



Drought decreases water storage capacity of two arboreal epiphytes with differing ecohydrological traits

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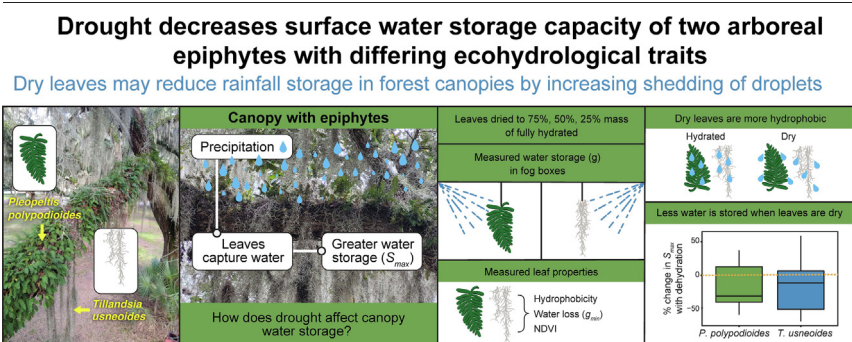
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HIGHLIGHTS

- Epiphytes growing in tree canopies capture and store rainwater, but this role may be vulnerable to increasing drought.
- We tested the effects of drought (leaf desiccation) on water storage capacity (S_{max}) and leaf properties of two epiphytes.
- Drought significantly reduced S_{max} and increased leaf hydrophobicity for both species.
- Plants' responses to drought may reduce rainfall storage in forest canopies, potentially altering hydrological cycling.

GRAPHICAL ABSTRACT



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ABSTRACT

Arboreal epiphytes, plants that grow on trees, can significantly increase rainwater storage and evaporation (i.e., “interception”) within canopies. Drought conditions may affect this hydrological role, as epiphytes' physiological responses change leaf properties that affect water retention. Drought-induced changes in epiphyte water storage capacity could substantially alter canopy hydrology, but have not been studied. We tested the effects of drought on the water storage capacity (S_{max}) of leaves and leaf properties of two epiphytes with distinct ecohydrological traits: resurrection fern (*Pleopeltis polypodioides*), and Spanish moss (*Tillandsia usneoides*). Both species are common in maritime forests of the Southeastern USA, where climate change is expected to decrease precipitation in spring and summer. To simulate drought, we dried leaves to 75 %, 50 %, and ~25 % of fresh weight, and quantified their S_{max} in fog chambers. We measured relevant leaf properties: hydrophobicity, minimum leaf conductance (g_{min} ; a measure of water loss under drought), and Normalized Difference Vegetative Index (NDVI). We found that drought significantly reduced S_{max} and increased leaf hydrophobicity for both species, indicating that lower S_{max} may be due to shedding of droplets. While the overall reduction in S_{max} did not differ between the two species, they exhibited distinct drought responses. Dehydrated *T. usneoides* leaves had lower g_{min} , demonstrating the ability to limit water loss under drought. *P. polypodioides* increased g_{min} when dehydrated, consistent with its extraordinary ability to withstand water loss. NDVI decreased with dehydration in *T. usneoides* but not *P. polypodioides*. Our results suggest that increased drought may have a dramatic effect on canopy water cycling by reducing the S_{max} of epiphytes. Reduced rainfall interception and storage in forest canopies could have widespread effects on hydrological cycling, thus understanding the potential feedbacks of plant drought response on hydrology is crucial. This study highlights the importance of connecting foliar-scale plant response with broader hydrological processes.

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1. Introduction

Forest canopies influence hydrological processes through rainfall interception, when a portion of precipitation is stored in the canopy and evaporated from surfaces or transpired through leaves back to the atmosphere (Savenije, 2004). The amount of stored and intercepted precipitation can then influence other important components of the water cycle, such as stemflow, throughfall, and infiltration (Klamerus-Iwan et al., 2020). When forest canopies experience high interception rates, evaporation of water from leaf surfaces can lead to significant effects on canopy microclimate including greater humidity and evaporative cooling (Angelini and Silliman, 2014; Stuntz et al., 2002), which can also affect tree transpiration (Oren and Pataki, 2001). The canopy's water storage capacity, or the maximum amount of rainwater that can be stored by canopy surfaces (S_{max}), determines evaporation through interception of rainfall that is prevented from reaching the ground and instead evaporates from the canopy (Klaassen et al., 1998). Thus, the amount of rainfall that is intercepted depends on forest characteristics that determine water storage capacity, such as leaf area index and tree morphology (Carlyle-Moses and Gash, 2011; Gash et al., 1995). The traits of the leaves themselves also influence water shedding, leaf wettability, and water absorption (Lenz et al., 2021). Leaf shape and surface hydrophobicity can be important determinants of rainfall interception, since these properties affect how easily water is retained or shed from the leaf surface (Holder, 2007; Liu and Zhao, 2020). In particular, traits that increase leaf water repellency can reduce canopy water storage and interception through increased shedding of water droplets from leaf surfaces (Rosado and Holder, 2013).

Arboreal epiphytes, plants that live on the surfaces of trees, are important components of canopy structure, adding substantial leaf area and biomass to the canopy and therefore influencing canopy hydrology and precipitation fluxes (Mendieta-Leiva et al., 2020; Van Stan and Pypker, 2015). Epiphytes increase rainfall interception (Zotz, 2016), by increasing canopy water storage capacity (Köhler et al., 2007) and related evaporation (Hargis et al., 2019). Epiphytes also influence canopy microclimate by increasing humidity and evaporative cooling (Stuntz et al., 2002), and have an important ecological role through habitat modification and facilitation (Angelini and Silliman, 2014; Jian et al., 2013). Because epiphytes lack access to soil moisture, these plants largely rely on atmospheric water resources and have morphological and physiological adaptations for capturing rainfall and atmospheric moisture, including foliar water uptake (Darby et al., 2016; Gotsch et al., 2015). Many epiphytes have traits that increase leaf wettability such as water-absorbing leaf trichomes (Zambrano et al., 2019). Water storage adaptations are also common among epiphytes, including water-holding leaf structures like those of tank bromeliads, and internal storage in specialized cells (e.g. hydrenchyma) (Gotsch et al., 2015; Hargis et al., 2019). Because these water capture and storage traits contribute to overall canopy water storage and interception, epiphytes have an outsized capacity to influence rainfall interception where they are abundant (Mendieta-Leiva et al., 2020). While the ecological strategies of epiphytes make them influential in canopy hydrology, their reliance on atmospheric water resources and lack of access to soil water resources may also make epiphytes particularly susceptible to atmospheric drought and increased vapor pressure deficit (Benzing, 1998; Gotsch et al., 2017).

As plant leaves become desiccated in response to longer periods without rainfall during drought, leaf traits that influence rainfall storage capacity and interception can change, including leaf area, leaf orientation, and surface properties that influence hydrophobicity (Ilyas et al., 2021; Kao and Forseth, 1992). For example, the tipping movement of leaves during rain that causes water shedding depends on leaf and petiole stiffness, which in turn depend on turgor pressure and the degree of internal hydration in plants (Lenz et al., 2021; Niklas, 1999). Plants can increase leaf trichome density in response to drought stress (Galdon-Armero et al., 2018; Shahzad et al., 2021), which may either increase wettability and interception capacity (Wang and Duan, 2010) or increase hydrophobicity and shedding (Brewer et al., 1991). Cuticular waxes are important for protecting plant leaves under water stress, and plants increase the thickness of this

wax layer and alter its composition in response to drought (Lewandowska et al., 2020; Seo and Park, 2011; Shepherd and Wynne Griffiths, 2006), potentially increasing water repellency and shedding from leaf surfaces (Rosado and Holder, 2013). While the effects of drought on plant leaves are well documented, the influence of foliar level drought response on water interception and storage capacity has received less attention. The potential effects of drought and altered precipitation on canopy interception are increasingly recognized through hydrological modeling at the forest stand level (Ferreira Rodrigues et al., 2021; Lian et al., 2022). However, the connection between rainfall interception and plant foliar response to drought has not been investigated.

Plant species with differing ecohydrological traits may also vary in their functional trait shifts in response to drought, potentially determining outcomes for canopy water cycling (Bittner et al., 2010). If some plants are better able to maintain hydrologic functions like rainfall interception, these species may be able to provide redundancy in the contribution of canopy plants to forest water cycling, potentially buffering this important ecosystem service against the effects of environmental change. In the case of canopy epiphytes, drought response may depend on trade-offs between drought avoidance and drought tolerance, with some plants having functional traits that promote foliar water uptake and drought tolerance but correspond to limited capacity for internal water storage versus traits of more succulent plants that encourage internal water storage ability and drought avoidance, but correspond to more limited tolerance of low water potentials (Gotsch et al., 2022, 2015). Epiphytes with succulent leaf traits are likely more able to withstand drought, with fewer changes to leaf traits, whereas plants more reliant on foliar water uptake may be more vulnerable (Ferguson et al., 2022; Gotsch et al., 2015). Such variation in species response to environmental change, and the potential for more tolerant species to provide functional redundancy, are key to maintaining ecosystem functions and services under large-scale anthropogenic changes to earth systems (Mori et al., 2021). Testing the effects of drought on water storage capacity of epiphyte species with differing ecohydrological traits will provide a more predictive understanding of the potential for canopies to maintain hydrological function in the face of altered precipitation.

Precipitation patterns are expected to change in many areas due to global climate change, causing shifts in the seasonal timing of precipitation and the severity of atmospheric drought periods (Easterling et al., 2017; Trenberth, 2011). Ultimately, the resilience of canopy water cycling to these changes will depend on the ability of plants to maintain hydrologic function despite physiological changes associated with drought response. In particular, the drought response of epiphytes could have far ranging implications. Epiphytes may have significant effects on rainfall interception and evaporative cooling, such that the loss of their contribution to storage and interception could lead to regional climate warming and further hydrological changes (Porada et al., 2023; Van Stan et al., 2018). If drought reduces the water storage capacity of forest canopies, this could create a positive feedback contributing to hotter, drier conditions as interception and evaporation decrease. Thus, it is important to examine how decreases in precipitation may influence canopy storage capacity through the drought responses of epiphytes, potentially contributing to feedbacks in hydrological and climate processes.

In this study, we examined the influence of simulated drought in terms of leaf desiccation on S_{max} , the maximum water storage capacity of leaves, and relevant leaf properties of two arboreal epiphytes: the resurrection fern (*Pleopeltis polypodioides*) and the bromeliad, Spanish moss (*Tillandsia usneoides*) (Fig. 1). These species are common and abundant throughout live oak (*Quercus virginiana*) dominated maritime forests of the Southeastern United States. The contribution of arboreal epiphytes to canopy water storage capacity may be especially high in these forests, where *T. usneoides* is known to have a significant role in rainfall interception (Van Stan et al., 2016), perhaps due to its curtain-like growth form (Garth, 1964; Gay et al., 2015). However, since precipitation is expected to decrease during the spring and summer in the Southeastern USA due to climate change (Easterling et al., 2017; Melillo et al., 2014), the hydrologic role of these epiphytes may depend on their response to drought



Fig. 1. The resurrection fern (*Pleopeltis polypodioides*) and the bromeliad. Spanish moss (*Tillandsia usneoides*), from maritime forests in Georgia, Southeastern USA, which are dominated by Live Oak trees (*Quercus virginiana*). Panel A shows the abundance and curtain like structure of *T. usneoides* festoons. Panel B. shows a closer view of the two species with labels.

conditions and the ability of drier leaves to capture rainwater. Our two focal species are taxonomically distinct and differ in functional traits that may be relevant to water relations. *P. polypodioides* is a “resurrection” plant that tolerates extreme desiccation by going into a state of quiescence and regains normal metabolic activity when rewetted, through foliar water uptake (John and Hasenstein, 2017; Prats and Brodersen, 2021). *T. usneoides* uses foliar water uptake but also stores water in its tissues (Haslam et al., 2003; Helliker and Griffiths, 2007). In this study, plants experiencing different degrees of drought in terms of leaf desiccation underwent water storage capacity trials to determine how drought would influence the S_{max} of *P. polypodioides* and *T. usneoides* leaves. We also examined how dehydration influenced two leaf properties related to S_{max} : minimum leaf conductance (g_{min}), a measure of leaf surface water loss following stomatal closure under dry conditions, and hydrophobicity, a measure of the potential for leaf surfaces to shed water. These metrics demonstrate how well water is retained by (g_{min}) or shed from (hydrophobicity) the canopy under drought stress. Lastly, we examined changes in photosynthetic capacity by measuring Normalized Difference Vegetative Index (NDVI) (Yang et al., 2017). We hypothesized that leaf desiccation would reduce S_{max} and that the degree of reduction might differ between the two species. We expected that g_{min} would be lower for *T. usneoides*, which may be better adapted for drought avoidance. We expected that hydrophobicity would be greater in drier leaves and that NDVI would decrease with dehydration, due to decreased photosynthetic activity under stress.

2. Materials and methods

2.1. Study system and sample collection

We collected specimens of our focal plants during the summer of 2021 at University of Georgia, Skidaway Institute of Oceanography (SkIO) campus, Savannah, GA, USA (31.9885°N, 81.0212°W), from mature *Q. virginiana* trees where the two plants co-occur (Fig. 1). *T. usneoides*, a rootless bromeliad, occurs in festoons (curtain-like bundles of leaves), which hang from branches (Fig. 1A). *P. polypodioides* grows along the surface of the tree trunks and branches, often creating a thick rhizome mat (Fig. 1B). Mats of *P. polypodioides* were collected near the base of trees and *T. usneoides* festoons were pulled down from branches. Samples were transported to the Plant Growth Facility at Franklin and Marshall College, Lancaster, PA. Plants were kept in a climate-controlled environment with

average temperatures of $22\text{ }^{\circ}\text{C} \pm 4\text{ }^{\circ}\text{C}$ during the day and $18\text{ }^{\circ}\text{C} \pm 4\text{ }^{\circ}\text{C}$ at night, and relative humidity ranged between 50 % and 90 %. Plants received natural light for 2 h each morning and light from grow lights for 4 h in the afternoon. All drought simulations, trials and measurements were done between October 2021 and April 2022.

2.2. Drought simulation

We simulated the effects of atmospheric drought conditions on epiphyte leaves by drying *P. polypodioides* and *T. usneoides* leaf samples to 75 %, 50 %, and ~25 % of their fully hydrated mass (100 % hydration) and examined the influence of these leaf desiccation treatments on water storage capacity (S_{max}) and related leaf traits (hydrophobicity, minimum leaf conductance) and the leaf spectral response (NDVI) at each hydration level. For our treatments and measurements, we created leaf samples consisting of a minimum 1.5 g of plant material at 100 % hydration mass. To minimize genetic variation within each sample of leaf material, we used 3–4 *P. polypodioides* leaves that were connected to a single root mat and *T. usneoides* leaves collected from a single festoon. The 100 % hydration treatment consisted of healthy leaves that had been stored at 80 % relative humidity and watered and misted every day for at least two months before the experiment. We created the desiccation treatments by allowing samples to dry at ambient indoor humidity or in a drying oven at 30–45 °C to promote desiccation without affecting the viability of the leaves. Samples were weighed on an analytical balance (A-160 Denver Instrument Company) until they reached the desired dehydration state. For the lowest hydration level, if sample mass would not decrease to 25 % over a long period of drying, we used the lowest mass that the samples could attain without causing the leaves to die. *T. usneoides* exhibited a great capacity to withstand desiccation; the lowest fresh weight for these samples ranged from 25 % to 32 % of the weight at full hydration.

Whenever possible, we repeated both leaf measurements and water storage trials measuring S_{max} across all dehydration levels on a given sample of leaf material. This was done sequentially, as the sample went from the most hydrated state (100 %) to the least hydrated state (~25 %). We measured the mass and leaf area of samples at each hydration level. We were unable to directly measure leaf area for *P. polypodioides* at the 50 % and 25 % hydration levels because the leaves break apart as they are flattened for the measurement. Since we attempted to use the same samples at different hydration states, our goal was to keep the samples intact.

2.3. Water storage capacity (S_{max}) trials

Water storage capacity trials took place in plexiglass fog boxes (41.91 cm × 23.62 cm × 27.94 cm) with misting systems that continuously deliver reverse osmosis water as a fine mist into the boxes. Water storage capacity as S_{max} was measured by weighing hanging leaf samples with monofilament line connected to single-point load cells HBM PW15AH or Precix SPM4 (HBK Inc., Marlboro, MA, USA). The mass of the sample was recorded at 1-minute intervals using CR1000 and CR1000X data loggers (Campbell Scientific, Logan, UT, USA). Maximum water storage capacity, S_{max} (g), was calculated as maximum sample mass minus the initial sample mass. The maximum sample mass was determined when the sample mass stopped increasing and remained stable for at least 15-min, with no further increase. We found that once the mass stabilized for this length of time, no further increases in mass would occur, even if we continued observing the mass for longer periods of time.

2.4. Leaf ecohydrological traits and spectral analysis

We examined two leaf traits relevant to the ecohydrological role of the plants: hydrophobicity and minimum leaf conductance (g_{min}). Hydrophobicity indicates the propensity for water droplets to be shed from leaves (Holder, 2013), and g_{min} is a common metric of water loss under drought conditions (Duursma et al., 2019) and thus a useful metric to characterize water loss behavior of leaves under different states of dehydration. Measurements were made at each hydration level of our drought treatment, whenever possible. We measured hydrophobicity as the contact angle of a drop of water placed on the leaf surface. A drop with a smaller contact angle has flattened more on the surface of the leaf, whereas a drop with a larger contact angle has maintained a rounder shape, with less of its surface touching the leaf, as we would expect on a less absorbent surface. A larger contact angle indicates a greater ability of the leaf surface to shed water, i.e., greater hydrophobicity (Holder, 2013). We used 5 μ l drops of water for *P. polypodioides* and 4 μ l drops for *T. usneoides*, since the leaf surface area of this species is smaller. Contact angles of the droplets were recorded by securing leaves in a flat position with good illumination and taking images using a digital Nikon D750 camera (Nikon Inc., Melville, NY, USA). The camera was positioned at the height of the droplet and was leveled to ensure that the bottom of the image would be parallel with the drop. We measured contact angles with image analysis using ImageJ (V 1.53) with the Drop Snake Analysis (Low-Bond Axisymmetric Drop Shape Analysis; LB-ADSA) extension. As our leaf samples contained multiple leaves, the contact angle measurements were made on each leaf individually and then averaged across each sample. We defined minimum leaf conductance (g_{min} , mmol m⁻² s⁻¹) as the average water loss following stomatal closure, calculated by the slope of the relationship between the sample weight and time elapsed since the beginning of the trial for a given mole fraction of vapor pressure deficit, per unit area of leaf surface (Duursma et al., 2019). To determine g_{min} we weighed each leaf sample every 30 min over the span of 4–6 h while simultaneously measuring temperature and relative humidity. Sample mass was measured using an analytical balance and relative humidity and temperature were recorded every 20–30 min using a HOBO MX2301A Wireless Temperature/RH Humidity Data Logger (Onset, Bourne, MA, USA). We estimated g_{min} as the slope from at least six mass measurements over time, divided by the average mole fraction of the vapor pressure deficit taken over the measurement period (Scoffoni et al., 2018). To account for changes in leaf area during dehydration, we calculated g_{min} using the average leaf area from the beginning to the end of the experiment (Scoffoni et al., 2018). Measurements were made at ambient humidity in the laboratory. *P. polypodioides* leaf petioles were sealed with petroleum jelly to prevent water loss. We measured the total leaf area of each sample of leaves three times using a CI-202 Portable Laser Leaf Area Meter (CID Bio-Science, Camas, WA, USA) and used the average of these three measurements as our response to account for variation in measurements. For *P. polypodioides* we could not evaluate cuticular conductance at 50 % and 25 % hydration levels

because the brittleness of dehydrated leaves prevented us from measuring leaf area for these samples.

We evaluated the health of leaves across the range of hydration levels in terms of normalized difference vegetation index (NDVI), measured with a leaf spectrophotometer (CI-710 s, CID Bio-Science, Camas, WA, USA). We measured NDVI of *T. usneoides* at all hydration levels, however we were only able to measure NDVI of *P. polypodioides* at 75 % and 100 % hydration levels. At lower hydration levels, the leaves of *P. polypodioides* become brittle and break, as described above. Because of the thin leaf structure of *T. usneoides*, we arranged 5–7 leaves in parallel to cover the entire sensor area during measurements.

2.5. Data analysis

We tested the effects of hydration level on each response variable with ANOVA and tested differences between hydration levels with Tukey H.S.D. tests. Because direct measurements of leaf area were not feasible for *P. polypodioides* samples at the 25 % and 50 % hydration levels (see above), we have used an estimated leaf area for *P. polypodioides* at these two levels of our treatment. We used linear regression to determine the relationship between sample mass and sample leaf area for *P. polypodioides* at the 75 % hydration level. We then estimated leaf area at 25 % and 50 % hydration levels by extrapolation, using the known mass of *P. polypodioides* samples at those two hydration levels and the relationship between sample mass and sample leaf area at 75 % hydration ($y = 18.207x - 2.2127$; $R^2 = 0.456$). We compared the overall percent change in S_{max} from highest to lowest hydration levels between *T. usneoides* and *P. polypodioides* with a Welch's two-sample *t*-test. For *T. usneoides*, the same leaf sample was used to calculate the difference in S_{max} between 100 % hydration and ~25 % hydration levels, such that negative numbers indicate a reduction in S_{max} . For *P. polypodioides* we used pairs ranked by mass to calculate the change in S_{max} with dehydration, as the leaf samples were often too fragile to be used repeatedly across hydration levels. All analyses were done using R, version 4.2.1. Data are available from the HydroShare data repository (Moore et al., 2023).

3. Results

3.1. Water storage capacity (S_{max})

Leaf dehydration significantly reduced the S_{max} of *P. polypodioides*, particularly at the lowest hydration level ($P = 0.012$, Table 1, Fig. 2A), however more dehydrated leaves had higher S_{max} per leaf area ($P < 0.0001$, Table 1, Fig. 2B), because the area of the fern leaves is reduced when dehydrated ($P < 0.0001$, Table 1, Fig. 2D). *T. usneoides* showed a similar pattern, with S_{max} reduced by dehydration ($P = 0.001$, Table 1, Fig. 3A), however, S_{max} per leaf area did not differ by dehydration level ($P > 0.3$, Table 1, Fig. 3B). For both species, the leaf mass decreased significantly with desiccation as expected ($P < 0.0001$, Table 1, Figs. 2C & 3C). Desiccation did not affect leaf area of *T. usneoides* ($P > 0.7$, Table 1, Fig. 3D), as it did for *P. polypodioides*. There was no significant difference between the two species in the overall percent change in S_{max} per sample with dehydration from 100 % to ~25 % ($P > 0.6$, Fig. 4).

3.2. Leaf properties

Hydrophobicity was greater in dehydrated leaves of both *P. polypodioides* ($P = 0.0001$, Table 2, Fig. 5A) and *T. usneoides* ($P < 0.0001$, Table 2, Fig. 5B), indicating that drought conditions may reduce canopy moisture through shedding of water droplets from leaves. For *P. polypodioides*, minimum leaf conductance (g_{min}), a metric of water loss under dehydration, increased at the 75 % hydration level, relative to full hydration ($P < 0.0001$, Table 2, Fig. 6A). For *T. usneoides*, g_{min} was significantly decreased at all dehydration levels below 100 % hydration ($P < 0.0001$, Table 2, Fig. 6B). Dehydration did not have a significant effect on NDVI in *P. polypodioides* ($P > 0.4$, Table 2, Fig. 7A). However,

Table 1

Results from ANOVA of the effect of hydration level treatments (100 %, 75 %, 50 %, and ~25 %) for *P. polypodioides* and *T. usneoides* on: water interception per trial, water interception per leaf area, leaf sample mass, and leaf area.

	Plant species	Variable	Df	MS	F	P-value
Water interception (g water per trial)	<i>P. polypodioides</i>	Hydration level	3	7.81	3.90	0.012
		Residuals	70	2.00		
	<i>T. usneoides</i>	Hydration level	3	16.68	5.86	0.001
		Residuals	71	2.85		
Water interception per leaf area (g water per cm ²)	<i>P. polypodioides</i>	Hydration Level	3	0.04	18.89	<0.0001
		Residuals	70	0.002		
	<i>T. usneoides</i>	Hydration level	3	0.05	1.05	0.38
		Residuals	71	0.04		
Leaf sample mass (g)	<i>P. polypodioides</i>	Hydration level	3	17.93	75.40	<0.0001
		Residuals	70	0.24		
	<i>T. usneoides</i>	Hydration level	3	9.55	22.83	<0.0001
		Residuals	70	0.42		
Leaf sample area (cm ²)	<i>P. polypodioides</i>	Hydration level	3	15,783.00	117.20	<0.0001
		Residuals	74	135.00		
	<i>T. usneoides</i>	Hydration level	3	14.41	0.37	0.77
		Residuals	72	38.83		

dehydration did significantly reduce NDVI in *Tillandsia* leaves, but only at the lowest hydration level ($P < 0.0001$, Table 2, Fig. 7B).

4. Discussion

Our results suggest that increased drought could have a dramatic effect on canopy rainwater cycling in Southeastern maritime forests due to a reduction in the water storage capacity, S_{max} , of arboreal epiphytes. We found that drought response in leaves significantly decreased S_{max} for both epiphyte species (Figs. 2A & 3A). Drought treatments also caused an increase in leaf hydrophobicity for both species, indicating that enhanced

water shedding from leaves is an important mechanism that decreases canopy water storage capacity and interception during drought conditions. Although the species differed in some drought responses, we found that the overall percent reductions in S_{max} with desiccation from 100 % to ~25 % hydration did not differ significantly between the two species, and that reductions in S_{max} were often quite large: –44.7 % median reduction for *P. polypodioides* and –25.1 % for *T. usneoides* (Fig. 4). Decreases of this magnitude are likely to have significant effects on canopy moisture across forests stands where these plants are abundant. For example, based on previous estimates, the S_{max} of *T. usneoides* alone may be as high as 6 mm for larger rain events (Van Stan et al., 2016), so the median S_{max} decrease of

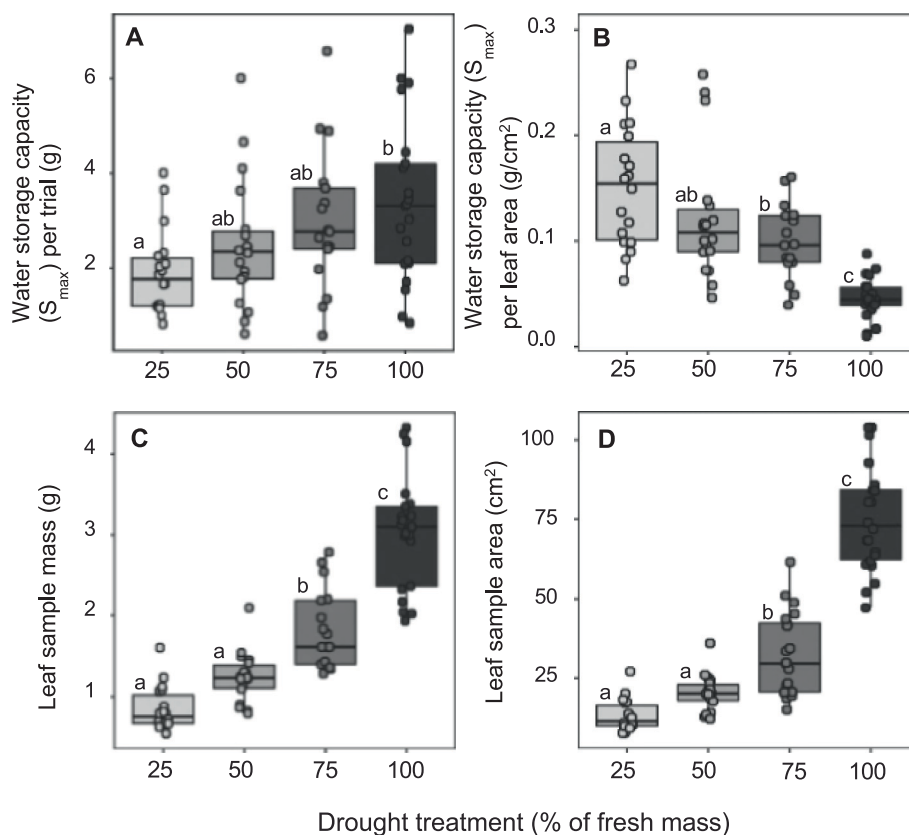


Fig. 2. Results for *P. polypodioides* at each leaf hydration level shown in box and whisker plots showing median, upper and lower quartiles (whiskers = 1.5 x Inter Quartile Range), with overlaid data points, including (A) interception by epiphytic plants per trial (g water), (B) interception per leaf area (g/cm²), (C) leaf sample mass (g), and (D) leaf area (cm²). Bars that significantly different ($P < 0.05$) are indicated with different letters above. Leaf area for *P. polypodioides* was estimated at the 25 % and 50 % hydration levels (see Methods section).

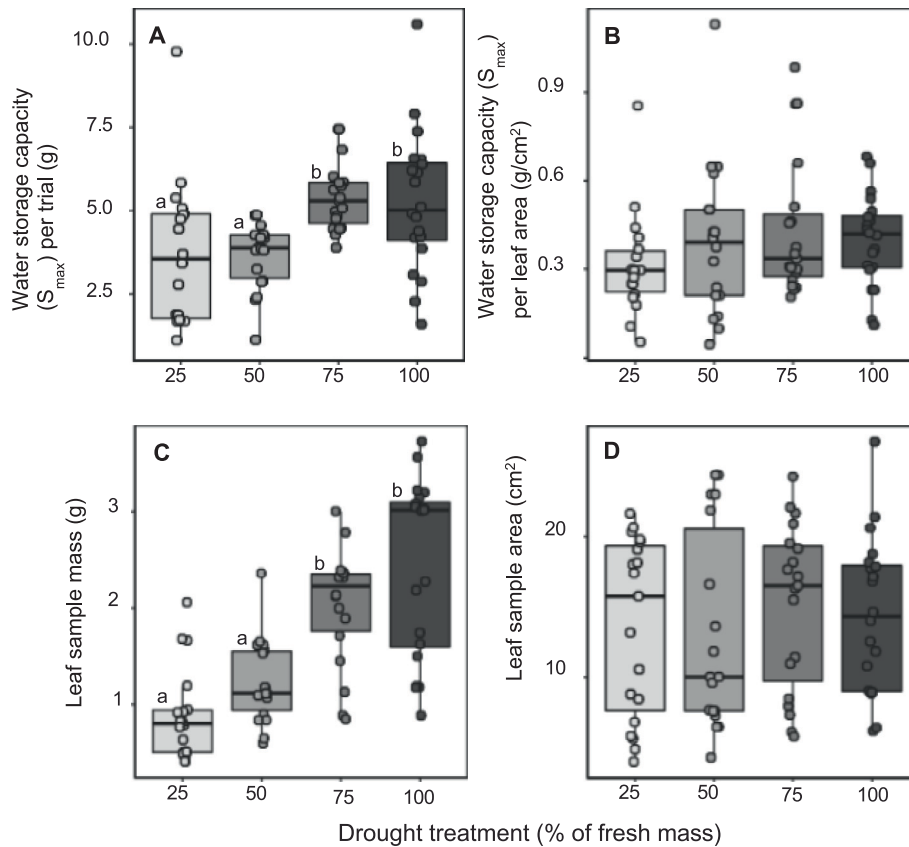


Fig. 3. Results for *T. usneoides* at each leaf hydration level shown in box and whisker plots showing median, upper and lower quartiles (whiskers = 1.5 x Inter Quartile Range), with overlaid data points, including (A) interception by epiphytic plants per trial (g water), (B) interception per leaf area (g/cm^2), (C) leaf sample mass (g), and (D) leaf area (cm^2). Bars that significantly different ($P < 0.05$) are indicated with different letters above.

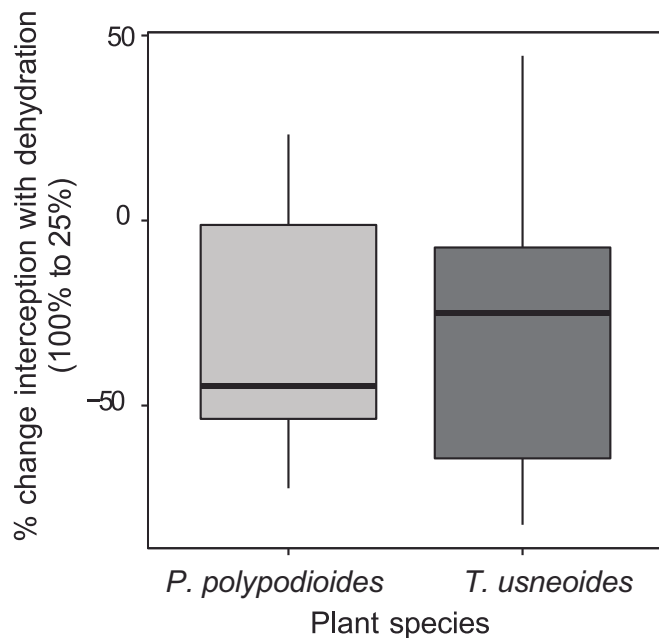


Fig. 4. Box and whisker plots of percent change in interception (g of water) per leaf sample, between 100 % hydration and ~25 % hydration, showing median, upper and lower quartiles (whiskers = 1.5 x Inter Quartile Range). The same leaf sample was compared at the two hydration levels for *T. usneoides*. For *P. polypodioides* we used pairs ranked by mass to calculate the change in interception with dehydration, as the leaf samples were often too fragile to be used repeatedly across hydration levels.

25 % under severe desiccation we found for this species could represent a large decrease in overall canopy water storage. Future studies could examine the length of drought periods necessary to dry leaves to the hydration levels of our treatments by measuring the relative water content of leaves in the field. Based on our results, we expect that the increased drought predicted with climate change in this region could significantly reduce canopy water storage contributions by epiphytes in this maritime forest ecosystem. Reduced water storage could hamper the ability of these forest canopies to reduce runoff and shelter soils through “smoothing” of rainfall intensities (Van Stan et al., 2018).

The overall effects of leaf desiccation on $S_{\max}$ appear to be similar for the two epiphyte species, likely due to increased leaf hydrophobicity, as seen in other plants under drought conditions (Łukowska, 2015; Oosterhuis et al., 1991). We may expect the drought response of these species to have similar effects on $S_{\max}$ rather than one providing some functional redundancy by maintaining its hydrological role. However, the degree of leaf desiccation under atmospheric drought may differ between species in the field. *P. polypodioides* likely spends a high proportion of time in a desiccated state, as leaves can become dehydrated after only three weeks without precipitation (Stuart, 1968). In contrast, for *T. usneoides* a state of desiccation to 25–50 % fresh weight may represent a significant drought response that causes a loss of internal water reserves. Dehydration clearly reduced the photosynthetic activity of *T. usneoides*, indicated by a significant reduction in NDVI at the lowest hydration level. However, NDVI did not change with desiccation treatments in *P. polypodioides*; results consistent with an ability to retain photosynthetic capacity rather than down-regulating photosynthetic enzyme pools in response to stress. As a resurrection plant, *P. polypodioides* decreases its metabolic activity including photosynthesis when dehydrated, and yet quickly recovers normal activity with rehydration (Prats and Brodersen, 2021; Stuart, 1968). *P. polypodioides* instead protects the photosynthetic machinery on the green upper surface of its leaves

Table 2
Results from ANOVA of the effect of hydration level treatments (100 %, 75 %, 50 %, and ~25 %) for *P. polypodioides* and *T. usneoides* on leaf properties, including: hydrophobicity, minimum leaf conductance (g_{min}), and NDVI.

	Plant species	Variable	Df	MS	F	P-value
Hydrophobicity	<i>P. polypodioides</i>	Hydration level	3	562.20	7.87	0.0001
		Residuals	78	71.50		
	<i>T. usneoides</i>	Hydration level	3	2501.50	15.93	<0.0001
		Residuals	72	157.10		
Minimum leaf conductance (g_{min} , $mmol\ m^{-2}\ s^{-1}$)	<i>P. polypodioides</i>	Hydration level	1	5852.00	22.13	<0.0001
		Residuals	36	264.00		
	<i>T. usneoides</i>	Hydration level	3	290.34	24.84	<0.0001
		Residuals	72	11.69		
NDVI	<i>P. polypodioides</i>	Hydration level	3	0.02	0.99	0.40
		Residuals	78	0.02		
	<i>T. usneoides</i>	Hydration level	3	0.03	11.22	<0.0001
		Residuals	72	0.002		

by curling up when dry, exposing only the underside of the leaf (Helseth and Fischer, 2005; Pessin, 1924). Although the effects of desiccation on S_{max} at the foliar scale may be similar, *T. usneoides* would likely take a longer drought period to reach the lower hydration levels we tested, based on its water storage capabilities (Helliker and Griffiths, 2007). Our results point to the importance of comparative work to determine whether variation in species-level traits translate to differences in the resilience of their contributions to ecosystem functions such as water cycling.

The two epiphytes responded to desiccation differently, consistent with the distinct ecohydrological traits of these species. For example, *T. usneoides* has the capacity to limit water loss under dehydration, as indicated by the lower minimum leaf conductance (g_{min}). In contrast, g_{min} increased with dehydration for *P. polypodioides*, a resurrection plant with an extraordinary ability to withstand water loss, rather than prevent it (John and Hasenstein, 2017; Stuart, 1968). *T. usneoides* allocates a substantial proportion of its cell structure to water storage (Martin and Schmitt, 1989) and has a high foliar water uptake capacity (Haslam et al., 2003; Helliker and Griffiths, 2007), which may provide an important buffer to drought. In contrast, for *P. polypodioides*, allowing severe desiccation could be considered a strategy for tolerating drought stress, and the plant may also be better able to withstand severe heat stress in its desiccated state, compared to a hydrated state (John and Hasenstein, 2020). Previous studies on epiphytes have found trade-offs between succulence and foliar water uptake (Gotsch et al., 2022, 2015), however *T. usneoides* has both the advantages of internal water storage and foliar uptake (Benz and Martin, 2006). We might expect *T. usneoides* to better sustain canopy water storage under drought conditions based on its ecohydrological traits and lower minimum leaf conductance. Both species use specialized trichomes to channel water on their surfaces for rapid hydration and foliar water uptake (Herppich

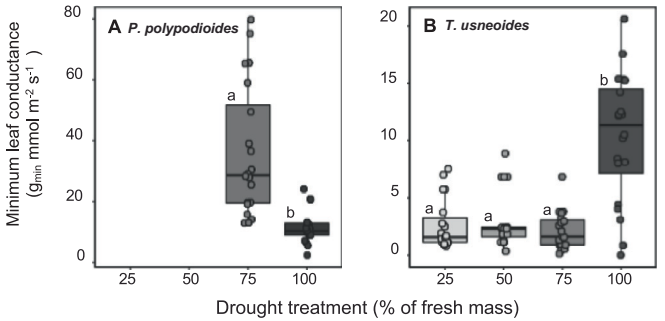


Fig. 6. Minimum leaf conductance of epiphytic plants (g_{min}) at each hydration level in box and whisker plots showing median, upper and lower quartiles (whiskers = $1.5 \times$ Inter Quartile Range), with overlaid data points, for (A) *P. polypodioides* and (B) *T. usneoides*. Bars that are significantly different ($P < 0.05$) are shown with different letters. Note the different y axes in panels A and B.

et al., 2019; John and Hasenstein, 2017; Martin and Schmitt, 1989), which may enhance the resilience of their roles in canopy water storage and interception. However, the reliance of these epiphytes on atmospheric water uptake likely renders them vulnerable to increasing drought (Benzing, 1998; Gotsch et al., 2017).

In this study, we found substantial reductions in S_{max} as leaves experienced drought. However, if we consider plants at a larger scale, the growth forms of these species might reduce the effects of canopy water storage loss at the stand level. For example, *T. usneoides* occurs in large bundles of strand-like leaves called festoons that hang from the trees in curtain-like formations (Garth, 1964; Gay et al., 2015) and are known to have a

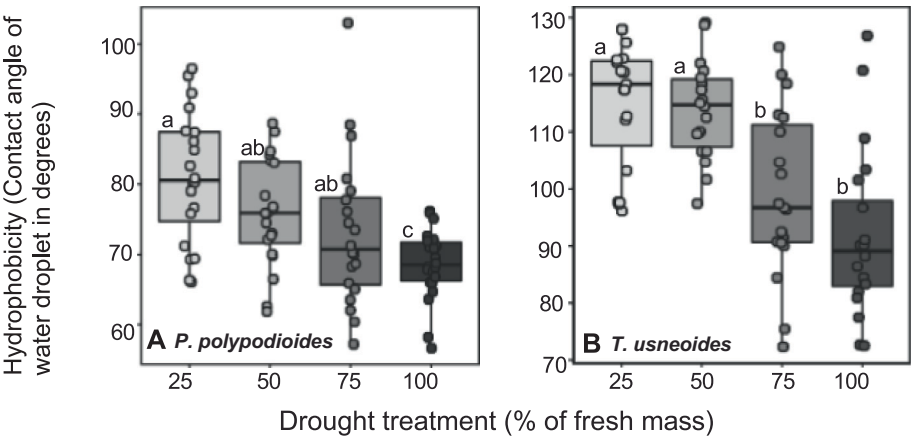


Fig. 5. Leaf hydrophobicity as contact angle of water droplet on leaf surface in degrees, at each hydration level, as box and whisker plots showing median, upper and lower quartiles (whiskers = $1.5 \times$ Inter Quartile Range), with overlaid data points for (A) *P. polypodioides* and (B) *T. usneoides*. Bars that are significantly different ($P < 0.05$) are shown with different letters. Note the different y axes in panels A and B.

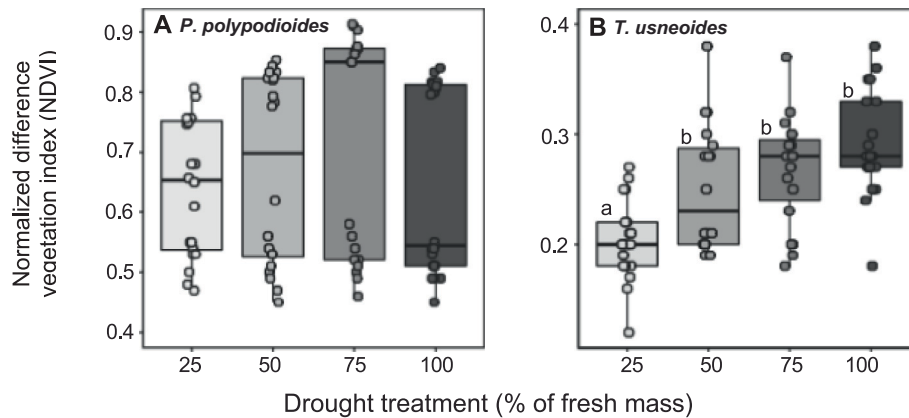


Fig. 7. Normalized Difference Vegetation Index (NDVI) at each hydration level in box and whisker plots showing median, upper and lower quartiles (whiskers = 1.5 x Inter Quartile Range), with overlaid data points, for (A) *P. polypodioides* and (B) *T. usneoides*. Bars that are significantly different ($P < 0.05$) are shown with different letters. Note the different y axes in panels A and B.

significant role in canopy hydrology at this scale (Gay et al., 2015; Van Stan II et al., 2015; Van Stan et al., 2016). Water may be caught and stored within the involutions of the festoon structure, which is often comprised of a tangle of densely crowded leaves (Billings, 1904; Garth, 1964). *P. polypodioides* grows along the surface of oak branches, forming a dense root mat that accumulates detritus and forms arboreal/canopy soil along the upper surface of large branches. Such canopy soils can be an important component of water storage for mats of epiphytes (Bohlman et al., 1995; Köhler et al., 2007). Temporary water storage in these plant structures and canopy soils might offset foliar level drought effects, however this has not been tested. Longer scale drought manipulations involving whole plants could incorporate other organismal responses to drought, such as changes to leaf development and structure, which could cause even greater reductions in water storage of plant structures than we observed based on shorter term physiological response of leaves. Future investigations of drought response and survival of plants at a larger spatial scale would improve our understanding of the influence of predicted drought on the canopy hydrology of this ecosystem. Further, similar studies in other forested ecosystems with high epiphyte densities could reveal different patterns, particularly in tropical forests, where the species diversity of epiphytes is very high (Nieder et al., 2001; Taylor et al., 2022) and thus may create more functional redundancy in hydrological roles.

Epiphytes increase rainfall interception by adding additional structure to forest canopies and through their adaptations for capture and storage of atmospheric water (Mendieta-Leiva et al., 2020), so we may expect that the degree of this increase for a given epiphyte species should depend on its abundance, as well as its ability to capture water per unit area. We found that S_{max} scaled per leaf area revealed different patterns in the two epiphytes. For *P. polypodioides*, the drier leaf tissue stored more water per unit area because the leaves shrink in size as they dry, although we could not measure the exact decrease at some hydration levels (see Materials and Methods). Under field conditions, *P. polypodioides* leaves also roll up as they desiccate to protect the leaf surface and expose the water absorbent trichomes on the ventral side (John and Hasenstein, 2020, 2017), which may further increase its water absorption per leaf area. In contrast, *T. usneoides* leaf area and S_{max} standardized per leaf area did not vary with dehydration treatment. Consistent leaf area coupled with a low g_{min} indicates that this species has strong stomatal regulation. However, dehydration likely reduced leaf mass both through loss of water tissue content (Martin, 1994) and water loss in leaf surface structures such as trichomes, which collect and hold water at the leaf surface (Martin and Schmitt, 1989). *T. usneoides* is densely covered with overlapping, fan-like trichomes that channel water quickly across the leaf surface, forming the primary means of water transport and uptake for this species (Ha et al., 2021; Herppich et al., 2019). Severe desiccation could cause a reduction in the trichome size and/or water trapping capacity, contributing to an overall

reduction in leaf mass and S_{max} without affecting leaf area. Greater abundance of *T. usneoides* in the field is directly related to reduced throughfall and thus presumably increased canopy storage capacity and interception (Gay et al., 2015; Van Stan et al., 2016). Since *T. usneoides* is more abundant than *P. polypodioides* in our study system (Moore et al., unpublished data) we would expect that its drought response will have a greater overall influence on canopy hydrology.

If changing precipitation patterns lead to decreased rainwater storage and evaporation in forest canopies through plant drought response at the foliar scale, this could have far reaching effects on hydrological cycling (Klamerus-Iwan et al., 2020; Savenije, 2004). Most obviously, reduced interception could increase throughfall and stemflow, increasing rainwater contributions to runoff, soil moisture, or infiltration to groundwater, depending on the surface cover and soil characteristics (Dunkerley, 2020). Rainfall interception by forest canopies returns water to the atmosphere for cloud formation, ultimately contributing to future precipitation (Ellison et al., 2019; Menenti, 2000) and influencing regional and global temperature predictions (Berg and Sheffield, 2019; Davies-Barnard et al., 2014). Observations and models have shown that arboreal epiphytes in particular, have a significant role in increasing rainfall interception and storage within the canopy (Mendieta-Leiva et al., 2020). Further, water capture and storage by epiphytes has a moderating effect on the microclimate of the canopy by increasing humidity and evaporative cooling (Stuntz et al., 2002). These habitat modifying effects can shape ecological communities by benefitting other plants (Jian et al., 2013; Spicer and Woods, 2022; Stanton et al., 2014) as well as fauna (Angelini and Silliman, 2014; Ellwood et al., 2011). Considering the expected effects of climate change on precipitation via hydrologic intensification (Lian et al., 2022; Trenberth, 2011), understanding changes in drought-mediated water storage capacity due to physiological plant response may be an important key to predicting ecosystem changes and future hydrological cycling. Such feedbacks between the effects of climate change and the physiological responses of organisms are key to understanding and predicting the effects of climate change on ecosystem processes and further climate change.

5. Conclusions

Our results demonstrate that foliar response to drought may significantly reduce rainwater storage capacity for two arboreal epiphytes with different ecophysiological strategies. This has considerable implications for canopy ecohydrology, as severe drought decreased *T. usneoides* and *P. polypodioides* water storage capacities by ~25 % and ~45 %, respectively. Despite their differing drought responses, the overall effects of leaf desiccation on water storage capacity (S_{max}) appear to be similar for both species, likely due in part to increased leaf hydrophobicity. This research highlights the need to link foliar scale plant response with broader

hydrology to better understand potential feedbacks in climate processes. The results emphasize the importance of comparative research to determine how plant traits affect the resilience of ecohydrological functions, and suggests the need for further studies to incorporate the diversity of epiphytes species. Future research is needed on epiphyte drought responses at the canopy scale, and in other types of forested ecosystems, to determine the potential consequences of reduced canopy water storage on ecological communities and associated hydrological processes. These findings will inform forest management and conservation efforts in the face of ongoing climate change.

CRediT authorship contribution statement

J. Van Stan, S. Gotsch and C. Buck obtained funding to support this research. S. Gotsch and J. Van Stan conceptualized the study. Data collection and initial data analyses were performed by undergraduate students: J. Antoine, L. Bedoya and A. Medina under the mentorship of S. Gotsch. A. Moore conducted the final analyses and wrote the manuscript with S. Gotsch. C. Buck and J. Van Stan provided feedback on the manuscript.

Data availability

Data are available from the HydroShare data repository: <https://doi.org/10.4211/hs.4e9723d9937f4adfa7e6f588a2f77ba4>.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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