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Foliar water uptake and diurnal water recharge-discharge cycle in *Pyrrosia piloselloides* (L.) M.G.Price (Polypodiaceae)

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ABSTRAK

Ketersediaan air merupakan faktor pembatas utama bagi tumbuhan epifit, yang tidak memiliki akses langsung ke tanah dan air tanah. Untuk mempertahankan fungsi fisiologisnya, banyak epifit memanfaatkan foliar water uptake *(FWU) sebagai sumber air tambahan. Penelitian ini bertujuan untuk mengkaji kapasitas FWU serta dinamika air harian pada tumbuhan paku epifit* Pyrrosia piloselloides *menggunakan perubahan ketebalan daun sebagai indikator penyimpanan dan kehilangan air. Ketebalan daun diukur setiap dua jam selama 48 jam pada sembilan individu, sedangkan kemampuan FWU diuji pada tujuh daun per individu. Hasil penelitian menunjukkan bahwa FWU meningkatkan kandungan air daun sebesar 0,44–1,37%. Ketebalan daun menurun pada siang hari seiring meningkatnya suhu dan menurunnya kelembapan, dan kembali meningkat pada malam hari ketika suhu menurun dan kelembapan relatif meningkat. Secara keseluruhan, ketebalan daun berkurang sekitar 14,11% selama periode terang. Temuan ini menunjukkan bahwa* P. piloselloides *mampu melakukan* foliar water uptake *dan menampilkan fluktuasi diurnal yang jelas pada status air daun, mencerminkan respons ekofisiologis yang dinamis terhadap variasi kondisi lingkungan.*

Kata kunci: biodiversitas urban, paku CAM, epifit, ketebalan daun, penyerapan kelembapan, sukulen

ABSTRACT

Water availability strongly constrains epiphytic plants, which lack direct access to soil water. To maintain physiological function under these conditions, many epiphytes rely on foliar water uptake (FWU) as a supplementary water source. This study examined FWU capacity and diurnal water dynamics in the epiphytic fern *Pyrrosia piloselloides* by analysing changes in leaf thickness as a proxy for water recharge and discharge. Leaf thickness was recorded every two hours over 48 hours in nine individuals, and FWU was quantified using seven leaves per individual. FWU increased leaf water content by 0.44–1.37%. Leaf thickness declined during daytime with increasing temperature and decreasing humidity, and increased at night under cooler, more humid conditions. Overall, leaf thickness decreased by approximately 14.11% during the light period. These results demonstrate *that P. piloselloides* is capable of foliar water uptake and exhibits pronounced diurnal fluctuations in leaf water status, reflecting dynamic ecophysiological responses to environmental variation.

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Keywords: CAM ferns, epiphyte, leaf thickness, moisture uptake, succulent, urban biodiversity

INTRODUCTION

Epiphytes are plants that grow upon their phorophytes without establishing direct contact with the soil. As a result, their roots do not penetrate the ground, therefore water and nutrients must be acquired from atmospheric sources such as fog, vapor, and rainfall (Gradstein, 2008). Although epiphytes are abundant in tropical regions characterised by high rainfall and humidity, dry periods still occur (Zhang et al., 2009), meaning precipitation is not available every day. During these dry periods, the only accessible water exists as atmospheric vapor (humidity). Yet, water is required daily to sustain all physiological processes in plants (Lambers et al., 2008). Thus, water availability becomes a critical environmental factor limiting growth and survival (Zhang et al., 2009).

Epiphytes exhibit diverse adaptations to cope with restricted water sources, such as specialised roots, rosette formation, succulence, thick cuticles, and the use of crassulacean acid metabolism (CAM) photosynthesis (Ong, Kluge & Friemert, 1986). *Pyrrosia piloselloides*, a fern species belonged to the family Polypodiaceae, adapts by developing succulent leaves and employing CAM photosynthesis (Rut et al., 2008). Many CAM plants stored water within tissues to support their physiological processes, significant amount of which is gradually depleted through transpiration (Lambers et al., 2008).

Because epiphytes lack direct contact with the soil, *P. piloselloides*, as an epiphytic fern, may rely on alternative strategies to acquire and retain water. Several plant species, including *Polystichum munitum* (Limm & Dawson, 2010), *Pseudotsuga menziesii*, and *Sequoia sempervirens*, have been shown to absorb water directly through their leaves via a mechanism known as foliar water uptake (FWU), particularly under conditions of limited water availability (Limm et al., 2009). The mechanism of foliar water uptake has also been studied in *Sloanea woollsii* (Yates & Hurtley, 1995) and in mangrove *Avicennia marina* (Nguyen et al., 2017). In many epiphytic plants, foliar water uptake has been documented in *Dendrobium* orchids (Pan et al., 2021) and in bromeliads (Ohrui et al., 2007). In succulent-leaved ferns such as *Pyrrosia*, the potential use of leaves for water recharge may occur but remains relatively under-observed and insufficiently explored.

In most plants, water lost via transpiration is replenished through root absorption (Taiz & Zeiger, 2002). However, studies on baobab trees (*Adansonia* spp.) by Chapotin et al. (2006) revealed that water absorption and release influence the water content of succulent organs, as evidenced by fluctuations in stem diameter. These stem diameter fluctuations in baobabs are considered a mechanism of daily water recharge and discharge. Similarly, *P. piloselloides* may exhibit fluctuations in leaf thickness, detectable in its succulent organs, as part of its diurnal water recharge-discharge cycle. Monitoring leaf thickness over at least 24 hours can therefore provide insights into the daily dynamics of water relations in this species. Most research on water relations in vascular epiphytes has focused on bromeliads and orchids, while epiphytic ferns have received comparatively little attention. Based on this gap, it is important to investigate the potential for foliar water uptake and the diurnal cycle of water recharge and discharge in the epiphytic fern *P. piloselloides*. As *P. piloselloides* is a common epiphytic component of tropical Asian urban biodiversity (Agatha et al., 2019; Sedayu et al., 2024; Muhaimin, 2015), it is becoming increasingly important for inhabitants of Jakarta and other large Asian cities to gain insight into how this interesting species withstands life on trees as an epiphyte, particularly in urban settings where the effects of heat and drought may be intensified.

METHODOLOGY

Study sites and species sampling

This study was conducted at the Universitas Negeri Jakarta garden for measurements of the diurnal cycle of water recharge and discharge, and at the UNJ Plant Physiology Laboratory for foliar water uptake (FWU) experiments.

Nine individuals of *P. piloselloides were* selected and cultivated on host trees—*Cocos nucifera, Dimocarpus longan, Ficus lyrata, Annona squamosa*, and *Veitchia merrillii*—in the Universitas Negeri Jakarta garden (Jl. Pemuda 10, Rawamangun, Jakarta Timur) for a period of ten months prior to data collection. The selection of phorophytes was not based on a specific scientific methodology; rather, these trees were chosen because they were readily available, had trunk diameters exceeding 20 cm, and are commonly found in the Jakarta area, making them potential phorophytes outside the UNJ garden as well. For FWU testing, seven leaves were sampled from each individual. For diurnal cycle measurements (fluctuations in leaf thickness), two leaves were selected from each individual. All leaves used in the experiments were mature, sterile leaves.

Foliar water uptake test

This *FWU* observation was directly adapted from Limm & Dawson (2010). Seven leaves of *P. piloselloides* were harvested from each individual immediately after sunset. The cut ends were sealed with nail polish to prevent evaporation and water loss, after which the initial mass was recorded (Mass 1). Nail polish application is also to prevent water absorption via stem, as occurring in cut flower. Leaves were then sprayed with distilled water using a hand fogger on the adaxial surface until fully covered. Excess water was removed by tilting the leaves at approximately 45° before re-weighing (Mass 2).

The wetted leaves were stored in sealed containers to minimise evaporation and kept for 10 hours. The following morning, surface water was removed by gently blotting with absorbent cloth, and the leaves were weighed again (Mass 3). Subsequently, leaves were air-dried for 15 minutes and weighed (Mass 4). Each leaf was then briefly wetted (1 second), blotted dry, and weighed (Mass 5). Finally, leaves were oven-dried at 60 °C for 72 hours to determine dry mass (Mass 6).

Those sequential mass measurements were used to calculate: (1) *Leaf Surface Water Retention Capacity* ($WRC_{surface}$) – the ability of leaves to retain water on their surface, (2) *Foliar Water Uptake (FWU)* – the amount of water absorbed through leaf tissues, and (3) *Leaf Water Content (LWC)* – the total water content of the leaf. Calculations followed the equations described by Limm and Dawson (2010).

Leaf thickness measurement

Leaf thickness was measured to assess the diurnal cycle of water recharge and discharge during the dry period. Measurements were taken on mature leaves of *P. piloselloides* using a digital caliper (Mitutoyo Absolute Digimatic Caliper Series 500) at three points along the central lamina, between the midrib and the leaf margin. Two leaves from each individual were selected, and thickness was recorded every two hours over a 48-hour period, beginning at 05:30.

At each measurement interval, environmental parameters—temperature and relative humidity—were also recorded. Correlation analyses were then performed to evaluate the relationship between leaf thickness fluctuations and environmental variables, thereby providing insights into the dynamics of water relations in response to microclimatic conditions.

Data standardisation and analysis

Values of $WRC_{surface}$ and *FWU* were standardised per unit leaf area using ImageJ software (US National Institutes of Health, Bethesda, MD). Statistical analyses included one-sample *t*-tests at $\alpha = 0.05$ to determine whether *FWU* significantly exceeded 0 mg H_2O/cm^2 and whether increases in *LWC* were significantly greater than 0%. Regression analyses were performed to examine the relationships between *FWU* and *LWC*, as well as between *FWU* and $WRC_{surface}$. Correlation analyses were also subsequently performed to evaluate the relationship between fluctuations in leaf thickness and temperature and relative humidity. The calculation was done manually with the help of MS-Excel spreadsheet.

RESULTS AND DISCUSSION

Foliar water uptake

The capacity of leaves to retain surface water ($WRC_{surface}$) ranged from 2.43 to 20.49 mg H_2O/cm^2, with an average of 8.99 mg H_2O/cm^2. Foliar water uptake (*FWU*) reached up to 0.55 mg H_2O/cm^2, with a mean value of 0.17 mg H_2O/cm^2. Leaf water content (*LWC*) increased by as much as 1.37%, with an average of 0.44%. One-sample t-tests for *FWU* and *LWC* indicated that leaves absorbed water through foliar uptake at statistically significant levels (p-value = 0.00000), with a mean *FWU* of 0.17 mg H_2O/cm^2. Leaf water content also increased significantly (p-value = 0.0000), with a mean of 0.44%.

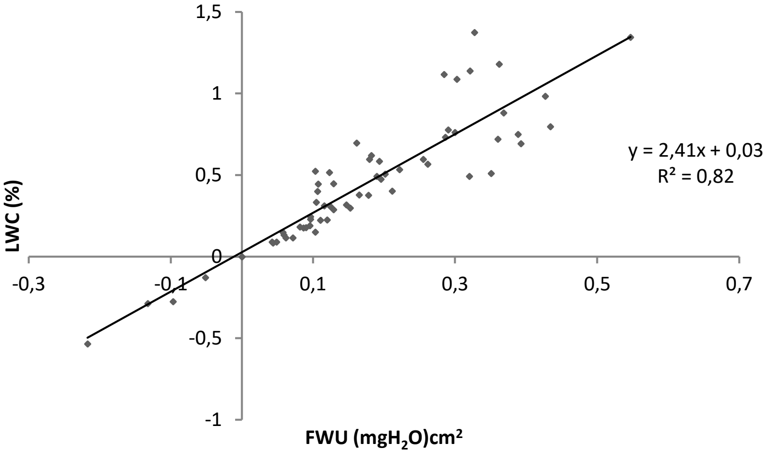

FIGURE 1. Linear relationship between foliar water uptake (*FWU*) and percentage increase in leaf water content (*LWC*).

Regression analysis revealed a strong linear relationship between *FWU* and *LWC* (p-value = 0.00000; r = 0.90; $r^2 = 0.82$). Thus, the magnitude of foliar water uptake was positively associated with the increase in leaf water content.

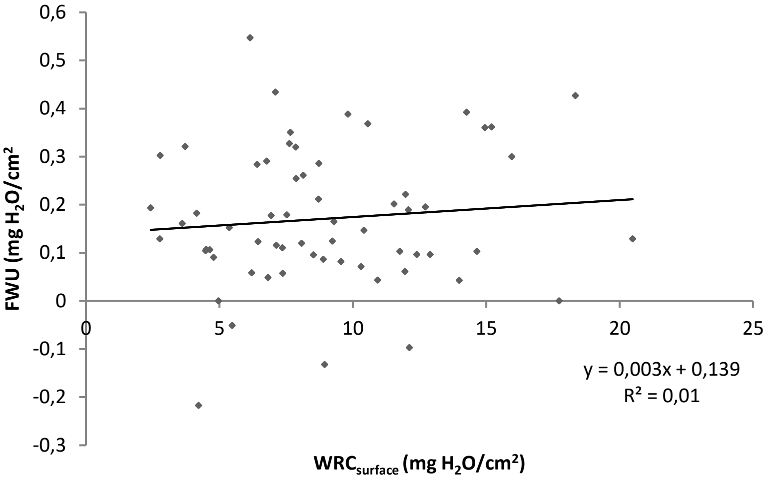

FIGURE 2. Linear relationship between foliar water uptake (*FWU*) and leaf surface water retention capacity ($WRC_{surface}$).

Regression analysis between *FWU* and $WRC_{surface}$ showed no significant relationship. This was evident from the very low coefficient of determination ($r^2 = 0.01$; p-value = 0.43; r = 0.1). In other words, the amount of water retained on the leaf surface did not determine the extent of water absorbed through foliar uptake.

The foliar water uptake (*FWU*) experiments demonstrated significant changes in leaf mass before and after treatment, with leaf mass increasing markedly (p = 0.00000). This confirms that water was absorbed through the leaf surface. *FWU* enhanced leaf water content (*LWC*), reaching a maximum of 1.37% with an average of 0.44%. These values are lower than those reported by Limm et al. (2009), where *LWC* in ten plant species increased by 2–11%, including *Polystichum munitum* at 7.2% (Limm & Dawson, 2010), and by Berry & Smith (2014), who found increases of 3.7–6.4% in *Abies fraseri* and *Picea rubens*. Although the increase in *P. piloselloides* was relatively small, one-sample t-tests confirmed that *FWU* significantly enhanced *LWC* (p = 0.0000). Regression analysis further revealed a strong positive relationship between *FWU* and *LWC* ($r^2 = 0.82$), indicating that absorbed water was retained within leaf tissues, thereby increasing leaf mass.

In *P. piloselloides*, the most probable entrance of water are through the cuticle and trichomes, as this species possesses both a cuticular layer and stellate hairs but lacks hydathodes (Hovenkamp, 1986). However, similar to the findings of Limm & Dawson (2010), the precise pathways of water entry remain uncertain. Experiments by Eller (2013) demonstrated that water can diffuse directly through the cuticle via apoplastic pathways into parenchyma tissues. The cuticle is a complex and dynamic structure capable of modifying its permeability in response to environmental conditions. Reduced cuticular resistance under high humidity facilitates direct absorption of atmospheric moisture (Moreshet, 1970).

Another potential pathway for *FWU* is via trichomes. *P. piloselloides* possesses stellate hairs, which Kato & Tsutsumi (2013) reported to have water-absorbing capacity in epiphytic fern fronds. However, the present study could not confirm whether water absorbed by trichomes penetrates deeper into leaf tissues. *FWU* may also occur through stomatal openings. As a *CAM* plant, *P. piloselloides* opens its stomata during the dark period, and *FWU* experiments were conducted after sunset. The presence of open stomata during testing suggests that water could have entered through stomatal pores.

Fundamentally, *FWU* is driven by water potential gradients between the leaf surface and internal tissues. Diffusion occurs when water potential differs, moving from higher to lower values. Water droplets condensed on the leaf surface have a higher potential (pure water, $\Psi = 0$) compared to leaf tissues, which contain solutes and thus exhibit more negative water potentials (Liu et al., 2012). Therefore, *FWU* can only occur when atmospheric vapor condenses into liquid droplets on the leaf surface, creating a favorable gradient for absorption.

Interestingly, the amount of water retained on the leaf surface ($WRC_{surface}$) was not correlated with the amount absorbed via *FWU*, as indicated by the very low coefficient of determination ($r^2 = 0.01$). This contrasts with findings by Limm & Dawson (2010) in *Polystichum munitum*. The discrepancy may be attributed to differences in cuticular permeability among individuals. As noted by Limm et al. (2009), variations in cuticle composition, surface architecture, or environmental disturbances strongly influence leaf surface permeability. In *P. piloselloides*, average $WRC_{surface}$ values were relatively high, yet *FWU* remained low. This suggests that while substantial water can be retained externally, absorption into tissues is limited. The variability among individuals may be explained by differences in trichome density, as trichomes are present in *P. piloselloides* but absent in species studied by Limm & Dawson (2010). According to Limm & Dawson (2010), high $WRC_{surface}$ values are often associated with trichome type, cuticular wax composition, and surface architecture.

Diurnal cycle of water recharge-discharge

During the 48-hour observation period, fluctuations in both temperature and relative humidity were recorded. The highest temperature (33.16 °C) occurred at 13:30, coinciding with the lowest humidity (51.56%). Conversely, the lowest temperature (25.50 °C) was observed at 05:30, when humidity reached its peak (88.94%). In general, temperature increased steadily from morning to midday (05:30–13:30) and declined from afternoon through night (13:30–05:30). Humidity showed the opposite trend, decreasing during the day and rising again in the evening and night. Correlation analysis revealed a strong and significant inverse relationship between temperature and humidity ($p\text{-value} = 0.00 < \alpha\ 0.05$; $r = -0.96$). Given this significant correlation, either parameter can be used to interpret leaf thickness dynamics.

FIGURE 3 illustrates the diurnal fluctuations in leaf thickness of *P. piloselloides* alongside changes in humidity over 48 hours. The maximum average leaf thickness was 0.91 mm (100%) at 05:30, when humidity was 88.94%. The minimum average thickness was 0.78 mm (85.89%) at 17:30, when humidity was 68.61%. The overall reduction in leaf thickness during the study period was calculated at 14.11%. In general, leaf thickness decreased during the light period (morning to midday) as temperature rose and humidity declined. During the dark period (afternoon to early morning), leaf thickness increased again, although it did not fully return to its initial value. Correlation analysis between leaf

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thickness and humidity, however, showed no significant relationship (p-value = 0.27 > α 0.05).

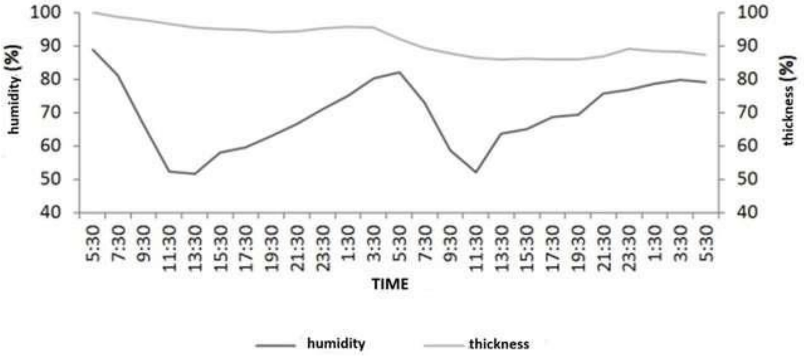

FIGURE 3. Average leaf thickness fluctuations (n = 9) in relation to humidity

Leaves of *P. piloselloides* exhibited continuous fluctuations in thickness, reflecting dynamic processes of water loss and uptake from the surrounding environment. As shown in **FIGURE 3**, leaf thickness varied over the 48-hour observation period. However, the pattern of thickness fluctuations (gray line) did not perfectly align with humidity fluctuations (black line). For instance, at times of minimum humidity (11:30 and 13:30), leaf thickness was low but not at its absolute minimum. Similarly, during periods of maximum humidity (03:30 and 05:30), leaf thickness increased but did not reach its maximum value.

The incomplete recovery of leaf thickness on the following day was likely due to the absence of direct rainfall during the study period. This suggests that atmospheric water uptake (from vapor) is less effective than direct absorption of rainwater. In other words, while *P. piloselloides* can absorb atmospheric moisture, rainfall provides a more substantial water supply. Because atmospheric water potential is highly negative compared to leaf water potential, uptake can only occur when humidity reaches saturation, allowing condensation on the leaf surface. Thus, most water available to *P. piloselloides* originates from rainwater flowing along host tree surfaces, which wets the roots.

As a succulent epiphyte, *P. piloselloides* stores water reserves in its leaves. Leaf thickness generally decreased during the day and increased at night. This pattern resembles fluctuations observed in *Larix decidua* × *leptolepis* (larch), or in Baobab tree where stem diameter varied diurnally due to water release by transpiration and subsequent refilling of tissues (Lambers, 2008; Chapotin et al., 2006). In *P. piloselloides*, the 24-hour cycle of thickness changes indicates both water loss and uptake. However, as an epiphyte without soil contact and in the absence of rainfall during the study, water supply must have been obtained through alternative mechanisms.

Mehltreter (2010) reported that *Pyrrosia adnascens* possesses hydrenchyma tissue, and it is likely that *P. piloselloides* also relies on hydrenchyma to store water in its succulent leaves. This adaptation enables survival under drought conditions by maintaining water reserves for metabolism and transpiration when direct water supply is absent. Over the 48-hour period, average leaf thickness decreased by approximately

14.11%, reflecting depletion of hydrenchyma water reserves. This finding is consistent with Mehltreter (2010), who noted that hydrenchyma cells in *Pyrrosia* species can shrink during dry periods, reducing leaf thickness by up to 50%.

Leaf shrinkage during daytime coincided with high temperatures and low humidity, conditions that increase vapor concentration gradients and transpiration rates. Although *P. piloselloides* is a CAM plant that closes its stomata during the day to minimise water loss, transpiration may still occur through other pathways. According to Ehler & Goss (2003), cuticular transpiration accounts for only ~5% of total water loss in most plants, but Lüttge (2004) argued that in CAM plants, water loss occurs primarily through the cuticle rather than stomata. This suggests that even with closed stomata, *P. piloselloides* may lose water via cuticular transpiration, though the magnitude of this pathway remains uncertain.

During the dark period, leaf thickness increased as temperature declined and humidity rose, despite the absence of direct water supply. Lower temperatures and higher humidity influence stomatal behaviour, allowing stomata to open (Lüttge, 2004). Open stomata facilitate CO_2 fixation, which is subsequently converted into malic acid and stored in vacuoles. The accumulation of malic acid increases vacuolar solute concentration, enhancing osmotic pressure and drawing water into cells, thereby raising turgor pressure. This process results in increased leaf mass and thickness. As Chen et al. (1983) observed, CAM plants exhibit increased leaf weight during the dark period due to internal acid accumulation from nocturnal CO_2 fixation.

Our data suggest that the capacity of *P. piloselloides* to repeatedly recharge and discharge water within its fleshy leaves, together with its ability to absorb atmospheric humidity, plays an important role in the survival of this epiphytic species in tropical urban environments. In such settings, rainfall does not occur on a daily basis, making the ability to store water during wetter periods critical for sustaining physiological functions during drier intervals while waiting for subsequent rainfall.

It is also noteworthy to consider whether rapid and extensive urbanisation in Jakarta (United Nations Department of Economic and Social Affairs, 2025). and other Indonesian and tropical cities has intensified the urban heat island (UHI) effect, potentially leading to further reductions in ambient humidity. If such conditions prevail, *P. piloselloides*—despite its capacity to absorb moisture from the air—may face increasing challenges in persisting within progressively hotter urban environments, particularly when rainfall becomes more intermittent.

CONCLUSIONS

Pyrrosia piloselloides demonstrates the capacity for foliar water uptake (*FWU*), though the possible pathway through cuticle, stellate hairs, or stomata is not demonstrated. *FWU* significantly enhances leaf water content (*LWC*), although it is not influenced by the amount of water retained on the leaf surface ($WRC_{surface}$). The species also exhibits a distinct diurnal cycle of water recharge and discharge, reflected in fluctuations of leaf thickness. Leaf thickness increases toward the end of the dark period due to water absorption and decreases toward the end of the light period as water is released to the environment. No significant correlation was found between leaf thickness

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fluctuations and environmental parameters such as temperature and humidity, indicating that internal physiological mechanisms play a dominant role in regulating water relations in this epiphytic fern.

AUTHOR CONTRIBUTIONS

AS, A, RI: project conception; AS, N, A: methodology; AS, N: data analyses; AS, N.: original manuscript draft; AS, N, A: manuscript review and editing.

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CONFLICTS OF INTEREST STATEMENT

There are no conflicts to declare

ETHICAL COMPLIANCE

The process of collecting data was conducted using non-invasive observation methods and did not involve human or animal subjects.

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