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Life in the treetops: ecophysiological strategies of canopy epiphytes in a tropical montane cloud forest

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Abstract. Tropical montane cloud forests (TMCFs) inhabit regions rich in biodiversity that play an important role in the local and regional water cycle. Canopy plants such as epiphytes and hemiepiphytes are an important component of the biodiversity in the TMCF and therefore play a significant role in the carbon, nutrient, and water cycles. With only partial or no access to resources on the ground, canopy plants may be vulnerable to changes in climate that increase canopy temperatures and decrease atmospheric humidity or precipitation inputs. Despite their importance in the TMCF, little is known about variation in functional strategies relating to drought avoidance or drought tolerance of canopy plants. In this study, we quantified variation in a number of functional traits in 11 species of epiphytes and hemiepiphytes in a Costa Rican TMCF. We also generated pressure–volume and xylem vulnerability curves that we used as indicators of drought tolerance. In addition, we hand-sectioned fresh leaves and examined cross sections under a microscope to quantify leaf thickness, mesophyll thickness and the thickness of water storage cell layers (i.e., hydrenchyma), if present. Lastly, we determined the capacity for foliar water uptake in the laboratory and measured whole-plant transpiration in the field.

A trade-off was found between traits that confer relative drought resistance and foliar water uptake capacity vs. traits that confer leaf capacitance and relative drought avoidance. This trade-off may represent an additional axis of the leaf economics spectrum that is unique to epiphytes. We also found that all species had the capacity for foliar uptake of water and that this process contributed substantially to their water balance. On average, foliar uptake of water contributed to the reabsorption of 70% of the water transpired over a relatively wet, 34-day study period. Our results indicate that canopy plants can mitigate water loss substantially via internal water storage or that they can directly utilize cloud water to offset losses. Our results indicate that species that rely on foliar uptake of water may be more vulnerable to projected changes in climate than species that buffer the effects of drought via internal water storage.

Key words: capacitance; drought tolerance; foliar water uptake; functional traits; hemiepiphytes; pressure–volume curves; vulnerability curves; water relations.

Introduction

Because water loss is an inevitable cost of carbon fixation, all plant communities are influenced by water availability. If water becomes limiting, plants may become increasingly vulnerable to water deficits and as a result, embolism and xylem cavitation can increase as tension in the xylem pathway builds (i.e., localized and widespread loss of function of xylem conduits, respectively). Drought can also have widespread effects on plant communities including changes in species distribution, decreases in primary productivity, and large-scale mortality due to physiological dysfunction such as hydraulic failure or poor carbon balance (McDowell et al. 2008, Brodribb and Cochard 2009, Kursar et al. 2009). These impacts of water limitation on plant communities are likely to become more important worldwide as temperatures rise and variability in precipitation patterns increase (IPCC 2007).

Despite high humidity and generally ample precipitation in tropical rainforests, water limitations can still influence species distribution and survival in these ecosystems (Engelbrecht et al. 2007, Kursar et al. 2009). In tropical montane cloud forests (TMCF), which are known for lush vegetation and abundant epiphyte communities, precipitation and cloud immersion can vary widely over short time scales, greatly influencing plant water balance (Holwerda et al. 2010, Goldsmith et al. 2013, Gotsch et al. 2014*a*, *b*). Increases in the evaporative demand of water from epiphytic

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plants that have little or no functional roots may lead to marked periods of water deficit or even stress, especially in canopy communities, which are largely disassociated from terrestrial soil resources (Benzing 1989).

Microclimatic conditions such as temperature, light availability, humidity, and wind can also vary greatly in TMCFs along vertical gradients from the soil to the canopy. As one moves up from the understory to the highest part of the canopy, light availability, vapor pressure deficit and wind speed all generally increase (Cardelús and Chazdon 2005, Watkins and Cardelús 2010; S. G. Gotsch, *unpublished data*). These conditions lead to a canopy microclimate that is considerably drier than in the understory (Cardelús and Chazdon 2005, Watkins and Cardelús 2010).

Despite drier conditions in the canopy, this habitat contains hundreds of plant species, which play an important role in ecosystem functions and services to the entire community aloft. In a TMCF in Costa Rica, epiphytes comprise 30% of the total foliar biomass and 45% of the nutrient capital in the forest (Nadkarni 1984). Canopy plants are important components of the hydrological cycle of tropical forests due to their high water storage capacity and additional surface area, which increases cloud and rainwater interception, and results in additional inputs of water to the ecosystem (Köhler et al. 2007, Tobón et al. 2010). Epiphytes and hemiepiphytes also promote the creation of dense aerial mats of soil and humus, which increase the water holding capacity of the forest and provide shelter for arboreal mammals and invertebrates (Foster 2001, Nadkarni et al. 2004).

The TMCF region of Costa Rica has experienced increased variability in rainfall over the last 40 years, which may be particularly detrimental for canopy communities. Although annual rainfall has generally increased, the number of consecutive days without rainfall has also increased while the frequency of mist has decreased (Pounds et al. 1999). Moreover, increases in the variability of rainfall and a general decrease in cloud immersion are projected for the Costa Rican TMCF region due to changes in land use (i.e., deforestation) and increases in sea surface temperatures (Still et al. 1999, Lawton et al. 2001). Epiphytes may be particularly vulnerable to changes in precipitation regimes and cloud cover because they are largely dependent on canopy soil inputs of water and nutrients. Although some epiphytes exhibit some traits that can be associated with drought avoidance (e.g., CAM photosynthesis, succulent leaves), there are many epiphytes in the TMCF that more closely resemble terrestrial herbaceous plants and shrubs and do not appear particularly well-adapted to drought (Fig. 1). Evaluating drought avoidance or resistance in epiphytes is critical to understanding how projected changes in climate will affect the diversity and abundance of canopy communities as well as the ecosystem services they provide.

In terrestrial plant communities, vulnerability to drought stress is determined in part by a plant's ability to maintain function as xylem tension increases. One important biological indicator of drought resistance or tolerance is wood or stem density. In dense wood, there are more xylem conduits of smaller diameter than in less dense wood and these smaller conduits are more resistant to cavitation (Hacke et al. 2001, Jacobsen et al. 2007, Willson et al. 2008). Although plants with high wood density may be well adapted to withstand moderate prolonged water limitation, high wood density is not a universal indicator of drought resistance. Although these species can withstand lower water potentials, they also function closer to their minimum critical water potential (i.e., they posses small safety margins), which may make species with high wood density more vulnerable to acute severe drought stress (Hoffmann et al. 2011). Xylem vulnerability to cavitation can also be directly determined by inducing a series of decreasing stem water potentials and measuring changes in hydraulic conductivity (Sperry and Saliendra 1994). Maintenance of hydraulic function at low water potentials may be related to an underlying trade-off between resistance to cavitation and the capacity to conduct large volumes of water and may also be influenced by shared evolutionary history (Tyree et al. 1994, Ackerly and Donoghue 1998, Piñol and Sala 2000). Drought also has impacts on live cells and the evaluation of the water potential at which cell walls collapse (i.e., the turgor loss point, ψ_{TLP}) is another trait that is used to evaluate resistance to drought (Niinemets 2001, Brodribb and Holbrook 2003, Lenz et al. 2006, Blackman et al. 2010, Bartlett et al. 2012). Despite the widespread assumption that epiphyte communities exhibit traits to avoid or resist drought, a community-wide evaluation of ecophysiological strategies in canopy communities is still lacking.

Another widespread assumption regarding epiphyte communities is that the leaves of these species can directly absorb cloud water and mist (Foster 2001). Elegant morphological descriptions of *Tillandsia* sp. have uncovered adaptations to capture and absorb cloud water although it is unknown whether these adaptations extend to other epiphytic taxa (Benzing 1989). Even without such specialized leaf structures, foliar water uptake has been detected in terrestrial species in the TMCF where this process comprises a significant component of whole plant water balance (Goldsmith et al. 2013, Gotsch et al. 2014*a*). The extent to which foliar water uptake occurs across canopy communities and the importance for this process in epiphytic water balance is unknown. Understanding the capacity for and prevalence of foliar water uptake is needed to determine how changes in cloud base heights and/or precipitation patterns will affect community dynamics in the canopy and ecosystem water balance.

In this study, we examined the water relations of common species of epiphytes and hemiepiphytes in the

FIG. 1. View from within the canopy of one of the study trees (*Ficus tuerckheimii*). All of the vegetation in the foreground consists of epiphytes or hemiepiphytes. On the right in the foreground, the red flowers of *Cavendishia melastomoides* can be seen. In the center of the photo towards the bottom are the palm-like leaves of *Chlorigyne ensiformis*. In the upper-right corner of the photo, the faint purple color of *Neomirandea croatii* flowers can be seen. This image is representative of the density of vegetation in the study crowns and the proximity of the study species within the crown.

TMCF of Monteverde, Costa Rica. We measured a number of functional traits and determined volumetric sap flow on species representing different canopy growth forms to ask the following questions: (1) Do canopy plant communities in the TMCF use a variety of strategies to cope with water limitation? (2) Do epiphytes use similar drought-tolerance strategies to those documented in terrestrial species? (3) Is foliar water uptake a widespread phenomenon in the canopy and if so, how important is this process to epiphyte and hemiepiphyte water balance?

We hypothesized that the relatively mild conditions in the TMCF would allow a variety of adaptations to cope with periodic water limitation. Despite the fact that short-term water limitation is an inescapable part of life in the treetops, some TMCFs have relatively consistent inputs of occult precipitation (fog and mist) promoting great diversity and biomass in the canopy (Clark et al. 2000). In the TMCF of Monteverde, Costa Rica, a wide array of epiphytic and hemiepiphytic life forms are visible in a single tree crown including bryophytes, ferns, leafy herbaceous species, succulents, shrubs, and treelets (Ingram and Nadkarni 1993). We hypothesized that adaptations to resist or avoid drought would vary based on these different life forms. We also hypothesized that these species would exhibit traits known to confer drought tolerance in terrestrial plants such as low ψ_{TLP} and resistance to cavitation. Lastly, we hypothesized that all species would possess some capacity for foliar uptake of water, given the importance of this water source for canopy plants, and that this process would be an important component of water balance.

METHODS

Study location

This research was conducted in the Monteverde Cloud Forest Reserve on the Pacific slope of the Cordillera de Tilarán in Costa Rica (10°18′ N, 84°48′ W; 1480–1550 m in elevation). The site consists of primary forest 20–30 m high with emergent trees reaching 35 m (Nadkarni and Matelson 1991). The soils in this region are Typic Dystrandepts and are characterized by high moisture content and porosity, as well as low clay content, and bulk density (Lawton and Dryer 1980, Nadkarni and Matelson 1991, Nadkarni and Wheelwright 2000). Epiphytes are a ubiquitous feature of this forest; there are approximately 800 species of epiphytes in the Monteverde Reserve and the biomass of this community has been estimated at ~1.92 t/ha (Haber 2000, Hölscher et al. 2004). Air temperature remains relatively constant throughout the year (daily average: 22°C) though diurnal changes in temperature are great and surpass yearly variation (Nadkarni 1994). The dry season generally extends from February to April while the wet season is generally from May to November

TABLE 1. Taxonomic names and growth forms for the study species, and the measurements of each species made during the study period.

Species	Family	Growth form	Measurements
Cavendishia capitulata	Ericaceae	shrub epiphyte	1,2,3,4,5
Cavendishia melastomoides	Ericaceae	shrub epiphyte	1,2,4
Chlorigyne ensiformis	Cyclantaceae	herbaceous	1,2,4,5
Clusia flavasepala	Clusiaceae	hemiepiphyte	1,2,3,4,5
Clusia palmana	Clusiaceae	hemiepiphyte	1,2,4
Cosmibuena valerii	Rubiaceae	hemiepiphyte	1,2,3,4
Maianthemum monteverdense	Asparagaceae	herbaceous	1,2,3,4
Neomirandea croatii	Asteraceae	small woody epiphyte	1,2,4,5
Notopleura piticobia	Rubiaceae	small woody epiphyte	1,2,4,5
Oreopanax vestitus	Areliaceae	hemiepiphyte	1,2,3,4,5
Schefflera rodrigueziana	Areliaceae	hemiepiphyte	1,2,3,4,5

Note: Explanations for each measurement number are as follows: 1, functional traits; 2, pressure–volume curves; 3, vulnerability curves; 4, foliar water uptake capacity; and 5, volumetric sap flow.

(Nadkarni 1985, 1994). December and January tend to be misty and windy; this period is considered the transition season (Nadkarni 1985, 1994). On average, this site receives 2500 mm of rainfall annually and there are additional inputs of 500–2000 mm provided by mist and fog, which are especially abundant in the transition and dry seasons (Nadkarni 1985, 1994). Despite generally mild conditions, there has been an increase in the number of dry days and a decrease in the frequency of mist at the site over the last 40 years (Pounds et al. 1999).

Study species

Eleven common epiphyte and hemiepiphyte species were the subject of this study. These species were chosen because they are common throughout the reserve and exhibit diverse life forms including herbaceous epiphytes, shrub epiphytes, and hemiepiphytes (Table 1, Fig. 1). Multiple individuals of all species were studied in the crowns of three to five host trees. Study species were representatives of nine different genera and nine different families.

Sample collection

Most samples were collected between June and August of 2013 from the canopies of five mature strangler fig trees (*Ficus tuerckheimii*). *F. tuerckheimii* is a common canopy tree in the TMCF; its large crown size supports abundant and diverse epiphytic communities (Fig. 1). All host trees contained canopy mats up to 25 cm thick and were densely populated with epiphytes and hemiepiphytes (Nadkarni 1985). Tree crowns were accessed using single-rope and double-rope climbing techniques. To measure functional traits, samples were cut, placed in black plastic bags to minimize dehydration, and then were lowered to the ground. Samples were then taken to the field laboratory where stems were recut underwater and plants were covered until measurement. The stem diameter of samples varied based on the plant growth form but generally ranged from 0.5–2.5 cm in diameter. Single stems had a minimum of five leaves distal to the cut portion and often times many more. For smaller growth forms with multiple stems, a number of adjacent stems were cut and treated as a single individual. Functional traits were measured on five individuals per species in a minimum of three tree crowns. Only the youngest mature leaves were measured. Sap flow was measured on a subset of the study species that were all common within five meters of one another in three crowns. Microclimate was measured near sap flow stations as well as on a tower that was between 20 and 500 m from study trees. Additional sap flow and microclimate data were collected in January of 2014. Microscopy measures were completed from June–August of 2014 on individuals from the same tree crowns.

Functional trait measures

Stem density.—Stem density was calculated by dividing the dry weight by the fresh volume (Table 2). Approximately six cm of woody tissue was measured for each sample. Bark was removed, the sample was cut directly down the middle and all pith was removed. *C. ensiformis* and *M. monteverdense* are herbaceous monocots; the arrangement of vascular bundles in these species did not permit pith removal prior to measurement. Volume of the prepared sample was determined using the displacement principle of Archimedes. Following the determination of volume, tissues were dried at 60°C for three days, which was sufficient for the samples to achieve a constant weight.

Leaf toughness.—Leaf toughness was determined by measuring the weight needed to pierce a leaf with a blunt cylinder of known diameter (Gotsch et al. 2010). The penetrometer used in this study was constructed at the machine shop at Franklin and Marshall College. Toughness was measured in the middle of the leaf blade in an area free of secondary veins (Table 2).

Specific leaf area.—Specific leaf area (SLA) was calculated as the fresh leaf area divided by the dry mass. Six leaf discs of a known area were removed from the leaf and samples were dried for three days at 60°C.

TABLE 2. Leaf and whole-plant physiological traits for 11 common epiphyte and hemiepiphyte species.

Species	WD (g/cm^3)	Tough (g)	SLA (cm^2/g)	LDMC	Huber	FWUC (MPa)	Mesophyll (mm)	Cuticle (mm)
Cav cap	0.71	789.57	361.08	0.25	0.00232	0.27	0.378	0.015
Cav mel	0.77	854.58	423.11	0.18	0.00022	0.36	0.301	0.013
Chl ens	0.14	2168.40	310.84	0.26	0.00067	0.15	0.405	0.011
Clu fla	0.61	1661.30	209.08	0.30	0.00040	0.16	0.387	0.019
Clu pal	0.56	1775.47	230.77	0.22	0.00028	0.16	0.504	0.024
Cos val	0.59	1234.29	296.84	0.26	0.00032	0.25	0.275	0.010
Mai mon	0.22	664.01	1228.43	0.26	0.00033	0.25	0.190	0.009
Neo cro	0.66	869.00	551.82	0.24	0.00034	0.20	0.535	0.013
Not pit	0.60	1111.13	524.77	0.25	0.00021	0.20	0.254	0.011
Ore ves	0.49	782.02	622.77	0.29	0.00027	0.21	0.226	0.010
Sch rod	0.53	1020.89	449.97	0.21	0.00045	0.24	0.236	0.010

Species	Thick (mm)	WS thick (mm)	Pi_o (MPa)†	ψ_{TLP} (MPa)†	RWC_{TLP} (%)†	ε (MPa)†	C_{FT} (MPa^{-1})†	C_{TLP} (MPa^{-1})†
Cav cap	0.49	0.074	−1.76	−1.85	89.06	18.66	0.07	1.29
Cav mel	0.42	0.086	−1.35	−1.48	85.44	15.93	0.09	1.04
Chl ens	0.50	NA	−1.08	−1.20	88.44	22.53	0.10	0.77
Clu fla	0.70	0.360	−0.76	−0.85	85.76	9.93	0.16	1.80
Clu pal	1.06	0.548	−0.77	−0.86	90.59	9.57	0.12	0.80
Cos val	0.59	0.256	−1.02	−1.16	86.97	10.11	0.11	0.68
Mai mon	0.26	NA	−0.95	−1.03	91.02	14.82	0.09	1.14
Neo cro	0.66	NA	−1.00	−1.08	90.24	13.21	0.09	1.06
Not pit	0.75	0.294	−1.07	−1.14	93.23	21.51	0.05	0.96
Ore ves	0.29	0.030	−0.98	−1.06	90.23	16.95	0.10	1.97
Sch rod	0.35	0.070	−1.19	−1.35	90.17	16.29	0.08	0.81

Notes: Species abbreviations are the first three letters of the species name followed by the first three letters of the genus name (see Table 1). Abbreviation meanings are as follows: WD, wood or stem density; Tough, leaf toughness measured as the weight needed to pierce the leaf; SLA, specific leaf area; LDMC, the ratio of dry mass to fresh mass of a leaf; Huber, Huber value calculated as the ratio of the sapwood area to leaf area; FWUC, foliar water uptake capacity measured as an improvement in water potential; mesophyll, mesophyll thickness; cuticle, cuticle thickness; thick, total leaf thickness; WS thick, thickness of the water storage cell layer; Pi_o, osmotic potential at full saturation; ψ_{TLP}, water potential at the turgor loss point; RWC_{TLP}, relative water content at the turgor loss point; ε, modulus of elasticity; C_{FT}, capacitance at full turgor; and C_{TLP} is the capacitance at the turgor loss point. "NA" indicates species for which WS thickness was not measured, as these species did not have a distinct water storage layer. All values are species averages.

† Parameters were determined with pressure–volume curves.

Care was taken to avoid primary veins and to choose the youngest mature leaves.

Leaf dry matter content.—Leaf dry matter content (LDMC) is the ratio of dry mass to fresh mass of a leaf. A minimum of five leaves were measured per individual. Fresh leaves were weighed and then dried at 60°C for three days to obtain the dry mass (Table 2).

Huber value.—Huber value is the ratio of sapwood area to leaf area (Table 2). One piece of leafy stem approximately 6 cm long was taken from each sample and the cross-sectional sapwood area was determined. All leaves were traced onto white paper and the area of the samples was determined in the lab at Franklin and Marshall College using a LI-3100C area meter (LI-COR Biosciences, Lincoln, Nebraska, USA).

Microscopy

Following collection in the field, sample stems were cut underwater in the field laboratory and stored in water under black plastic until they were processed the following day. Three fresh leaves were hand-sectioned per individual and stained with safranin to increase contrast. Leaf cross-sections were viewed under 40× or 100× power with a light microscope (Motic BA210E, Richmond, British Colombia, Canada). Digital images were taken of all samples and the leaf thickness, mesophyll thickness, total cuticle thickness, and total hydrenchymal thickness were quantified using Image J Software (v1.48, U.S. National Institutes of Health, Bethesda, Maryland, USA). All measurements were taken away from major veins (Table 2).

Foliar water uptake capacity

Samples were recut under water, covered with dark plastic and left overnight to rehydrate. In the morning, water potential was measured on the leaves to ensure that they were fully rehydrated. Following the initial measurement, leaves were dehydrated by applying 1.0 MPa of pressure for one minute in a pressure chamber (PMS model 1505D-EXP, Albany, Oregon, USA). During this minute, a paper towel was held to the exposed petiole to remove water from the cut surface. After a minute, water potential was measured again to establish pre-rehydration water status. Leaf blades were then submerged in water for 60 minutes. The cut petiole was exposed, but wrapped in parafilm to limit water loss. After an hour of submersion, leaves were wiped dry and the water potential was measured again. Foliar

water uptake capacity was calculated as the improvement in water potential following submersion (Table 2). Three leaves were measured per individual and five individuals were measured per species. Methods followed those described by Goldsmith et al. (2013).

Pressure volume curves

Samples were rehydrated overnight prior to analysis. A leaf or branchlet was measured from each individual depending on the sturdiness and length of the petiole. Five individuals per species were measured from at least three host trees. As soon as samples were removed from the rehydrated branches, their water potential was measured and the sample was then immediately weighed. Leaves were allowed to bench dry and the water potential and weight were measured 15–20 times throughout the desiccation process until approximately 40% of the weight was lost due to dehydration. If desiccation occurred slowly, samples were placed in a light box with a fan to accelerate evaporation. The relationship between the inverse water potential and relative water content was plotted and analyzed following methods described by Sack et al. (2011). This analysis was used to determine the turgor loss point (ψ_{TLP}), relative water content at the turgor loss point (RWC_{TLP}), osmotic potential at full saturation (Pi_o) and the bulk elastic modulus (ε) (Table 2).

Vulnerability to cavitation

Vulnerability to cavitation was measured on the following woody epiphyte and hemiepiphyte species: *Clusia flavasepala*, *Cosmibuena valerii*, *Cavendishia capitulata*, *Oreopanax vestitus* and *Schefflera rodrigueziana* following the methods of Sperry and Saliendra (1994). The maximum vessel length for each species was measured by attaching a long branch (>1 m) to a hose with pressurized N_2. The end of the branch not connected to the hose (i.e., the distal end) was placed in a tub of water and short segments of the branch were cut back until bubbles were observed in the water which indicated that a vessel had been isolated. The length of this segment was considered the maximum vessel length of the sample. A minimum of three samples per species were measured and the greatest value obtained was considered the maximum vessel length of the species. Branch samples larger than the maximum vessel length were used. Minor lateral branchlets and leaves were removed and scars were sealed with quick-dry adhesive glue. The bark was removed from approximately 1 cm of the ends of each segment and ends were trimmed with a razor to expose any vessels that had been damaged when segments were initially cut. As many as four stems were then attached to a plastic manifold of hysteresis-resistant polytetrafluoroethylene that allowed water to flow from a 4-L Nalgene source solution (10 mmol/L KCl degassed distilled water) that was placed one meter above branch height (Markesteijn et al. 2011). Surgical latex tubing of various diameters, parafilm, and hose clamps were used to ensure a secure fit between stems and the plastic manifold tubing. The plastic manifold was attached to a pressurized water tank used to flush stems initially (150 kPa) for 30 minutes to remove emboli from the stems. We found that this initial flush was sufficient to remove latex from the stem of *Clusia flavasepala* so that conductivity could be measured. We had intended to also remove latex from *F. tuerckheimii* using this method but latex in this species continued to flow following the initial flush and therefore a quantification of conductivity in the host tree was not possible. Stems were allowed to equilibrate for 10 minutes before maximum hydraulic conductivity was measured (Markesteijn et al. 2011). To measure conductivity, Eppendorf tubes were filled with cotton and weighed to obtain an initial mass. Cotton-filled tubes were placed on the ends of the exposed xylem of the stems and were weighed every minute until there was no change in mass. The rate at which water was absorbed by the cotton was calculated to determine conductivity.

After determining the maximum conductivity, cavitation was induced by air injection. Overlapping notches, 50 mm apart, were cut into bark to expose xylem. Segments, fitted with rubber stoppers on both ends, were placed in a sealed steel cavitation chamber with an air vent connected to a pressure manifold of US standard tubing (CGA-580, PMS Instrument, Albany, Oregon, USA; Sperry and Saliendra 1994). Air pressure was regulated by a Pressure Chamber Instrument (Model 1505D-EXP, PMS Instrument Company, Albany, Oregon, USA) attached to the pressure manifold and to a N_2 tank (Sperry and Saliendra 1994). The cavitation chambers were initially pressurized to 0.25 MPa for 10 minutes. Stems were allowed to rest for three minutes before conductivity was measured (Sperry and Saliendra 1994, Markesteijn et al. 2011). Following a measurement of conductivity, pressurization of the stems was increased by an additional 0.25 MPa and hydraulic conductivity was measured again. If an increase in pressurization of 0.25 MPa resulted in no change in conductivity, the pressure increment was increased to 0.5 MPa. Greater pressure increments were applied to the stem until a conductivity of zero was measured. Scatterplots were created for water potential as a function of percent loss of hydraulic conductivity (PLC). Vulnerability curves were fit using the following equation:

$$\mathrm{PLC} = 100/\Big(1 + \exp\Big(a(\mathrm{WP} - b)\Big)\Big). \qquad (1)$$

where WP is the xylem pressure, a is the slope of the curve, and b is the xylem pressure at 50% loss of hydraulic conductivity (Pammenter and Vander Willigen 1998, Markesteijn et al. 2011). Eq. 1 did not significantly fit data for *C. capitulata*. The equation $\mathrm{PLC} = a \times \mathrm{WP}^b/(c^b + \mathrm{WP}^b)$, where WP is the xylem pressure and a, b, and c are constants, was used for this species. A minimum of five individuals were measured per species; data were pooled to create an average vulnerability curve for each species (Table 2).

Sap flow

To characterize transpiration, we measured sap flow using the heat ratio method, which allows for the determination of reverse and low flow rates (Burgess et al. 2001). Small external sensors were custom built in the laboratory at Franklin and Marshall College following the design of Clearwater et al. (2009; also see Roddy and Dawson 2012). These sensors had been successfully used on small-stemmed individuals but, to our knowledge, had never been used in canopy communities (Goldsmith et al. 2013, Skelton et al. 2013). Sixteen sensors were installed on the stems of epiphytes and hemiepiphytes in each of the study trees. The following seven species were measured: *Cavendishia capitulata*, *Chlorigyne ensiformis*, *Clusia palmana*, *Neomirandea croatii*, *Oreopanax vestitus*, *Notopleura piticobia*, and *Schefflera rodrigueziana*. These species were chosen because they are common and live in close proximity to one another within a tree crown (~5 m). A maximum of 16 sensors could be connected to a single data logger, which limited the number of species we could instrument with sap flow sensors. Two individuals were measured in each tree and data were collected using a CR-1000 Campbell Scientific data logger attached to a multiplexer (AM16/32B, Campbell Scientific, Logan, Utah, USA).

The sensors were attached to the outside of a small branch and were wrapped extensively with Parafilm to isolate the sensor from direct sunlight and to keep the sensor and stem dry. Every 10 minutes, a 6-second heat pulse was applied to the sensor and then 20 seconds later, the temperature was measured upstream and downstream of the heater for 40 seconds. Heat pulse velocity, V_h (cm/hr), was determined from the following equation:

$$V_h = k/x \ln(\delta T_1/\delta T_2) \times 3600 \quad (2)$$

where x represents the distance between the heater and the thermocouple, δT_1 and δT_2 are the downstream and upstream temperature changes, and k represents the thermal diffusivity constant. A diffusivity constant of 2.83×10^{-3} cm^2/s has been found across a number of species and was used in this study (Clearwater et al. 2009, Goldsmith et al. 2013). Corrections are needed to determine sap flow velocity from heat pulse velocity in small stems since the heat pulse diffuses through non-conductive materials (i.e., bark, phloem, and pith) as well as through xylem (Burgess et al. 2001, Clearwater et al. 2009). Sap flow velocity, V_s, was determined using the following equation:

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

where ρ_b is the stem density, c_w is the specific heat capacity of the wood matrix at 20°C (1200 J·kg^{-1}·°C^{-1}), c_s is the specific heat capacity of water at 20°C (4182 J·kg^{-1}·°C^{-1}), m_c is the water content of the xylem, and ρ_s is the density of water (Burgess et al. 2001). The correction factor was employed because it did not require destructive harvesting of study individuals, which are under continued observation.

Sap flow stations were installed in early July of 2013. A study window was chosen from 7 August to 15 August, as this was a period of drier weather immediately following the rewrapping of all the sensors in all three trees. A sap flow station was also deployed during the misty-windy transition season in 2014, data from 26 December to 27 January of 2014 were also included in this study.

Sap flow data management

Electrical noise and/or mechanical failure resulted in a few erroneous sap flow data points that were orders of magnitude above or below surrounding values. Sap flow data were scanned visually for such anomalous data, which were removed from the data set. The data set was then gap filled by averaging the values on either side of the erroneous value. Erroneous data comprised less than 1% of the data set. Sap flow data were then corrected for smaller errors resulting from variation in sensor construction. Sensor variation resulted in baseline values slightly above or below zero. Zero-flow corrections were performed by taking the average sap flow rate during a nighttime period when vapor pressure deficit (VPD) was low but leaves were dry (i.e., when we would not expect either transpiration or reverse flow) and adjusting the data set for each sensor by adding or subtracting this "true" zero transpiration value to the rest of the data set (Ambrose et al. 2009, 2010, Gotsch et al. 2014*a*).

Volumetric sap flow and error analyses

Following corrections, volumetric sap flow was calculated by multiplying rates of sap velocity by the estimated leaf area supplied to each stem. To estimate leaf area, the number of leaves upstream of the sensor were counted and multiplied by the average leaf area, which was measured on individuals used for destructive measurements. The percentage of hours that sensors underwent reverse flow (i.e., foliar water uptake) and nighttime flow were calculated along with total flow attributed to each of these processes (Table 3).

A number of errors may be introduced as sap flow data are scaled from point velocity measurements to whole-individual volumetric flows (Gotsch et al. 2014*a*). We considered the errors included in data screening, gap filling, zero-flow correction, and scaling up of sap flow using estimates of leaf area. Because so few data points were removed in screening procedures, this source of error is excluded from our analysis. Zero-flow calculations also resulted in very low variation in sap flow rates (<1%) and were excluded from the error analysis. The single largest source of potential error in our study resulted from the scaling up of sap flow based on leaf area estimates. Leaves were counted precisely but these numbers were converted to an area by multiplying by the average leaf area for the species. The error in

TABLE 3. Volumetric water balance parameters for seven common epiphyte and hemiepiphyte species over a 30-day period (26 December–26 January) in the tropical montane cloud forest (TMCF) of Monteverde, Costa Rica.

	Foliar water uptake				Nighttime sap flow			
Species	Time (%)	Transpiration (%)	Volume (L)	σ	Time (%)	Flow (%)	Volume (L)	σ
Cav cap	56.4	96.4	66.5	1.1	29.0	6.9	4.7	0.1
Chl ens	50.6	79.5	2.2	0.2	38.1	15.0	0.4	0.0
Clu pal	42.1	75.8	33.8	1.9	58.6	33.4	14.9	0.8
Neo cro	56.2	80.5	14.8	1.2	30.1	12.8	2.4	0.2
Not pit	39.0	64.2	2.6	0.3	55.8	22.6	0.9	0.1
Ore ves	53.3	59.5	8.6	0.6	31.1	10.0	1.4	0.1
Sch rod	42.2	37.9	30.1	1.0	42.2	17.7	14.1	0.5
Avg	48.5	70.5	22.6	0.9	40.7	16.9	5.5	0.3
SE	2.8	7.1	8.7	0.2	4.6	3.4	2.4	0.1

Notes: The species instrumented with sap flow sensors were *Cavendishia capitulata* (Cav cap), *Chlorigyne ensiformis* (Chl ens), *Clusia palmana* (Clu pal), *Neomirandea croatii* (Neo cro), *Notopleura piticobia* (Not pit), *Oreopanax vestitus* (Ore ves), and *Schefflera rodrigueziana* (Sch rod). Values shown for foliar water uptake are time, the percentage of the total study hours when reverse flow was occurring; transpiration, the percentage of total transpiration that is recovered during the period; volume, the total volume of water that was recovered during the study period; and σ, the error term associated with volume. Values shown for nighttime flow are time, the percentage of the total nighttime study hours when the sensors detected upward movement of sap; flow, the percentage of the total volume of sap moved above the level of the sensor that occurred at night; volume, the total volume of water moved up from the height of the sensor at night; and σ, the error term associated with volume. Across-species averages (Avg) and standard errors (SE) are reported at the bottom of the table.

nighttime sap flow (NF) resulting from scaling point measurements of sap velocity to whole-plant transpiration was therefore calculated using the following equation derived from Stull (1999)

$$\sigma\mathrm{NF} = \mathrm{NF} \times (\sigma\mathrm{LA}/\mathrm{LA}). \quad (4)$$

where LA is the leaf area of each branch. The error in foliar water uptake (σFWU) was similarly calculated

$$\sigma\mathrm{FWU} = \mathrm{FWU} \times (\sigma\mathrm{LA}/\mathrm{LA}). \quad (5)$$

The errors were then converted to a percentage and the volume of the percentage was calculated (Table 3).

Microclimate

A microclimate station was installed in each of the study trees as well as at a meteorological tower located 20 m from one of our study trees. The station on the meteorological tower consisted of a full decagon microclimate monitoring system (Decagon Devices, Pullman, Washington, USA), which included a high-resolution rain gauge, a solar radiation sensor, a Davis cup anemometer, a leaf wetness sensor, and a temperature and relative humidity sensor. Data from these systems were collected via an Em50 data logger (Decagon Devices, Pullman, Washington 99163). Crown microclimate stations had a similar setup but without the rain gauge or solar radiation gauge. Also installed in the study trees were soil moisture smart sensors (S-SMD-M005, Onset Computer Corporation, Bourne, Massachusetts, USA) as well as two air temperature and relative humidity data loggers (HOBO U23 Pro v2 External U23-002, Onset Computer, Bourne, Massachusetts, USA).

Data analysis

For all parametric analyses, data that were not normally distributed were log-transformed to achieve normality. A MANOVA test was performed to determine the effect of species on trait combinations. Following this initial analysis, ANOVAs were performed on each trait. A two-way ANOVA was conducted on the volumetric sap flow data to determine the relative effect of the month of measurement (August vs. January) and species identity on the average daily maximum volumetric sap flow as well as the average daily range of sap flow. Average values for the water potential at which the stem experiences a 50% loss of conductivity, P_{50}, for each species were determined using a non-linear regression analysis. Linear regression analyses were conducted to determine the strength of the relationships between all functional traits, water relations and microscopy measures. On the subset of species instrumented with sap flow gauges, the relationship between foliar water uptake capacity and foliar water uptake in situ as well as the relationships between nighttime flow and hydrenchymal thickness, foliar water uptake capacity and the relative water content at the turgor loss point were analyzed. All analyses were performed using JMP V.10 (SAS Institute, Cary, North Carolina, USA). To determine variation in ecological strategies, we performed a cluster analysis based on functional traits, which created groupings of species. This analysis was performed using PC-ORD, V.6 (Gleneden Beach, Oregon, USA). Significance between groupings was determined using a Multi-Response Permutation Procedure (MRPP) analysis, which was also completed using PC-ORD.

RESULTS

Functional traits

Traits that have been documented to play an important role in plant ecophysiological strategies such as stem density, SLA, leaf toughness, leaf thickness, LDMC, and Huber value all varied greatly across canopy species

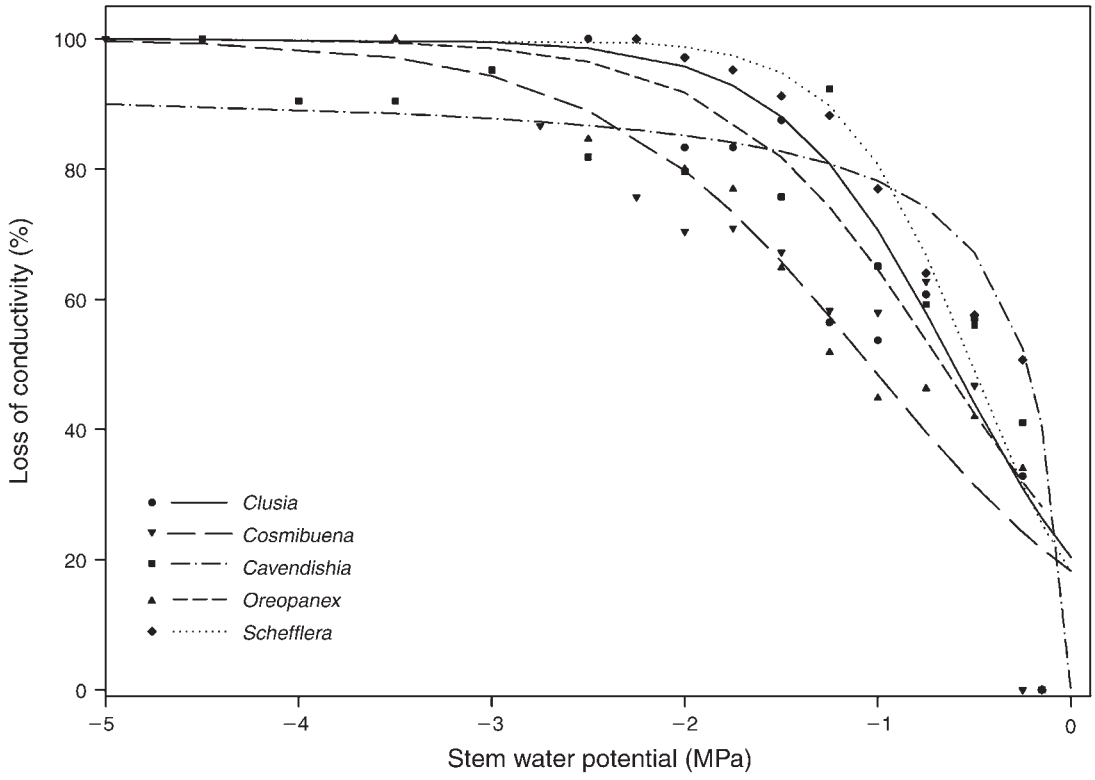

FIG. 2. Loss of hydraulic conductivity as a function of stem water potential. Five individuals were measured per species. At each water potential, identical symbols represent different individuals within a species. The water potential at which 50% of the conductivity is lost (P_{50}) was −0.61 MPa for *Clusia*, −1.00 MPa for *Cosmibuena*, 0.4 MPa for *Cavendishia*, −0.67 MPa for *Oreopanax*, and −0.51 MPa for *Schefflera*.

(Table 2). For example, stem density of woody species ranged from 0.49 g/cm^3 in a hemiepiphyte (*O. vestitus*) to 0.77 g/cm^3 in a shrub epiphyte (*C. melastomoides*). Leaf toughness ranged from 664 g in an herbaceous monocot (*M. monteverdense*) to 2168 g in another herbaceous monocot (*C. ensiformis*). SLA ranged from 209 cm^2/g in a succulent hemiepiphyte (*C. flavasepala*) to 1228 cm^2/g in an herbaceous monocot (*M. monteverdense*, Table 2). Leaf thickness varied from 0.26 mm in *M. monteverdense* to 1.06 mm in *C. palmana* while hydrenchymal thickness varied greatly, even just across hemiepiphytes (0.03 mm in *O. vestitus* to 0.55 mm in *C. palmana*; Table 2). The MANOVA analysis indicated a significant effect of species identity in functional trait variation (Roy's greatest root; approximate $F = 24.2$, df = 10, 45; $P < 0.0001$). In post-hoc ANOVAs, there were significant species effects ($P < 0.0001$) for all traits with the exception of foliar water uptake capacity.

We also found significant variation in water relations traits. ψ_{TLP} values ranged from −0.85 MPa in *C. flavasepala* to −1.85 MPa in *C. capitulata*, and ε values ranged from 9.6 in *C. palmana* to 22.5 in *C. ensiformis* (Table 2). We also found that all species had the capacity for foliar water uptake. The improvement in water status caused by an hour of foliar submersion following desiccation ranged from 0.15 to 0.36 MPa (Table 2). On a subset of woody-stemmed species, we also conducted vulnerability curves. The P_{50} values for these five species ranged from −0.4 MPa in *C. capitulata* to −1.0 MPa in *C. flavasepala* (Fig. 2).

Linear regression analyses indicated significant negative relationships between foliar water uptake capacity and ψ_{TLP} ($r^2 = 0.45$; Fig. 3a), leaf toughness ($r^2 = 0.47$; Fig. 3b) and osmotic potential at full saturation ($r^2 = 0.45$; Fig. 3c), These analyses also indicated significant relationships between hydrenchymal thickness and foliar water uptake capacity ($r^2 = 0.43$; Fig. 3d), ψ_{TLP} ($r^2 = 0.47$; Fig. 3e), leaf toughness ($r^2 = 0.88$; Fig. 3f) and cuticle thickness ($r^2 = 0.6$; $P = 0.03$; relationship not shown in Fig. 3). Foliar water uptake capacity decreased with an increase in hydrenchymal thickness while ψ_{TLP} and leaf toughness increased. All significant correlations are reported in Table 4.

Relationships between the functional traits and sap flow were examined on the seven species instrumented with sap flow gauges. Linear regression analyses indicated that foliar water uptake in situ (total volume) was positively correlated with foliar water uptake capacity ($r^2 = 0.4$; Fig. 4a) while nighttime flow (percentage of total volume at night) was positively correlated with the relative water content at the turgor loss point ($r^2 = 0.52$; Fig. 4b) and hydrenchymal thickness ($r^2 = 0.88$; Fig. 4c) and negatively

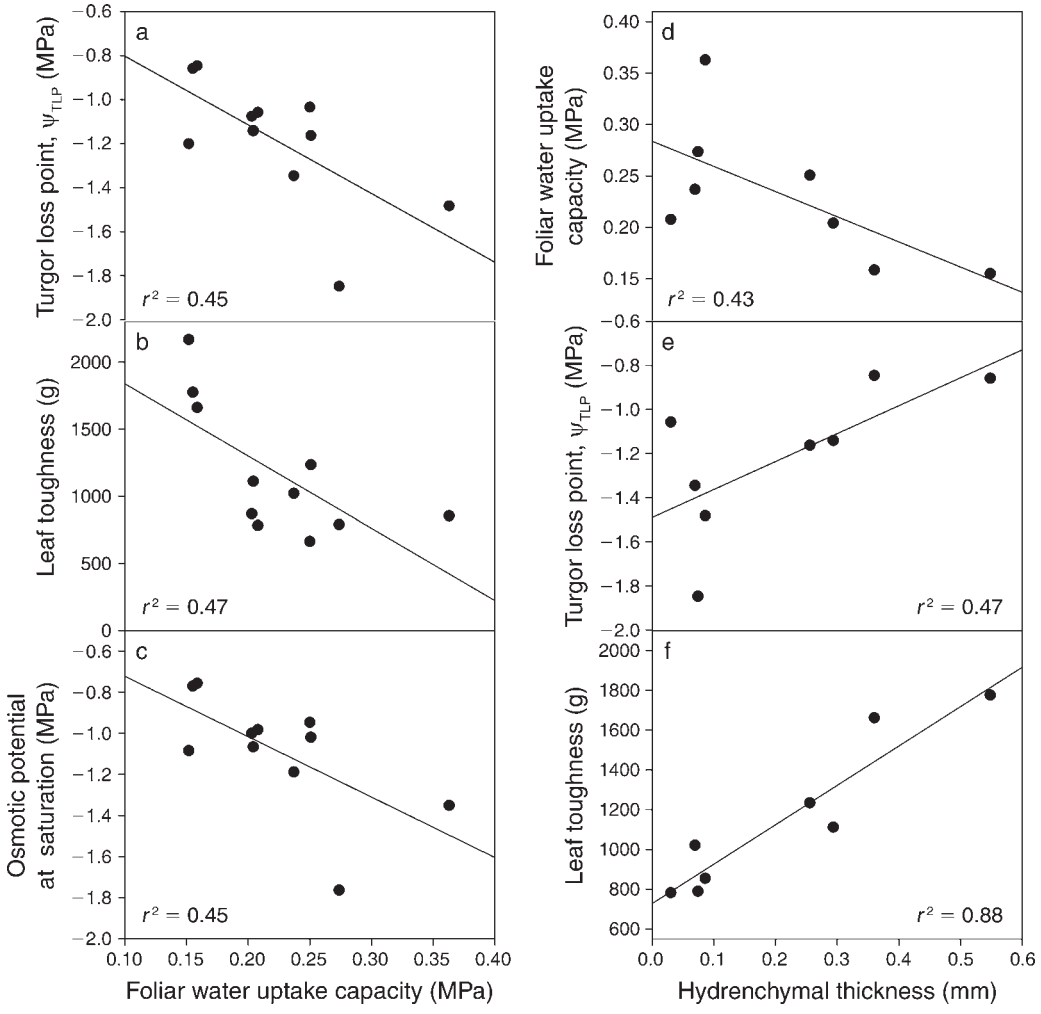

FIG. 3. (a–c) Turgor loss point, leaf toughness, and the osmotic potential at saturation as a function of the foliar water uptake capacity for 11 canopy species (epiphytes and hemiepiphytes) in the tropical montane cloud forest (TMCF) of Monteverde, Costa Rica. (d–f) Foliar water uptake capacity, turgor loss point, and leaf toughness as a function of the hydrenchymal thickness (mm) for the species identified in panels (a–c); see Table 1 for species descriptions. All relationships were significant at $P < 0.05$.

correlated with foliar water uptake capacity ($r^2 = 0.37$; Fig. 4d). All regressions presented were significant at $P < 0.05$ with the exception of the relationship between nighttime flow and foliar water uptake capacity ($P = 0.1$). There were fewer data points in Fig. 4c because not all of the species instrumented with sap flow gauges had a hydrenchymal layer. Variation in cell structure for representative species can be seen in Fig. 5.

One of the reasons for the quantification of ecological and water relations traits in this study was to determine whether variation in traits led to distinct ecophysiological groups based on life forms within the canopy community. A cluster analysis dendrogram produced species groupings based on trait data but in subsequent MRPP analyses, no combination of groups resulted in statistical significance between groups (Fig. 6). These results indicate that there was significant variation within than rather than between groups.

Water balance

We successfully obtained data from a relatively dry nine day period in the wet season in August, as well as a 34-day period in the misty-windy transition season in January. We found clear diurnal patterns of sap flow data in the absence of precipitation (Figs. 7 and 8). In both seasons, the greatest volumetric flow occurred in *S. rodrigueziana*, a hemiepiphyte (Figs. 7–9). *C. capitulata*, a shrub epiphyte, and *O vestitus*, a hemiepiphyte had intermediate rates of sap flow while smaller epiphytes (e.g., *N. piticobia*, *C. ensiformis* and *N. croatii*) transpired much less (Figs. 7–9). *C. palmana*, a hemiepiphyte, experienced more erratic flow rates, throughout the study (Figs. 7 and 8). A two-way ANOVA revealed significant effects of species ($F = 33.9$, df = 6, $P < 0.001$), and the interaction between the season and species ($F = 34.7$, df = 6, $P < 0.001$) on the average daily maximum sap flow. The main effect of season was not

significant in this analysis. In general, sap flow was greater in the misty-windy season but this pattern varied across species (Fig. 9a). In the two-way ANOVA, which included data on the average daily range in volumetric sap flow, the main effects of season and species were significant ($F = 27.3$, df = 1, $P < 0.001$ and $F = 96.7$, df = 6, $P < 0.001$, respectively) as well as the interaction between season and species ($F = 122.2$, df = 6, $P < 0.001$). The average daily range in sap flow was greater for all species in the misty-windy season when conditions were more variable (Fig. 9b).

The degree to which plants absorbed foliar water (indicated by sap flow reversals; FWU) varied among species. Species underwent FWU between 39% and 56% of the time (Table 3). These reversals led to an average FWU percentage (i.e., the percentage of total positive flow that was recovered via FWU) of 70.5%. *C. capitulata* recovered the greatest percentage of transpired water (96.4%), while *S. rodrigueziana* recovered the least amount (37.8%; Table 3). These sap flow reversals led to an average of 22.65 L reabsorbed during the month-long period in the misty-windy season (Table 3). *C. ensiformis* reabsorbed the least amount of water (2.2 L) due to its overall low rates of transpiration, while *C. capitulata* absorbed the greatest amount of water via foliar uptake (66.5 L; Table 3).

TABLE 4. Significant pairwise correlations of functional traits, water relations, and microscopy measures for 11 common epiphyte and hemiepiphyte species.

Correlated variable 1	Correlated variable 2	r^2	P
C_{FT}	Pi_o	0.37	0.046
C_{FT}	RWC_{TLP}	−0.37	0.047
C_{FT}	ε	−0.50	0.015
C_{TLP}	LDMC	0.37	0.045
Cuticle	Mesophyll	0.48	0.018
Cuticle	Thick	0.62	0.004
FWUC	Tough	−0.47	0.020
Mesophyll	Thick	0.47	0.019
Pi_o	FWUC	−0.40	0.035
Pi_o	Huber	−0.60	0.005
SLA	Tough	−0.38	0.042
WS thick	Cuticle	0.58	0.029
WS thick	Mesophyll	0.51	0.044
WS thick	Thick	0.94	<0.0001
WS thick	Tough	0.88	0.001
ψ_{TLP}	FWUC	−0.43	0.028
ψ_{TLP}	Huber	−0.56	0.008
ψ_{TLP}	Pi_o	0.99	<0.0001

Note: See Table 2 for definitions of variables.

In addition to examining dry season patterns of FWU, we also examined the prevalence of nighttime flow (NF) during the study period. In general, we found that NF was less important to overall water balance than FWU and that variation across species was great.

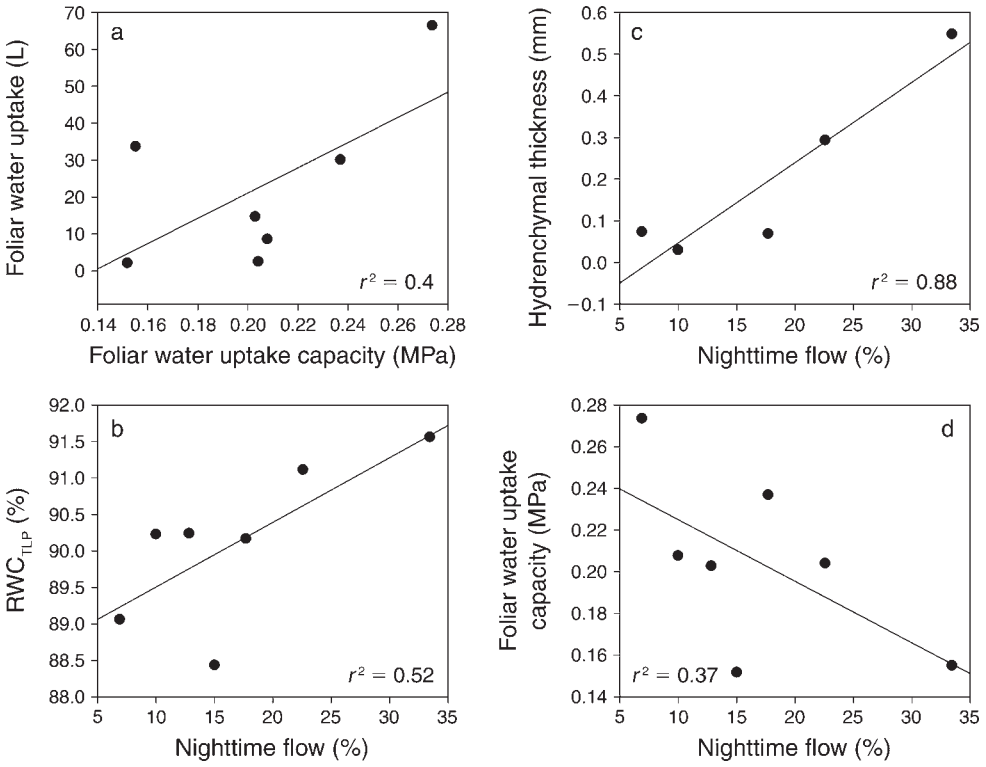

FIG. 4. (a) The relationship between foliar water uptake capacity and in situ foliar water uptake (amount recovered via foliar absorption) for seven species that were instrumented with external sap flow gauges. (b–d) The relationships between relative water content at the turgor loss point (RWC_{TLP}), hydrenchymal thickness, foliar water uptake capacity, and the nighttime sap flow (percentage of total volume transpired during the study period). All relationships were significant at $P < 0.05$, with the exception of panel (d) ($P = 0.1$). Species instrumented with sap flow gauges are listed in Table 3 and species information can be found in Table 1.

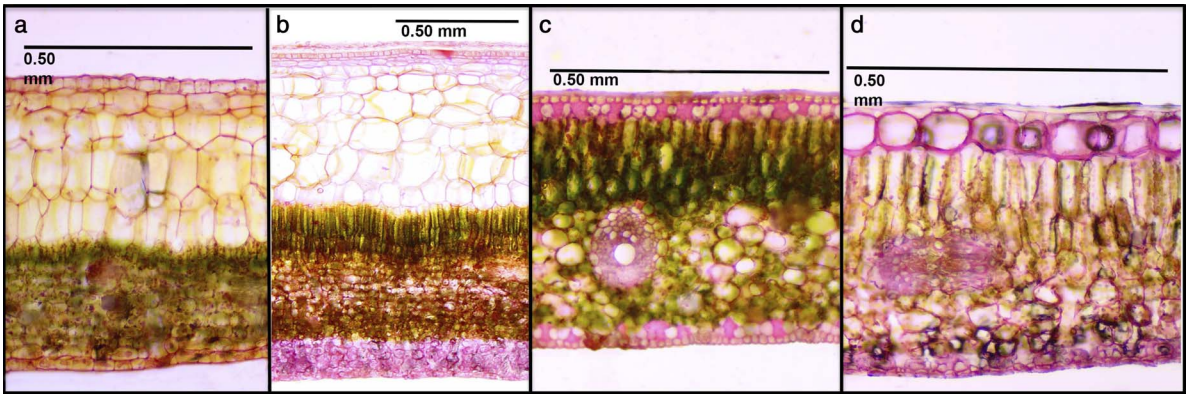

FIG. 5. Variation in leaf anatomy in common epiphytes of the TMCF. All upper portions of the four panels correspond to the adaxial side of the leaves. (a) A semi-succulent, *Notopleura piticobia*, contains a thick hydrenchymal (i.e., water storage) layer on the adaxial side of the leaf. (b) A hemiepiphyte, *Clusia palmana*, contains a clear hydrenchymal layer on the adaxial side of the leaf and a reduced layer on the abaxial side of the leaf as well. (c) *Chlorigyne ensiformis*, a herbaceous monocot, does not exhibit a hydrenchymal layer. (d) *Cavendishia capitulata*, is a shrub epiphyte that does not appear to be succulent and yet contains a thin layer of hydrenchymal cells.

The study species on average underwent NF for 40.7% of the nighttime hours (Table 3). *C. palmana* experienced the greatest NF (33.4% of total L transpired), while *C. capitulata* had the least amount of NF (6.8% of total L transpired; Table 3). Given the relationships presented in Figs. 3 and 4, NF is most likely due to refilling of hydrenchymal layers at night rather than nighttime transpiration.

DISCUSSION

The goals of this research were to enhance our understanding of the ecophysiological strategies of drought tolerance or avoidance in a TMCF epiphytic plant community and quantify the importance of fog and mist in their water balance. Here we present the first data set of functional trait relationships and water balance metrics of common vascular epiphytes in the TMCF of Monteverde, Costa Rica. We have found that plants in this community exhibit a continuum of strategies. At one extreme, plants allocate to traits that confer relative drought resistance and rely heavily on foliar water uptake to offset transpiration losses. At the other extreme, plants specialize in water storage and drought avoidance at the expense of foliar water uptake.

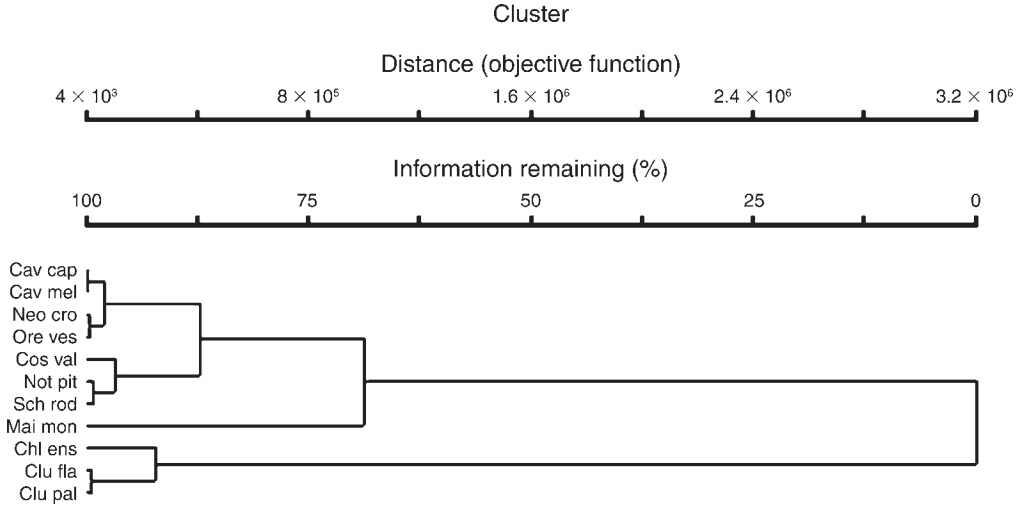

FIG. 6. Cluster analysis for 11 common canopy species based on the following functional traits: wood density, leaf toughness, specific leaf area, leaf thickness, leaf dry matter content, Huber value, foliar water uptake capacity, turgor loss point, bulk elastic modulus, and the relative water content at the turgor loss point. The "Information remaining (%)" is the amount of variation in the distances that is accounted for at a given step in the clustering process. The "Distance (objective function)" is computed with Ward's method using the Euclidian distance. An MRPP analysis in PC-ORD indicated that the groups depicted in the cluster analysis are not significantly different from one another due to substantial trait variation within groups. Species abbreviations are the first three letters of the species name followed by the first three letters of the genus name (see Table 1).

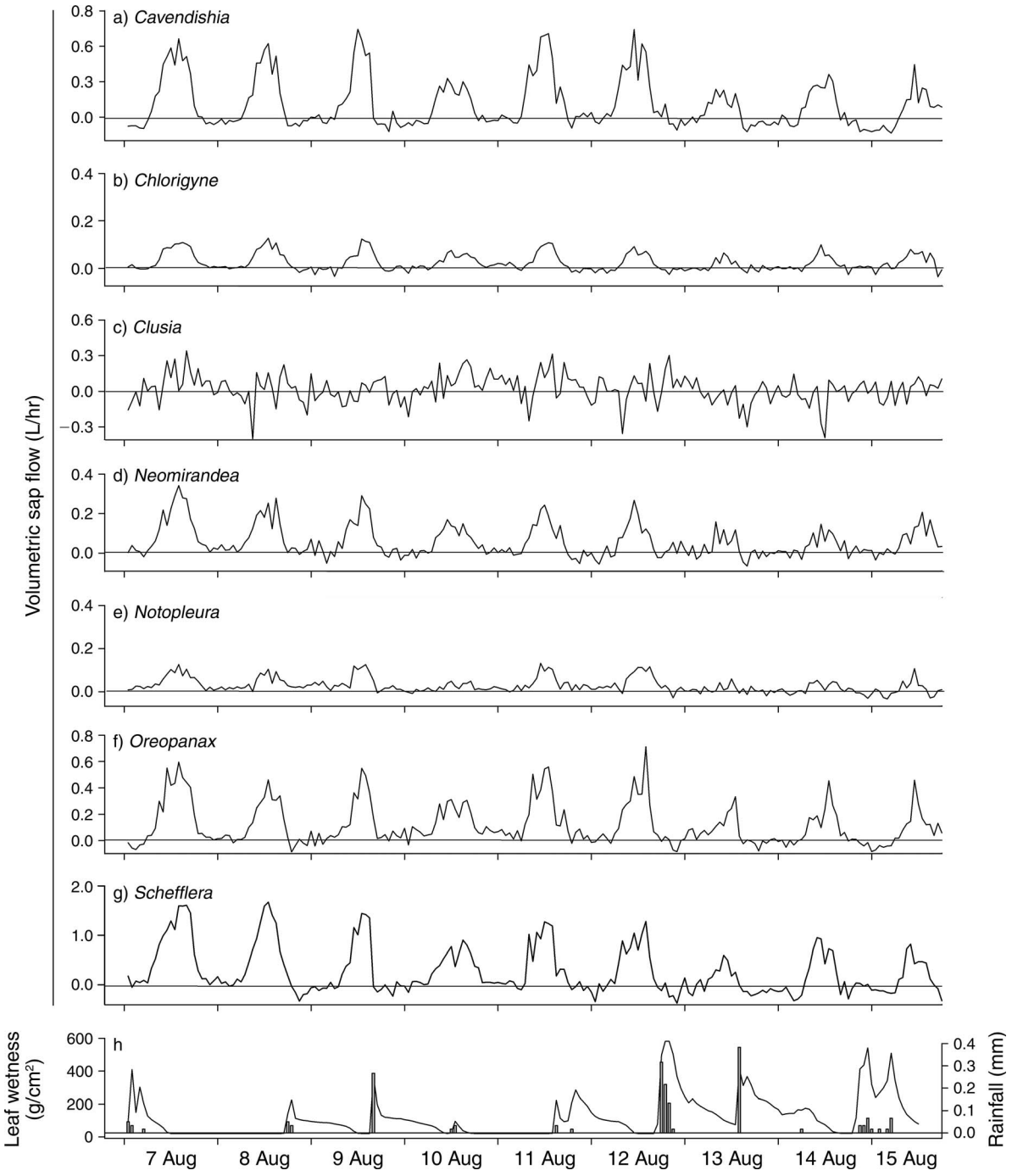

FIG. 7. Volumetric sap flow for seven common canopy species in the TMCF of Monteverde, Costa Rica over a nine-day period (7–15 August 2013) in the wet season when there was relatively little rainfall. (a) *Cavendishia capitulata* is a woody epiphyte, (b) *Chlorigyne ensiformis* is an herbaceous monocot, (c) *Clusia flavasepala* is a hemiepiphyte, (d) *Neomirandea croatii* is a woody epiphyte, (e) *Notopleura piticobia* is a woody epiphyte, (f) *Oreopanax vestitus* is a hemiepiphyte, and (g) *Schefflera rodrigueziana* is a hemiepiphyte. The bottom panel (h) shows rainfall (bars) and leaf wetness (solid line). Each panel of sap flow data is an average of four to six individuals per species.

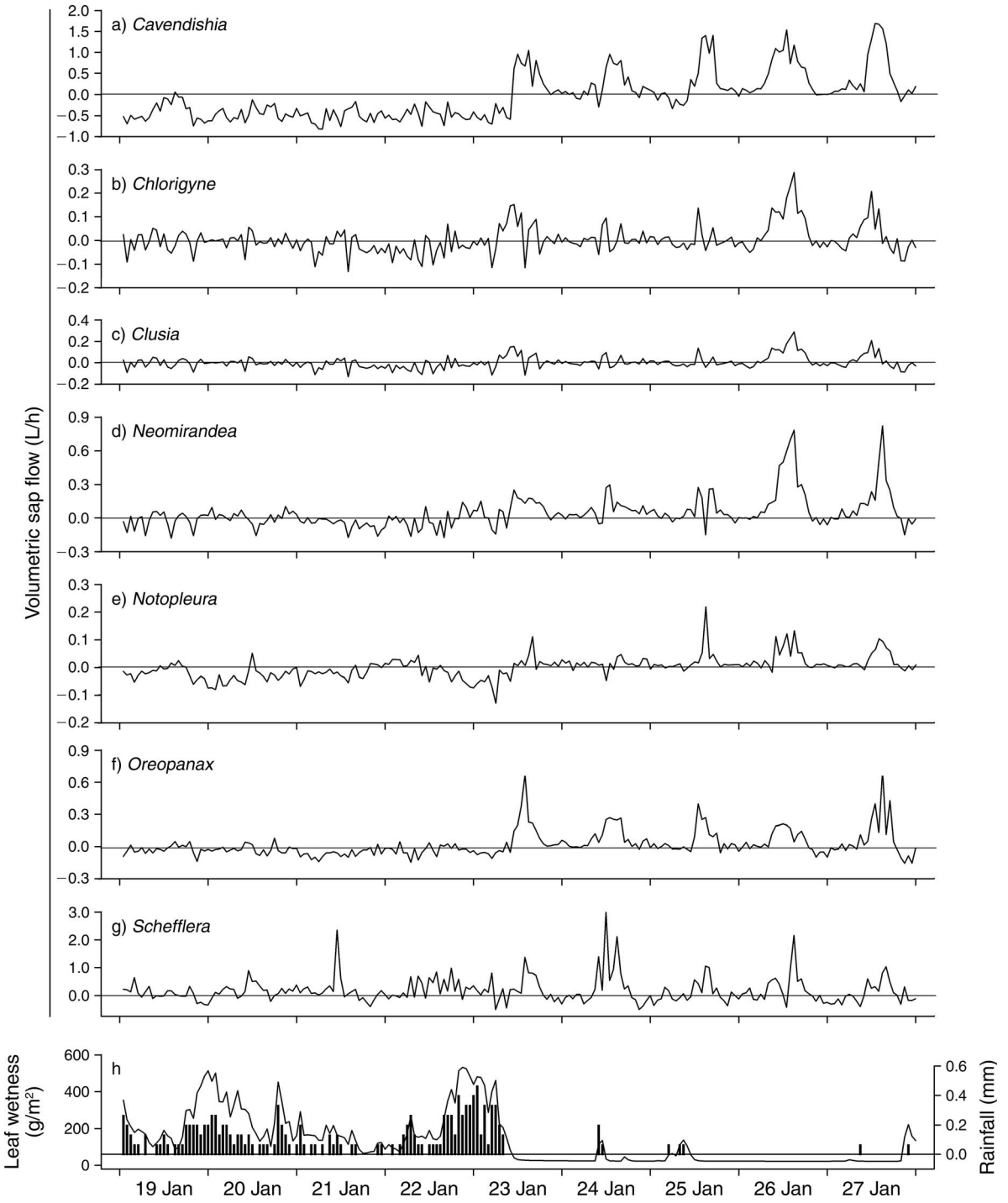

FIG. 8. Volumetric sap flow for seven common canopy species in the TMCF of Monteverde, Costa Rica over a nine-day period (19–27 January 2013) in the dry season. (a) *Cavendishia capitulata* is a woody epiphyte, (b) *Chlorigyne ensiformis* is an herbaceous monocot, (c) *Clusia flavasepala* is a hemiepiphyte, (d) *Neomirandea croatii* is a woody epiphyte, (e) *Notopleura piticobia* is a woody epiphyte, (f) *Oreopanax vestitus* is a hemiepiphyte, and (g) *Schefflera rodrigueziana* is a hemiepiphyte. The bottom panel (h) shows rainfall (bars) and leaf wetness (solid line). Each panel of sap flow data is an average of two individuals per species.

Our findings indicate that these species tolerate the water limitations that plants commonly experience in their environment in a variety of ways and that drought tolerance cannot be accessed solely based on traits commonly quantified in terrestrial habitats.

Functional trait variation

We found a great deal of variation in most functional traits in this study, indicating that the ways in which traits can combine are not only multifaceted but also increase the range of possible functional strategies that can coexist in this treetop community. Said another way, it seems clear from the data collected that plants in this TMCF community may achieve drought tolerance or avoidance in a wide variety of ways and use different combinations of traits. For example, SLA, a commonly measured trait that relates to photosynthetic capacity and leaf longevity, varied threefold across the 12 species measured (Table 2). Leaf toughness, which relates to structural defense allocation, varied 2.5-fold, though values were generally high ($\geq$600 g). Leaf thickness, which in this system is likely most related to succulence, varied fourfold (Table 2).

While trait variation is generally substantial across species, much of this variation appears to lie along an axis relating to drought resistance and avoidance. Our data indicate that there is a trade-off between foliar water uptake capacity and succulence. Succulent plants often have a distinct hydrenchymal layer that can act as a supply of water to photosynthetically active cells (Ogburn and Edwards 2010). Species with a thicker hydrenchymal layer in this study also tended to have tougher (Fig. 3f) and thicker leaves, and they also had a higher turgor loss point (Fig. 3e) and a thicker cuticle. These species may avoid reaching the turgor loss point by maintaining high structural allocation and water storage. The limitation of this strategy is that foliar water uptake capacity is limited (Fig. 3d). Species with higher foliar water uptake capacity tended to have limited water storage capacity (i.e., thinner and less tough leaves) but they likely resist moderate drought by having lower ψ_{TLP} and osmotic potential at full turgor. In addition, these species have a greater ability to offset water loss by absorbing water directly through their leaves (Fig. 3a–c). It is important to recognize that our measures of leaf drought resistance (i.e., ψ_{TLP}) were on bulk leaf samples. Averaging of hydrenchymal and mesophyll cell properties may overestimate the drought sensitivity of photosynthetically active cells due to the high level of sensitivity of hydrenchymal tissue. Further studies should extend such trait analyses to different cell types within the leaf to confirm if such trait relationships between water relations traits and functional traits persist.

The examination of relationships between volumetric sap flow and functional traits also indicates a trade-off in ecological strategies in this community. As expected, foliar water uptake in situ correlated with foliar water uptake capacity (Fig. 4a). Furthermore, there is a negative relationship between nighttime flow and foliar water uptake capacity (Fig. 4d), as well as positive relationships between nighttime flow and the relative water content at the turgor loss point (Fig. 4b) and hydrenchymal thickness (Fig. 4c). The greatest nighttime flow was measured in species that had the greatest capacity for drought avoidance via leaf water storage. While in many ecosystems, nighttime sap flow is an indication of nighttime transpiration (Dawson et al. 2007, Gotsch et al. 2014*a*, *b*), in the TMCF canopy, nighttime flow is more likely a signal of refilling of succulent leaves; however, stomatal conductance measurements at night would be needed to confirm the degree to which this signal is indeed refilling.

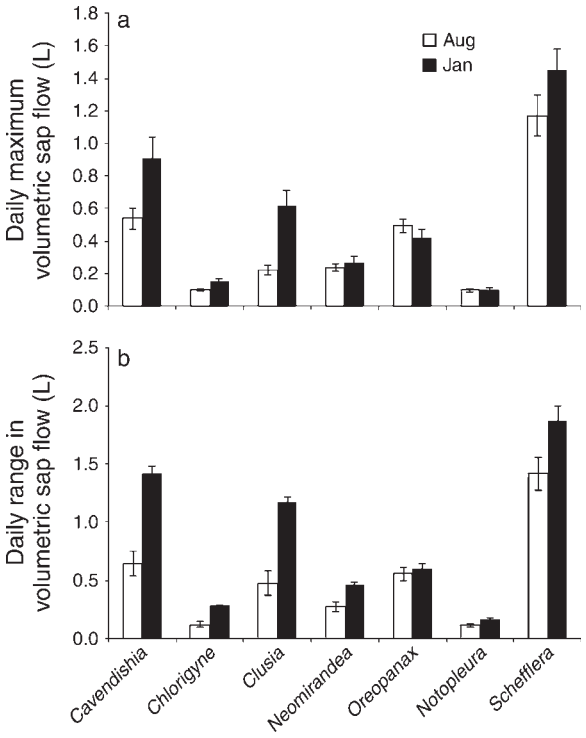

FIG. 9. (a) Maximum volumetric flow (mean and SE) and (b) daily range (mean and SE) in volumetric sap flow for the seven species in the wet (August; nine-day observation period) and dry (January; 30-day observation period) seasons in the TMCF.

Evaluation of drought resistance

In studies conducted across a wide range of species and ecosystems, there is growing evidence that the ψ_{TLP}, or water potential at the turgor loss point, may be a good indicator of drought resistance (Bartlett et al. 2012). In habitats that experience greater water limitation such as semi-deserts or dry temperate forests, the average ψ_{TLP} is approximately three times higher than that of crops or species in a tropical rainforest (Bartlett et al. 2012). Epiphytes and hemiepiphytes, despite living in relatively wet tropical forests, are disassociated from

the ground during all or part of their life cycle and therefore are more water limited than their terrestrial counterparts. Given the water limitation in this community, we expected these plants to have generally low ψ_{TLP} values and we expected the true epiphytes to have a lower ψ_{TLP} than hemiepiphytes. In contrast to these expectations, the average ψ_{TLP} was −1.1 MPa across species. This value is in line with the average ψ_{TLP} for tropical wet forest terrestrial species (Bartlett et al. 2012) and does not indicate that this community is more drought resistant than species that have access to soil resources. While the two *Clusia* species had higher ψ_{TLP} values than true epiphytes (−0.85 and −0.86), the other hemiepiphytes we studied had ψ_{TLP} values more similar to the ψ_{TLP} of true epiphytes (Table 2).

Another indicator of drought resistance is the degree of resistance to the loss of stem conductivity as water potential declines. Stems that maintain high flow rates despite increasing tension in the xylem are considered drought resistant since this ability will facilitate continued conductivity despite soil water limitation. Although a somewhat arbitrary value, the water potential at which the stem experiences a 50% loss of conductivity, or P_{50}, has been used to compare plants across a wide range of ecosystems to indicate drought resistance (Sperry et al. 1994, Sobrado 1997, Pockman and Sperry 2000, Maherali et al. 2004, Bhaskar et al. 2007). Like ψ_{TLP}, P_{50} values tend to correlate with water availability (Maherali et al. 2004). While there is generally considerable variation in P_{50} within ecosystems, average P_{50} values range from approximately −1.0 MPa in tropical rain forests to −5.0 MPa in mediterranean ecosystems (Maherali et al. 2004). In this study, P_{50} values were higher than expected and ranged from −0.4 MPa in *C. capitulata* to −1.0 MPa in *C. flavasepala* (Fig. 2). Despite seasonal water limitation, these species are not able to maintain conductivity if high tensions exist in the xylem. Since woody stem segments are needed to generate vulnerability curves, these measurements were limited to five species that exhibit large shrub-like or treelet growth forms. Hemiepiphytes spend part of their lifecycle as true epiphytes but for many species, large individuals eventually develop connections with the ground. Given the size of these individuals, it is possible they had a direct connection to ground water supplies, which would reduce the need for a low P_{50}.

Despite ψ_{TLP} and P_{50} values that suggest that epiphytes and hemiepiphytes may not be adapted to withstand drought, it is more likely that these measures do not adequately characterize strategies to survive drought in canopy communities. One additional way that plants can buffer the effects of seasonal water loss is by having high capacitance (i.e., water storage capacity) in leaves, stems, and underground organs (Chaves et al. 2002, Ogburn and Edwards 2010). A trade-off between capacitance and stem P_{50} has been recognized whereby xylem elements that have a greater degree of capacitance are more vulnerable to cavitation (Meinzer et al. 2009). High capacitance in leaves, or succulence, is a common growth strategy in dry areas and is also common in *Clusia* sp. and *Notopleura* sp. that have low SLA and high leaf thickness (Table 2). While most of the species in this study did not have conspicuously succulent leaves, leaf cross sections revealed that a number of species have leaves with a distinct hydrenchymal layer (Fig. 5). Even in species that do not contain a distinct water storage layer, often times there are cells that appear to be specialized for water storage interspersed with photosynthetically active cells (Fig. 5; S. G. Gotsch, *personal observation*). These observations indicate that capacitance is likely high in this community.

Even though the turgor loss point is high in these plants, high capacitance may provide an important buffer to keep the water potential within an appropriate range to maintain function. In fact, a high water storage capacity was observed directly in the process of carrying out pressure–volume curves. In the experience of the authors, pressure–volume curves on terrestrial species in the TMCF can be completed generally within 24 hours. In this study, many of the species required facilitated bench drying (using fans and light boxes) for up to four days in order to lose enough mass to complete the analyses. We suggest that, despite having a high ψ_{TLP} and P_{50}, many of the species in this study have other leaf-level adaptations that maintain leaf water potentials above the ψ_{TLP}. In addition to high leaf capacitance, some of the species in this study appeared to have additional adaptations to avoid drought. For example, *Cavendishia* species exhibit tuber-like growth forms that appear well-suited for storage. *C. ensiformous* excretes mucilage from cut stems which may be an additional source of stored water (Robichaux and Morse 1990). Large statured hemiepiphytes such as *Oreopanax* sp. and *Schefflera* sp. may not require adaptations that confer high capacitance if they have access to ground water (see Field and Dawson 1998).

Sap flow and water balance in the canopy

All species instrumented with sap flow gauges exhibited diurnal and seasonal variation in sap flow and responded quickly to changes in microclimate (Figs. 7–9). Sap flow trials were conducted during one period without rain in the wet season, which followed three months of almost daily rainfall (S. G. Gotsch, *unpublished data*). During this dry and sunny period, epiphytes exhibited diurnal courses of sap flow (Fig. 7). While rates were lower during wet periods in January, daily maximal rates were generally higher during this period and the ranges of sap flow were greater due to greater fluctuations in microclimate (Figs. 8 and 9). These data indicate that, despite water storage in canopy soils and plants, water limitation likely occurs soon after precipitation ceases and canopy plants limit water loss by closing stomata.

We also found that all species in this study have the capacity to absorb water via the leaf surface (i.e., foliar

water uptake capacity; Table 2). The degree of improvement in water potential was related to ψ_{TLP}, the osmotic potential at saturation and leaf toughness (Fig. 3a–c). These improvements in water status are much lower than the average improvement of 0.8 MPa, which has been recently observed in terrestrial species in the TMCF of Monteverde (Goldsmith et al. 2013). This disparity is likely due to the impact that thick epiphyte leaves have on the capacity for absorption.

Despite lower levels of foliar water uptake capacity when compared with terrestrial TMCF plants, in situ measurements of whole-plant transpiration indicate that foliar water uptake occurs frequently and is an important component of both the ecophysiology of the plants that compose this community as well as the water balance. To our knowledge, this is the first data set to describe patterns of whole plant water use in vascular epiphytes. During the month-long study period in the misty-windy transition season, foliar water uptake occurred on average, 48.5% of the hours and resulted in the reabsorption of 70.5% of the water transpired during this period. *C. capitulata*, in an extreme case, absorbed 96.4% of the total water transpired. This species is an epiphytic shrub with a high degree of branching. Each branch tip contains dozens of small leaves. Such architecture may be specialized for cloud water interception. On the low end of the spectrum, foliar water uptake led to the recovery of 37.8% of transpired water in the hemiepiphyte, *S. rodrigueziana*. These values are much higher than recently published rates of foliar water uptake in terrestrial species in the TMCF (Goldsmith et al. 2013, Gotsch et al. 2014*a*), and indicate that the presence of cloud water and conditions that maintain leaf wetness are of great importance for water balance in the canopy community. We suspect that these values were high due to the presence of mist and fog during the study period.

Another potentially important component of water balance in plant communities is nighttime transpiration (Dawson et al. 2007). Although initially assumed to be non-existent, this process, which occurs under generally moist conditions when evaporative demand, or VPD, is high, has subsequently been found across a wide range of ecosystems (Feild and Holbrook 2000, Bucci et al. 2004, Dawson et al. 2007, Goldstein et al. 2008, Novick et al. 2009, Goldsmith et al. 2013, Gotsch et al. 2014*a*). In the TMCF, which experiences generally moist conditions, VPD can vary greatly, even within a single day, leading to high evaporative demand and water loss (Holwerda et al. 2010, Muñoz-Villers et al. 2012, Gotsch et al. 2014*a*). In a recent study in the TMCF of Veracruz, Mexico, total nighttime water loss comprised on average, 17% of the total branch-level water loss in a dominant canopy tree (Gotsch et al. 2014*a*). Monteverde is a wetter TMCF than Veracruz due to a greater incidence of cloud immersion and higher annual precipitation (Nadkarni 1985, 1994, Holwerda et al. 2010, Muñoz-Villers et al. 2012). In this study we also found a signal for nighttime sap flow, but given the trait relationships discussed above, it is more likely that this signal is due to refilling of succulent leaves rather than transpiration from the leaf surfaces.

Conclusions

We present some of the first data on whole-plant water balance and functional trait allocation in the TMCF canopy community. We have found that plants in this community exhibit a range of functional trait combinations including highly conservative growth forms (i.e., succulent, well-defended leaves) that live in close proximity to species that exhibit trait combinations more indicative of high growth rates and photosynthetic capacity. We have also found that quantifying drought resistance in this community is not as straightforward as in many terrestrial plants given the variation in potential adaptations to withstand water shortage and the high degree of capacitance of these plants. This complexity is largely due to an additional axis of trait variation in the leaf economics spectrum (Reich et al. 1999, Wright et al. 2004) in canopy plants relating to the foliar water uptake capacity (and relative drought resistance) vs. leaf succulence (drought avoidance). Plant functional traits in species across ecosystems have been found to co-vary in ways that relate to allocation to defense and photosynthetic ability. In the TMCF canopy, plant allocation is likely primarily driven by water storage and foliar water uptake capacity rather than traits such as specific leaf area or leaf dry matter content, which relate to growth rate and tissue longevity. The ψ_{TLP} and P_{50} values in this community were high, but rather than an indication of vulnerability to drought stress, these traits may indicate a strategy of drought avoidance by storing water rather than withstanding low water potentials. Lastly, we found that foliar water uptake is an important component of water balance in this community. These results indicate that conditions leading to leaf wetness (i.e., heavy or long periods of fog and light rain) are critical factors in the water balance and canopy water storage of this community. Projected changes in climate, such as increases in cloud base heights or periods without rain, will likely have substantial impacts on epiphyte and hemiepiphyte water relations and water balance. These impacts may influence larger processes including ecosystem water cycling.

Future directions

This work provides an important beginning in our understanding of the ecological strategies and water balance patterns of epiphytes and hemiepiphytes in the TMCF, but much remains to be investigated. The number of species included in this study was limited due to the difficulty accessing and conducting experiments in the canopy. We suggest an expansion of this data set to include a greater proportion of the community and to include canopy communities in drier microclimates. In addition, future research should include annual or

seasonal variation in leaf water potentials experienced by these plants. By quantifying the monthly or seasonal minimum in leaf water potential of these species, we can determine the operating safety margins of plants along a spectrum of drought resistance and drought avoidance. We also suggest that future research include manipulative experiments. By directly controlling the water supply, we can determine the effectiveness of different adaptations to withstand water stress (i.e., tubers, stem mucilage, leaf water storage, low ψ_{TLP}.). Such experiments can also elucidate trade-offs in the allocation to traits that aid in the maintenance of low water potential (i.e., traits that lead to low ψ_{TLP} and P_{50}) vs. high water storage.

The canopy community has been described as having an important role in nutrient cycling and water cycling of the TMCF; understanding how these physiological processes scale up to affect whole-forest processes, especially water cycling and balance is still an unanswered question and warrants greater attention given the importance of the TMCF in biodiversity and regional hydrology.

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