls below zero as precipitation and leaf wetness increase



**Fig. 4** Representative diurnal courses of sap velocity ( $\text{cm h}^{-1}$ ) for *Cavendishia capitulata* (a) and *Neomirandea croatii* (b) during a period of peak soil moisture (January 26–27, at the beginning of the wet season following a number of rainy days) and during the period with the driest recorded soil moisture (March 18–19)

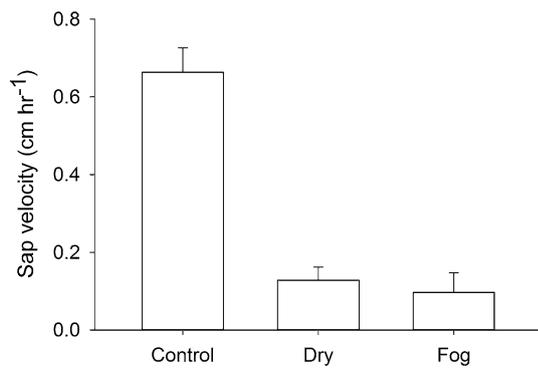


divided by the leaf area upstream of the sensor. While *C. capitulata* still had a high sap flow rate per unit leaf area relative to most of the other individuals, one individual of *N. croatii* and one individual of *O. vestitus* were similar in magnitude. The number of hours throughout the study period that FWU occurred varied as well, but less than the amount of water recovered (average: 28 %, range 16.5–37.1 %, Table 3).

Throughout the study, positive sap flow occurred at night. Across species, nighttime sap flow led to the upward movement of 34.6 % of the total positive sap flow over the

study period (Table 3). Nighttime sap flow was highest in *Chlorogyne ensiformis* (47.7 %) and lowest in *Cavendishia capitulata* (16.3 %). The percent of the total nighttime hours when positive flow occurred averaged 34.3 % with a range of 26.8 % (*Cavendishia capitulata*) to 43.2 % (*Neomirandea croatii*). In contrast to FWU, there was less variation across species between the percent of total sap flow that occurred at night and the percentage of time (hours) that nighttime flow was occurring (Table 3).

The sample size in the water balance calculations was lower than planned due to sensor failure. The sap



**Fig. 5** Average sap velocity ( $\text{cm h}^{-1}$ ) across eight species during a control period (clear 5-day period at the beginning of the dry season), a drought period (clear 5-day period at the end of the dry season) and during fog events (daytime hours throughout the study period that had at least 50 % reduced visibility but no rain was registered). Error bars represent the standard error of the mean

flow sensors are fragile and are susceptible to damage by weather and canopy dwelling animals once they are deployed in the field. Sensors were secured with parafilm, zip ties and electrical tape to try to avoid physical sensor damage. Sensors were maintained throughout the study period but only sensors that were functional for the entire period could be used for water balance calculations since a complete dry season sap flow response was needed.

### Observational study: drivers of daytime sap flow

In the first analysis, we examined the effect that variation in microclimate had on transpiration, which was defined as positive daytime values of sap flow. There were  $n = 1099$  observations in this analysis. After examining the explanatory variables for multicollinearity, the full model contained 20 fixed effects (main and quadratic effects for temperature, VPD, soil moisture, visibility, and precipitation, and 10 two-way interactions). Scaled estimates of the final model obtained by performing the backward selection that are shown in Table 4 were calculated to allow for comparison of the relative effect of the different terms in the model. Surprisingly, both VPD and precipitation had the largest estimated main effects on daytime positive flow and these effects were both positive. These results may be due to the complex patterns of water balance in this system. Weather in the TMCF is very dynamic and daytime conditions can often be cloudy and wet. While tissue refilling presumably happens in plants overnight when evaporative demand is lower, in this system, refilling may also happen during the day as well. Precipitation may be driving refilling which would be expressed as daytime sap flow values during wet periods while VPD may be driving positive sap flow values during dry periods (i.e., transpiration). Daily average air

**Table 4** A summary of fixed effects in the final model examining the effect of microclimate on transpiration (i.e., positive, daytime sap flow values)

Effect	Estimate	Scaled estimate	<i>t</i> value	<i>p</i> value
Temperature	-1.2227	-1.3697	-1.93	0.0541
VPD	0.0194	2.6322	4.51	<0.0001
Soil moisture	9.9411	0.6131	9.62	<0.0001
Precipitation	9.8653	2.4994	3.62	0.0003
Temperature <sup>2</sup>	0.0399	0.0501	2.14	0.0328
Soil moisture <sup>2</sup>	-16.6408	-0.0633	-2.33	0.0200
Precipitation <sup>2</sup>	0.4505	0.0289	3.82	0.0001
Temperature × VPD	-0.0010	-0.1512	-4.20	<0.0000
Temperature × precipitation	-0.5020	-0.1425	-3.30	0.0010
Soil moisture × precipitation	-11.2658	-0.1760	-3.08	0.0022

The Effect column lists the effects that were significant in the final model. The Estimate column shows the estimated values of the regression coefficients on the original scale, while the Scaled Estimate column lists the estimated values of the regression coefficients when each explanatory variable was scaled to have a standard deviation of 1 prior to analysis. This metric was calculated to examine the relative effect of the different drivers on transpiration. The last two columns correspond to the *t* and two-sided *p* values for each of the effects, respectively

temperature as well as the interactions between temperature and VPD, temperature and precipitation and soil moisture and precipitation all led to a suppression in daytime sap flow rates. Of these, temperature had an effect that was an order of magnitude larger than any of the interaction terms. Daily average temperature generally increases throughout the dry season. There may be a correlation between higher temperatures and reduced transpiration towards the end of the dry season (Fig. 4).

In the second analysis, we examined the effect that variation in microclimate had on FWU (i.e., negative sap flow values). There were  $n = 210$  observations in this analysis. After examining the explanatory variables for multicollinearity, the full model contained 14 fixed effects (main and quadratic effects for temperature, VPD, visibility, and precipitation, and 6 two-way interactions). In this final model obtained through the backward selection procedure, final model shown in Table 5, precipitation had the largest effect on FWU and this effect was an order of magnitude larger than any of the other significant effects. Days with more rainfall resulted in more negative sap flow. An increase in temperature also led to more FWU though this effect was minor. Temperature increases into the wet season, which may explain this significant effect. VPD had a significant negative effect on FWU, which is not surprising since days with higher VPD are likely to be drier. The interaction between temperature and precipitation also had a slight

**Table 5** A summary of fixed effects in the final model examining the effect of microclimate on FWU (i.e., negative sap flow values)

Effect	Estimate	Scaled estimate	<i>t</i> value	<i>p</i> value
Temperature	0.2694	0.2647	2.42	0.0163
VPD	-0.0069	-0.6640	-2.47	0.0144
Precipitation	28.0064	5.1110	3.63	0.0004
VPD <sup>2</sup>	0.0000	0.2056	2.58	0.0105
Temperature × precipitation	-1.6264	-0.2916	-3.55	0.0005

The Effect column lists the effects that were significant in the final model. The Estimate column shows the estimated values of the regression coefficients on the original scale, while the Scaled Estimate column lists the estimated values of the regression coefficients when each explanatory variable was scaled to have a standard deviation of 1 prior to analysis. This metric was calculated to examine the relative effect of the different drivers on transpiration. The last two columns correspond to the *t* and two-sided *p* values for each of the effects, respectively

negative effect on FWU. This result may be due to the types of rain events throughout the season. In the beginning of the dry season it is cooler and the rain events tend to be smaller (mist and wind driven rain). These events may lead to more FWU than the intense rainstorms that punctuate the beginning of the wet season, when it is warmer (Table 5).

The third analysis examined the effect that variation in microclimate had on nighttime sap flow (i.e., positive sap flow values at night). There were *n* = 957 observations in this analysis. After examining the explanatory variables for multicollinearity, the full model contained 20 fixed effects (main and quadratic effects for temperature, VPD, soil moisture, visibility, and precipitation, and 10 two-way interactions). Solar radiation, which was used to determine the nighttime period, was excluded from this model. The final model obtained through backward selection procedure is shown in Table 6. The main effects of temperature, VPD, soil moisture and precipitation were significant and all led to an increase in nighttime sap flow. Precipitation had the largest effect in this model by an order of magnitude. More precipitation in a nighttime period resulted in greater NT. Soil moisture also had a positive effect on NT, though this effect was much smaller than precipitation. Surprisingly VPD and temperature also had a significant (but slight) positive effect on NT. Warm dry air is likely to be a driver of nighttime transpiration (Dawson et al. 2007) while wet nights are more likely to drive tissue refilling. The fact that both dry and wet conditions had some effect on positive sap flow at night is an indication that we had both nighttime transpiration as well as nighttime refilling in this system, but that refilling is a much more significant process since precipitation is by far the largest driver. Table 7 and Fig. 6 show the simple linear regression analyses results and plots between observed and predicted sap flow values.

**Table 6** A summary of fixed effects in the final model examining the effect of microclimate on nighttime sap flow (i.e., positive, nighttime sap flow values)

Effect	Estimate	Scaled estimate	<i>t</i> value	<i>p</i> value
Temperature	0.1137	0.1324	3.08	0.0022
VPD	0.0029	0.1457	3.20	0.0014
Soil moisture	4.5099	0.2944	6.56	<0.0001
Precipitation	12.5110	1.9907	3.67	0.0003
Temperature × precipitation	-0.5059	-0.0938	-2.59	0.0098
VPD × precipitation	-0.0663	-0.5244	-2.44	0.0150
Soil moisture × precipitation	-20.7737	-0.2158	-3.82	0.0001

The Effect column lists the effects that were significant in the final model. The Estimate column shows the estimated values of the regression coefficients on the original scale, while the Scaled Estimate column lists the estimated values of the regression coefficients when each explanatory variable was scaled to have a standard deviation of 1 prior to analysis. This metric was calculated to examine the relative effect of the different drivers on transpiration. The last two columns correspond to the *t* and two-sided *p* values for each of the effects, respectively

**Table 7** A summary of simple linear regression analyses carried out to assess how well the models fit the data

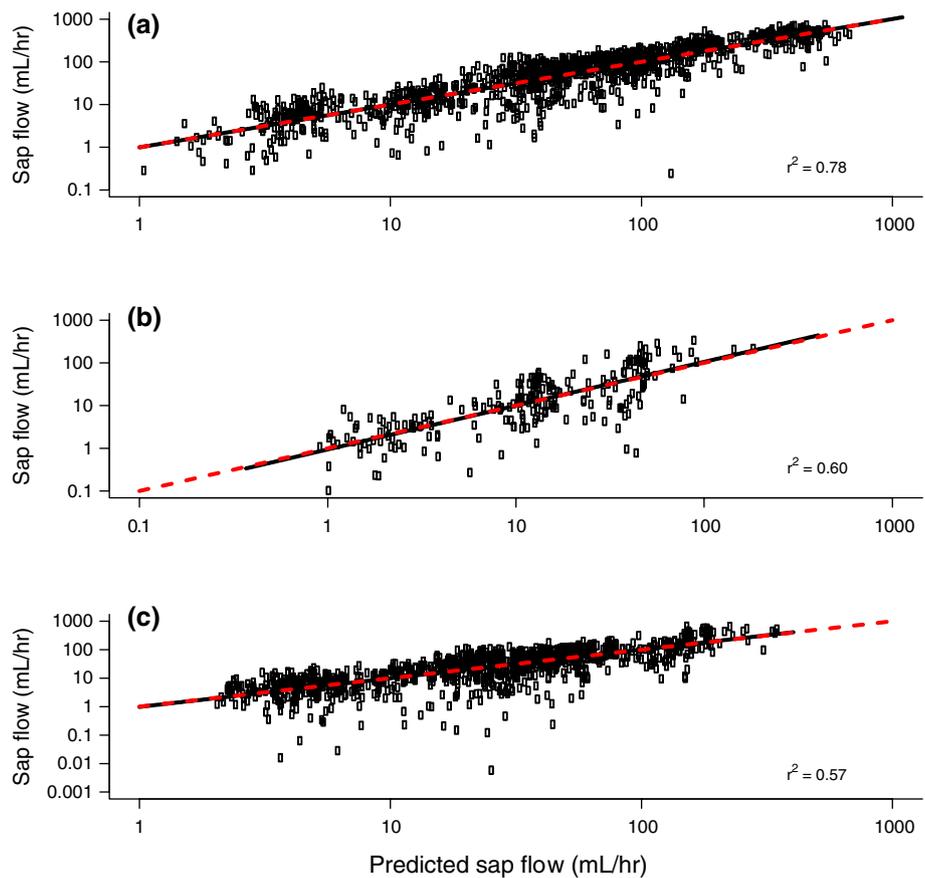
Analysis	Coefficient	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> <sup>2</sup>
Model 1	$\beta_0$	-0.0079	-0.12	0.9040	0.78
	$\beta_1$	1.0021	62.44	<0.0001	
Model 2	$\beta_0$	-0.0617	-0.39	0.6980	0.60
	$\beta_1$	1.0251	17.65	<0.0001	
Model 3	$\beta_0$	-0.0201	-0.21	0.8330	0.57
	$\beta_1$	1.0064	35.58	<0.0001	

The response variable was the ln of the observed sap flow values and the explanatory variable was the ln of the predicted sap flow values. See Fig. 6 for a graphical display of these analyses. Model 1 analyzes the effect of microclimatic drivers on transpiration, Model 2 analyzes the effect of microclimatic drivers on nighttime sap flow while Model 3 analyzes the effect of microclimate on foliar water uptake

The linear regression analyses indicated good fits between the observed and predicted values. All slope and intercept estimates were near 1 and 0, respectively, and the *R*<sup>2</sup> values were 0.78, 0.60, and 0.57 for models 1, 2, and 3, respectively.

The quantile regression analysis indicated that the distribution of sap velocity is greatly impacted by the number of days without rain (Table 8; Fig. 7). With each additional dry day, the predicted decrease in the median and 97.5th quantile was 4.30 and 56.76 ml h<sup>-1</sup>, respectively. For the 2.5th quantile the predicted increase was 17.39 ml h<sup>-1</sup>. As conditions dried, there was a considerable reduction in maximum sap velocity as well as FWU while the median values only decreased slightly (Fig. 7).

**Fig. 6** Performance of the models created to evaluate the effect of microclimatic drivers on transpiration (a), nighttime sap flow (b) and foliar water uptake (c). The response variable was the ln of the observed sap flow values and the explanatory variable was the ln of the predicted sap flow values. A 1:1 dashed reference line is plotted in each panel but is barely visible due to the agreement between the model and predictions. A solid line represents the simple linear regression line



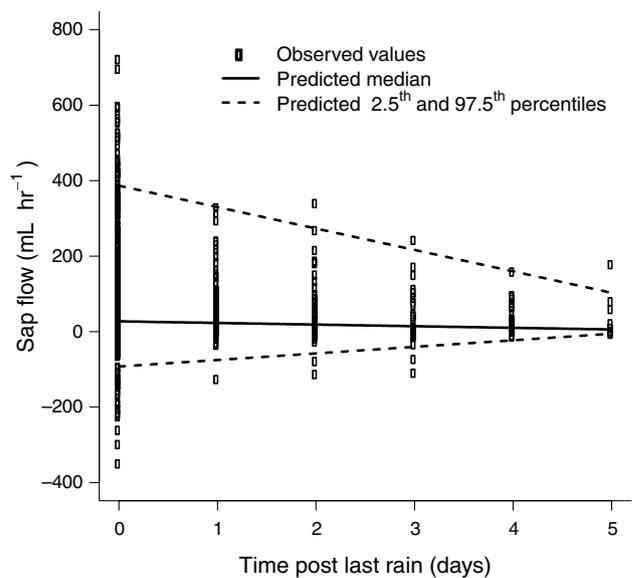
**Table 8** A summary of quantile regression analyses carried out to model the quantiles (2.5th, 50th, and 97.5th) as function of number of days post-last rain

Quantile	Coefficient	Estimate	<i>t</i> value	<i>p</i> value
2.5th	$\beta_0$	-92.47	-4.73	<0.0001
	$\beta_1$	17.39	2.12	0.0339
50th (median)	$\beta_0$	27.29	9.12	<0.0001
	$\beta_1$	-4.30	-2.86	0.0044
97.5th	$\beta_0$	386.78	18.89	<0.0001
	$\beta_1$	-56.76	-6.16	<0.0001

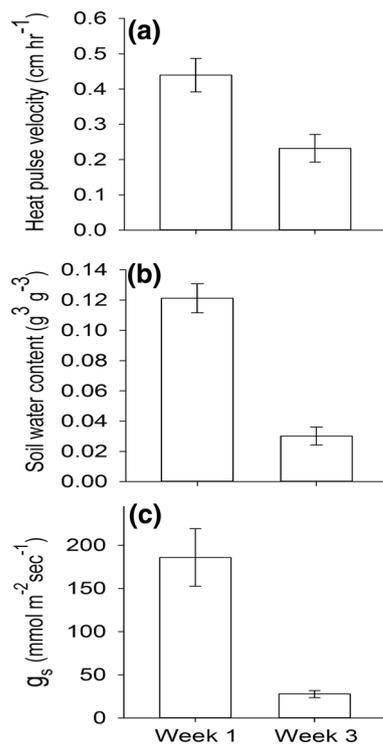
See Fig. 7 for graphical display of these analyses

**Drought experiment**

Sap flow also decreased significantly over the course of the drought experiment (Friedman Test,  $P < 0.001$ ,  $df = 20$ ,  $\chi^2 = 90.37$ , Fig. 8a). Average heat pulse velocity decreased from 0.42 cm h<sup>-1</sup> (SE = 0.006) at the beginning of the experiment to 0.22 cm h<sup>-1</sup> (SE = 0.0003) after 19 days of drought (Fig. 8a). In addition to sap flow, a number of other parameters changed dramatically throughout the course of the experiment. The relative



**Fig. 7** Effect of dryness (number of days after the last rain) on volumetric sap flow (ml h<sup>-1</sup>). The solid line represents the estimated 50th percentile (median) value of the distribution of the sap flow as a function of dryness. The dashed lines represent 2.5th (lower line) and 97.5th (upper line) percentile of the distribution of the sap flow as a function of dryness



**Fig. 8** Physiological responses of 11 individuals across six species in the first and last weeks of the drought experiment. Average heat pulse velocity ( $\text{cm h}^{-1}$ ), volumetric soil water content, and stomatal conductance deficit are represented in panels a–c, respectively. Error bars represent the standard error of the mean

volumetric soil water content decreased from  $0.12 \text{ g}^3 \text{ g}^{-3}$  in the first week of the experiment to  $0.03 \text{ g}^3 \text{ g}^{-3}$  in the final week (Fig. 8b). The average vapor pressure deficit was 0.3 kPa during the experiment and values ranged from 0.06 to 0.7 kPa. These values were higher than the vapor pressure deficit in the observational tree crown during the same time period (average = 0.004 kPa, range 0–0.01). The average stomatal conductance significantly decreased from  $185 \text{ mmol m}^{-2} \text{ s}^{-1}$  in the first week of the experiment to  $27.7 \text{ mmol m}^{-2} \text{ s}^{-1}$  in the last week (ANOVA,  $df = 1$ ,  $F$  ratio = 32.9,  $P < 0.0001$ , Fig. 8c). Leaf thickness also decreased significantly over the course of the drought experiment for most species. Across all species, there was an average decrease in 28.4 % of the thickness of the leaf lamina (ANOVA,  $df = 1$ ,  $F$  ratio = 17.19,  $P < 0.0001$ , Fig. 9). Percent loss ranged from  $-1.3 \%$  (SE = 1.1 %) in *Neomirandea* sp. to 77 % (SE = 4.3 %) in *Notopleura* sp. The greatest percent reduction occurred in succulent species. Across species, 56 % of individuals experienced branch dieback or complete mortality by the end of the experiment and all plant types experienced some mortality with the exception of bromeliads.

## Discussion

The goal of this research was to characterize the responsiveness of common epiphytes to drought and changes in microclimate. This is the first project that we are aware of to document the significance of FWU to dry season water balance in epiphytes. In addition, our work furthers our understanding of the importance of habitat moisture on sap flow. Last, the results of our drought experiment indicate that despite adaptations to withstand seasonal drought, epiphytes are vulnerable to the extended dry periods that may become more common as changes in climate continue.

### Drought effects on sap velocity, stomatal conductance and leaf thickness

Sap velocity patterns exhibited clear diurnal courses while daily average values decreased as the dry season progressed (Figs. 2a, 4). Flow rate reduction occurred rapidly over the first 3 weeks, followed by little further reduction over the rest of the dry period (Fig. 2a). This suggests that any water storage capacity in these species is insufficient to alleviate drought stress during prolonged dry periods.

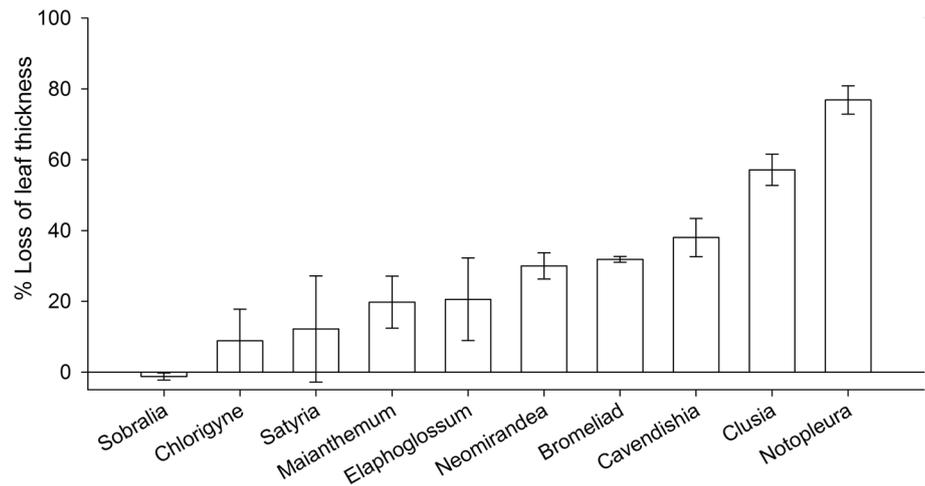
Drought decreased sap flow in both the manipulative and observational experiments, although the rate and amount of reduction varied with the severity of the drought. During the experimentally imposed drought, sap flow rates decreased by 64 % following 14 days without rain (Fig. 8). Although a sap flow reduction was also seen throughout the dry season in the field experiment, this response was faster in the greenhouse, which was likely due to the complete exclusion of rain and higher VPDs.

Stomatal conductance and leaf thickness also decreased significantly by the end of the drought experiment (Figs. 8, 9). Changes in leaf thickness varied greatly across species but in most cases drought led to significant reductions in leaf thickness (Fig. 9). This occurred largely due to the drawdown of water stored in leaf hydrenchymal cells which have been identified in a number of these species and are part of a drought avoidance strategy in epiphytes (Ogburn and Edwards 2010; Gotsch et al. 2015, Gotsch *unpubl data*). Despite stomatal regulation and high leaf capacitance, many of the individuals were partially desiccated by the end of the experiment and the majority did not recover from the drought.

### Water balance

The study species relied heavily on FWU for a large portion of their dry season water intake. On average, 31.18 % of total positive flow was offset via FWU over the course of the study although there was considerable

**Fig. 9** Decrease in leaf thickness (%) of 10 common groups of epiphytes (>3 individuals per species) exposed to a 3-week drought experiment. *Sobralia*, *Satyria*, *Elaphoglossum*, and *Clusia* were identified to genus only. 'Bromeliad' included multiple genera of this functional group. All other species are listed in Table 2. Error bars represent the standard error of the mean



variation across species and individuals. The greatest amount of FWU occurred in *C. capitulata* although when the leaf area upstream of the sensor was taken into consideration, the FWU of *C. capitulata* was similar in magnitude to one individual of *N. croatii* and one individual of *O. vestitus*. While *C. capitulata* and *O. vestitus* are relatively large species, *N. croatii* is a small, single-stemmed woody epiphyte. Properties of leaves (including leaf age and surface colonization of moss or lichen) or canopy position may confer greater relative success in FWU than plant size.

In this study, FWU was lower than the recently published rates of Gotsch et al. (2015). This previous work documented an average FWU of 70 % of total positive flow during a month-long misty and foggy period (Gotsch et al. 2015). The current study quantifies the effect of drought on water balance and, therefore, took place during a period that was considerably drier and experienced less fog and mist. In contrast, our rates of FWU were greater than recently published rates in terrestrial species suggesting that epiphytes may exhibit a greater reliance on clouds than their terrestrial neighbors (Goldsmith et al. 2013; Gotsch et al. 2014a). Furthermore, the large variation in FWU across species suggests that species-specific differences in foliar uptake capacity may be more important to the overall amount of water recovered than differences in the amount of time species are engaged in FWU.

Nighttime sap flow also occurred frequently (34.3 %) throughout the study and accounted for an average of 34.6 % of total positive sap flow. Nighttime sap flow can either be the result of nighttime transpiration or tissue refilling. While nighttime transpiration has been documented in TMCFs, we have found in a previous study that nighttime positive sap flow is likely indicative of tissue refilling (Gotsch et al. 2014a, 2015). Our modeling work, which we discuss below, further supports this hypothesis.

### Microclimatic drivers of sap flow

Our modeling efforts indicate that precipitation is the most important driver of FWU and nighttime sap flow in this system. Nighttime sap flow has been documented across many ecosystems and is often the result of relatively high VPDs at night (Dawson et al. 2007 and references therein). In our study, nighttime sap flow is driven by habitat moisture and is likely an indication of tissue refilling rather than transpiration. Our values of daytime positive sap flow maybe a signal for both transpiration as well as refilling since both VPD and precipitation had a large positive effect on daytime positive flow rates. In the TCMF canopy where daytime microclimate may often include wet conditions with low-lying clouds, both transpiration and refilling may occur during daylight hours. In future studies we plan to explore the effect of microclimate on refilling in these species using controlled greenhouse experiments.

This work adds to recent efforts to determine the environmental controls of transpiration in the TCMF. In the cloud forests of Brazil, Eller et al. (2015) found that VPD, soil water content and leaf wetness were all important drivers of sap flow in *Drimys brasiliensis*, a common Neotropical cloud forest tree. Berry et al. (2016) also found that VPD was an important environmental driver of transpiration in three common tree species in a TCMF in Mexico and that slope position also affected the importance of different microclimatic variables on transpiration. Our results further these efforts by examining these relationships in a wetter TCMF and in epiphytes, an understudied plant community that plays an important role in TCMF ecosystem function.

While this study took place in the dry season, it was a particularly wet-dry season due to consistent inputs of rain and mist. Plants utilized wet periods to replenish lost water via FWU and tissue refilling but nonetheless, transpiration was suppressed rapidly during dry periods. These results

indicate that despite adaptations to store or conserve water, the epiphytes studied are very responsive to changes in climate and are, therefore, vulnerable to even subtle changes in atmospheric conditions.

## Conclusions

We have found that epiphytes depend on atmospheric moisture deposited from clouds (fog) and rain in the dry season. Our results indicate that these plants are vulnerable to projected changes in this region, including reduced and more variable precipitation patterns as well as increases in temperature and cloud base heights (Pounds et al. 2006; Ray et al. 2006; Karmalkar et al. 2008; Pounds unpublished data). Dry season air temperature is projected to rise in this region by approximately 3.8 °C and variability is also projected to increase (Karmalkar et al. 2008). Dry season precipitation is also projected to decrease by 25 % (Karmalkar et al. 2008) with an increase in the number of consecutive days without precipitation (Pounds et al. 2006). Our experiments have found that epiphytes will likely respond rapidly to such changes. Combined with changes in orographic cloud base heights (Ray et al. 2006), future dry seasons will likely cause an increase in water stress, particularly in the canopy community. The heavy reliance of epiphytes on clouds, as shown here, suggests that epiphytes may be vulnerable to projected changes in climate. Changes in the abundance or distribution of canopy species will likely lead to a decrease in the important ecosystem services that this community provides to the larger TMCF ecosystem.

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**Author contribution statement** SGG formulated the ideas resulting in the research. AD, AG and SGG conducted the fieldwork. AD, and SGG conducted the non-modeling statistical analyses. DD conducted modeling analyses and contributed text regarding those analyses. AD and SGG wrote the manuscript. All authors edited the manuscript.

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