

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

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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 on the leaf energy and water cycle has not yet been studied in details. We provide new insight on a common phenomenon, and do so by developing 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 extends prior results by looking at how non-meteoric water impacts the energy and water balance of hydrophobic leaves. We show that the two phenomena 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

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

82 II. Materials and Methods

83 II.1 The added value of stable isotopes

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

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

90 of isotope ratios [Mook, 2006], where δ_i is expressed in ‰, and the index i stands for either ^{18}O or D.
91 $R_{^{18}O} = [H_2^{18}O]/[H_2^{16}O]$ and $R_D = [HD^{16}O]/[H_2^{16}O]$ are the isotope ratios, while the R_{r_i} are the ratios of
92 the corresponding reference standard. For water, the reference is the Vienna Standard Mean Ocean Water
93 (VSMOW).

94 Because precipitation condenses under conditions of equilibrium fractionation, $\delta^{18}O$ and δD in precip-
95 itation evolve along a line with slope c. 8, the global meteoric water line (GMWL) [Voelker et al., 2014].
96 However, kinetic isotope effects associated with differences in diffusivity among the different isotopologues of
97 water can lead to deviations from the GMWL [Farquhar et al., 2006]. For example, since $HD^{16}O$ diffusivity
98 is greater than that of $H_2^{18}O$, the water of a leaf that has undergone heavy transpiration will be more depleted
99 in D than in ^{18}O (see Figure 1). Deuterium excess (d-excess) is a widely used measure of how evaporated
100 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
101 for precipitation is c. 10‰. Lower d-excess values generally indicate that the pool has undergone some
102 evaporation [Brooks et al., 2014] (see Figure 1).

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

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

111 Our first experiment examines leaf scale spatial and temporal patterns of water isotopes induced by the
112 presence or the absence of dew under natural conditions. Six bulbs of *Colocasia esculenta* were planted in
113 separate pots. All pots were placed outside and received full sun for four weeks. During this time, all plants
114 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
115 plants reached maturity, watering stopped and the plants were moved to a shaded area to remove any sun
116 exposure differences between the plants.

117 Watering stopped two days before the beginning of the treatment. The upper-leaf surfaces in three of
118 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
119 using a spray bottle. Any extra water would run off the leaves, leaving them covered in submillimeter-size
120 droplets, which is approximately the natural size for dew-deposition drops [Defraeye et al., 2013]. The
121 misting simulated dew and was always performed around 08:00h.

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

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

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

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

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

146 **II.5 Isotope analysis**

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

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

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

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

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

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

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

210 II.6 Linking d-excess and transpiration

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

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

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

$$\epsilon_k^{\text{H}_2^{18}\text{O}} = \frac{32r_s + 22r_b}{r_b + r_s} \quad \text{and} \quad \epsilon_k^{\text{HDO}} = \frac{16r_s + 10r_b}{r_b + r_s} \quad (3)$$

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

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

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

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

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

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

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

232 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
233 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
234 kPa) is the saturated vapor pressure at air temperature, which is also taken to be 25°C . In our analysis, we
235 study the ratio of $E_{\text{dew}}/E_{\text{control}}$, expressed in %.

236 II.7 Statistical analysis

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

243 III. Results

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

245 The results of Experiments 1a are presented as maps of the analyzed half leaves (Figure 2). The maps were
246 obtained using an inverse distance interpolation and show the evolution of the d-excess of leaves from the
247 control and misted treatments collected at 0, 12 (dew), 14 (control) and 21 (dew and control) days from the
248 beginning of the experiment. All the maps of δD and $\delta^{18}O$ (Supporting Information, Figures S1 and S2)
249 show a progressive enrichment [Cernusak and Kahmen, 2013] of leaf water when moving away from the
250 main stem towards the rims of the leaf. The average difference between the center and the rim of the leaf for
251 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
252 composition of the bulk water at the end of the experiment, the dew-treated leaf exhibits a d-excess higher
253 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
254 treatment is not apparent for days 12/14 ($\Delta d\text{-excess} \approx 10.2 \text{ ‰}$, two-sample t-test: $t = -1.6$, $v = 35$, $P = 0.11$).

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

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

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

265 Experiment 2 looked at the temporal evolution of water potential in artificially drying leaves (see Figure 4).
266 Strong differences in drying pattern are shown for the misted or drought leaves. In both the control and the the
267 high heat and mist cases, the leaf water potential experiences a slow decline, which is well approximated by a
268 linear function. However, the high heat treated leaves experience a faster decline and are better approximated
269 by a parabola. Table 2 presents the average decline from initial to final leaf water potential for the three
270 different treatments. All the data is normalized for leaf size and drying time. The misted leaves exhibit a
271 much smaller decline in water potential than the leaves subjected to the same high heat treatment but that
272 did not get sprayed (two-sample t-test: $t = 2.37$, $v = 7$, $P < 0.05$). The decline observed for misted leaves is
273 not statistically different to the one observed for naturally drying leaves (two-sample t-test: $t = -1.46$, $v = 6$,
274 $P = 0.19$).

275 IV. Discussion

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

277 Since dew treated leaves have higher d-excess values in Experiments 1a and 1b, we might conclude that foliar
278 shielding decreased leaf transpiration. Yet, we must first consider two other processes that will also influence
279 the leaf water isotopes. First, the dew droplets might actually penetrate the dew-treated leaves through foliar
280 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
281 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
282 would have shown an enrichment over the control ones. We observe a decrease in both $\delta^{18}\text{O}$ and δD for the
283 dew-treated plant compared to the control, which is consistent with a lack of foliar uptake. Second, depleted
284 source water contained in the soil and stem of the plant is constantly entering the leaf. We expect this effect
285 has the same impact on both dew treated and control plants, and so we exclude it when interpreting differences
286 between the two treatments. We conclude that foliar shielding is the primary phenomenon impacting leaf
287 water d-excess composition.

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

293 To calculate the systematic error associated with our choices for those parameters, we calculate $E_{\text{dew}}/E_{\text{control}}$
294 for a range of leaf temperatures from 10° to 40°C and for a stomatal conductance g_s from 0.1 to
295 0.8 $\text{mmol m}^{-2} \text{s}^{-1}$. We find that the systematic error associated with our choice of g_s is negligible, while
296 that associated with the choice of T_{leaf} is important. For Experiment 1a, the transpiration rate obtained
297 for the dew treated leaf is significantly lower than that of the control ($t = -9.4$, $\mu = 38$, $P < 0.001$) by
298 30 ± 2.6 (stat) ± 1.6 (syst) %. Similar results were found for Experiment 1b, where the dew treatment signifi-
299 cantly ($t = -3.9$, $\mu = 28$, $P < 0.001$) decreased transpiration by 30 ± 9.1 (stat) ± 0.09 (syst) %. These values are
300 consistent with the one existing study on the impacts of dew on plant water use: [Garratt and Segal, 1988]
301 estimated that the reduction in transpiration due to dewfall could reduce daily plant water use by c. 10%. This
302 value was obtained for wheat plants associated with a low transpiration rate. Since our leaves were larger and
303 because our control plants had a higher transpiration rate, we expect the reduction to be larger in our case (see
304 Section IV.2).

305 **Interpreting temporal patterns** Leaves collected from both treatments on day 12 or 14 present results
306 that disagree with the trends formed by the results of day 0 and 21 (Figure 2). For the control, d-excess is
307 generally decreasing between day 0 and day 21, but the leaf collected on day 14 shows values of d-excess
308 higher than expected. In the dew treatment case, the general trend is reverse and d-excess at the end of
309 the experiment (day 21) is much higher than on day 0. However, the dew treated leaf collected on day 12
310 presents lower values of d-excess than expected from this trend. It is important to note that the plants were
311 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.

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

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

350 foliar shielding will allow the leaf to maintain its water status and increase CO₂ assimilation through multiple
351 mechanisms.

352 **IV.3 Implications for foliar uptake studies using stable isotopes**

353 The three mechanisms described in section IV.2 will also decrease leaf water isotopic enrichment. Indeed,
354 by decreasing evaporation, foliar shielding suppresses the isotopic enrichment associated with leaf water
355 transpiration [Farquhar et al., 2006]. Therefore, leaves undergoing foliar shielding will have a bulk isotopic
356 composition lower (more depleted) than leaves that do not experience it. The average δD enrichment
357 between the first and last days of collection for Experiment 1A were $-9.1 \pm 3.7 \text{ ‰}$ for the control leaf and
358 $-27.9 \pm 2.9 \text{ ‰}$ for the dew treated leaf. This corresponds to a $-18.8 \pm 6.6 \text{ ‰}$ difference in enrichment between
359 sprayed and control treatments. In the case of highly water stressed leaves (Figure 3), the difference in
360 enrichment reaches $-45.2 \pm 35.8 \text{ ‰}$. In both cases, the fog-treated leaf was more depleted in heavy isotopes
361 than the control.

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

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

384 Foliar uptake has the largest impact on conifers (see Figure 5), where the difference in enrichment between
385 treatment and control reaches up to c. 20 ‰. Foliar shielding for the non-water stressed case (Experiment 1a)
386 exhibits the opposite effect, with a magnitude similar to the largest foliar uptake case. In the water stressed
387 case (Experiment 1b), the depletion observed is as large as c. 45.2 ‰. The true effect of foliar shielding

388 on leaves in the field during a drought likely lies in between the two cases shown here. The three foliar
389 experiments presented here all used nighttime treatment, so foliar shielding did not impact the enrichment
390 observed. However, the competing effects of foliar uptake and foliar shielding are likely to be very important
391 when analyzing field or day time foliar uptake experiment data. For example, [Berry et al., 2014b] observed
392 a significantly larger enrichment when fogging saplings in the morning than in the afternoon or the evening.
393 This results is well explained if the effects of foliar shielding on temperature and transpiration are taken into
394 account. Our results suggest that, in the field, foliar shielding has a larger impact on leaf isotopes than foliar
395 uptake. The relative importance of foliar uptake VS foliar shielding will depend on many factors, including
396 the isotopic composition of the non-meteoric water, the timing and length of the wetting event, the size of the
397 leaf, the atmospheric conditions and of course, the specie. To properly interpret isotope data, future studies
398 on foliar uptake should include foliar shielding into their isotope balance calculation.

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

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

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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.

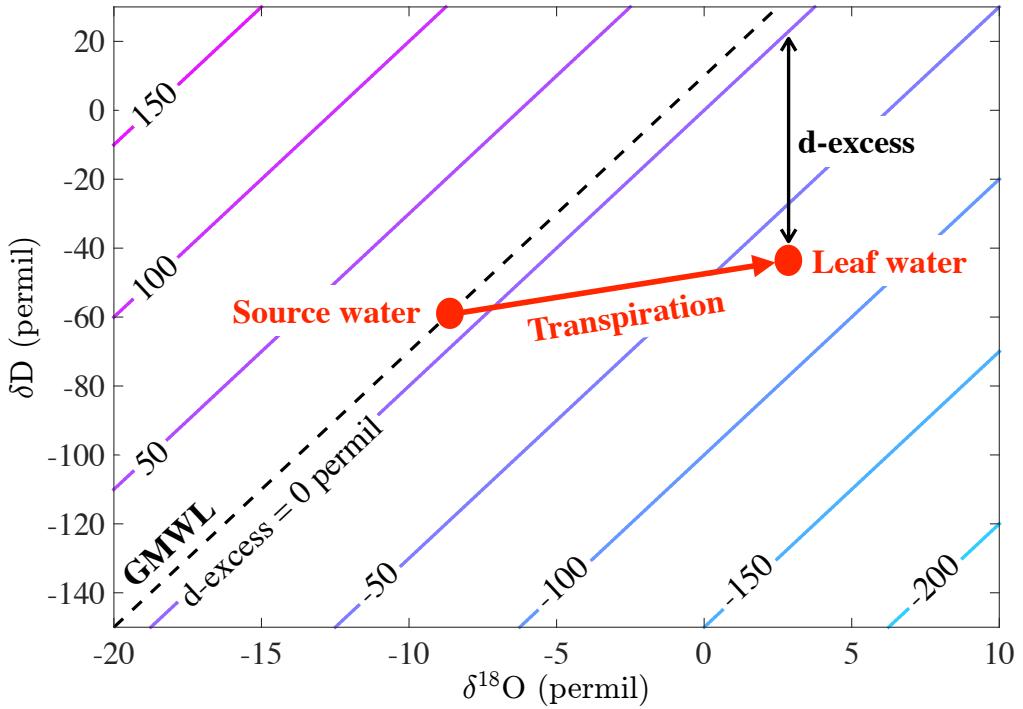


Figure 1: Adapted from [Voelker et al., 2014]: Conceptual figure showing the evaporative conditions controlling the evolution of $\delta^{18}\text{O}$ and δD in leaf water from source water located on the global meteoric water line (GMWL, dashed black line). The slope of the transpiration line depends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

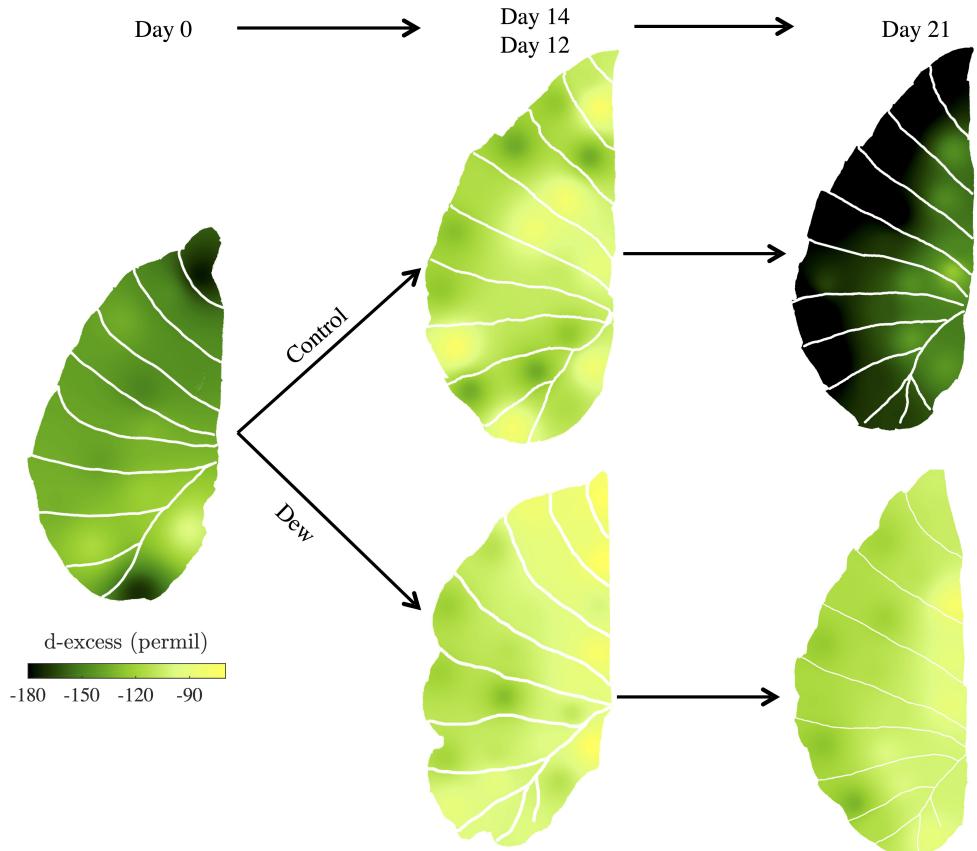


Figure 2: Maps of the spacial distribution of d-excess of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial 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.

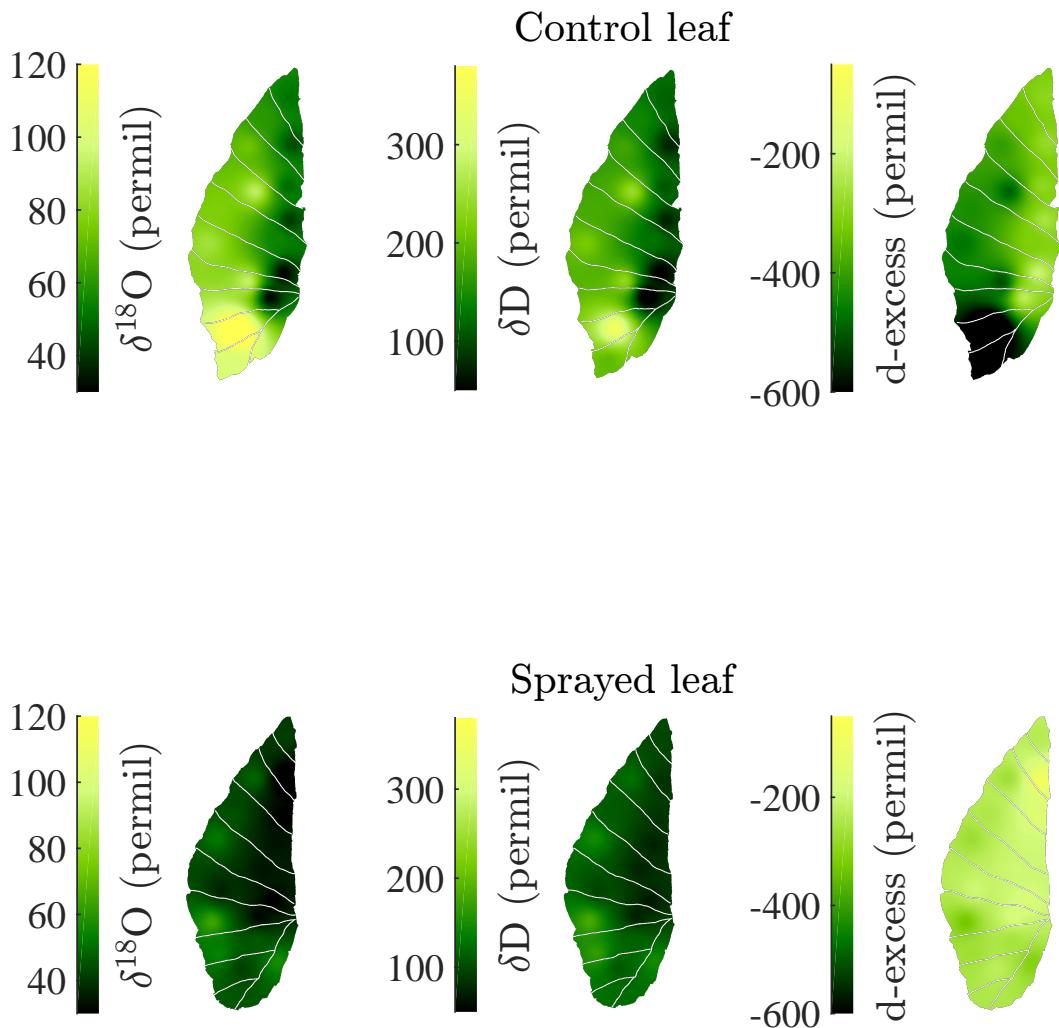


Figure 3: Maps of two leaves left to dry under a 500W blue light for four hours. **Top row:** $\delta^{18}\text{O}$, δD and d-excess of the control (not sprayed) leaf. **Bottom row:** $\delta^{18}\text{O}$, δD and d-excess of the leaf sprayed with isotopically enriched water ($\delta^{18}\text{O} \approx 8.85\text{‰}$, $\delta\text{D} \approx 737.64\text{‰}$) 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.

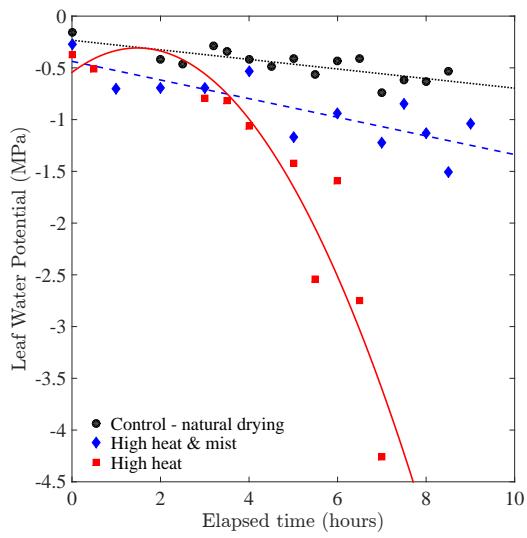


Figure 4: Typical examples of the temporal evolution of the leaf water potential of *Colocasia esculenta* leaves under three different treatments. All the leaves under the natural drying (black circles) and the high heat and mist (blue diamonds) treatments are well fit by a linear relation (black dotted 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.

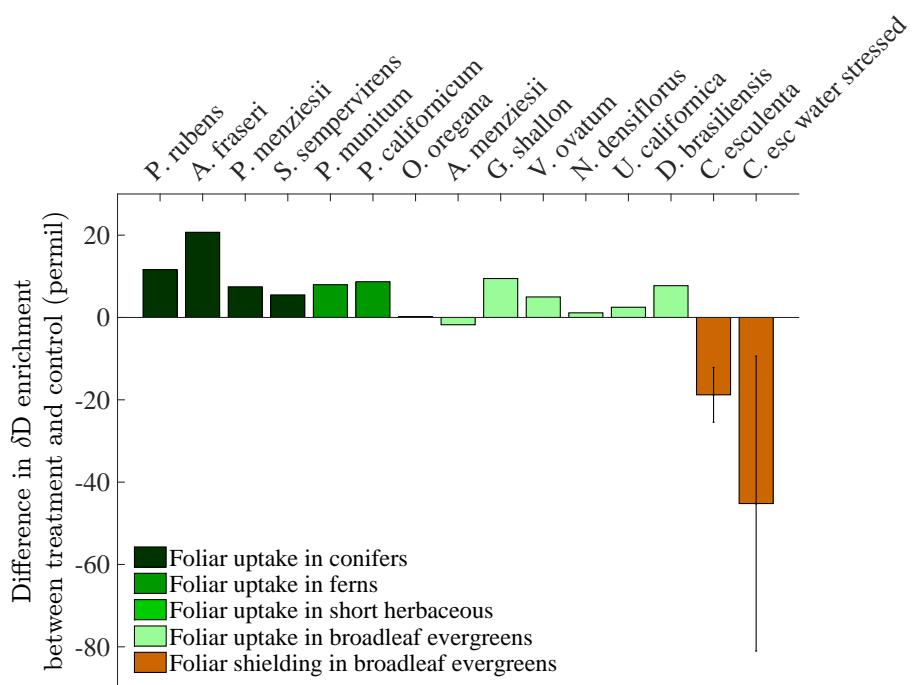


Figure 5: A comparison between the impact of foliar uptake of nighttime fog in three studies [Limm et al., 2009, Eller et al., 2013, Berry and Smith, 2014] to foliar shielding in *Colocasia esculenta*. Bars represent the magnitude of the difference in enrichment between fogged/sprayed and control plants. 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.

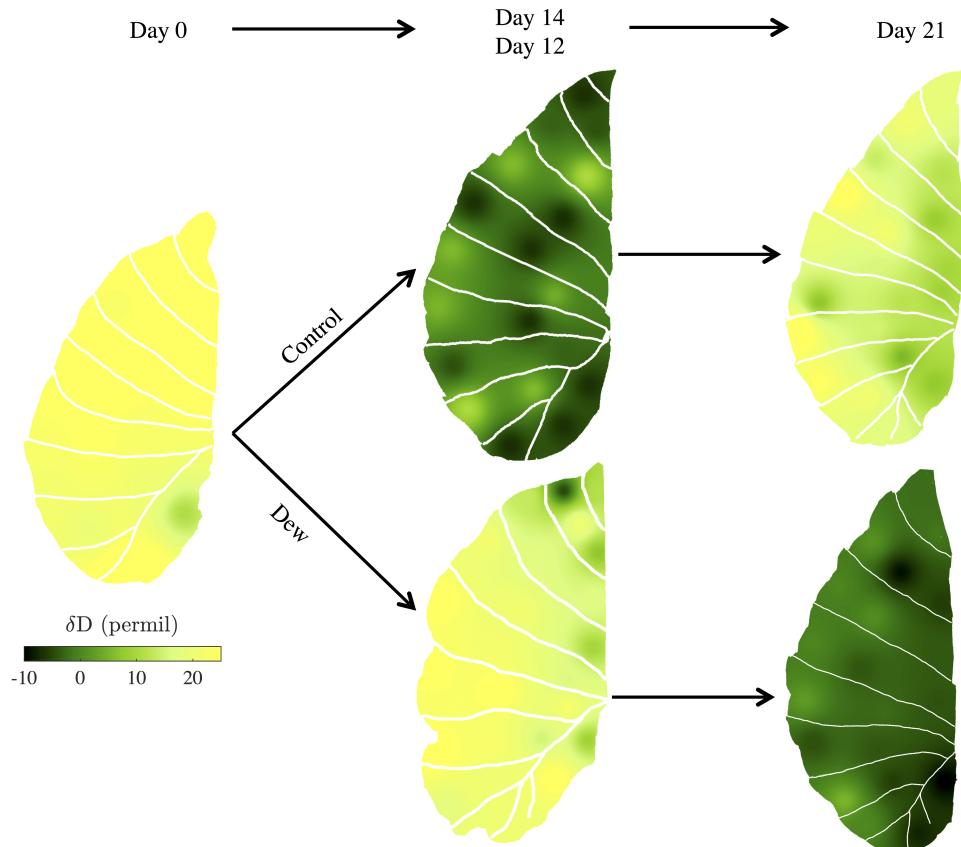


Figure S1: Maps of the spacial distribution of δD of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial leaf 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.

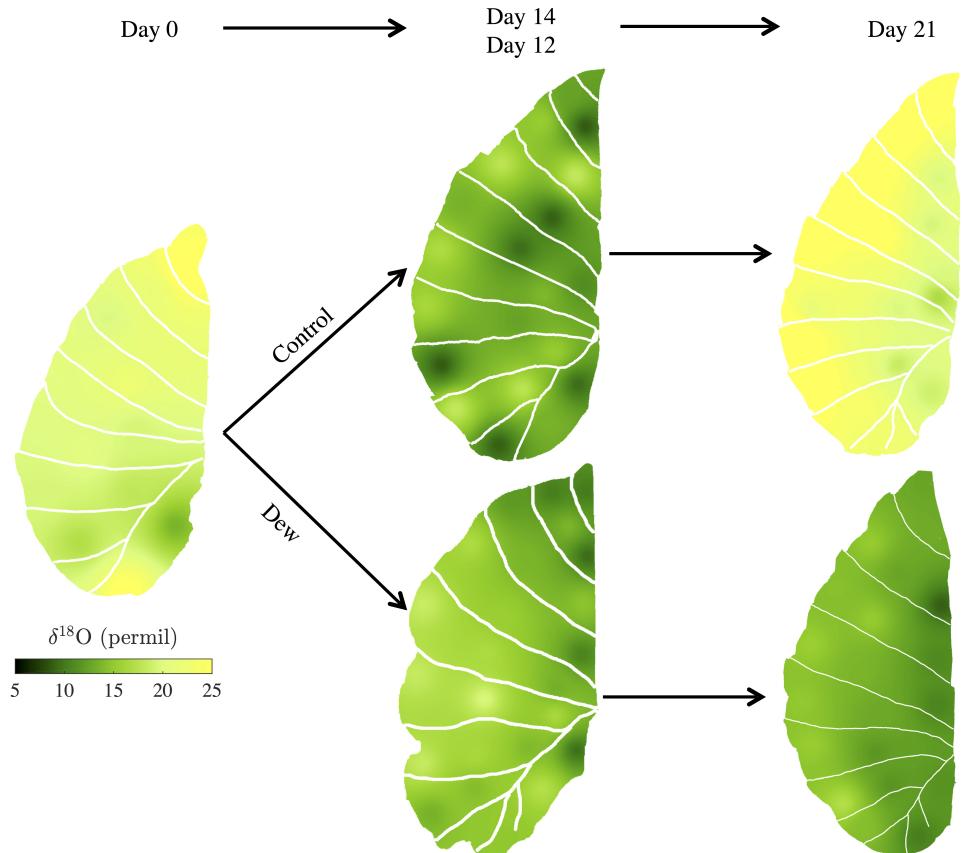


Figure S2: Maps of the spacial distribution of $\delta^{18}\text{O}$ of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** 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 ($\delta^{18}\text{O} \approx 8.85\text{\textperthousand}$, $\delta D \approx 737.64\text{\textperthousand}$) every two days. The color scheme is the same for all rows.

