

## RESEARCH ARTICLE

Functional Ecology



# Vascular epiphytes show low physiological resistance and high recovery capacity to episodic, short-term drought in Monteverde, Costa Rica

Cameron B. Williams<sup>1</sup> | Jessica G. Murray<sup>2</sup> | Andrew Glunk<sup>1</sup> | Todd E. Dawson<sup>3</sup> |  
Nalini M. Nadkarni<sup>4</sup> | Sybil G. Gotsch<sup>1</sup>

<sup>1</sup>Department of Biology, Franklin and Marshall College, Lancaster, PA, USA

<sup>2</sup>Department of Biology and the Ecology Center, Utah State University, Logan, UT, USA

<sup>3</sup>Department of Integrative Biology, University of California, Berkeley, CA, USA

<sup>4</sup>School of Biological Sciences, University of Utah, Salt Lake City, UT, USA

**Correspondence**

Cameron B. Williams  
Email: cameron.williams@fandm.edu

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**Abstract**

1. Tropical montane cloud forests support abundant epiphytic vascular plant communities that serve important ecosystem functions, but their reliance on atmospheric inputs of water may make them susceptible to the drying effects of rising cloud bases and more frequent droughts.
2. We conducted a common garden experiment to explore the combined effects of decreasing cloud influence—lower humidity, warmer temperature, brighter light—and meteorological drought (i.e. absence of rain) on the physiology and morphology of vascular epiphytes native to primary forests of Monteverde, Costa Rica. The epiphytes, which exhibited C<sub>3</sub> photosynthesis, were sourced from a lower montane cloud forest (CF) or a rainforest (RF) below the current cloud base and transplanted into nearby shadehouses (CF or RF shadehouse respectively). Vapour pressure deficit (VPD) and light availability, measured as photosynthetically active radiation, were 2.5 and 3.1 times higher in the RF than the CF shadehouse. Half of the plants were subjected to a severe 4-week drought followed by a recovery period, and the other half were watered controls.
3. Plants subjected to low VPD/light conditions of the CF shadehouse were physiologically and morphologically resistant to the drought treatment. However, compared to control plants, both sources of plants subjected to high VPD/light conditions of the RF shadehouse experienced declines in maximum net photosynthesis ( $A_{max}$ ), stomatal conductance ( $g_s$ ) and the proportion of healthy leaves (those not exhibiting chlorosis, desiccation or necrosis). At peak drought, leaves from the RF were 19% thinner than controls. Within 7–14 days after rewatering,  $A_{max}$ ,  $g_s$  and leaf health recovered to nearly the levels of controls. Growth rate, mortality and phenology were unaffected by the treatments.
4. The divergent responses to drought in the CF versus RF shadehouses, combined with the recovery in the RF shadehouse, indicate that these epiphytes possess adaptive properties that confer low resistance, but high recovery capacity, to episodes of short-term drought over a range of cloud influence. In addition, the reduction in  $A_{max}$  suggests stomatal regulation that favours water conservation over

carbon acquisition, a strategy that may inform epiphyte responses to rising clouds and increasing drought frequency expected in the long term.

#### KEYWORDS

climate change, community composition, drought resilience, epiphyte physiology, shadehouse experiment, stomatal regulation, tropical cloud forest epiphytes

## 1 | INTRODUCTION

One of the most conspicuous features of tropical montane cloud forests (TMCFs) is their rich and abundant epiphyte communities (Brujinzeel, Scatena, & Hamilton, 2011; Foster, 2001; Gentry & Dodson, 1987; Zotz, 2016). Individual trees support up to 190 species (Catchpole & Kirkpatrick, 2011), and stands accumulate up to 44 t/ha of epiphytic material (Gotsch, Nadkarni, & Amici, 2016). Epiphytes may contribute 50% of the within-crown leaf area of tropical forests (Hofstede, Wolf, & Benzing, 1993). They are capable of storing thousands of litres of water per hectare (Hölscher, Köhler, van Dijk, & Brujinzeel, 2004; Köhler, Tobón, Frumau, & Brujinzeel, 2007; Richardson, Richardson, Scatena, & McDowell, 2000), which helps to control surface water run-off, flooding and erosion (Gotsch et al., 2016; Still, Foster, & Schneider, 1999; Veneklaas & Van Ek, 1990). This storage capacity, along with the increased boundary layer epiphytes provide, also moderate the temperature and relative humidity of tree crowns (Freiberg, 2001; Stanton et al., 2014; Stuntz, Simon, & Zotz, 2002).

Because epiphytes occupy a niche dissociated from groundwater, they must routinely cope with meteorological drought that may rapidly lead to hydrological drought as their canopy soils desiccate. Poikilohydry enables lichens and bryophytes to tolerate extreme desiccation without physiological damage, but this strategy in vascular plants is not well-understood (Zotz, 2016). Vascular epiphytes resist desiccation via specialized traits such as succulent leaves, tuber-like storage structures and Crassulacean acid metabolism (CAM) photosynthesis (Benzing, 1998; Gotsch et al., 2015; Luteyn, 2002). Despite these putative adaptations to routine drought, the segregation of epiphyte communities is strongly correlated with variation in temperature, humidity and rainfall (Amici, Nadkarni, Williams, & Gotsch, 2020; Cardelús, Colwell, & Watkins Jr., 2006; Ding et al., 2016). Vapour pressure deficit (VPD)—a function of temperature and relative humidity that is a measure of atmospheric demand for water—has a stronger effect on transpiration than temperature, is an important driver of evapotranspiration in tropical climates and is a good predictor of local epiphyte abundance (Eamus, Boulain, Cleverly, & Breshears, 2013; Gotsch, Davidson, Murray, Duarte, & Draguljić, 2017; Massmann, Gentine, & Lin, 2019). This sensitivity to atmospheric conditions may explain the high variability of epiphytes across microclimatic gradients, although segregation of species among habitats can also occur indirectly via biotic interactions (e.g. Fine, Mesones, & Coley, 2004).

Many have noted that sensitivity to atmospheric conditions would make epiphytes likely to suffer climate change effects (Benzing, 1998; Gradstein, 2008; Lugo & Scatena, 1992). Extreme

events such as El Niño-influenced droughts are predicted to increase in frequency and severity in the tropics (IPCC, 2014). In recent decades, warmer air and sea surface temperatures have caused a rise in the elevation of orographic cloud formation over TMCFs, leading to a decline in the frequency of horizontal precipitation (e.g. fog, mist), a larger number of rainless days and an increase in VPD (Karmalkar, Bradley, & Diaz, 2008; Lawton, Nair, Pielke, & Welch, 2001; Pounds et al., 2006; Pounds, Fogden, & Campbell, 1999; Still et al., 1999; Ray, Nair, Lawton, Welch, & Pielke Sr, 2006). The compounding effects of these changes in atmospheric conditions will likely affect TMCF epiphytes via higher desiccation rates during the dry seasons. Rising cloud bases will also intensify the solar radiation received by TMCFs, which may further exacerbate desiccation due to higher temperatures and light-induced stomatal opening that increases leaf conductance (Bittencourt, Barros, Eller, Müller, & Oliveira, 2019; Brujinzeel et al., 2011; Roelfsema & Hedrich, 2005).

The potential effects of climate change on epiphytes are rarely addressed experimentally even though their small stature and minimal substrate connection facilitate transplantation. Transplantation is a powerful approach to understand epiphyte responses to climate change. Such experiments have documented reductions in stomatal conductance, sap flow, leaf thickness, leaf production, growth rates and recruitment, as well as increases in leaf mortality and die-back (Darby, Draguljić, Glunk, & Gotsch, 2016; Jácome, Gradstein, & Kessler, 2011; Nadkarni & Solano, 2002; Rapp & Silman, 2014; Song, Liu, & Nadkarni, 2012). Changes in individual growth and survival are particularly relevant to population growth rates (Buckley et al., 2010) and may therefore indicate potential shifts in community composition.

These experiments have improved our understanding of epiphyte responses to warming and drought, but questions remain. Deviations in the timing of leaf shedding and flushing confer drought resistance in some tropical trees (Borchert, 1994; Harrison, 2001), and changes in herbivory and reproduction can influence population growth (Maron & Crone, 2006), yet these phenological variables remain unexplored in vascular epiphytes. In addition, the ability for epiphytes to physiologically resist and recover from drought is poorly understood. For example, after an El Niño-influenced drought through which all study plants survived, cloud forest (CF) epiphytes recovered sap flow rates more slowly than epiphytes at lower elevations, hinting at a vulnerability to rising clouds but suggesting some drought resilience because a recovery was underway and the mortality threshold was not reached (Gotsch, Dawson, & Draguljić, 2018). Survival through and recovery from severe drought may

hinge upon stomatal regulation that maintains high water potential to prevent cavitation from disrupting the hydraulic pathway (Tyree & Sperry, 1989). The trade-off between hydraulic failure caused by cavitation versus carbon deficit caused by long-term stomatal closure can inform potential modes of drought-induced mortality (McDowell et al., 2008), about which little is known in epiphytes. For example, in TMCF epiphytes, cavitation occurs at relatively high water potentials and sap flow nearly ceases during drought (Gotsch et al., 2015, 2018), suggesting that tight stomatal control may be critical to resist hydraulic failure. Whether this behaviour translates into reduced carbon fixation remains unknown.

The sensitive responses of epiphytes to warmer and drier conditions suggest that those occupying TMCFs would be more susceptible to the drying effects of rising cloud bases and longer rainless periods projected by climate change, compared to epiphytes from below the cloud base (Benzing, 1998). Using epiphytes sourced from a CF and a nearby rainforest (RF) below the cloud base, we conducted a common garden experiment to address two questions. (a) How do CF epiphytes respond to decreasing cloud influence—lower humidity, warmer temperature, brighter light—and meteorological drought, compared to epiphytes from below the cloud base? (b) Do epiphytes from these two habitats recover differently after drought? We formulate our hypotheses as components of a resilience framework; that is, the relative stability of ecological communities in response to disturbance can be partitioned into ‘resistance’ defined as the change during disturbance and ‘recovery’ defined as the capacity to return to the original state after the disturbance (Hodgson, McDonald, & Hosken, 2015; Ingrisch & Bahn, 2018). We hypothesized that, compared to CF epiphytes, those from below the cloud base would be physiologically and morphologically more resistant to changes during the drought and exhibit a stronger capacity to recover after drought.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and epiphytes

We collected epiphytes in Costa Rica from a lower montane CF in the Monteverde Cloud Forest Reserve (N10°18′19″, W84°47′39″, 1,550 m) and a lower montane RF in the Curi-Cancha Reserve located slightly below the cloud base (N10°18′23″, W84°48′16″, 1,480 m). These sites fit the descriptions of CF and RF outlined by Bruijnzeel et al. (2011). Weathered volcanic geology at both sites supported canopy heights reaching 25–35 m, steep topography and Andisol (Udands) soils overlain with histosols, the latter frequently developing on canopy branches (Clark, Lawton, & Butler, 2000). Mean annual temperature, relative humidity, VPD and total rainfall in the CF were 17.0°C, 98.2%, 0.038 kPa and 3,148 mm respectively; conditions in the RF were warmer and drier at 17.9°C, 94.0%, 0.131 kPa and 2,993 mm respectively (temperature, relative humidity and VPD collected every 15 min; rainfall collected daily; January 2015 through December 2017; S.G. Gotsch, J.A. Pounds, and Monteverde Institute, unpubl. data). Mean daytime solar irradiance

and wind speed measured in the canopy at the RF site were 63 W/m<sup>2</sup> and 0.6 m/s, while at a site (N10°19′18″, W84°46′2″, 1,552 m) close to our CF site the means were 18 W/m<sup>2</sup> and 1.1 m/s (data collected every 15 min; August 2017 through July 2018; S.G. Gotsch, unpubl. data). Horizontal precipitation can augment CF precipitation by as much as 20% in Monteverde, and the region experiences a dry season historically characterized by roughly 100 mm of rain falling February through April (Clark et al., 2000). We selected these sites because they exhibited clear differences in microclimate and community composition (Amici et al., 2020; Gotsch et al., 2017) and fall along an elevation gradient where cloud base heights are rising (Pounds et al., 1999, 2006; Ray, Nair, Lawton, Welch, & Pielke, 2006).

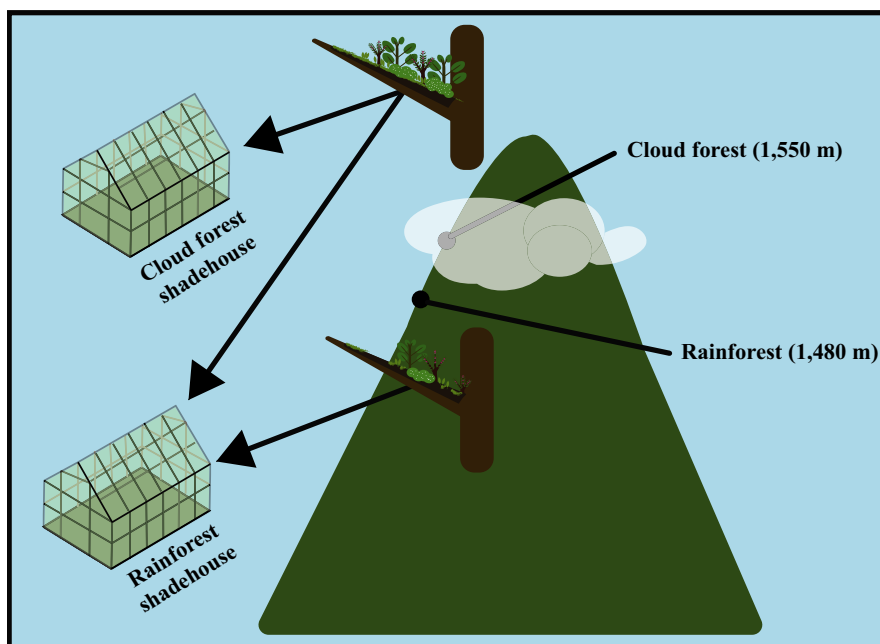
We selected epiphyte species based on qualitative assessments of commonness and abundance in Monteverde to represent the epiphyte community at each site. The crowns of dominant canopy trees were accessed using arborist techniques (Jepson, 2000). Soil mats containing target species were peeled from the tree bark, lowered to the ground and then transferred into two experimental shadehouses (‘CF shadehouse’ or ‘RF shadehouse’), each located within 200 m of the respective collection site. Previous studies indicate that careful transplantation of canopy soil mats does not adversely affect vascular epiphytes (Darby et al., 2016; Nadkarni & Solano, 2002). Our experiment featured 12 families, 16 species and 463 individuals representing herbs, single-stemmed woody plants and shrubs that ranged in mean size from a 16-cm-tall fern (*Elaphoglossum lingua* [C. Presl] Brack.) to a 71-cm-tall shrub (*Macleania insignis* M. Martens & Galeotti; Table 1; Table S1). Carbon isotope ratios available for 13 of the species ranged from –33.9‰ to –27.1‰ (T. Dawson, unpubl. data), were consistent with C<sub>3</sub> photosynthesis and excluded C<sub>3</sub>-CAM intermediates (Cornwell et al., 2018; Winter, Holtum, & Smith, 2015).

### 2.2 | Experimental design

Shadehouses were outfitted with clear plastic roofs to exclude precipitation, and with 70% shade cloth to simulate canopy light environments. The choice of shade cloth was informed by comparing in-canopy photosynthetically active radiation (PAR) at the CF and RF sites to PAR inside each shadehouse, measured with the photodiode on an AP4 Porometer (Delta-T Devices). Shadehouse benches were surfaced with wood planks to mimic canopy substrates. To minimize disturbance, epiphyte mats were kept intact rather than dissected into individual epiphytes, the consequence of which was an unbalanced design wherein sample size and species representation varied among factor levels (Table S1). Epiphyte mats from the CF were distributed evenly between the two shadehouses to enable monitoring of drought responses under two different treatment conditions; the CF shadehouse had lower VPD and lower light conditions similar to the CF, whereas the RF shadehouse had higher VPD and higher light conditions similar to those expected with continued climate change. All RF-sourced epiphytes were placed in the RF shadehouse alongside the CF-sourced epiphytes to compare responses in a common

| Taxon   | Family           | Growth form           | Habitat |    |
|---|------------------|-----------------------|---------|----|
| <i>Cavendishia capitulata</i><br>Donn. Sm.                        | Ericaceae        | Woody, multi-stemmed  | CF      |    |
| <i>Clusia</i> spp. L.   | Clusiaceae       | Woody, single-stemmed | CF      | RF |
| <i>Cybianthus costaricanus</i> Hemsl.                             | Primulaceae      | Woody, multi-stemmed  | CF      | RF |
| <i>Disterigma humboldtii</i><br>(Klotzsch) Nied.                  | Ericaceae        | Woody, multi-stemmed  | CF      | RF |
| <i>Elaphoglossum lingua</i><br>(C. Presl) Brack.                  | Elaphoglossaceae | Herbaceous            | CF      |    |
| <i>Elleanthus glaucophyllus</i> Schltr.                           | Orchidaceae      | Herbaceous            | CF      |    |
| <i>Macleania insignis</i><br>M. Martens & Galeotti                | Ericaceae        | Woody, multi-stemmed  |         | RF |
| <i>Neomirandea croatii</i><br>R.M. King & H. Rob.                 | Asteraceae       | Woody, single-stemmed | CF      |    |
| <i>Notopleura pithecobia</i><br>(Standl.) C.M. Taylor             | Rubiaceae        | Woody, single-stemmed | CF      | RF |
| <i>Oreopanax anomalus</i><br>M.J. Cannon & Cannon                 | Araliaceae       | Woody, single-stemmed |         | RF |
| <i>Peperomia</i> sp. Ruiz & Pav.                                  | Piperaceae       | Herbaceous            | CF      |    |
| <i>Pleurothallis dolichopus</i> Schltr.                           | Orchidaceae      | Herbaceous            |         | RF |
| <i>Schefflera rodriguesiana</i> Frodin<br>ex M.J. Cannon & Cannon | Araliaceae       | Woody, single-stemmed | CF      |    |
| <i>Sobralia carazoi</i> C.H. Lank. &<br>Ames                      | Orchidaceae      | Herbaceous            | CF      | RF |
| <i>Sphaeradenia praetermissa</i><br>R. Erikss.                    | Cyclanthaceae    | Herbaceous            | CF      |    |
| <i>Stenospermation sessile</i> Engl.                              | Araceae          | Herbaceous            | CF      | RF |

**TABLE 1** Epiphyte taxa, growth forms and habitats for a common garden experiment in Monteverde, Costa Rica. Habitats include lower montane cloud forest (CF) and rainforest (RF)



**FIGURE 1** Experimental design for an investigation of vascular epiphyte responses to drought and decreasing cloud influence in Monteverde, Costa Rica. Plants sourced from a cloud forest were distributed evenly into shadehouses representing a cloud forest or rainforest below the cloud base, whereas plants from the rainforest were transplanted into only the rainforest shadehouse. The combination of habitat from which the epiphytes were sourced and the shadehouse into which they were transplanted represents a three-level factor in a common garden experiment. For each level, half of the plants were subjected to a 4-week drought treatment while the other half were watered controls [Correction added on 23 July 2020, after first online publication: acronym 'RF' ('rainforest') has been removed.]

garden. We did not transplant epiphytes from the RF uphill into the CF shadehouse because climate models forecast declining cloud influence in Monteverde; this fractional factorial design prevented the full separation of drought versus cloud effects. The combination of

habitat (CF vs. RF) from which the epiphytes were sourced and the VPD/light conditions (low vs. high) of the CF or RF shadehouse into which they were transplanted represents a three-level factor ('forest-VPD/light') in a common garden experiment (Figure 1).

To ensure revival from potential transplant stress, epiphytes were watered two times daily for 6 weeks before the experiment began, at which point we established baseline values for physiological and morphological variables. The plants were then subjected to a 4-week treatment period from 7 April to 7 May when they were either thoroughly watered two times daily (control) or received no water (drought). This 4-week duration is a realistic expectation for severe meteorological drought, such as the 2016 El Niño-influenced drought that coincided with this study and precipitated just 7 and 13 mm of rain over the RF and CF sites in March (Monteverde Institute and J.A. Pounds, unpubl. data). Finally, all plants received water for a 2-week recovery period. Weekly measurements tracked individual epiphyte responses to the treatment and recovery periods. Radiation-shielded temperature and relative humidity in each shadehouse were recorded every 15 min by HOBO Pro v2 dataloggers (Onset Computer Corporation, Bourne, MA). Soil moisture was not measured. The transition from treatment to recovery periods coincided with the beginning of the wet season.

### 2.3 | Physiological variables

Maximum net photosynthesis ( $A_{\max}$ ) was measured using the LI-6400XT Portable Photosynthesis System (LI-COR). We used light-response curves to determine optimal PAR levels for measuring  $A_{\max}$ . On each of three individuals per species per site, net photosynthesis was measured at each of 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  increments, descending from 1,600 to 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The PAR level at which net photosynthesis was highest, which varied from 600 to 1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  depending on species and site, was selected for measuring  $A_{\max}$ . Chamber conditions were regulated at 400  $\mu\text{mol/s}$  flow rate, 400  $\mu\text{mol/mol CO}_2$ , 20°C and 53%–67% relative humidity. Leaf stomatal conductance to water vapour ( $g_s$ ) and associated PAR were measured using the AP4 Porometer. We measured  $A_{\max}$  between 8 a.m. and 4 p.m. and  $g_s$  between 10 a.m. and 2 p.m. under mostly sunny conditions. The daily sequence of all physiological measurements was randomized to minimize the effect of time of day.

### 2.4 | Morphological variables

We measured plant length to the nearest 5 mm (stem base to shoot apical meristem), except for rhizomatous herbs and taxa with very short above-soil stems (*E. lingua*, *Pleurothallis dolichopus* Schltr., *Sphaeradenia praetermissa* R. Erikss.) for which the longest leaf was measured. Plant length was used to calculate growth rate ( $G$ ; mm/day) as a daily change from the previous measurement:

$$G = (L_n - L_{n-1}) / (D_n - D_{n-1}), \quad (1)$$

Here,  $L_n$  and  $D_n$  denote plant length and Julian Day at measurement period  $n$ , and  $L_{n-1}$  and  $D_{n-1}$  represent length and Julian Day of the

previous measurement (Chiariello, Mooney, & Williams, 2000). On four leaves per plant we measured blade thickness to 0.01-mm precision and 0.025-mm accuracy using a thickness gauge (model 547-500S; Mitutoyo USA). We counted the total number of leaves on herbs and single-stemmed woody plants. For shrubs, we counted a subset of leaves on a marked branch. Leaves exhibiting chlorosis, desiccation or necrosis were counted separately so that the proportion of healthy leaves could be quantified. We removed the expected large variation in leaf health among species by calculating the change in the proportion of healthy leaves since baseline ( $\Delta H$ ) using,

$$\Delta H = H_n - H_0, \quad (2)$$

where  $H_n$  is the proportion of healthy leaves at measurement period  $n$ , and  $H_0$  is the proportion at baseline. We also noted plant mortality if all above-soil parts were dry and non-green.

Phenology was monitored by estimating the proportions of leaves that were newly shedding, flushing or exhibiting the signs of herbivory since the previous measurement, and the proportions of leaf axils or shoot tips that were flowering or fruiting, using percentage bins (0 = 0%, 1 = 1%–25%, 2 = 26%–50%, 3 = 51%–75%, 4 = 76%–100%) that were later converted to midpoint percentages. Identifying the transition from flower to fruit was difficult, so we summed flowering and fruiting into one variable characterizing reproductive output. We quantified the reproductive output of *E. lingua* via the proportion of fertile fronds. Similar to the calculation of  $\Delta H$ , we expressed each phenological variable as a change from baseline (Equation 2).

### 2.5 | Statistical analyses

The response variables  $A_{\max}$ ,  $g_s$  and leaf thickness were transformed to achieve normality and homogeneity of variances before conducting parametric tests (Table 2). We used three-way repeated measures analysis of variance (ANOVA) to test for differences in  $A_{\max}$ ,  $g_s$ ,  $G$ ,  $\Delta H$ , leaf thickness, shedding, flushing, herbivory and reproductive output among the three levels of forest-VPD/light and two water regimes for the entire experiment. Using individual epiphytes as subjects, we analysed forest-VPD/light, water regime and their interaction as between-subjects factors, while measurement period, forest-VPD/light, water regime and their interactions were analysed as within-subjects factors. Most of the covariance matrices failed to meet the assumption of compound symmetry as evaluated by Mauchly's test of sphericity, so we report Huynh-Feldt corrected significance levels for within-subjects effects (Potvin, Lechowicz, & Tardif, 1990). When differences were significant, we used one-way ANOVA to further test the effects of forest-VPD/light and water regime on epiphyte responses at each measurement period, and to compare among measurement periods for taxa with sufficient sample sizes. Mortality counts were compared among the forest-VPD/light and water treatments using Pearson's chi-squared test. Analyses were performed in SPSS v26 (IBM Corporation) using a

**TABLE 2** Summary of three-way repeated measures ANOVA *p*-values and effect sizes {eta squared} for treatment effects on physiology (maximum photosynthesis [ $A_{\max}$ ] and stomatal conductance [ $g_s$ ]) and morphology during an experimental drought imposed on vascular epiphytes from Monteverde, Costa Rica. 'Forest-VPD/light' refers to the source of epiphytes by habitat (cloud forest vs. rainforest below the cloud base) and the VPD/light conditions (low vs. high) of the shadehouse into which the epiphytes were transplanted [Correction added on 23 July 2020, after first online publication: acronym 'RF' ('rainforest') has been removed.]

| Source of variation                   | Response variables (transformation) |                                    |                                |   |                                |
|---------------------------------------|-------------------------------------|------------------------------------|--------------------------------|---|--------------------------------|
|                                       | $A_{\max}$<br>( $A_{\max}^{1/2}$ )  | $g_s$<br>( $\log_{10} [g_s + 1]$ ) | Growth rate<br>(untransformed) | Leaf thickness<br>(thickness <sup>1/3</sup> ) | Leaf health<br>(untransformed) |
| Within-subject                        |                                     |                                    |                                |   |                                |
| Period                                | <0.0001 {0.24}                      | <0.0001 {0.33}                     | <0.0001 {0.04}                 | <0.0001 {0.09}                                | <0.0001 {0.16}                 |
| Period × forest-VPD/<br>light         | <0.0001 {0.16}                      | <0.0001 {0.07}                     | 0.1566 {0.01}                  | <0.0001 {0.06}                                | <0.0001 {0.04}                 |
| Period × water                        | <0.0001 {0.16}                      | <0.0001 {0.21}                     | 0.2855 {0.00}                  | <0.0001 {0.01}                                | <0.0001 {0.08}                 |
| Period × forest-VPD/<br>light × water | <0.0001 {0.12}                      | <0.0001 {0.06}                     | 0.8799 {0.00}                  | <0.0001 {0.02}                                | <0.0001 {0.03}                 |
| Between-subject                       |                                     |                                    |                                |   |                                |
| Forest-VPD/light                      | 0.1509 {0.02}                       | <0.0001 {0.27}                     | 0.0715 {0.01}                  | <0.0001 {0.02}                                | <0.0001 {0.06}                 |
| Water                                 | <0.0001 {0.25}                      | <0.0001 {0.34}                     | 0.0572 {0.01}                  | 0.3688 {0.00}                                 | <0.0001 {0.04}                 |
| Forest-VPD/light ×<br>water           | <0.0001 {0.20}                      | <0.0001 {0.09}                     | 0.3903 {0.00}                  | 0.1905 {0.00}                                 | <0.0001 {0.05}                 |
| Source of variation                   | Response variables (transformation) |                                    |                                |   |                                |
|                                       | Leaf shedding<br>(untransformed)    | Leaf flushing<br>(untransformed)   | Herbivory<br>(untransformed)   | Reproduction<br>(untransformed)               |                                |
| Within-subject                        |                                     |                                    |                                |   |                                |
| Period                                | <0.0001 {0.13}                      | <0.0001 {0.05}                     | <0.0001 {0.42}                 | 0.0079 {0.01}                                 |                                |
| Period × forest-VPD/<br>light         | 0.0041 {0.01}                       | 0.0395 {0.01}                      | <0.0001 {0.02}                 | 0.3367 {0.01}                                 |                                |
| Period × water                        | 0.0155 {0.01}                       | 0.0025 {0.01}                      | 0.0007 {0.01}                  | 0.3961 {0.00}                                 |                                |
| Period × forest-VPD/<br>light × water | 0.1012 {0.0}                        | 0.5673 {0.00}                      | 0.2154 {0.00}                  | 0.6672 {0.00}                                 |                                |
| Between-subject                       |                                     |                                    |                                |   |                                |
| Forest-VPD/light                      | 0.9195 {0.00}                       | 0.3308 {0.01}                      | 0.0789 {0.01}                  | 0.5152 {0.00}                                 |                                |
| Water                                 | 0.2782 {0.00}                       | 0.1434 {0.00}                      | 0.5573 {0.00}                  | 0.3296 {0.00}                                 |                                |
| Forest-VPD/light ×<br>water           | 0.5062 {0.00}                       | 0.6103 {0.00}                      | 0.2248 {0.01}                  | 0.3384 {0.00}                                 |                                |

Boldface values are statistically significant.

significance cut-off of  $\alpha = 0.05$ . Untransformed means are presented for all response variables to ease interpretation.

test,  $p < 0.0001$ ) and within the range of in-canopy PAR previously reported from a different cloud forest (León-Vargas, Engwald, & Proctor, 2006).

### 3 | RESULTS

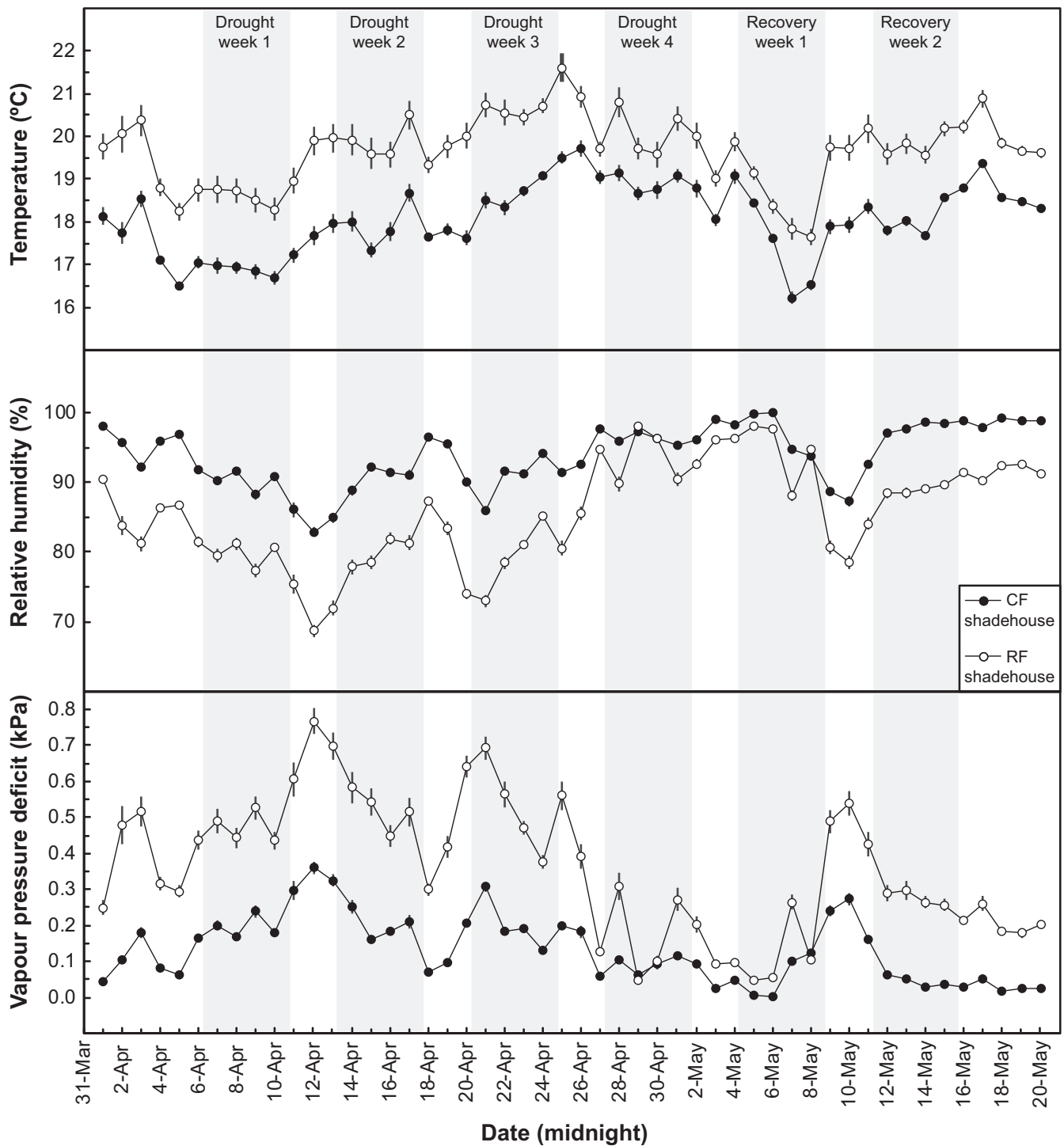
#### 3.1 | Microclimate

The CF shadehouse maintained lower temperature and higher humidity (means: 18.1°C, 91.4% RH, 0.186 kPa VPD) than the RF shadehouse (means: 19.9°C, 81.7% RH, 0.461 kPa VPD; Figure 2). The difference between daily averages inside the shadehouses was more pronounced than at the field sites, which were generally cooler and more humid (Figure S1). PAR was significantly lower in the CF than in the RF shadehouse (means: 53 and 162  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; one-tailed *t*

#### 3.2 | Physiological responses to drought

In the low VPD/light conditions of the CF shadehouse, all plants maintained relatively stable and significantly higher  $A_{\max}$  throughout the study (mean 5.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; Table 2; Figure 3), compared to drought-treated plants in the high VPD/light conditions of the RF shadehouse where  $A_{\max}$  fell to  $<1 \mu\text{mol m}^{-2} \text{s}^{-1}$  during peak drought (Table S2). All plants returned to nearly baseline levels by recovery week 2 (Figure 3) when drought versus control plants exhibited no difference in  $A_{\max}$  (Table S2). Our dataset for  $g_s$  exhibited overall

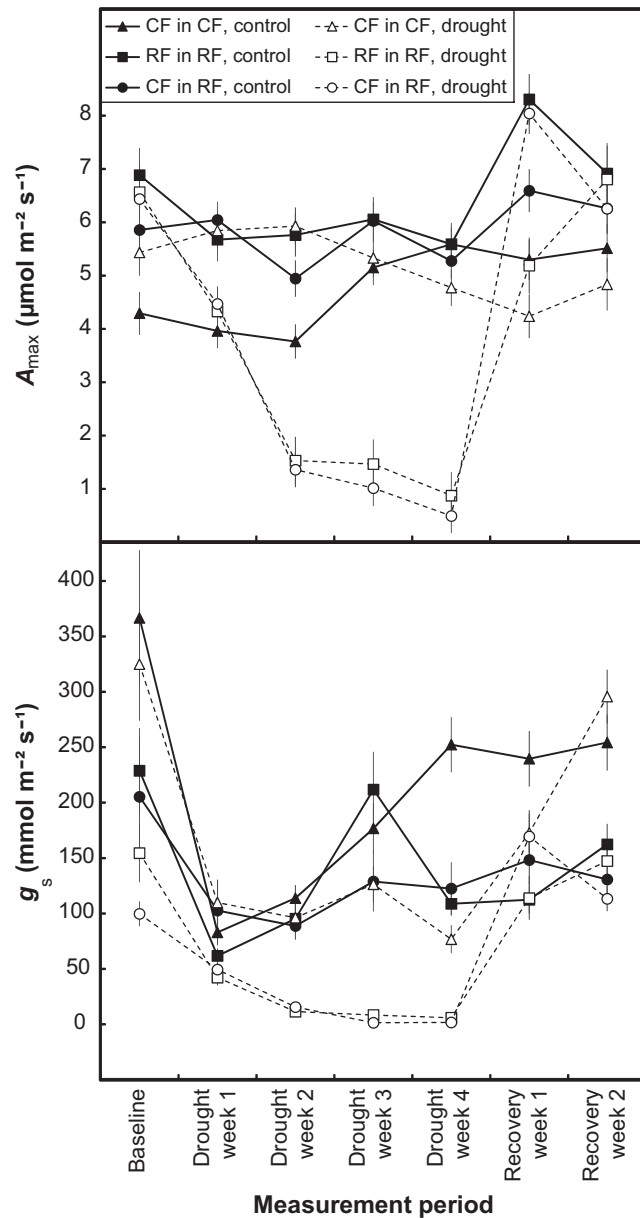




**FIGURE 2** Micrometeorological conditions inside experimental shadehouses representing a cloud forest (CF) or a rainforest (RF) below the cloud base during a common garden experiment with vascular epiphytes. Points are daily means ( $\pm 1$  SE) of data collected every 15 min. Shaded regions indicate 3-day measurement campaigns during a 4-week drought, followed by a 2-week recovery period

similar patterns to  $A_{\max}$ , reflecting the importance of stomatal response to drought. Drought-treated plants in the RF shadehouse experienced a clear reduction in  $g_s$ , whereas all other groups maintained significantly higher values (Table 2; Figure 3). In the RF shadehouse, the separation in  $g_s$  between drought versus control plants was significant at drought weeks 2 through 4 as  $g_s$  approached zero, but in the CF shadehouse this separation was significant only at

drought week 4 (Table S2). Drought-treated plants recovered to the  $g_s$  levels of controls by recovery week 2 (Table S2). This  $g_s$  dataset contained large amounts of unexplained variability; standard errors were a relatively large fraction of their estimates, and baseline values were much higher than drought week 1 for all groups (Table S2). Physiological responses to drought in the RF shadehouse were similar among species (Table S3; Figure 4).



**FIGURE 3** Maximum net photosynthesis ( $A_{\max}$ ) and stomatal conductance ( $g_s$ ) in vascular epiphytes during a common garden experiment. Epiphytes sourced from a cloud forest (CF) or a rainforest (RF) below the cloud base were transplanted into CF or RF shadehouses nearby where they were watered (control) or received no water for 4 weeks (drought). Points are means  $\pm$  1 SE

### 3.3 | Morphological responses to drought

On average, epiphytes grew in length 0.3 mm/day (Table S2), but forest-VPD/light, water regime and their interactions had no effect on growth rate (Table 2). Leaf thickness responded to forest-VPD/light, water regime and their interactions among measurement periods, and also differed among levels of forest-VPD/light independent of measurement period (Table 2). During peak drought, leaves were 0.2 mm (19%) thinner on drought-treated plants compared to controls in the high VPD/light conditions of the RF

shadehouse, but did not differ among other groups (Figure 5; Table S2). Leaf health ( $\Delta H$ ) was affected by all within-subjects and between-subjects sources of variation (Table 2). By drought week 4, drought-treated plants in the RF shadehouse experienced a 34%–46% decline in  $\Delta H$  compared to baseline, whereas all other groups were relatively stable (Tables S2 and S3; Figures 4 and 6). All plants returned to nearly baseline values of  $\Delta H$  after the 2-week recovery period (Table S3; Figures 4 and 6). Recovery of  $\Delta H$  occurred primarily via blade rehydration after wilting with a small component of flushing in a few cases. Changes in leaf shedding, leaf flushing, herbivory and reproductive output occurred among measurement periods, with forest-VPD/light and water regime additionally influencing shedding, flushing and herbivory (Table 2). However, these phenological variables were not systematically affected by drought (Table S2). Mortality counts were low (16 deaths, 447 survivors) and not significantly different among treatments ( $\chi^2_{(5, N=463)} = 10.39, p = 0.0649$ ).

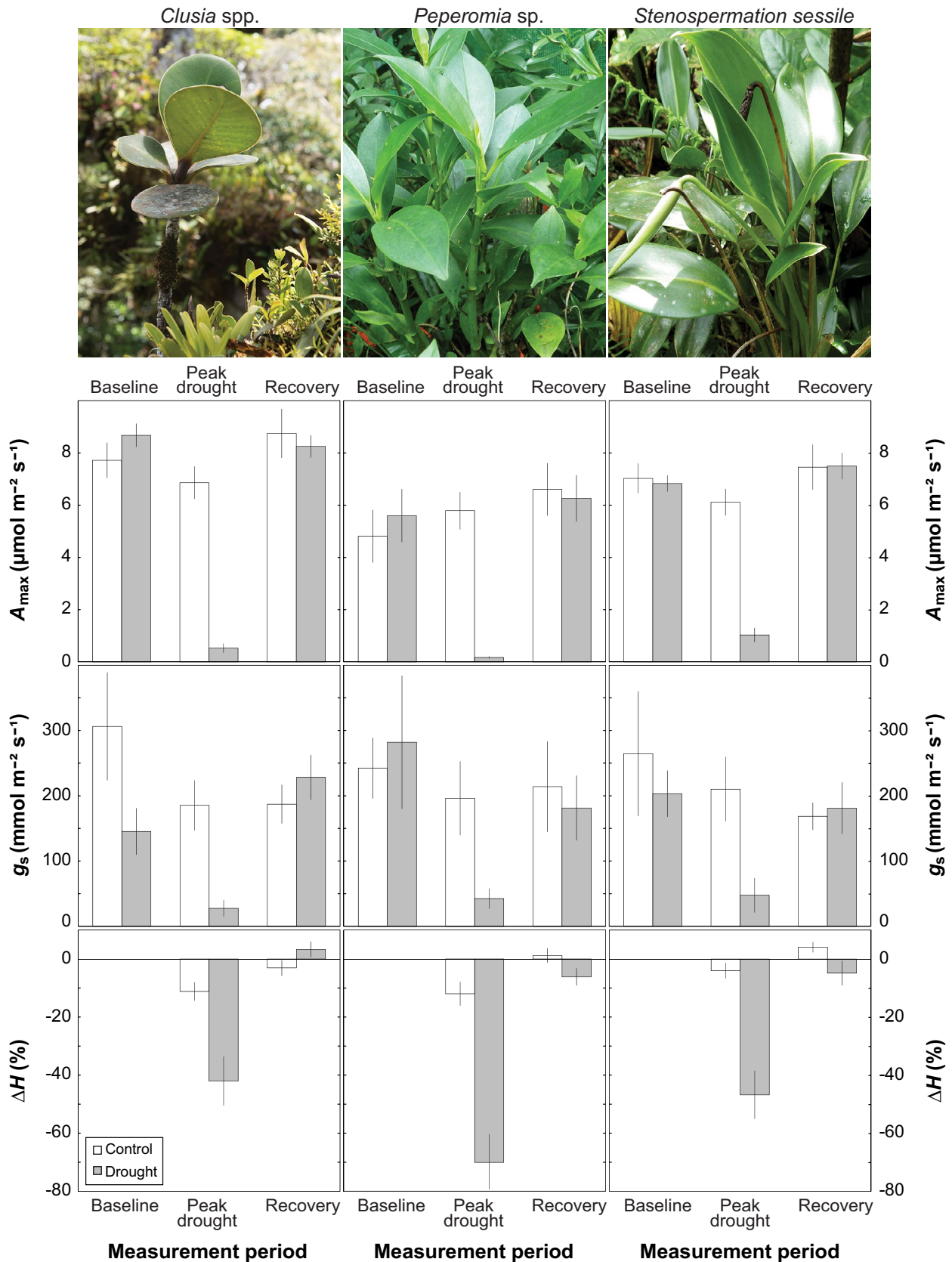
## 4 | DISCUSSION

In response to severe drought with relatively high VPD, epiphytes in our common garden experiment experienced substantial declines in  $A_{\max}$ ,  $g_s$  and  $\Delta H$ . However, when water became available, the drought-treated plants rebounded surprisingly well. This rapid and nearly full recovery suggests that vascular epiphytes may be more resilient to episodic, short-term drought than we had predicted. The decline we observed in  $A_{\max}$  reflects stomatal regulation that favours water conservation over carbon acquisition, a strategy that may inform epiphyte responses to rising clouds and increasing drought frequency expected in the long-term future. Our inferences are limited to  $C_3$  epiphytes because CAM photosynthesizers were not represented in this study.

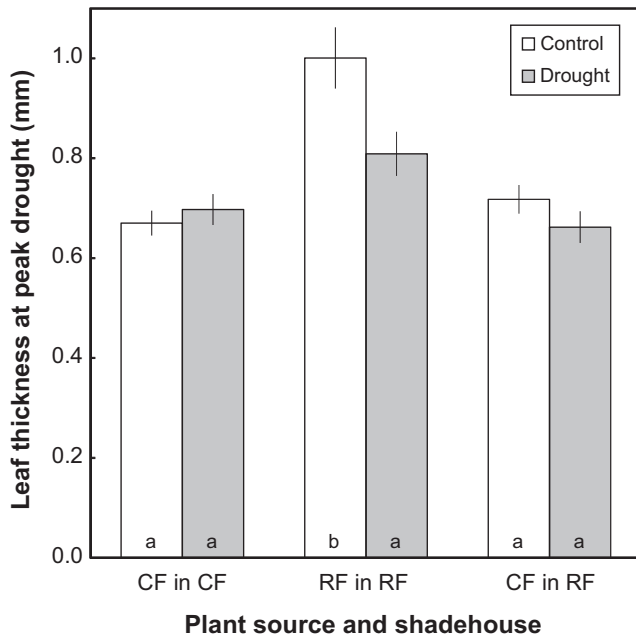
### 4.1 | Habitat segregation among epiphyte species

The clear differences in microclimate and community composition that we have shown between the sites (Amici et al., 2020; Gotsch et al., 2017) led to the hypotheses that epiphytes from the RF would be physiologically and morphologically more resistant to changes during the drought, and exhibit a stronger recovery after drought. However, the single short-term drought we imposed on established epiphytes yielded results that did not support these hypotheses. In the RF shadehouse at peak drought,  $A_{\max}$ ,  $G$ ,  $\Delta H$  and phenology were not significantly different in CF compared to RF epiphytes, and the difference in  $g_s$  was just 4 mmol m<sup>-2</sup> s<sup>-1</sup>. After the 2-week recovery period,  $A_{\max}$  and  $g_s$  were similar between control and drought-treated plants, and  $\Delta H$  was close to a full recovery. These results do not indicate that RF epiphytes are more resilient to the projected drying effects of climate change, but they do suggest that the variables we measured may not directly mediate the segregation of plant species into CF versus RF habitats. Other factors, such as the trade-off between investment in chemical defence

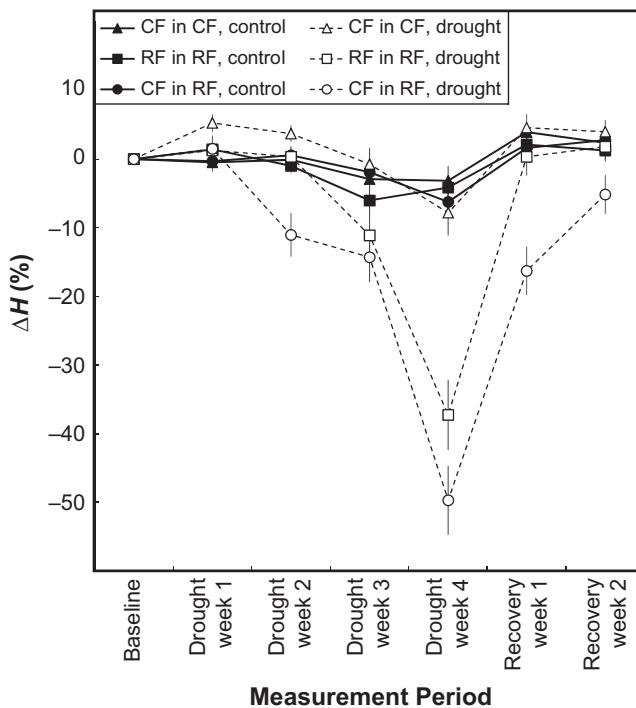




**FIGURE 4** Maximum net photosynthesis ( $A_{max}$ ), stomatal conductance ( $g_s$ ) and change in the proportion of healthy leaves since baseline ( $\Delta H$ ) in the rainforest shadehouse for the three most common taxa used in the experiment. For each variable and taxon, only drought-treated plants at the peak drought measurement period were significantly different (one-way ANOVA, Tukey's HSD;  $p < 0.0001$ ). Columns are means  $\pm 1$  SE. Photographs by Sybil G. Gotsch and Rikke Reese Næsborg (*Clusia*), used with permission [Correction added on 23 July 2020, after first online publication: acronym 'RF' ('rainforest') has been removed.]



**FIGURE 5** Leaf thickness on vascular epiphytes during peak drought in a common garden experiment. Epiphytes sourced from a cloud forest (CF) or a rainforest (RF) below the cloud base were transplanted into CF or RF shadehouses nearby where they were watered (control) or received no water for 4 weeks (drought). Letters refer to significant differences obtained from a one-way ANOVA and Tukey's HSD ( $p < 0.0001$ ). Columns are means  $\pm 1$  SE



**FIGURE 6** Change in the proportion of healthy leaves since baseline ( $\Delta H$ ) on epiphytic vascular plants during a common garden experiment. Epiphytes sourced from a cloud forest (CF) or a rainforest (RF) below the cloud base were transplanted into CF or RF shadehouses nearby where they were watered (control) or received no water for 4 weeks (drought). Points are means  $\pm 1$  SE

versus plant growth, variation in xylem hydraulic traits and host tree specificity, are known contributors to local species turnover in the tropics (Benavides, Vasco, Duque, & Duivenvoorden, 2011; Cosme, Schietti, Costa, & Oliveira, 2017; Fine et al., 2004).

#### 4.2 | Resistance to and recovery from episodic, short-term drought

Our results indicate that vascular epiphytes in the Monteverde region are resilient to episodes of short-term drought. Drought-treated plants in the RF shadehouse experienced clear declines in  $A_{\max}$ ,  $g_s$  and  $\Delta H$  whereas plants in the CF shadehouse showed no adverse physiological or morphological responses, suggesting that CF epiphytes can be resistant to drought in the absence of cloud attenuation. Although we lack soil moisture data for confirmation, we speculate that cloudiness at the CF shadehouse maintained VPD that prevented the meteorological drought we imposed from becoming hydrological, thus allowing the soil to remain sufficiently moist for normal physiological and morphological processes in the CF but not the RF shadehouse. Alternatively, perhaps direct contact with low-lying clouds in the CF shadehouse enabled foliar water uptake that is common among TMCF epiphytes (Darby et al., 2016; Gotsch et al., 2015). And while  $A_{\max}$ ,  $g_s$  and  $\Delta H$  declined in response to drought in the RF shadehouse, a rapid recovery occurred within 2 weeks after rewatering. Moreover, we noted no difference in mortality between control and drought-treated plants, consistent with a sap flow recovery trend measured in wild epiphytes after a severe drought through which all individuals—including those above and below the cloud base—survived (Gotsch et al., 2018).

Water stored in succulent organs likely moderated the drops in  $A_{\max}$ ,  $g_s$  and  $\Delta H$  that defined resistance to the experimental drought in the RF shadehouse. Drawdown of stored water is known to stabilize water potential against rapid fluctuations in VPD and replenish evaporative losses through the lamina after stomata close (Martins, McAdam, Deans, DaMatta, & Brodrigg, 2016; Sack, Cowan, Jaikumar, & Holbrook, 2003). Leaf hydrenchymal layers are a common trait among vascular epiphytes (Gotsch et al., 2015; Ogburn & Edwards, 2010), and epiphytes occurring below the cloud base, where VPD is higher and direct cloud water inputs are lower, should be more reliant on leaf water storage compared to cloud forest epiphytes. Accordingly, at peak drought, leaves on drought-treated plants from below the cloud base were 19% thinner than controls, but we observed no difference among the other groups. Similar leaf blade thinning occurred during an experimental drought using several of the same taxa (Darby et al., 2016). Some epiphytic shrubs in Ericaceae produce swollen, tuber-like bodies known as 'lignotubers' that serve a water storage function and can grow to 1-m diameter (Evans & Vander Kloet, 2010; Luteyn, 2002). The lignotubers we observed on most of the *Cavendishia capitulata* Donn. Sm. and *Macleania insignis* in our experiment likely also conferred drought resistance, but we did not measure their size or hydraulic capacitance.

The probability of recovering from short-term drought may be improved by stomatal regulation that reduces the risk of cavitation because the cost of replacing embolized conduits is likely to exceed the benefit of keeping stomata open (Eller et al., 2018). However, this strategy comes at the cost of reduced carbon fixation and, therefore, drought resistance. The trade-off between hydraulic failure and carbon deficit represents a continuum of drought-response strategies that can inform the mechanisms causing plant death and community turnover (West et al., 2012) and can even predict vulnerability to drought (Skelton, West, & Dawson, 2015). Our physiological data suggest that the epiphytes we surveyed employ a conservative water-use strategy. Brighter conditions tend to stimulate stomatal opening that boosts leaf conductance (Roelfsema & Hedrich, 2005). However, in the RF shadehouse, both  $A_{\max}$  and  $g_s$  fell to near-zero values for three full weeks in drought-treated plants, indicating stomatal closure even though PAR was higher there than in the CF shadehouse where stomata remained open. This conservative strategy, which we interpret as resistance being sacrificed to improve recovery capacity, appears adequate to survive short-term droughts and may be common among vascular epiphytes because of their heavy reliance on direct atmospheric inputs of water.

#### 4.3 | Long-term effects of drought with higher VPD

Reductions in population growth rates can influence species proportions. Epiphytes transplanted downslope to simulate climatic warming experienced reduced growth, less recruitment and shifts in relative abundances over 2 years (Jácome et al., 2011; Nadkarni & Solano, 2002; Rapp & Silman, 2014; Song et al., 2012). However, our experimental treatments did not yield changes in growth rate, herbivory, reproduction or mortality that are known to alter population growth rates (Buckley et al., 2010). Our 4-week experimental drought, although realistic for a severe event, may have been too brief to affect these variables because the impact of chronic drought is difficult to predict from a single short-term episode (Meir et al., 2018). In particular, our failure to push the epiphytes beyond their mortality thresholds strongly limits comparisons of long-term drought resilience between CF and RF epiphytes.

Nonetheless, our results offer an opportunity to speculate about how a higher frequency of droughts, in combination with higher VPD, may have long-term impact. In the RF shadehouse, drought-treated plants exhibited significant physiological and morphological responses—reduced  $A_{\max}$ ,  $g_s$  and  $\Delta H$ —that were symptomatic of an overall decline in performance, whereas plants in the CF shadehouse appeared mostly unaffected. A primary dissimilarity in CF versus RF shadehouse conditions was a combination of temperature and relative humidity that amounted to a difference in VPD of 0.27 kPa, a range over which significant changes in epiphyte abundance and community composition occur among sites in the Monteverde region (Amici et al., 2020; Gotsch et al., 2017). The severe drought conditions we imposed in the RF shadehouse elicited responses similar to other manipulation experiments with

vascular epiphytes, including the thinning of leaf blades coupled with a reduction in  $g_s$  as well as increased leaf damage and dieback (Darby et al., 2016; Nadkarni & Solano, 2002). The additional decline in  $A_{\max}$  we observed is consistent with a strategy of stomatal regulation that favours water conservation over carbon acquisition and could help explain the decreased vascular epiphyte longevity and recruitment previously observed in response to downhill transplants (Nadkarni & Solano, 2002; Rapp & Silman, 2014). Drought-induced carbon starvation, however, is a controversial hypothesis that merits further research (McDowell et al., 2011; Sala, Piper, & Hoch, 2010); vascular epiphytes may represent a model ecosystem element for investigating the interaction between plant hydraulics and carbon metabolism.

## 5 | CONCLUSIONS

Vascular epiphytes from forests both above and below the cloud base experienced significant declines in physiological and morphological performance in response to a severe but realistic 4-week drought. However, they exhibited quick post-drought recovery, suggesting that epiphytes from both habitats are resilient to episodic, short-term drought. Conversely, the observed decrease in  $A_{\max}$  leads us to speculate that the higher frequency of severe droughts and cloudless episodes predicted by climate models may promote extended periods of stomatal closure that could impact these epiphyte communities in the long term.

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### AUTHORS' CONTRIBUTIONS

S.G.G., N.M.N. and T.E.D. formulated the research ideas; J.G.M., A.G. and S.G.G. collected the data and conducted the preliminary analyses; C.B.W. performed the final analyses and wrote the manuscript. All the authors edited, revised and enjoyed the research that led to this manuscript.

### DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.ngf1vhr9> (Williams et al., 2020).

## ORCID

Cameron B. Williams  <https://orcid.org/0000-0002-8503-3762>

Todd E. Dawson  <https://orcid.org/0000-0002-6871-3440>

Nalini M. Nadkarni  <https://orcid.org/0000-0002-0841-7391>

Sybil G. Gotsch  <https://orcid.org/0000-0002-8685-6576>

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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