

Experimental evidence of the impacts of dew-induced foliar shielding on the energy, water and isotope balance of hydrophobic leaves

Cynthia Gerlein-Safdi¹, Craig James Sinkler², Kelly Krispin Caylor¹

¹ Princeton University, Department of Civil and Environmental Engineering,
E-208 E-Quad, Princeton, NJ 08544, USA

² Rider University, 2083 Lawrenceville Road, Lawrenceville, NJ 08648, USA

Author for correspondence: *Cynthia Gerlein-Safdi*

Tel: +1-609-865-5428

Email: *cgerlein@princeton.edu*

Total word count (excluding summary, references and legends)	6988
Summary	199
Introduction	1207
Materials and Methods	2894
Results	489
Discussion	2340
Acknowledgements	58
No. of Figures	7 (all color except 6)
No. of Tables	2
No. of Supporting Information files	2 figures (all color)

For Cover Letter (max. 50 words per question):

What hypotheses or questions does this work address?

The deposition of water droplets from dew or fog will block part of the energy coming into a leaf. We hypothesize that this decrease of incoming energy will induce a significant decrease in transpiration, which will in turn affect leaf water status and leaf water isotopes.

How does this work advance our current understanding of plant science?

The importance of non-meteoric water deposition on the leaf energy and water cycle has yet to be studied in details. We provide new insight on a common phenomenon, and developed a new protocol for the rapid analysis of leaf samples using a laser spectrometer and an induction module.

Why is this work important and timely?

Foliar uptake of non-meteoric water is an important source of water for many ecosystems. This work challenges prior results by showing that foliar uptake and the impact of non-meteoric water on the leaf energy cycle have an effect of similar amplitude but opposite direction on leaf water isotopes.

Summary

- The uptake of water from the surface of the leaves, called foliar uptake, is common when rainfall is scarce and non-meteoric water (dew or fog) is the only water source. However, many species have very water repellent leaves. Past studies have not differentiated between the uptake of water and the impact of the droplets on the energy balance of the leaf, which we call ‘foliar shielding’.
- Leaves of the hydrophobic *Colocasia esculenta* were sprayed with isotopically enriched water. We developed a protocol using a laser spectrometer for the rapid analysis of leaf samples. The leaf water potential and water isotopes were monitored for different water-stress conditions.
- Dew-treated leaves exhibited a higher leaf water potential ($P < 0.05$) and c. 30% decrease in transpiration rate ($P < 0.001$) compared to the control. The dew treated leaves also had a depleted water isotopic composition compared to the control ($P < 0.001$). Three possible mechanisms are proposed for the interaction of water droplets with the leaf energy and water balance.
- Comparing three previous foliar uptake studies to our results, we conclude that foliar shielding has a comparable and opposite effect to foliar uptake on leaf water isotopes, especially when considering isotopic non-steady-state.

Key words: *Colocasia esculenta*, foliar uptake, foliar shielding, induction module, laser spectrometer, leaf energy balance, leaf water isotopes, non-meteoric water

¹ I. Introduction

² Non-meteoric water is an important source of water for many plants, because it occurs consistently in all
³ environments. But since it only provides small amounts of water, it is often overlooked in large scale
⁴ models greater than the ecosystem level. Plants from many different environments have long been known
⁵ to be using fog [Stanton and Horn, 2013, Eller et al., 2013, Berry and Smith, 2014] or dew [Andrade, 2003,
⁶ Clus et al., 2008, Lakatos et al., 2012] through foliar uptake. The literature suggesting the importance of this
⁷ mechanism is growing and includes a wide range of plant species and areas.

⁸ So far, most studies have focused on determining circumstances in which specific plants use foliar uptake
⁹ as a source of water. Vegetation in dry and fog-prone areas like coastlands [Burgess and Dawson, 2004,
¹⁰ Stanton and Horn, 2013] or mountain hillsides [Berry et al., 2014a] have adapted to using fog as their main
¹¹ source of water. Similarly, dew water has been shown to be a major source of water on islands where fresh
¹² water is scarce [Clus et al., 2008] or by species that have physical features allowing them to collect dew water,
¹³ like epiphytic bromeliads [Andrade, 2003] or lichens [Lakatos et al., 2012]. Both of these plants grow on
¹⁴ other plants, often without any access to soil water.

¹⁵ In this paper, we will focus on the interaction of non-meteoric water droplets on the leaf energy
¹⁶ balance, which we call ‘foliar shielding’. It is known that many species have water-repellent leaves
¹⁷ [Neinhuis and Barthlott, 1997] which are not adapted to uptake water from their leaves. For most plants,
¹⁸ non-meteoric water deposition is a source of nuisance as it may freeze and cause damages to the leaf in cold cli-
¹⁹ mate, or stagnate and cause rotting and pathogen infection in warm environments [Evans et al., 1992]. Leaves
²⁰ that are repeatedly exposed to dew have been shown to become more water-repellent [Aryal and Neuner, 2009].
²¹ However, micro-droplets of water will indeed form on the surface of even very hydrophobic leaves. The
²² interaction of these droplets on the leaf energy balance (foliar shielding) has not yet been studied, despite its
²³ potentially large impact on both leaf water resources and leaf water isotopes.

²⁴ **Leaf energy balance —** Because they are unable to move to the shade, leaves are vulnerable to sun
²⁵ radiation, and they can often be warmer than the surrounding air. The leaf temperature will in turn affect the
²⁶ saturation vapor pressure, isotope fractionation, transpiration, and photosynthesis. Smaller leaves tend to
²⁷ be at a temperature closer to the ambient air, since their boundary layer is thinner. This is the reason why,
²⁸ on a single tree, leaves exposed to the sun are usually smaller than shaded ones. To stay cool, leaves use a
²⁹ combination of re-radiation (transfer of energy to the surroundings), convection (heat loss as cool air moves
³⁰ over the surface of the leaf) and evaporative cooling (evaporation of water inside the leaf into water vapor,
³¹ which is an exothermic process) [Vogel, 2012]. During a drought, leaves have to preserve water to maintain
³² turgor pressure, which competes with evaporative cooling. In this case, leaves are left with re-radiation and
³³ convection to cool themselves down. This is sometimes not enough to maintain a low temperature. If its
³⁴ duration extends for too long, the drought might lead to plant mortality.

³⁵ Non-meteoric water can supply the plants with a pool of water that will supplement the scarce leaf
³⁶ water by depositing a layer of small water droplets on the surface of the leaves. This provides a form of
³⁷ externalized evaporative cooling. Moreover, the presence of the droplets will both increase the albedo of

38 the leaves, allowing it to reflect more energy [Pinter, 1986], and increase surface roughness, which increases
39 the leaf boundary layer, therefore decreasing the vapor pressure deficit (VPD) and lowering the evaporative
40 demand. This later mechanism was proposed by [Limm et al., 2009] to explain how fog suppresses nighttime
41 respiration in redwoods.

42 Foliar shielding is therefore directly affecting the water status of the leaf by influencing the leaf energy
43 cycle. Depending on the location and climate, dew deposition can take from c. 1.5 [Abtew and Melesse, 2012]
44 to 6 hours [Monteith, 1957] after sunrise to completely evaporate from the surface of the leaves. Dew and fog
45 can also form in the late afternoon before sunset [Wilson et al., 1999, Kabela et al., 2009]. Although neither
46 dew nor fog is usually present at the hottest hour of the day, they can effectively shorten the duration of the
47 water-stressed part of the day. This may significantly help the plant maintain its water status over an extended
48 period of drought [Madeira et al., 2002, Proctor, 2012].

49 Dew formation is usually included in global climate models (GCMs) as it merely involves tracking dry
50 bulb temperatures going below the dewpoint temperature. However, its interaction with vegetation is not
51 commonly taken into account. Non-meteoric water deposition events occur around the world, even in dryland
52 ecosystems [Agam and Berliner, 2006], and may affect large areas at the same time. The small changes in
53 the energy, water and carbon balance of each single leaf can therefore have a large cumulative impact at
54 the ecosystem level. Including this interaction into GCMs would allow modelers to better understand the
55 response of vegetation to climate change and the feedback on CO₂ atmospheric concentrations.

56 **Leaf water isotopes** Foliar shielding will influence leaf water isotopes by decreasing leaf transpiration
57 [Farquhar et al., 2006, Cernusak and Kahmen, 2013]. The balance of the stable isotopologues of water has
58 been used for decades to understand plant water fluxes [Allison et al., 1985, Ehleringer and Dawson, 1992,
59 Werner et al., 2012], but as the number of water sources and sinks increases, the interpretation of isotope
60 data can become difficult. The effect of foliar shielding on leaf water isotopes is, for example, likely to be
61 opposite to that of foliar uptake of heavy fog or dew [Scholl et al., 2010], which will enrich leaf water in
62 heavy isotopes. However, foliar uptake studies have so far not taken foliar shielding into account, even though
63 it likely results in an underestimation of the amount of water uptaken by the leaf.

64
65 In this study, we present three experiments that focus on the effects of water droplets deposition at the
66 surface of *Colocasia esculenta* leaves. This specie is native to South East Asian tropical forests but has
67 been cultivated across the world for many centuries under the name of taro. With a contact angle of ~164°
68 [Neinhuis and Barthlott, 1997], *Colocasia esculenta* is considered to have highly water-repellent leaves. Its
69 leaves can reach a size of up to c. 50 cm in length and c. 40 cm in width. We present the first protocol for the
70 fast analysis of small sized leaf samples, allowing for spatial and temporal high-resolution mapping of the
71 leaf-water properties. Using isotopically-labelled water as well as traditional plant physiology techniques, we
72 confirm that the *Colocasia esculenta* leaves do not uptake water from the surface of the leaves. So far, few
73 studies have attempted to map leaf isotopes because it is both time and labor intensive. While the number of
74 replica presented in this study was limited by the novelty of the protocol, c. 550 plant samples were analyzed.
75 This still largely exceeds the number of samples analyzed by previous studies focused on spatial patterns of

leaf-water isotopes [Gan et al., 2002, Šantrůček et al., 2007]. We analyze the spatial patterns of leaf water isotopic enrichment and compare them to three different models. In addition, we show that foliar shielding decreases leaf transpiration and increases water potential, and we present three mechanisms that explain the influence of water droplet deposition on the energy and water cycles of water-repellent leaves. Finally, we compare our results to multiple foliar uptake studies. We conclude that foliar shielding has an opposite and larger effect on leaf isotopes than foliar uptake. It is therefore crucial to include foliar shielding in leaf isotope models to properly interpret isotope data of foliar uptake.

II. Materials and Methods

II.1 The added value of stable isotopes

Stable isotopes of water hold great potential for resolving transpiration and evaporation fluxes across multiple scales [Griffis et al., 2010, Rothfuss et al., 2012, Wang et al., 2013]. The process of evaporation is accompanied by a high degree of isotopic fractionation that leads to evaporated water with an isotopic composition depleted in the heavy isotopologues $H_2^{18}O$ and $HD^{16}O$. This is due to the difference in vapor pressure of the different isotopologues [Farquhar et al., 2006]. Isotopic compositions are commonly expressed in terms of the relative ratios

$$\delta_i = \left(\frac{R_i}{R_{r_i}} - 1 \right) \times 10^3 \quad (1)$$

of isotope ratios [Mook, 2006], where δ_i is expressed in ‰, and the index i stands for either ^{18}O or D. $R_{^{18}O} = [H_2^{18}O]/[H_2^{16}O]$ and $R_D = [HD^{16}O]/[H_2^{16}O]$ are the isotope ratios, while the R_{r_i} are the ratios of the corresponding reference standard. For water, the reference is the Vienna Standard Mean Ocean Water (VSMOW).

Because precipitation condenses under conditions of equilibrium fractionation, $\delta^{18}O$ and δD in precipitation evolve along a line with slope c. 8, the global meteoric water line (GMWL) [Voelker et al., 2014]. However, kinetic isotope effects associated with differences in diffusivity among the different isotopologues of water can lead to deviations from the GMWL [Farquhar et al., 2006]. For example, since $HD^{16}O$ diffusivity is greater than that of $H_2^{18}O$, the water of a leaf that has undergone heavy transpiration will be more depleted in D than in ^{18}O (see Figure 1). Deuterium excess (d-excess) is a widely used measure of how evaporated a pool of water (ocean, lake, leaf) is and is defined as $d\text{-excess} = \delta D - 8 \times \delta^{18}O$. The average d-excess for precipitation is c. 10‰. Lower d-excess values generally indicate that the pool has undergone some evaporation [Brooks et al., 2014] (see Figure 1).

Stable isotopes are also very efficient in helping identify different water sources in plants [Ehleringer and Dawson, 1992]. Simple mixing models allow one to separate the composition and the fluxes coming from different sources [Phillips and Gregg, 2001]. For this reason, stable isotopes are great natural labels that can be used to track pathways of water within plants without harming them; they have been the method of choice for many studies looking at foliar uptake [Breshears et al., 2008, Limm et al., 2009, Eller et al., 2013, Berry et al., 2014b]. Indeed, non-meteoric water is usually enriched in heavy isotopes [Scholl et al., 2010], making it easy to trace even after entering the leaf.

111 II.2 Experiment 1a: Effects of foliar shielding on leaf isotopes in natural conditions

112 Our first experiment examines leaf scale spatial and temporal patterns of water isotopes induced by the
113 presence or the absence of dew under natural conditions. Six bulbs of *Colocasia esculenta* were planted in
114 separate pots. All pots were placed outside and received full sun for four weeks. During this time, all plants
115 were heavily watered with tap water ($\delta^{18}\text{O} \approx -5.96\text{\textperthousand}$, $\delta\text{D} \approx -37.63\text{\textperthousand}$) to allow plant growth. Once the six
116 plants reached maturity, watering stopped and the plants were moved to a shaded area to remove any sun
117 exposure differences between the plants.

118 Watering stopped two days before the beginning of the treatment. The upper-leaf surfaces in three of
119 the six pots were misted with isotopically-enriched water ($\delta^{18}\text{O} \approx 8.85\text{\textperthousand}$, $\delta\text{D} \approx 737.64\text{\textperthousand}$) every two days
120 using a spray bottle. Any extra water would run off the leaves, leaving them covered in submillimeter-size
121 droplets, which is approximately the natural size for dew-deposition drops [Defraeye et al., 2013]. The
122 misting simulated dew and was always performed around 08:00h.

123 The three control pots were not watered and did not receive any mist. To avoid contact between the misted
124 water and the soil in the pots, the surfaces of all pots were covered in wrapping plastic. Six leaves were
125 collected between the beginning of the control/dew treatments and the end of the experiments, three weeks
126 later. The sampling and the analysis are described in Section II.5.

127 II.3 Experiment 1b: Effects of foliar shielding on leaf isotopes under high water stress

128 Our second experiment was designed to artificially increase the contrast between the control and misted
129 treatments from Experiment 1a. The plants from this former experiment were moved into the laboratory and
130 well watered for multiple weeks to offset any effects from the first experiment. Two leaves of similar size and
131 of the same *Colocasia esculenta* plant were cut at the junction of the petiole and the rachis and left to dry c.
132 80 cm under a blue light (Eiko 1960 EBW, 500 W, 10500 lumens, color temperature of 4800 K). The entire
133 experiment lasted four hours. During that time, the treated leaf was misted with isotopically-labelled water
134 ($\delta^{18}\text{O} \approx 8.85\text{\textperthousand}$, $\delta\text{D} \approx 737.64\text{\textperthousand}$) every half-hour. The control leaf was left to dry without any intervention.
135 After four hours, samples were collected from both leaves as described in Section II.5.

136 II.4 Experiment 2: Effects of foliar shielding on leaf water potential

137 In this final experiment, we focused on the effect of water droplet deposition on leaf water potential under
138 high water stressed conditions. One leaf was cut at the junction of the petiole and the rachis and left to dry.
139 Three different water stress conditions were tested here: natural drying (control), high heat drying, and high
140 heat and mist. In the high heat case, the leaf was placed 80 cm under a blue light (Eiko 1960 EBW, 500 W,
141 10500 lumens, color temperature of 4800 K) and left to dry between 8 and up to 10 hours. In the high heat
142 and mist case, the leaf was also misted with ultra pure water every hour using a spray bottle. Again, surplus
143 water was allowed to runoff, leaving the leaf covered in submillimeter size water droplets. Leaf disks of
144 1 inch diameter were collected every hour. The surface of each leaf disk was wetted with ultra pure water,
145 immediately sanded with ultra-fine sandpaper (3M, 600 grit sandpaper), and the water potential analyzed on a
146 WP4C (Decagon Devices Inc.).

147 **II.5 Isotope analysis**

148 For the water isotope analysis, each analyzed leaf was sampled in 12 to 25 different locations depending on the
149 size of the leaf. All of the sampling points were located on the same half of the leaf, and each point consisted
150 of four holes (6 mm diameter) punched next to each other forming a square. Each hole was punched as
151 quickly as possible to avoid evaporation, which would influence the isotopic composition of the neighboring
152 holes. Each leaf disk was then secured in an aluminum foil and inserted in a sealed vial. The entire leaf was
153 sampled in one go. The prepared vials were then stored in the fridge until being analyzed.

154 The leaf samples were analyzed using an Induction Module (IM) combined to a Cavity Ring Down
155 Spectrometer (CRDS) L2103-i from Picarro Inc. (Sunnyvale, CA, USA). The IM was set on the ‘normal
156 leaf’ setting: the leaf disks did not appear carbonized, and after being dried in the oven at 60°C for 48 hours,
157 they showed no decline in weight, proving that this setting dried the leaf samples completely. The IM was
158 equipped with a micro-combustion module (MCM). The MCM has been proven to efficiently reduce the
159 interferences due to the presence of organics in water samples extracted from plants (Kate Dennis, private
160 communication). On average, each half-leaf was sampled in c. 18 different locations, which corresponds to c.
161 73 punched holes.

162 The entire sampling and IM analysis process lasted from 1.5 to 2 days per half leaf depending on the size
163 of the leaf, which limited the number of replicas we were able to conduct for this study. However, the number
164 of leaf disks sampled per leaf far exceeded the c. 25 samples per half leaf collected by [Gan et al., 2002]. In a
165 different study, [Šantrůček et al., 2007] sampled c. 50 disks per half leaf, but the study was carried out only
166 in one replicate for each of the two treatments because of time and money constraints. The size of our study
167 is therefore a significant improvement on previous efforts to map spatial patterns of leaf water isotopes. In
168 addition, the sampling scheme allowed us to look at the temporal evolution of the spatial patterns, which to
169 the best of our knowledge, had never been done before.

170 **IM-CRDS analysis sequence** The M-CRDS analysis sequence was based on [van Geldern and Barth, 2012].
171 Following their notation, Table 1 presents the sequence of standards and samples. Six empty vials were run at
172 the beginning of each run. The average water vapor content, $\delta^{18}\text{O}$, and δD for the six vials were measured
173 and introduced in a mixing model that allowed us to retrieve the true isotopic composition of the sample
174 analyzed. Reference water samples were run using the paper filter provided with the instrument and the
175 same piece of filter paper was reused for all the injections of a single reference water. We found that 3 μl of
176 reference water was necessary to reproduce the amount of water contained by one punch hole of *Colocasia*
177 *esculenta*. The data was corrected for drift and memory effects, and it was also rescaled back to VSMOW.
178 The central vein and the half of the leaf that had not been sampled for IM-CRDS analysis were placed in a
179 vial, and the water was extracted using cryogenic vacuum distillation. This water was then analyzed both by
180 Isotope Ratio Infrared Spectrometry (IRIS) and Isotope Ratio Mass Spectrometry (IRMS) for comparison
181 with the IM-CRDS.

182 **IRIS and IRMS analysis** Ten samples were sent to the Center for Stable Isotope Biogeochemistry at the
183 University of California in Berkeley for IRMS analysis. For the IRMS method, δD was obtained by chromium

184 combustion using an H/Device (labelled as HDEV; Thermo Finnigan, Bremen). Microliters of water were
185 injected in the HDEV and reduced to H₂ gas. The ratio of D/H was then measured on a Thermo Delta Plus
186 mass spectrometer. For the δ¹⁸O analysis, water from standards and samples were pipetted into glass vials
187 and quickly sealed. The vials were then purged with 0.2% CO₂ in Helium and allowed to equilibrate at room
188 temperature for at least 48 hours. The ¹⁸O in the CO₂ was then analyzed by continuous flow using a Thermo
189 Gas Bench II interfaced to a Thermo Delta Plus XL mass spectrometer. In this H₂O-CO₂ equilibration method,
190 the dissolved components (organic and/or inorganic) do not affect the values of δ¹⁸O. For the IRIS analysis,
191 1.8 μl of water was injected into a vaporizer and the vapor was pushed through a MCM. The concentrations
192 of H₂¹⁸O and HD¹⁶O were measured on a water isotope analyzer (L2103-i) from Picarro Inc. (Sunnyvale, CA,
193 USA).

194 The ten samples analyzed both by IRMS and IRIS were used to calculate the offset between the two
195 techniques. All the samples that had been run exclusively by IRIS or IM-CRDS (and had not been analyzed
196 by IRMS) were then corrected for this offset. The IM-CRDS method has not been widely used yet and
197 protocols and precision analyses are still absent from the scientific literature. To justify the results from the
198 IM-CRDS, we compared the values obtained from the extracted water of the half-leaf analyzed by IRIS to the
199 average leaf water composition obtained using a nearest neighbor interpolation on the half-leaf analyzed by
200 IM-CRDS. For the seven leaves analyzed by IM-CRDS, the average difference between those two methods
201 was 2.6±0.88‰ in δ¹⁸O (mean ± SE) and 3.4±2.4‰ in δD. One potential source of error comes from the
202 IM-CRDS analyses being conducted on a different half of a leaf than the IRMS analyses. However, the
203 average difference we observed between two halves of the same *Colocasia esculenta* leaf was 0.3±0.2‰ in
204 δ¹⁸O and 1.9±1.2‰ in δD. The differences between the results obtained with the IM-CRDS and the IRMS
205 are therefore not attributable to the analyses being conducted on different halves of the same leaf. Further
206 testing is clearly necessary before using the IM-CRDS technique as an absolute method. However, our goal in
207 this paper is to compare strongly enriched water samples and the order of the differences presented in the next
208 section are up to two orders of magnitude greater than the error observed for the IM-CRDS. We therefore
209 believe that the IM-CRDS is an appropriate method for our applications, as it allowed us to quickly process
210 many small samples, therefore increasing the spatial and temporal resolution of our analysis.

211 II.6 Linking d-excess and transpiration

212 While d-excess is commonly used in Atmospheric Science [Risi et al., 2013] and for the interpretation
213 of ice core data [Luz et al., 2009], it has not been widely used in plant physiology. However, because
214 it combines both deuterium and ¹⁸O, d-excess contains more information than the isotopologues taken
215 separately. Indeed, lower (more negative) d-excess values are associated with higher transpiration rates
216 [Voelker et al., 2014]. To interpret our d-excess differences in terms of transpiration rates, we link d-excess to
217 steady-state relative humidity. The steady-state enrichment of leaf water Δ_E above source water is expressed
218 in [Farquhar et al., 2006] as

$$\Delta_E = (1 + \epsilon^*)[(1 + \epsilon_k)(1 - h) + h(1 + \Delta_v)] - 1 \quad (2)$$

219 where h is the relative humidity, ϵ^* is the equilibrium fractionation; $\epsilon^* = 9.2 \text{‰}$ (74‰) for H_2^{18}O (HDO) at
220 25°C [Craig and Gordon, 1965]. The kinetic fractionation factor, ϵ_k , is and is taken as

$$\epsilon_k^{\text{H}_2^{18}\text{O}} = \frac{28.5r_s + 18.9r_b}{r_b + r_s} \quad \text{and} \quad \epsilon_k^{\text{HDO}} = \frac{16r_s + 10r_b}{r_b + r_s} \quad (3)$$

221 for H_2^{18}O and HDO, respectively [Farquhar et al., 1989, Farquhar et al., 2006]. r_s is the stomatal resistance,
222 and it is taken to be constant and equal to 217 s m^{-2} [Hughes et al., 2014]. The resistance of the boundary
223 layer, r_b , depends on leaf size and wind speed. Here we choose a constant leaf size of 40 cm and a wind
224 speed of 0.2 m s^{-1} , resulting in an $r_b = 1.13 \cdot 10^5 \text{ s m}^{-2}$. Δ_v is the enrichment of ambient water vapor, which
225 was calculated for a measured composition of $\delta^{18}\text{O} = -17 \text{‰}$ and $\delta\text{D} = -100 \text{‰}$.

226 The enrichment relative to a source can be linked back to isotopic compositions expressed in δ notation
227 through the relative ratios R :

$$\Delta_i = \frac{R_i}{R_{\text{source}}} - 1. \quad (4)$$

228 Using Equation 1 to express R_i as a function of δ_i , we obtain a relation between Δ_i and δ_i

$$\delta_i = \left[\frac{(\Delta_i + 1) R_{\text{source}}}{R_{r_i}} - 1 \right] \times 1000. \quad (5)$$

229 By replacing Δ_i in Equation 5 by its expression from Equation 2 and combining the expressions for $\delta^{18}\text{O}$ and
230 δD , we obtain an expression for the d-excess as a function of the relative humidity h . We then solve for h ,
231 bounding its value between 0 and 1. Assuming that the vapor pressure inside the leaves, e_i , is at saturation,
232 we may calculate the estimated transpiration rate E (in $\text{mmol m}^{-2} \text{ s}^{-1}$) as

$$E = g_s \frac{e_i^* - h e_{\text{air}}^*}{P}. \quad (6)$$

233 Here, P is the atmospheric pressure taken to be 101.3 kPa and g_s (in $\text{mmol m}^{-2} \text{ s}^{-1}$) is the stomatal conductance
234 equal to $1/r_s$. e_i^* (in kPa) is the saturated vapor pressure calculated for a leaf temperature of 25°C . e_{air}^* (in
235 kPa) is the saturated vapor pressure at air temperature, which is also taken to be 25°C . In our analysis, we
236 study the ratio of $E_{\text{dew}}/E_{\text{control}}$, expressed in %.

237 II.7 Understanding spatial patterns

238 Leaf water isotopic composition is often compared to the isotopic composition of freely evaporating water
239 as described by the Craig-Gordon (CG) model [Craig and Gordon, 1965]. In this model, the fractionation is
240 driven by the difference of saturation vapor pressure between the interior of the leaf and the atmosphere, and
241 by the difference of diffusivity of the isotopologues. However, this simplistic model has been shown to largely
242 underestimate the actual isotopic enrichment. Two main models have since then been proposed to better
243 describe the complexity of leaf water isotopes patterns. The effect of the backward diffusion of enriched
244 water, a form of Péclet effect [Farquhar and Lloyd, 1993, Barbour et al., 2004], has been shown to improve
245 the prediction of bulk water enrichment, as well as the progressive enrichment of leaf water between the xylem

and the sites of evaporation [Gan et al., 2002]. The string-of-lakes effect takes into account the progressive enrichment of leaf water along the path of water flow [Yakir et al., 1990, Helliker and Ehleringer, 2000], and improves the modeling of large scale variations of leaf water enrichment.

The Craig-Gordon model of evaporation is expressed as [Gan et al., 2002]

$$\Delta_{CG} = \epsilon_k + \epsilon^* + (\Delta_v - \epsilon_k) \frac{h e_{air}}{e_i^*}, \quad (7)$$

with Δ_v the isotopic enrichment of atmospheric water vapor relative to source water (Eq. 4). ϵ_k , r_b , and e_i^* depend on leaf temperature. Using an infrared picture of a *Colocasia esculenta* leaf, we are able to calculate Δ_{CG} at each pixel to obtain a map of Δ_{CG} that we can then compare to the spatial patterns of the measured isotopic enrichment of leaf water relative to source water (Δ_{lw} , as defined in Eq. 4). Pressure and relative humidity were taken to be constant and equal to 1013 hPa and 80%, respectively.

II.8 Understanding the competing effects of foliar uptake and foliar shielding

To compare the relative effects of foliar uptake and foliar shielding, we analyze the results of three different studies that conducted similar experiments on different species. [Limm et al., 2009] looked at a ten different species from the coast redwood ecosystem of California (*Pseudotsuga menziesii* and *Sequoia sempervirens* (two conifers), *Polystichum munitum* and *Polystichum californicum* (two types of fern), *Oxalis oregana* (a short herbaceous), *Arbutus menziesii*, *Gaultheria shallon*, *Vaccinium ovatum*, *Notholithocarpus densiflorus* and *Umbellularia californica* (all evergreen broadleaf)), while [Eller et al., 2013] focused on *Drimys brasiliensis*, a woody broadleaf evergreen native from Central and South America, and [Berry and Smith, 2014] concentrated on *Abies fraseri* and *Picea rubens*, two montane conifers found in the Appalachian Mountains. All the studies conducted glasshouse experiments in which saplings experienced nighttime fog. Leaf samples were collected in the evening before the fogging treatment and in the morning, right after the treatment. Every study used isotopically labeled fog with a different composition ($\delta D_{fog} - \delta D_{soil} = 16\text{\textperthousand}$ in [Berry and Smith, 2014], $78\text{\textperthousand}$ in [Limm et al., 2009] and $712\text{\textperthousand}$ in [Eller et al., 2013]). To compare the different experiments, we normalized the results to reflect the leaf water enrichment that would have been observed if the fog water had been $20\text{\textperthousand}$ heavier than soil water, since this is within the range of natural values [Scholl et al., 2010].

II.9 Statistical analysis

Responses for the different experiments were analyzed using a two-sample t-test (Welch's t-test) with a 5% significance level. This test has been recognized as a better alternative to the Student's t-test when dealing with groups of unequal sample size or variance [Ruxton, 2006]. In the following, we will report the p-value, P, the test statistics, t, and the degrees of freedom of the test, v. When comparing the results of the different treatments in Experiments 1a and 1b, we treated the multiple samples collected on each leaf as a single population. stat and syst refers to the statistical and the systematic errors, respectively.

277 III. Results

278 **III.1 Effects of foliar shielding in natural conditions**

279 The results of Experiments 1a are presented as maps of the analyzed half leaves (Figure 2). The maps were
280 obtained using an inverse distance interpolation and show the evolution of the d-excess of leaves from the
281 control and misted treatments collected at 0, 12 (dew), 14 (control) and 21 (dew and control) days from the
282 beginning of the experiment. All the maps of δD and $\delta^{18}O$ (Supporting Information, Figures S1 and S2)
283 show a progressive enrichment [Cernusak and Kahmen, 2013] of leaf water when moving away from the
284 main stem towards the rims of the leaf. The average difference between the center and the rim of the leaf for
285 the five leaves presented is $\Delta^{18}O = 11.1 \pm 1.2 \text{ ‰}$ (mean \pm SE) and $\Delta D = 23.9 \pm 3.3 \text{ ‰}$. When comparing the
286 composition of the bulk water at the end of the experiment, the dew-treated leaf exhibits a d-excess higher
287 by c. 63.0‰ than the control one (two-sample t-test: $t = -9.4$, $v = 29$, $P < 0.001$). The effect of the dew
288 treatment is not apparent for days 12/14 ($\Delta d\text{-excess} \approx 10.2 \text{ ‰}$, two-sample t-test: $t = -1.6$, $v = 35$, $P = 0.11$).

289 **III.2 Effects of foliar shielding in high water stress conditions**

290 Similar maps were produced for Experiment 1b (Figure 3). In this case, the heat lamp artificially increased
291 the transpiration rate in both the control and the misted leaves, leading to significantly enriched $\delta^{18}O$ and
292 δD values and low d-excess values for both treatments. The d-excess in the control case is c. 173.0 ‰ more
293 negative than for the dew treated leaves (two-sample t-test: $t = 3.9$, $v = 29$, $P < 0.001$). This experiment was
294 merely an extreme version of Experiment 1a, with the objective of accentuating the contrast between the
295 two treatments. While the high heat treatment led to a strong drying of some areas of the leaf, in particular
296 those far away from the central vein, the significant difference observed between the control and the misted
297 treatments do confirm the results of Experiment 1a.

298 **III.3 Effects of foliar shielding on leaf water potential**

299 Experiment 2 looked at the temporal evolution of water potential in artificially drying leaves (see Figure 4).
300 Strong differences in drying pattern are shown for the misted or drought leaves. In both the control and the the
301 high heat and mist cases, the leaf water potential experiences a slow decline, which is well approximated by a
302 linear function. However, the high heat treated leaves experience a faster decline and are better approximated
303 by a parabola. Table 2 presents the average decline from initial to final leaf water potential for the three
304 different treatments. All the data is normalized for leaf size and drying time. The misted leaves exhibit a
305 much smaller decline in water potential than the leaves subjected to the same high heat treatment but that
306 did not get sprayed (two-sample t-test: $t = 2.37$, $v = 7$, $P < 0.05$). The decline observed for misted leaves is
307 not statistically different to the one observed for naturally drying leaves (two-sample t-test: $t = -1.46$, $v = 6$,
308 $P = 0.19$).

309 IV. Discussion

310 **IV.1 Foliar shielding-induced decrease in transpiration**

311 Since dew treated leaves have higher d-excess values in Experiments 1a and 1b, we might conclude that foliar
312 shielding decreased leaf transpiration. Yet, we must first consider two other processes that will also influence
313 the leaf water isotopes. First, the dew droplets might actually penetrate the dew-treated leaves through foliar
314 uptake. However, the sprayed water was highly enriched ($\delta^{18}\text{O} \approx 8.85\text{\textperthousand}$, $\delta\text{D} \approx 737.64\text{\textperthousand}$) compared to the
315 source water ($\delta^{18}\text{O} \approx -5.96\text{\textperthousand}$, $\delta\text{D} \approx -37.63\text{\textperthousand}$): if foliar uptake had been occurring, the dew treated leaves
316 would have shown an enrichment over the control ones. We observe a decrease in both $\delta^{18}\text{O}$ and δD for the
317 dew-treated plant compared to the control, which is consistent with a lack of foliar uptake. Second, depleted
318 source water contained in the soil and stem of the plant is constantly entering the leaf. We expect this effect
319 has the same impact on both dew treated and control plants, and so we exclude it when interpreting differences
320 between the two treatments. We conclude that foliar shielding is the primary phenomenon impacting leaf
321 water d-excess composition.

322 We apply the model described in Section II.6 to interpret our results in terms of the transpiration rate, E .
323 In the model, all of the changes in leaf isotopic composition are absorbed by the difference in relative humidity.
324 While this is a simplified description of the processes, it allows us to estimate the difference in transpiration
325 rates between the treated and control leaves. In particular, the use of a constant stomatal conductance and leaf
326 temperature are most likely the largest sources of systematic error in this model.

327 To calculate the systematic error associated with our choices for those parameters, we calculate $E_{\text{dew}}/E_{\text{control}}$
328 for a range of leaf temperatures from 10° to 40°C and for a stomatal conductance g_s from 0.1 to 0.8 $\text{mmol m}^{-2} \text{s}^{-1}$.
329 We find that the systematic error associated with our choice of g_s is negligible, while that associated with the
330 choice of T_{leaf} is important for Experiment 1a, but not for Experiment 1b. For Experiment 1a, the transpiration
331 rate obtained for the dew treated leaf is significantly lower than that of the control ($t = -9.4$, $\mu = 38$, $P < 0.0001$)
332 by 29.9 ± 2.6 (stat) ± 1.1 (syst) %. Similar results were found for Experiment 1b, where the dew treatment
333 significantly ($t = -3.9$, $\mu = 29$, $P < 0.0001$) decreased transpiration by 29.9 ± 9.1 (stat) %. These values are
334 consistent with the one existing study on the impacts of dew on plant water use: [Garratt and Segal, 1988]
335 estimated that the reduction in transpiration due to dewfall could reduce daily plant water use by c. 10%. This
336 value was obtained for wheat plants associated with a low transpiration rate. Since our leaves were larger and
337 because our control plants had a higher transpiration rate, we expect the reduction to be larger in our case (see
338 Section IV.2).

339 **Interpreting spatial patterns** To understand the spatial patterns observed in Figures 2 and 3, we calculate
340 the expected CG enrichment for ^{18}O as described in Section II.7. We compare the results to the leaf water
341 enrichment above source water, Δ_{lw} measured for three leaves from Experiment 1a (see Figure 5). All three
342 leaves tested show an enrichment on both side of the 1:1 line, which corresponds to the CG enrichment.

343 Leaf water depleted from the expected CG model points toward a larger importance of the Péclet effect
344 while samples located above and below the CG model show a larger importance of the string-of-lakes effect
345 [Gan et al., 2002]. *Colocasia esculenta* leaves seem to generally behave like a string-of-lakes, in which

the enriched water leftover after transpiration increases the expected enrichment of the next pool. This effect has been shown to be particularly important in monocots, since they tend to have parallel veins with stomata located in-between them that act as enrichment sites [Helliker and Ehleringer, 2000]. Since *Colocasia esculenta* is a monocot itself, our result confirms the main importance of the string-of-lakes effect in monocots, and expand previous work that has so far been concentrating on dicots [Yakir et al., 1990, Gan et al., 2002, Šantrůček et al., 2007], and a few monocots [Helliker and Ehleringer, 2000, Gan et al., 2003]. We find a strong linear correlation ($R^2 = 0.84$, $P < 0.001$) between Δ_{lw}/Δ_{CG} and distance from the petiole (Figure 6). Δ_{lw}/Δ_{CG} appears to be smaller than 1 for samples close to the petiole, and larger than 1 at the tip of the leaf and at the rims. This pattern has already been observed in cotton leaves [Gan et al., 2002], and was pointed out as a characteristic trait of the string-of lakes effect.

Interpreting temporal patterns Leaves collected from both treatments on day 12 or 14 present results that disagree with the trends formed by the results of day 0 and 21 (Figure 2). For the control, d-excess is generally decreasing between day 0 and day 21, but the leaf collected on day 14 shows values of d-excess higher than expected. In the dew treatment case, the general trend is reverse and d-excess at the end of the experiment (day 21) is much higher than on day 0. However, the dew treated leaf collected on day 12 presents lower values of d-excess than expected from this trend. It is important to note that the plants were kept outside throughout the experiment and were therefore subjected to the daily variations of temperature and relative humidity, which both influence the transpiration rate as well as the isotopic composition. The dew-treated leaf collected on day 12 was sampled after a prolonged period of dry and hot weather that might have enhanced the transpiration despite the artificial dew treatment. This may explain why this leaf presents lower d-excess values than expected. During the experiment, the plants were kept in a shaded, protected area below a building where the temperature is often lower and the relative humidity higher than outside, which lead to natural dew formation on some nights. We believe this to be particularly relevant for the four days preceding the collection of the first control leaf on day 14. Finally, a series of small rain events happened on the day preceding this collection, which may have decreased the transpiration rate and increased the d-excess composition of the leaf.

IV.2 Effects of foliar shielding on the leaf energy cycle

Our results show that the deposition of submillimeter size droplets allow the leaf to decrease its transpiration rate and maintain its water potential. The water balance of the leaf is influenced by the change in energy balance associated with the water droplets deposited at the surface through three distinct processes.

First, the deposited droplets increase the albedo of the leaf, allowing more of the radiation to be reflected away from the leaf. The albedo is the reflection coefficient for solar radiation off natural surfaces. Depending on the direction of the incoming solar radiation, water can have an albedo as high as 1 (perfect reflector) whereas typical values for leaves are c. 0.2 for visible light. The increase of vegetation albedo due to dew deposition has been observed in the field many times [Pinter, 1986, Zhang et al., 2012]. By reflecting more radiation when they are wet, leaves will decrease the incoming shortwave radiation and consequently keep their temperatures lower. This will in turn reduce the evaporative demand and the leaf transpiration.

383 Second, part of the on-coming energy will be dissipated through the evaporation of the droplets, which
384 also provides evaporative cooling to the surface of the plant. The energy that is not reflected by the droplets
385 will be used to evaporate them; because of the high heat capacity of water, the evaporation of the droplets
386 will dissipate energy that will not contribute to the leaf energy budget. Moreover, because evaporation is an
387 exothermic process, the evaporation of the water droplets will result in a cooling of the leaf surface. This will
388 again reduce the evaporative demand and the transpiration.

389 Finally, the evaporating droplets increase the boundary layer [Defraeye et al., 2013] and locally decrease
390 the VPD, creating a moister environment around the leaf. The increase in surface roughness associated
391 with the presence of the droplets at the surface of the leaf will also contribute to increasing the size of the
392 boundary layer. The evaporation of the droplets will cause the air close to the leaf to have a higher relative
393 humidity than the surrounding air, creating a moist micro-climate around the leaf [Jones, 1992]. This will
394 decrease the difference between the interstitial and the air vapor pressures. This decrease in gradient will
395 therefore reduce the flux of water vapor out of the leaf, namely transpiration. By decreasing the outward
396 flow of water vapor, more CO₂ will be able to enter the leaf, increasing interstitial CO₂ concentration,
397 photosynthesis, and water use efficiency. Water potential values are correlated with leaf relative water content
398 [Maxwell and Redmann, 1978] and with stomatal conductance [Lhomme et al., 1998]; by maintaining a
399 higher water potential, the leaf will be able to open its stomata wider. CO₂ assimilation is in turn linearly
400 correlated to stomatal conductance [Lambers et al., 2008]. As a result, by affecting the leaf energy cycle,
401 foliar shielding will allow the leaf to maintain its water status and increase CO₂ assimilation through multiple
402 mechanisms.

403 IV.3 Implications for foliar uptake studies using stable isotopes

404 By decreasing evaporation, foliar shielding suppresses the isotopic enrichment associated with leaf water
405 transpiration [Farquhar et al., 2006]. Therefore, leaves undergoing foliar shielding will have a bulk isotopic
406 composition lower (more depleted) than leaves that do not experience it. The average δD enrichment
407 between the first and last days of collection for Experiment 1A were $-9.1 \pm 3.7 \text{ ‰}$ for the control leaf and
408 $-27.9 \pm 2.9 \text{ ‰}$ for the dew treated leaf. This corresponds to a $-18.8 \pm 6.6 \text{ ‰}$ difference in enrichment between
409 sprayed and control treatments. In the case of highly water stressed leaves (Figure 3), the difference in
410 enrichment reaches $-45.2 \pm 35.8 \text{ ‰}$.

411 Non-meteoric water is usually more enriched in deuterium than rain and soil water by up to 50 ‰
412 [Scholl et al., 2010]. If foliar uptake is indeed happening in a leaf, the uptake of heavy fog water will then
413 enrich the leaf water, while foliar shielding depletes leaf water in heavy isotopes. [Limm et al., 2009] pointed
414 out the tension between foliar uptake and nighttime suppression of respiration due to the saturated atmosphere
415 during fog events. Transpiration is a much larger water loss for plants than respiration and the effects of foliar
416 shielding during day time is expected to be have a even larger impact on leaf isotopes than that discussed by
417 [Limm et al., 2009].

418 Using previous studies on foliar uptake (described in Section II.8), we were able to compare the relative
419 impact of both processes. Foliar uptake has the largest impact on conifers (see Figure 7), where the difference
420 in enrichment between treatment and control reaches up to c. 20 ‰. Foliar shielding for the non-water stressed

case (Experiment 1a) exhibits the opposite effect, with a magnitude similar to the largest foliar uptake case. In the water stressed case (Experiment 1b), the depletion observed is as large as c. 45.2 %. The three foliar experiments presented here all used nighttime treatment, so foliar shielding did not impact the enrichment observed. However, the competing effects of foliar uptake and foliar shielding are likely to be very important when analyzing field or day time foliar uptake experiment data. For example, [Berry et al., 2014b] observed a significantly larger enrichment when fogging saplings in the morning than in the afternoon or the evening. This results is well explained if the effects of foliar shielding on temperature and transpiration are taken into account. Our results suggest that, in the field, foliar shielding has a larger impact on leaf isotopes than foliar uptake. The relative importance of foliar uptake VS foliar shielding will depend on many factors, including the isotopic composition of the non-meteoric water, the timing and length of the wetting event, the size of the leaf, the atmospheric conditions and of course, the specie. To properly interpret isotope data, future studies on foliar uptake should include foliar shielding into their isotope balance calculation.

The results of our study show a larger impact of foliar shielding in times of drought than in well-watered conditions. The simultaneous occurrence of non-meteoric water deposition and drought is common in drylands [Agam and Berliner, 2006], where many plants rely on non-meteoric water as their primary source of water [Stanton and Horn, 2013]. Regular dew formation has also been observed in the upper canopy of the Amazon forest during the dry season [Satake and Hanado, 2004, Frolking et al., 2011]. In those cases, energy balance is thought to be the main driver of leaf water isotopic composition, with a response much larger than that of soil water availability, for example [Wayland, 2015]. Foliar shielding will delay the time when leaves reach their maximum transpiration rate and attain isotopic steady state [Dubbert et al., 2014]. Isotopic steady state is often assumed when interpreting transpiration data, but [Dubbert et al., 2013] recently showed that this assumption is typically unjustified and can lead to errors in estimated transpiration fluxes by up to 70%, since steady state models systematically overestimate the isotopic enrichment of leaf water. Isotopic steady state depends on the leaf transpiration rate, which changes quickly as energy flux incident on the leaf changes, for example when the leaf goes from the shade to the sun. Foliar shielding will have a large impact at short time scales on both leaf transpiration and water isotopes because of this fast response.

In this study, we used the highly hydrophobic leaves of *Colocasia esculenta* to look at the impacts of dew water droplets deposition (called foliar shielding) on the leaf energy, water and isotope balance. We show that the spatial patterns of enrichment are consistent with the string-of-lakes model, which is common in monocots. Our results show that foliar shielding significantly decreases leaf transpiration by c. 30%, maintains leaf water potential, and limits leaf water isotopic enrichment. We highlight the opposite effects of foliar uptake, which enriches leaf water in heavy isotopes, and foliar shielding, which depletes it. Because both effects are of similar magnitude, taking into accounts both processes is crucial to properly interpret field data of foliar uptake. Our results are also in agreement with recent studies pointing at the importance of non-isotopic steady state for the proper understanding of leaf water fluxes. More experiments are now required to understand the effects of foliar shielding on different species and for a range of leaf shapes and sizes. Introducing stable isotopes of water in a model of leaf energy and water balance could help to interpret the competing effects of foliar uptake and foliar shielding, give a new insight into non-steady-state transpiration, and improve the general understanding of the interaction of leaves with their environment.

460 Acknowledgments

461 The authors thank Todd Dawson and Wenbo Yang for the IRMS analysis, and Fulton Rockwell for the
462 discussion on spatial patterns. C.Gerlein-Safdi and K.K. Caylor acknowledge the financial support of NASA
463 Headquarters under the NASA Earth and Space Science Fellowship Program - Grant 14-EARTH14F-241 -
464 and of the Science, Technology, and Environmental Policy Fellowship from the Princeton Environmental
465 Institute.

REFERENCES

- [Abtew and Melesse, 2012] Abtew, W. and Melesse, A. (2012). *Evaporation and Evapotranspiration - Measurements and Estimations*. Springer Science & Business Media.
- [Agam and Berliner, 2006] Agam, N. and Berliner, P. R. (2006). Dew formation and water vapor adsorption in semi-arid environments—A review. *Journal of Arid Environments*, 65(4):572–590.
- [Allison et al., 1985] Allison, G. B., Gat, J. R., and Leaney, F. W. J. (1985). The relationship between deuterium and oxygen-18 delta values in leaf water. *Chemical Geology: Isotope Geoscience section*, 58(1-2):145–156.
- [Andrade, 2003] Andrade, J. L. (2003). Dew deposition on epiphytic bromeliad leaves: an important event in a Mexican tropical dry deciduous forest. *Journal of Tropical Ecology*, 19(5):479–488.
- [Aryal and Neuner, 2009] Aryal, B. and Neuner, G. (2009). Leaf wettability decreases along an extreme altitudinal gradient. *Oecologia*, 162(1):1–9.
- [Barbour et al., 2004] Barbour, M. M., Roden, J. S., Farquhar, G. D., and Ehleringer, J. R. (2004). Expressing leaf water and cellulose oxygen isotope ratios as enrichment above source water reveals evidence of a Pécel effect. *Oecologia*, 138(3):426–435.
- [Berry et al., 2014a] Berry, Z. C., Hughes, N. M., and Smith, W. K. (2014a). Cloud immersion: an important water source for spruce and fir saplings in the southern Appalachian Mountains. *Oecologia*, 174(2):319–326.
- [Berry and Smith, 2014] Berry, Z. C. and Smith, W. K. (2014). Experimental cloud immersion and foliar water uptake in saplings of *Abies fraseri* and *Picea rubens*. *Trees*, 28(1):115–123.
- [Berry et al., 2014b] Berry, Z. C., White, J. C., and Smith, W. K. (2014b). Foliar uptake, carbon fluxes and water status are affected by the timing of daily fog in saplings from a threatened cloud forest. *Tree Physiology*, 34(5):459–470.
- [Breshears et al., 2008] Breshears, D. D., McDowell, N. G., Goddard, K. L., Dayem, K. E., Martens, S. N., Meyer, C. W., and Brown, K. M. (2008). Foliar absorption of intercepted rainfall improves woody plant water status most during drought. *Ecology*, 89(1):41–47.

- [Brooks et al., 2014] Brooks, J. R., Gibson, J. J., Birks, S. J., Weber, M. H., Rodecap, K. D., and Stoddard, J. L. (2014). Stable isotope estimates of evaporation: inflow and water residence time for lakes across the United States as a tool for national lake water quality assessments. *Limnology and Oceanography*, 59(6):2150–2165.
- [Burgess and Dawson, 2004] Burgess, S. and Dawson, T. E. (2004). The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell & Environment*, 27(8):1023–1034.
- [Cernusak and Kahmen, 2013] Cernusak, L. A. and Kahmen, A. (2013). The multifaceted relationship between leaf water ^{18}O enrichment and transpiration rate. *Plant, Cell & Environment*, 36(7):1239–1241.
- [Clus et al., 2008] Clus, O., Ortega, P., Muselli, M., Milimouk, I., and Beysens, D. (2008). Study of dew water collection in humid tropical islands. *Journal of Hydrology*, 361(1-2):159–171.
- [Craig and Gordon, 1965] Craig, H. and Gordon, L. I. (1965). Deuterium and oxygen-18 variations in the ocean and the marine atmosphere . *Proceedings of a Conference on Stable Isotopes in Oceanographic Studies and Palaeotemperatures*, pages 9–130.
- [Defraeye et al., 2013] Defraeye, T., Verboven, P., Derome, D., Carmeliet, J., and Nicolai, B. (2013). Stomatal transpiration and droplet evaporation on leaf surfaces by a microscale modelling approach. *International Journal of Heat and Mass Transfer*, 65:180–191.
- [Dubbert et al., 2013] Dubbert, M., Cuntz, M., Piayda, A., Maguás, C., and Werner, C. (2013). Partitioning evapotranspiration – Testing the Craig and Gordon model with field measurements of oxygen isotope ratios of evaporative fluxes . *Journal of Hydrology*, 496(C):142–153.
- [Dubbert et al., 2014] Dubbert, M., Cuntz, M., Piayda, A., and Werner, C. (2014). Oxygen isotope signatures of transpired water vapor: the role of isotopic non-steady-state transpiration under natural conditions. *New Phytologist*, 203(4):1242–1252.
- [Ehlner and Dawson, 1992] Ehleringer, J. R. and Dawson, T. E. (1992). Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell & Environment*, 15(9):1073–1082.
- [Eller et al., 2013] Eller, C. B., Lima, A. L., and Oliveira, R. S. (2013). Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis*(Winteraceae). *New Phytologist*, 199(1):151–162.
- [Evans et al., 1992] Evans, K. J., Nyquist, W. E., and Latin, R. X. (1992). A model based on temperature and leaf wetness duration for establishment of alternaria leaf-blight of muskmelon. *Phytopathology*, 82(8):890–895.
- [Farquhar et al., 1989] Farquhar, G., Hubick, K., Condon, A., and Richards, R. (1989). *Stable Isotopes in Ecological Research*, chapter Carbon isotope fractionation and plant water-use efficiency, pages 21–40. Springer New York.

- [Farquhar and Lloyd, 1993] Farquhar, G. and Lloyd, J. (1993). *Stable Isotopes and Plant Carbon-water Relations*, chapter Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the atmosphere, pages 47–70. Academic Press, New York.
- [Farquhar et al., 2006] Farquhar, G. D., Cernusak, L. A., and Barnes, B. (2006). Heavy water fractionation during transpiration. *Plant Physiology*, 143(1):11–18.
- [Frolking et al., 2011] Frolking, S., Milliman, T., Palace, M., Wisser, D., Lammers, R., and Fahnestock, M. (2011). Tropical forest backscatter anomaly evident in SeaWinds scatterometer morning overpass data during 2005 drought in Amazonia. *Remote Sensing of Environment*, 115(3):897–907.
- [Gan et al., 2003] Gan, K. S., Wong, S. C., and Yong, Jean Wan Hongand Farquhar, G. D. (2003). Evaluation of models of leaf water ^{18}O enrichment using measurements of spatial patterns of vein xylem water, leaf water and dry matter in maize leaves. *Plant, Cell & Environment*, 26(9):1479–1495.
- [Gan et al., 2002] Gan, K. S., Wong, S. C., Yong, J. W. H., and Farquhar, G. D. (2002). ^{18}O spatial patterns of vein xylem water, leaf water, and dry matter in cotton leaves. *Plant Physiology*, 130(2):1008–1021.
- [Garratt and Segal, 1988] Garratt, J. R. and Segal, M. (1988). On the contribution of atmospheric moisture to dew formation. *Boundary-Layer Meteorology*, 45(3):209–236.
- [Griffis et al., 2010] Griffis, T. J., Sargent, S. D., Lee, X., Baker, J. M., Greene, J., Erickson, M., Zhang, X., Billmark, K., Schultz, N., Xiao, W., and Hu, N. (2010). Determining the Oxygen Isotope Composition of Evapotranspiration Using Eddy Covariance. *Boundary-Layer Meteorology*, 137(2):307–326.
- [Helliker and Ehleringer, 2000] Helliker, B. R. and Ehleringer, J. R. (2000). Establishing a grassland signature in veins: ^{18}O in the leaf water of C3 and C4 grasses. *PNAS*, 97(14):7894–7898.
- [Hughes et al., 2014] Hughes, N. M., Carpenter, K. L., Keidel, T. S., Miller, C. N., Waters, M. N., and Smith, W. K. (2014). Photosynthetic costs and benefits of abaxial versus adaxial anthocyanins in Colocasia esculenta ‘Mojito’. *Planta*, 240(5):971–981.
- [Jones, 1992] Jones, H. G. (1992). *Plants and microclimate: a quantitative approach to environmental plant physiology*. Cambridge University Press.
- [Kabela et al., 2009] Kabela, E. D., Hornbuckle, B. K., Cosh, M. H., Anderson, M. C., and Gleason, M. L. (2009). Dew frequency, duration, amount, and distribution in corn and soybean during SMEX05. *Agricultural and Forest Meteorology*, 149(1):11–24.
- [Lakatos et al., 2012] Lakatos, M., Obregón, A., Büdel, B., and Bendix, J. (2012). Midday dew - an overlooked factor enhancing photosynthetic activity of corticolous epiphytes in a wet tropical rain forest. *New Phytologist*, 194(1):245–253.
- [Lambers et al., 2008] Lambers, H., Chapin, III, F. S., and Pons, T. L. (2008). *Plant Physiological Ecology*. Springer Science & Business Media.

- [Lhomme et al., 1998] Lhomme, J. P., Elguero, E., Chehbouni, A., and Boulet, G. (1998). Stomatal control of transpiration: Examination of Monteith's formulation of canopy resistance. *Water Resources Research*, 34(9):2301–2308.
- [Limm et al., 2009] Limm, E. B., Simonin, K. A., Bothman, A. G., and Dawson, T. E. (2009). Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. *Oecologia*, 161(3):449–459.
- [Luz et al., 2009] Luz, B., Barkan, E., Yam, R., and Shemesh, A. (2009). Fractionation of oxygen and hydrogen isotopes in evaporating water. *Geochimica et Cosmochimica Acta*, 73(22):6697–6703.
- [Madeira et al., 2002] Madeira, A. C., Kim, K. S., Taylor, S. E., and Gleason, M. L. (2002). A simple cloud-based energy balance model to estimate dew. *Agricultural and Forest Meteorology*, 111(1):55–63.
- [Maxwell and Redmann, 1978] Maxwell, J. O. and Redmann, R. E. (1978). Leaf water potential, component potentials and relative water content in a xeric grass, *Agropyron dasystachyum* (Hook.) Scribn. *Oecologia*, 35(3):277–284.
- [Monteith, 1957] Monteith, J. L. (1957). Dew. *Quarterly Journal of the Royal Meteorological Society*, 83:322–341.
- [Mook, 2006] Mook, W. G. (2006). *Introduction to Isotope Hydrology Stable and Radioactive Isotopes of Hydrogen, Carbon and Oxygen*. Taylor & Francis, London.
- [Neinhuis and Barthlott, 1997] Neinhuis, C. and Barthlott, W. (1997). Characterization and distribution of water-repellent, self-cleaning plant surfaces. *Annals of Botany*, 79(6):667–677.
- [Phillips and Gregg, 2001] Phillips, D. L. and Gregg, J. W. (2001). Uncertainty in source partitioning using stable isotopes. *Oecologia*, 127(2):171–179.
- [Pinter, 1986] Pinter, P. J. (1986). Effect of dew on canopy reflectance and temperature. *Remote Sensing of Environment*, 19(2).
- [Proctor, 2012] Proctor, M. C. F. (2012). Dew, where and when? 'There are more things in heaven and earth, Horatio, than are dreamt of in your philosophy...'. *New Phytologist*, 194(1):10–11.
- [Risi et al., 2013] Risi, C., Landais, A., Winkler, R., and Vimeux, F. (2013). Can we determine what controls the spatio-temporal distribution of d-excess and ^{17}O -excess in precipitation using the LMDZ general circulation model? *Climate of the Past*, 9(5):2173–2193.
- [Rothfuss et al., 2012] Rothfuss, Y., Braud, I., Le Moine, N., Biron, P., Durand, J.-L., Vauclin, M., and Bariac, T. (2012). Factors controlling the isotopic partitioning between soil evaporation and plant transpiration: Assessment using a multi-objective calibration of SiSPAT-Isotope under controlled conditions. *Journal of Hydrology*, 442-443:75–88.
- [Ruxton, 2006] Ruxton, G. D. (2006). The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U test. *Behavioral Ecology*, 17(4):688–690.

- [Šantrůček et al., 2007] Šantrůček, J., Kveton, J., Setlík, J., and Bulícková, L. (2007). Spatial variation of deuterium enrichment in bulk water of snowgum leaves. *Plant Physiology*, 143(1):88–97.
- [Satake and Hanado, 2004] Satake, M. and Hanado, H. (2004). Diurnal change of Amazon rain forest σ^0 observed by Ku-band spaceborne radar. *IEEE Transactions on Geoscience and Remote Sensing*, 42(6):1127–1134.
- [Scholl et al., 2010] Scholl, M., Eugster, W., and Burkard, R. (2010). Understanding the role of fog in forest hydrology: stable isotopes as tools for determining input and partitioning of cloud water in montane forests. *Hydrological Processes*, 25(3):353–366.
- [Stanton and Horn, 2013] Stanton, D. E. and Horn, H. S. (2013). Epiphytes as “filter-drinkers”: life-form changes across a fog gradient. *The Bryologist*, 116(1):34–42.
- [van Geldern and Barth, 2012] van Geldern, R. and Barth, J. A. C. (2012). Optimization of instrument setup and post-run corrections for oxygen and hydrogen stable isotope measurements of water by isotope ratio infrared spectroscopy (IRIS). *Limnology and Oceanography: Methods*, 10:1024–1036.
- [Voelker et al., 2014] Voelker, S. L., Brooks, J. R., Meinzer, F. C., Roden, J., Pazdur, A., Pawelczyk, S., Hartsough, P., Snyder, K., Plavcová, L., and Šantrůček, J. (2014). Reconstructing relative humidity from plant $\delta^{18}\text{O}$ and δD as deuterium deviations from the global meteoric water line. *Ecological Applications*, 24(5):960–975.
- [Vogel, 2012] Vogel, S. (2012). *The Life of a Leaf*. The University of Chicago Press.
- [Wang et al., 2013] Wang, L., Niu, S., Good, S. P., Soderberg, K., McCabe, M. F., Sherry, R. A., Luo, Y., Zhou, X., Xia, J., and Caylor, K. K. (2013). The effect of warming on grassland evapotranspiration partitioning using laser-based isotope monitoring techniques. *Geochimica et Cosmochimica Acta*, 111:28–38.
- [Wayland, 2015] Wayland, H. (2015). An ecohydrological characterization of two African savanna trees under water stress. Master’s thesis, Princeton University.
- [Werner et al., 2012] Werner, C., Schnyder, H., Cuntz, M., Keitel, C., Zeeman, M. J., Dawson, T. E., Badeck, F. W., Brugnoli, E., Ghashghaei, J., Grams, T. E. E., Kayler, Z. E., Lakatos, M., Lee, X., Máguas, C., Ogée, J., Rascher, K. G., Siegwolf, R. T. W., Unger, S., Welker, J., Wingate, L., and Gessler, A. (2012). Progress and challenges in using stable isotopes to trace plant carbon and water relations across scales. *Biogeosciences*, 9(8):3083–3111.
- [Wilson et al., 1999] Wilson, T. B., Bland, W. L., and Norman, J. M. (1999). Measurement and simulation of dew accumulation and drying in a potato canopy. *Agricultural and Forest Meteorology*, 93(2):111–119.
- [Yakir et al., 1990] Yakir, D., DeNIRO, M. J., and Gat, J. R. (1990). Natural deuterium and oxygen-18 enrichment in leaf water of cotton plants grown under wet and dry conditions: evidence for water compartmentation and its dynamics. *Plant, Cell & Environment*, 13(1):49–56.

[Zhang et al., 2012] Zhang, Y.-f., Wang, X.-p., Pan, Y.-x., and Hu, R. (2012). Diurnal and seasonal variations of surface albedo in a spring wheat field of arid lands of Northwestern China. *International journal of Biometeorology*, 57(1):67–73.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1: Interpolated maps showing the δD of the leaves analyzed in Experiment 1a.

Fig. S2: Interpolated maps showing the $\delta^{18}\text{O}$ of the leaves analyzed in Experiment 1a.

Identifiers		
ID	Type	Injections
Blank 1 to	Empty vial	1
Blank 6	Empty vial	1
DEST	Drift ref. water	10
HIS	High ref. water	10
ANTA	Low ref. water	10
DEST	Drift ref. water	10
HERA	QC ref. water	4
Sample 1 to	Sample	4
Sample 10	Sample	4
DEST	Drift ref. water	6
Sample 11 to	Sample	4
Sample 20	Sample	4
DEST	Drift ref. water	6

Table 1: Typical sequence layout of an IM-CRDS run with four reference waters. Following [van Geldern and Barth, 2012], HIS and ANTA are the names of the reference waters with high and low delta values, DEST and HERA are intermediate waters. DEST is the drift monitoring reference water whereas HERA is treated as a sample for quality control. All reference waters except HERA are used for memory correction.

Treatment	Average drop in leaf water potential over 8h (MPa)	SE
Natural drying	0.43	0.03
High heat & mist	1.05	0.31
High heat	2.9	0.77

Table 2: Average drop in water potential (MPa) for the three treatments of Experiment 2: ‘Natural drying’ (control), ‘High heat & mist’ and ‘High heat’. All the data was normalized to reflect the drop in water potential for a 40 cm long leaf over 8 hours.

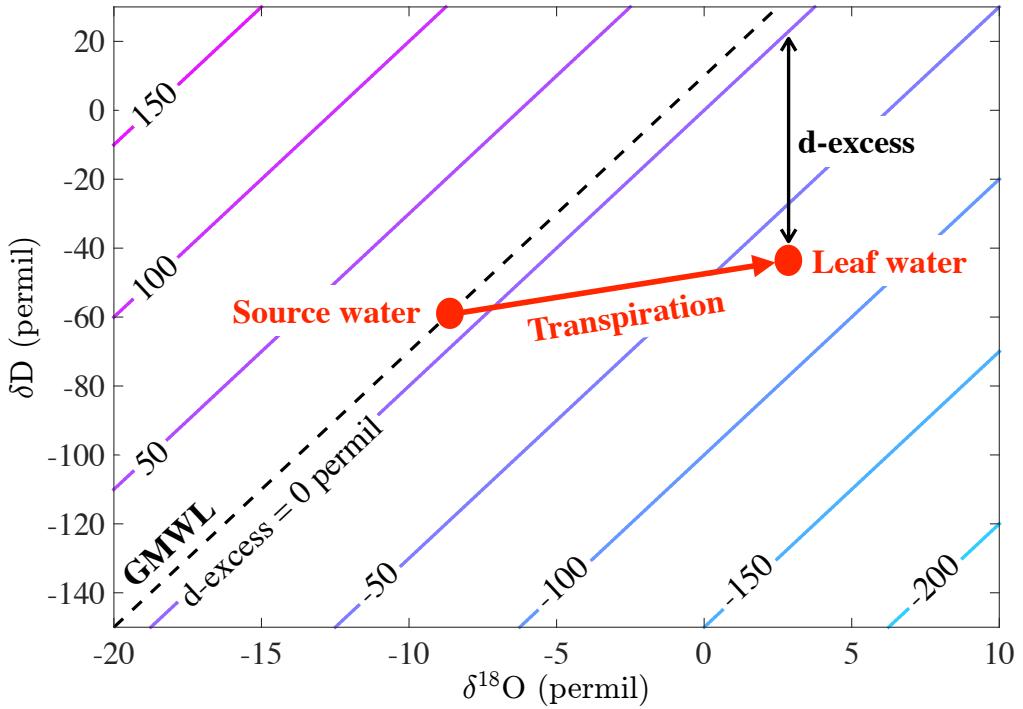


Figure 1: Adapted from [Voelker et al., 2014]: Conceptual figure showing the evaporative conditions controlling the evolution of $\delta^{18}\text{O}$ and δD in leaf water from source water located on the global meteoric water line (GMWL, dashed black line). The slope of the transpiration line depends on the relative humidity. The d -excess of a sample is the vertical distance from that sample to the d -excess reference line. The position of the source water along the GMWL depends on the temperature at which the water condensed and on the isotopic composition of the vapor.

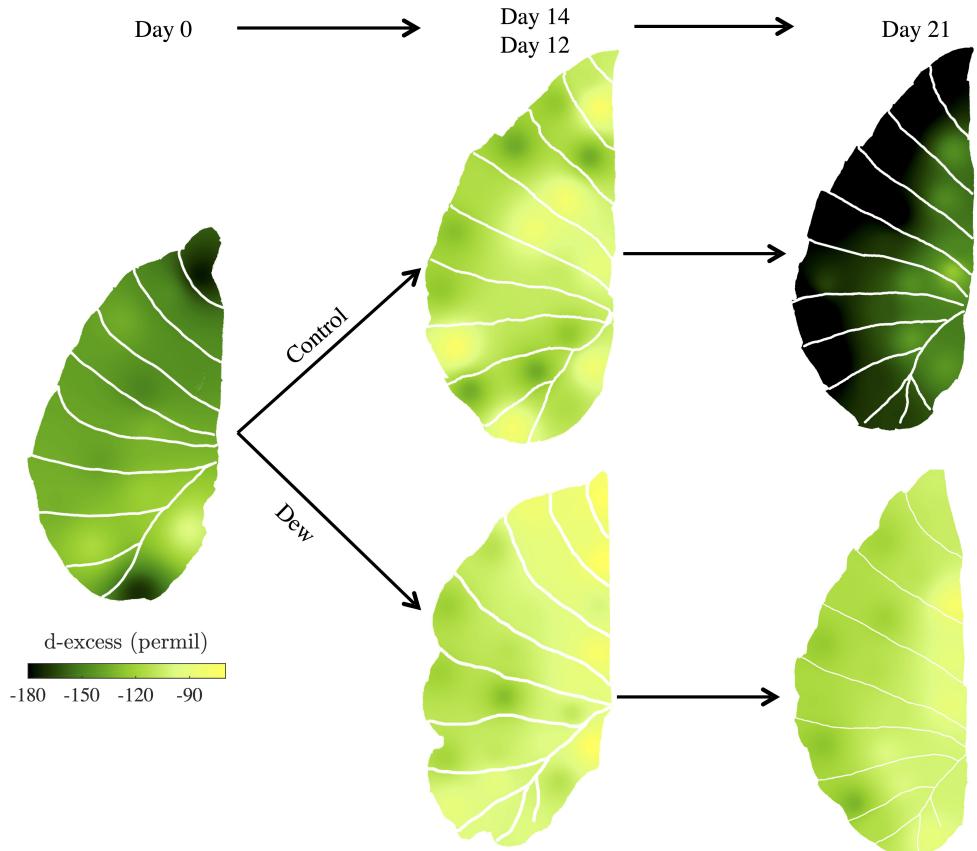


Figure 2: Maps of the spacial distribution of d-excess of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial leaf collected on day 0. **Top row:** leaves collected on day 14 (center) and 21 (far right) from the control. **Bottom row:** leaves collected on day 12 (center) and 21 (far right) from the sprayed treatment, where the leaves were sprayed with isotopically enriched water ($\delta^{18}\text{O} \approx 8.85\text{\textperthousand}$, $\delta D \approx 737.64\text{\textperthousand}$) every two days. The color scheme is the same for all rows.

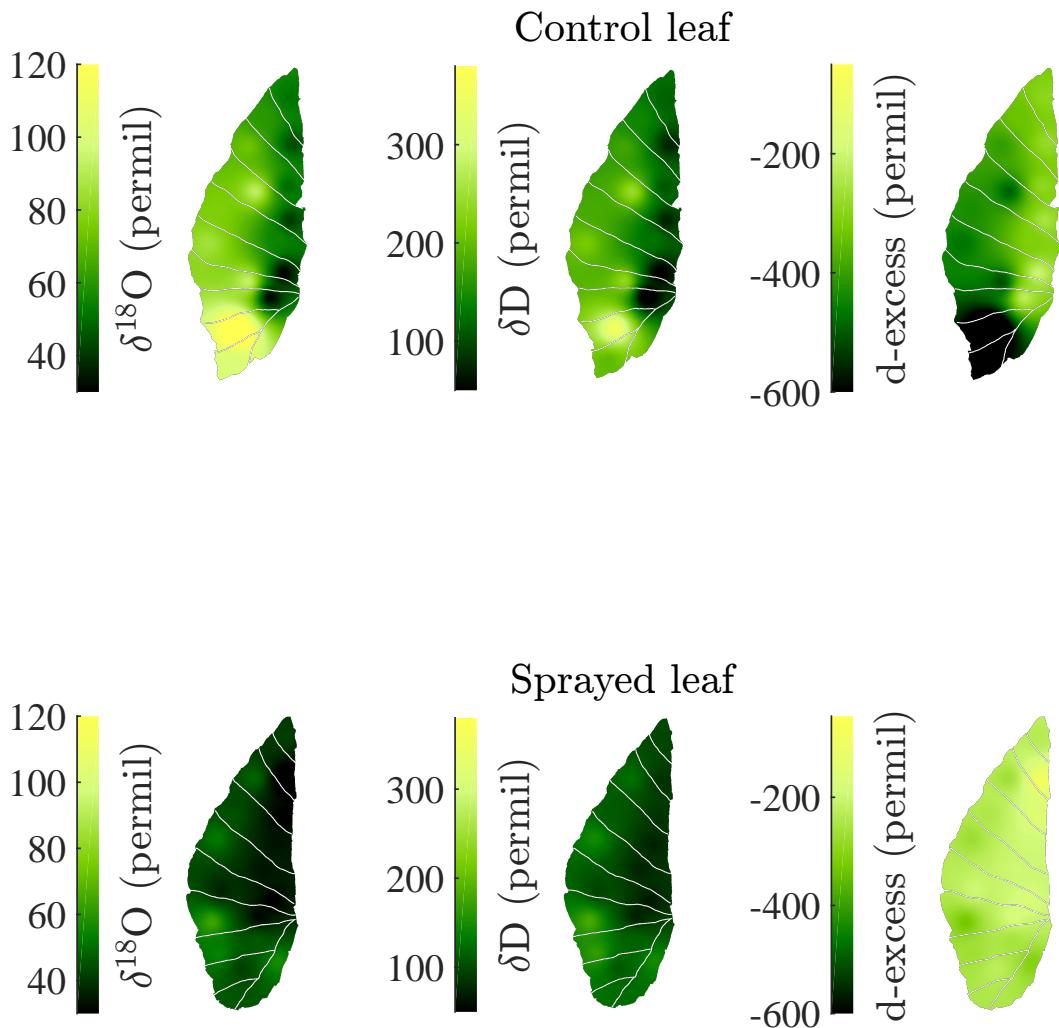


Figure 3: Maps of two leaves left to dry under a 500W blue light for four hours. **Top row:** $\delta^{18}\text{O}$, δD and d-excess of the control (not sprayed) leaf. **Bottom row:** $\delta^{18}\text{O}$, δD and d-excess of the leaf sprayed with isotopically enriched water ($\delta^{18}\text{O} \approx 8.85\text{‰}$, $\delta\text{D} \approx 737.64\text{‰}$) every half-hour. The control leaf shows higher enrichment and lower d-excess values that are associated with enhanced transpiration compared to the sprayed leaf.

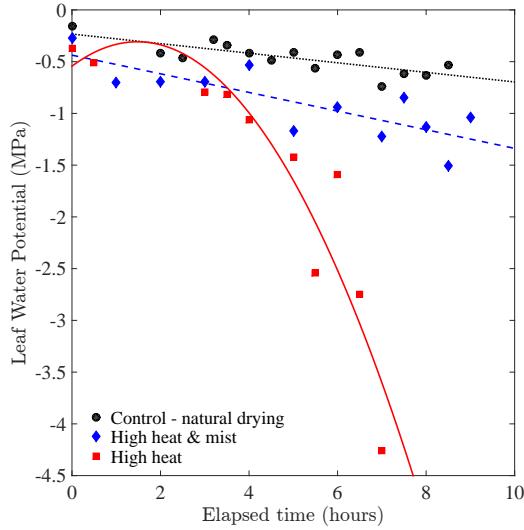


Figure 4: Typical examples of the temporal evolution of the leaf water potential of *Colocasia esculenta* leaves under three different treatments. All the leaves under the natural drying (black circles) and the high heat and mist (blue diamonds) treatments are well fit by a linear relation (black dotted and blue dashed lines, respectively). All but one of the leaves under the high heat drying case (red squares) are better fit by a parabola (red solid line). All the leaves shown here are c. 38 cm long.

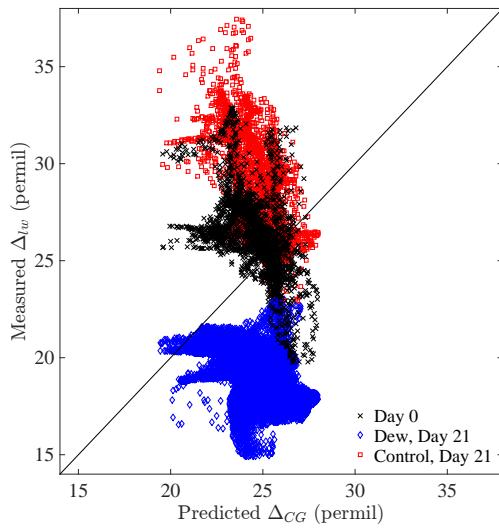


Figure 5: Comparison of the measured Δ_{Iw} and the Craig-Gordon predicted Δ_{CG} for ^{18}O in three leaves from Experiment 1a. **Black crosses:** initial leaf collected at day 0, **blue diamonds:** leaf collected on day 21 from the spray treatment, **red squares:** leaf collected on day 21 from the control. The black line represents a 1:1 relationship.

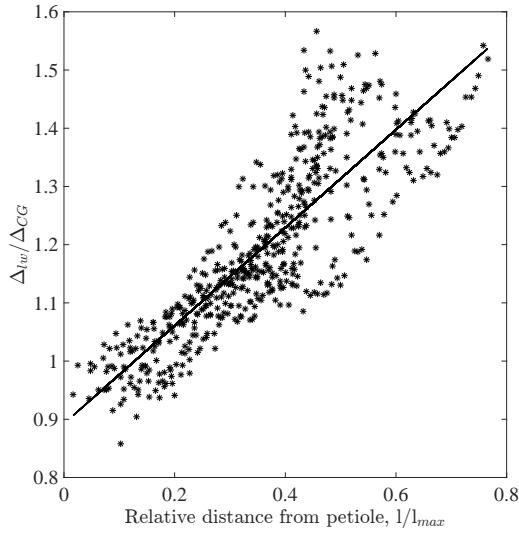


Figure 6: Ratio Δ_{Iw}/Δ_{CG} for ^{18}O in the leaf collected on day 21 from the control plant of Experiment 1a as a function of distance from the petiole relative to leaf total length (l_{max}). The black line represents a linear fit.

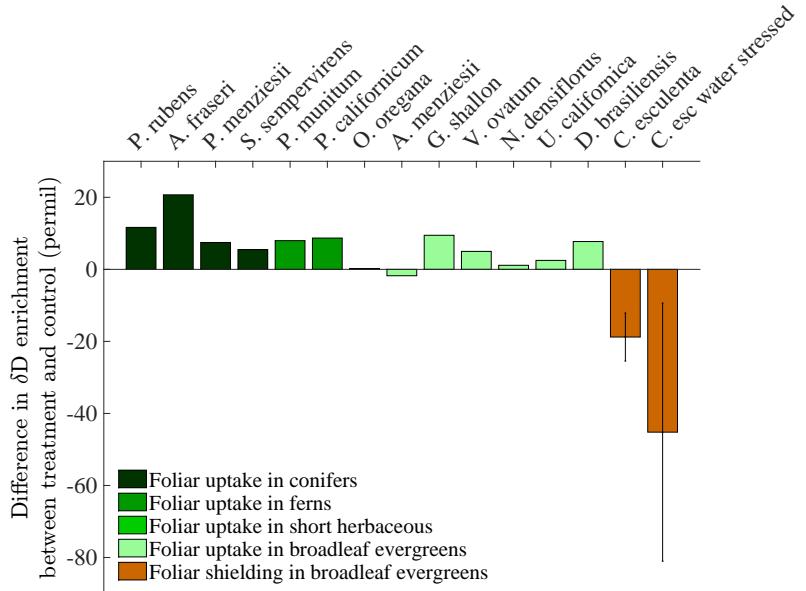


Figure 7: A comparison between the impact of foliar uptake of nighttime fog in three studies [Limm et al., 2009, Eller et al., 2013, Berry and Smith, 2014] to foliar shielding in *Colocasia esculenta*. Bars represent the magnitude of the difference in enrichment between fogged/sprayed and control plants. Enrichment is the difference between pre- and post-treatment leaves. All the foliar uptake data were normalized to reflect enrichment corresponding to a realistic difference of 20‰ between rain and fog water [Scholl et al., 2010]. Error bars show the standard error. Because we did not obtain the raw data from the foliar experiments, error bars were not added for those, please refer to the original articles for more details.

Supplemental Information

Article title: Experimental evidence of the impacts of dew-induced foliar shielding on the energy, water and isotope balance of hydrophobic leaves

Authors: Cynthia Gerlein-Safdi, Craig James Sinkler, Kelly Krispin Caylor

The following Supporting Information is available for this article:

Fig. S1: Interpolated maps showing the δD of the leaves analyzed in Experiment 1a.

Fig. S2: Interpolated maps showing the $\delta^{18}O$ of the leaves analyzed in Experiment 1a.

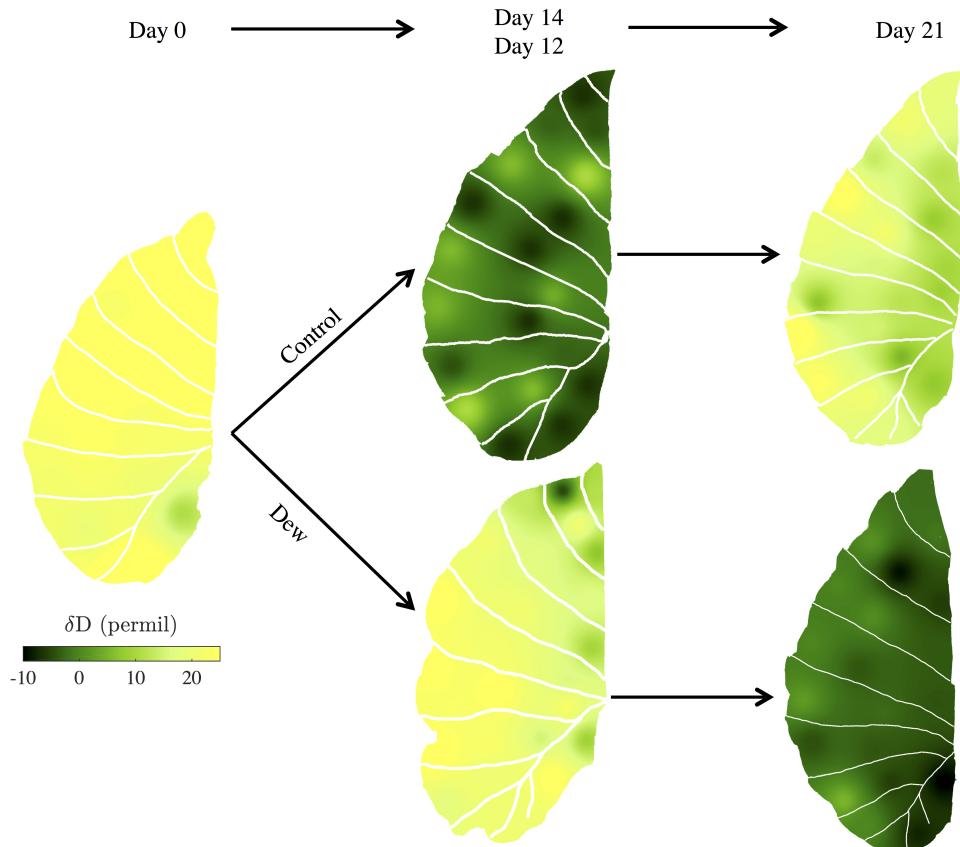


Figure S1: Maps of the spacial distribution of δD of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial leaf collected on day 0. **Top row:** leaves collected on day 14 (center) and 21 (far right) from the control. **Bottom row:** leaves collected on day 12 (center) and 21 (far right) from the sprayed treatment, where the leaves were sprayed with isotopically enriched water ($\delta^{18}O \approx 8.85 \text{‰}$, $\delta D \approx 737.64 \text{‰}$) every two days. The color scheme is the same for all rows.

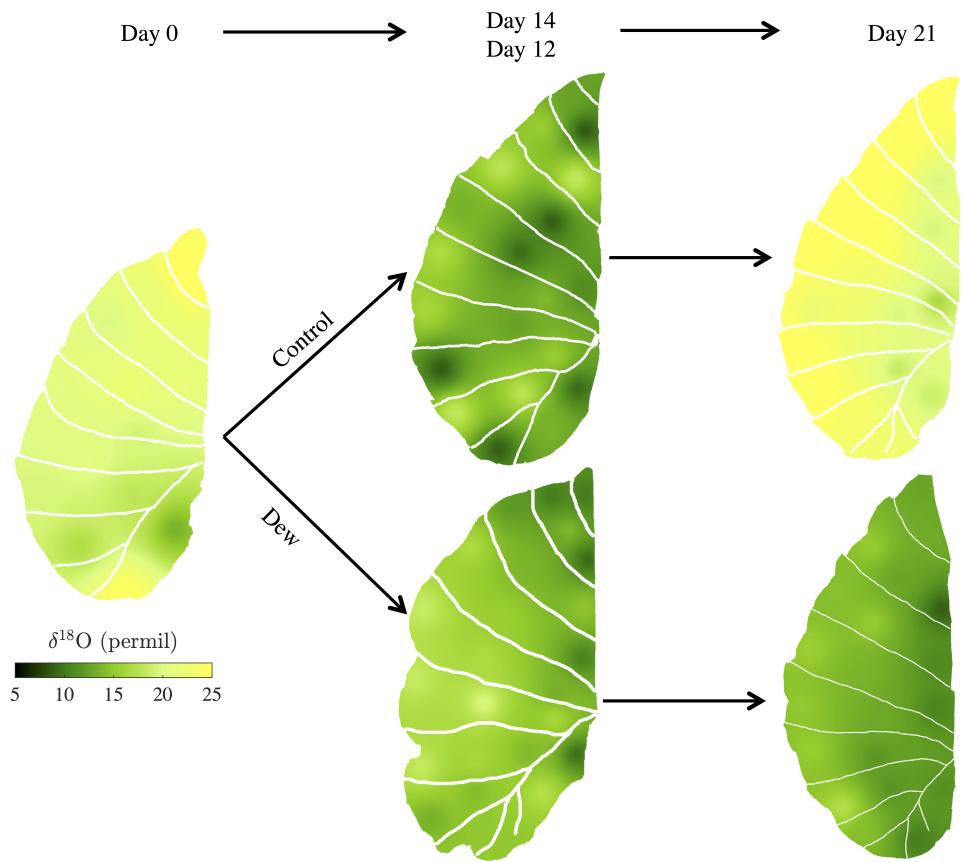


Figure S2: Maps of the spacial distribution of $\delta^{18}\text{O}$ of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial leaf collected on day 0. **Top row:** leaves collected on day 14 (center) and 21 (far right) from the control. **Bottom row:** leaves collected on day 12 (center) and 21 (far right) from the sprayed treatment, where the leaves were sprayed with isotopically enriched water ($\delta^{18}\text{O} \approx 8.85\text{\textperthousand}$, $\delta\text{D} \approx 737.64\text{\textperthousand}$) every two days. The color scheme is the same for all rows.