

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)	6052
Summary	196
Introduction	1117
Materials and Methods	1852
Results	1110
Discussion	1900
Acknowledgements	73
No. of Figures	7 (all color)
No. of Tables	1
No. of Supporting Information files	3 figures

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 on the leaf energy and water cycle has not yet been studied in details. We provide new insight on a very 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 a similar yet opposite effect 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 and none of the past studies 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 an induction module coupled to 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 and a lower transpiration rate than the control. The dew leaves also had a depleted water isotopic composition compared to the control. Three possible mechanisms are proposed for the interaction of water droplets with the leaf energy and water balance.
- Comparing the results of three foliar uptake studies to our results, we conclude that foliar shielding as 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 Because it occurs consistently in all environments, non-meteoric water is an important source of water
³ for many plants. But because it only provides small amounts of water, it is often overlooked in large
⁴ scale models past 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 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] has adapted to using fog as its 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 grow on other plants, often
¹⁴ without any access to soil water. All those case studies focus on very specific plants, particular either by their
¹⁵ morphology or the ecosystem they grow in.

¹⁶ But many species have very water-repellent leaves [Neinhuis and Barthlott, 1997]. Those hydrophobic
¹⁷ species are not adapted to uptake water from their leaves. For most plants, non-meteoric water deposition is
¹⁸ a source of nuisance as it may freeze and cause damages to the leaf in cold climate, or stagnate and cause
¹⁹ rotting and pathogen infection in warm environments [Evans et al., 1992]. [Aryal and Neuner, 2009] even
²⁰ showed that leaves that are repeatedly exposed to dew tend to become more water-repellent. However, not all
²¹ hydrophobic leaves are as water repellent as the iconic water lilies: micro-droplets of water will indeed form
²² on the surface of even very hydrophobic leaves. The interaction of those droplets on the leaf energy balance,
²³ which we call ‘foliar shielding’, has not yet been studied, despite its potentially large impact on both leaf
²⁴ water resources and leaf water isotopes.

²⁵ **Leaf energy balance** Because they are unable to move to the shade, leaves are vulnerable to sun radiations,
²⁶ and they can often be warmer than the surrounding air. Leaf temperature will in turn affect saturation vapor
²⁷ pressure, isotope fractionation, transpiration, and photosynthesis. Because their boundary layer is thinner,
²⁸ smaller leaves tend to be at a temperature closer to the ambient air. This is the reason why, on a single tree,
²⁹ sun leaves are usually smaller than shade ones. To stay cool, leaves use a combination of re-radiation (transfer
³⁰ of energy to the surroundings), convection (heat loss as cool air moves over the surface of the leaf) and
³¹ evaporative cooling (evaporation of water inside the leaf into water vapor, which is an exothermic process)
³² [Vogel, 2012]. During a drought, leaves have to preserve water to maintain turgor pressure, which competes
³³ with evaporative cooling. In this case, leaves are left with re-radiation and convection to cool themselves
³⁴ down, which is sometimes not enough to maintain a low temperature. If the duration of the drought extends
³⁵ for too long, it might lead to plant mortality.

³⁶ By depositing a layer of small water droplets on the surface of the leaves, non-meteoric water can provide
³⁷ the plants with a pool of water that will supplement the scarce leaf water and provide a form of externalized

38 evaporative cooling. Moreover, the presence of the droplets will both increase the albedo of the leaves,
39 allowing it to reflect more energy [Pinter, 1986], and increase surface roughness which will increase the leaf
40 boundary layer, therefore decreasing the vapor pressure deficit (VPD) and lowering the evaporative demand.
41 This later mechanism has already been proposed by [Limm et al., 2009] to explain how fog suppresses
42 nighttime respiration in redwoods.

43 By affecting the leaf energy cycle, foliar shielding is therefore directly affecting the water status of the
44 leaf. Depending on the location and climate, dew deposition can take from 1.5 [Abtew and Melesse, 2012] to
45 6 hours [Monteith, 1957] after sunrise to completely evaporate from the surface of the leaves. Dew and fog
46 can also form in the late afternoon before sunset [Wilson et al., 1999, Kabela et al., 2009]. Although neither
47 dew nor fog is usually present at the hottest hour of the day, they can effectively shorten the duration of the
48 water-stressed part of the day. This will significantly help the plant maintain its water status over an extended
49 period of drought [Madeira et al., 2002, Proctor, 2012]. Dew formation is usually included in global climate
50 models (GCMs) as it merely involves tracking dry bulb temperatures going below the dew point temperature.
51 However, its interaction with vegetation is never taken into account. Non-meteoric water deposition events
52 occur all around the world, even in dryland ecosystems [Agam and Berliner, 2006] and affect large areas at a
53 once. The small changes in the energy, water and carbon balance of each single leaf can therefore have a large
54 cumulative impact at the ecosystem level and including this interaction into GCMs would allow modelers to
55 better understand vegetation response to climate change and its feedback on CO₂ atmospheric concentrations.

56 **Leaf water isotopes** By decreasing leaf transpiration, foliar shielding will influence leaf water isotopes
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 will result 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 from 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 50 cm in length and 40 cm in width, allowing for spatially high-resolution
70 mapping of the leaf water properties. Using isotopically labelled water as well as traditional plant physiology
71 techniques, we confirm that the *Colocasia esculenta* leaves do not uptake water from the surface of the leaves.
72 We also show that foliar shielding decreases leaf transpiration and increases water potential and we present
73 three mechanisms that explain the influence of water droplets deposition on the energy and water cycles of
74 water-repellent leaves. We conclude by comparing our results to three foliar uptake studies to show that foliar
75 shielding has an opposite and larger effect on leaf isotopes and that it is crucial to include it in leaf isotope

76 models to properly interpret isotope data of foliar uptake.

77 II. Materials and Methods

78 II.1 The added value of stable isotopes

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

$$85 \delta_i = \left(\frac{R_i}{R_{r_i}} - 1 \right) \times 10^3$$

86 of isotope ratios [Mook, 2006], where δ_i is expressed in ‰ and the index i stands for ^{18}O or D. $R_{^{18}O} = [H_2^{18}O]/[H_2^{16}O]$
87 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
88 standard. For water, the reference is the Vienna Standard Mean Ocean Water (VSMOW).

89 Because precipitation condenses under conditions of equilibrium fractionation, $\delta^{18}O$ and δD in precipita-
90 tion evolve along a line with slope 8, the global meteoric water line (GMWL) [Voelker et al., 2014]. However,
91 kinetic isotope effects associated with the difference in diffusivity of the different isotopologues of water can
92 lead to deviation from the GMWL [Farquhar et al., 2006]. For example, since $HD^{16}O$ diffusivity is greater
93 than that of $H_2^{18}O$, the water of a leaf that has undergone heavy transpiration will be more depleted in D than
94 in ^{18}O (see Figure 1). Deuterium excess (d-excess) is a widely used measure of how evaporated a pool of
95 water (ocean, lake, leaf) is and is defined as: $d\text{-excess} = \delta D - 8 \times \delta^{18}O$.

96 The average d-excess for precipitation is 10. Lower d-excess values generally indicate that the pool under-
97 gone some evaporation [Brooks et al., 2014] (see Figure 1). Stable isotopes are also very efficient in helping
98 identify different water sources in plants [Ehleringer and Dawson, 1992]. Simple mixing models allow one
99 to separate the composition and the fluxes coming from different sources [Phillips and Gregg, 2001]. For
100 this reason, stable isotopes are great natural labels that can be used to track pathways of water within plants
101 without harming them and they have been the method of choice for many studies looking at foliar uptake
102 [Breshears et al., 2008, Limm et al., 2009, Eller et al., 2013, Berry et al., 2014b]. Indeed, non-meteoric wa-
103 ter is usually enriched in heavy isotopes [Scholl et al., 2010], making it easy to trace it even after it enters the
104 leaf.

105 II.2 Experiment 1a: Effects of foliar shielding on *Colocasia esculenta* water isotopes in natural con- 106 ditions

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

exposition difference between the plants. The area was very protected and temperature was usually lower than outside of it. Similarly, relative humidity was usually slightly higher. Watering stopped two days before the beginning of the treatment. The upper surface of the leaves of the three of the six pots were misted with isotopically enriched water ($\delta^{18}\text{O} = 8.85 \text{ ‰}$, $\delta\text{D} = 737.64 \text{ ‰}$) every two days using a spray bottle. Any extra water would run off the leaves, leaving them covered in submillimeter size droplets, which is a realistic size for dew deposition drops [Defraeye et al., 2013]. The misting simulated dew and occurred as early as possible in the morning. The three control pots were not watered and did not receive any mist. In order to avoid contact between the misted water and the soil in the pots, the surface of all pots was covered in wrapping plastic. Six leaves were collected between the beginning of the control/dew treatments and the end of the experiments, three weeks later. The sampling and the analysis are described in Section II.5.

II.3 Experiment 1b: Effects of foliar shielding on *Colocasia esculenta* leaf water isotope under high water stress conditions

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

II.4 Experiment 2: Effects of foliar shielding on *Colocasia esculenta* leaf water potential under high water stress conditions

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

II.5 Sampling and processing methods for the isotopic analysis

For the water isotope analysis, each analyzed leaf was sampled in 12 to 25 different locations depending on the size of the leaf. All the sampling points were located on the same half of the leaf and consisted in four

holes (6 mm diameter) punched next to each other forming a square. Each hole was punched as quickly as possible to avoid evaporation, which would influence the isotopic composition of the neighboring holes. Each leaf disk was then secured in an aluminum foil and inserted in a sealed vial. The entire leaf was sampled in one go and as fast as possible. The prepared vials were then stored in the fridge until being analyzed. The leaf samples were analyzed using an Induction Module (IM) combined to a Cavity Ring Down Spectrometer (CRDS) L2103-i from Picarro Inc. (Sunnyvale, CA, USA). The IM was set on the ‘normal leaf’ setting: the leaf disks did not appear carbonized and after being dried in the oven at 60°C for 48 hours, they show no decline in weight, proving that this setting dried the leaf samples completely. The IM was equipped with a micro-combustion module (MCM). The MCM has been proven to efficiently reduce the interferences due to the presence of organics in water samples extracted from plants (Kate Dennis, private communication). The entire sampling and IM analysis process lasted from 1.5 to 2 days per leaf depending on the size of the leaf.

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

IRIS and IRMS analysis Ten samples were sent to the Center for Stable Isotope Biogeochemistry at the University of California in Berkeley for IRMS analysis. For the IRMS method, δD was obtained by chromium combustion using an H/Device (labelled as HDEV; Thermo Finnigan, Bremen). Microliters of water were injected in the HDEV and reduced to H_2 gas. The ratio of D/H was then measured on a Thermo Delta Plus mass spectrometer. For the $\delta^{18}\text{O}$ analysis, water from standards and samples were pipetted into glass vials and quickly sealed. The vials were then purged with 0.2% CO_2 in Helium and allowed to equilibrate at room temperature for at least 48 hours. The ^{18}O in the CO_2 was then analyzed by continuous flow using a Thermo Gas Bench II interfaced to a Thermo Delta Plus XL mass spectrometer. In this $\text{H}_2\text{O}-\text{CO}_2$ equilibration method, the dissolved components (organic and/or inorganic) do not affect the values of $\delta^{18}\text{O}$. For the IRIS analysis, 1.8 μl of water were injected into a vaporizer and the vapor pushed through a MCM. The concentrations of H_2^{18}O and HD^{16}O were measured on a water isotope analyzer (L2103-i) from Picarro Inc. (Sunnyvale, CA, USA).

The ten samples analyzed both by IRMS and IRIS were used to calculate the offset between the two techniques. All the samples that had been run exclusively by IRIS or IM-CRDS (and had not been analyzed by IRMS) were then corrected for this offset. The IM-CRDS method has not been widely used yet and

184 protocols and precision analysis are still absent from the scientific literature. In order to justify the results
185 from the IM-CRDS, we compared the values obtained from the extracted water of the half-leaf analyzed by
186 IRIS to the average leaf water composition obtained using a nearest neighbor interpolation on the half-leaf
187 analyzed by IM-CRDS. For the seven leaves analyzed by IM-CRDS, the average difference between those
188 two methods was 2.6‰ in $\delta^{18}\text{O}$ and 3.4‰ in δD . These values are higher than the average difference we
189 observed between two halves of the same *Colocasia esculenta* leaf, both extracted by cryogenic vacuum
190 distillation and analyzed by IRIS (0.3‰ in $\delta^{18}\text{O}$ and 1.9‰ in δD). The observed error is therefore not
191 attributable to the analysis on IM-CRDS and IRMS being conducted on each half of the same leaf. Further
192 testing is clearly necessary before using the IM-CRDS technique as an absolute method. However, our goal in
193 this paper is to compare strongly enriched waters and the order of the differences presented in the next section
194 are up to two orders of magnitude bigger than the error observed for the IM-CRDS. We therefore believe
195 that the IM-CRDS is an appropriate method here, as it allowed us to quickly process many small samples,
196 therefore increasing the spatial and temporal resolution of our analysis.

197 II.6 Statistical analysis

198 Responses for Experiments 1a and 1b were analyzed using a Welch's t-test with a 5% significance level,
199 conducted using the multiple samples collected on each leaf as a single population and assuming unequal
200 variance. We assigned weight to each sample to match the proportional area of the leaf corresponding to each
201 sample location and calculated using a nearest neighbor interpolation. The interpolation and the tests were all
202 performed using Matlab v. 2014b (Mathworks, Natick, MA, USA).

203 III. Results

204 III.1 Effects of foliar shielding in natural conditions

205 The results of Experiments 1a are presented as maps of the analyzed half leaves (Figure 2). The maps were
206 obtained using an inverse distance interpolation in Matlab and show the evolution of the d-excess of leaves
207 from the control and misted treatments collected at 0, 12 (dew), 14 (control) and 21 (dew and control) days
208 from the beginning of the experiment. All the maps of δD and $\delta^{18}\text{O}$ (Supporting Information, Figures S1 and
209 S2) show the expected progressive enrichment [Cernusak and Kahmen, 2013] of leaf water when moving
210 away from the main stem towards the rims of the leaf (Average difference between the center and the rim of
211 the leaf: $\Delta^{18}\text{O} = 11.1 \pm 2.6 \text{‰}$ and $\Delta\text{D} = 23.9 \pm 7.4 \text{‰}$).

212 [PLACE IN DISCUSSION] This enrichment is due to the progressive transpiration of the leaf water as
213 it moves away from the source water that enters the leaf through the petiole. The lighter isotopologues are
214 transpired first, leaving the heavier ones in the leaf [Farquhar et al., 2006]. This translates into a decrease
215 in d-excess from the center of the leaf towards the edges. Those results reinforced our confidence in the
216 IM-CRDS method.

217

218

Comparing the results for both treatments at the end of the experiment, we see that the dew treated plants exhibits a significantly higher d-excess values than the control ones ($d\text{-excess}_{\text{dew}} - d\text{-excess}_{\text{control}} = 63.2\%$, two-sample t-test: $t = -5.5$, $P < 0.001$). The lower (more negative) d-excess values are associated with higher transpiration rate. On the other hand, the misted leaves had a lower rate of transpiration, which led to higher values of d-excess. The leaf average isotopic composition of the dew treated and control leaves (see Figure 3. Figure 1 provides an explanation on how to interpret this figure.) shows that the isotopic composition of the control leaves evolved directly from evaporated source water (tap water), while the dew treated leaves are evolving on a line parallel to the GMWL. Before the treatment started the water in the dew treated leaves most likely followed an evaporation line similar to that of the control leaves. However, after the treatment started, transpiration in the dew treated leaves stopped and the water in those leaves followed a line parallel to the GMWL. For the samples to evolve on such a line, only equilibrium isotopic fractionation is happening within the leaf. Indeed, any kinetic fractionation would induce a slope of less than 8. In terms of leaf physiology, this is the sign that water vapor is not diffusing out of the leaf, i.e. that little transpiration is occurring.

The effect of the dew treatment was not apparent for days 12/14 ($d\text{-excess}_{\text{dew}} - d\text{-excess}_{\text{control}} = 9.7\%$, two-sample t-test: $t = -0.79$, $P = 0.43$).

One must recall 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 explains 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 of the shelter. During the four days preceding the collection of the first control leaf (day 14), the air temperature came within 1°C from the dew point temperature every night (see Figure S3). Because of the locally lower temperature and higher relative humidity under the sheltered area, natural dew probably formed at the surface of the leaves. Indeed, natural dew formation was observed on the leaves multiple times. Moreover, a series a small rain events happened on the day preceding the collection, which would have greatly affected the transpiration rate and the resulting isotopic composition of the the leaf.

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

Similar maps were produced for Experiment 1b (Figure 4). In this case, the heat lamp artificially increased the transpiration rate in both the control and the misted leaves, leading to highly enriched $\delta^{18}\text{O}$ and δD values and very low d-excess values for both treatments. However, the d-excess in the control case is a lot more negative (reaching values down to $\sim -800\%$) than for the dew treated leaves (reaching values down to $\sim -300\%$). This experiment was merely an extreme version of Experiment 1a, with the objective of accentuating the contrast between the two treatments. While the high heat treatment led to a strong drying of some areas of the leaf, in particular those far away from the central vein, the large differences observed between the control and the misted treatments do confirm the results of Experiment 1a.

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

256 Experiment 2 was design to look at the temporal evolution of water potential in artificially drying leaves
257 (see Figure 5). Strong differences in drying pattern are shown for the misted or drought leaves. In both the
258 control and the the high heat & mist cases, the leaf water potential experiences a slow decline, which is best
259 approximated by a linear function. However, the high heat treated leaves experience a faster decline and are
260 best approximated by a parabola. Without the results of Experiments 1 and 2, that confirmed the leaves' high
261 hydrophobicity, this results could easily be mistaken for a foliar uptake process.

262 Large differences in water potential patterns were also observed as a function of leaf size for the high
263 heat treatment: smaller leaves had a stronger decline in water potential than big leaves did. This difference
264 disappears when the leaf is misted. In order to verify that this leaf size difference was not related to a
265 difference in water repartition within the leaf (on a short time scale, transpiration occurs mainly in the lamina),
266 eight *Colocasia esculenta* leaves of length ranging from 14 to 64 cm were weighted, their veins and lamina
267 (inter-vein tissues) separated and re-weighted before being oven-dried for 48 hours and weighted one last
268 time. On average, veins accounted for 39% and the lamina for 41% of the total leaf water. This values are
269 uncorrelated with leaf size (Figure 6), showing that the size dependent change in water potential in the high
270 heat treatment is due to the process of the drying itself, and not due to pre-existing differences in water
271 distribution.

272 **IV. Discussion**

273 Dew and fog have been shown to have a direct impact on plants water status through direct uptake of water
274 from the leaves or needles [Stanton and Horn, 2013, Eller et al., 2013, Clus et al., 2008, Lakatos et al., 2012,
275 Berry et al., 2014a, Berry and Smith, 2014]. As mentioned before, *Colocasia esculenta* is native to tropical
276 wetlands and posses highly hydrophobic leaves [Neinhuis and Barthlott, 1997] that allow the plant to prevent
277 the development of fungus. This is confirmed by Experiments 1a and 1b in which the misted leaves all exhibit
278 lower isotopic enrichment in ^{18}O and D than the control leaves. This is the sign that none of the highly
279 enriched sprayed water is being uptaken by the leaves, even in artificially dry and hot conditions.

280 **IV.1 Effects of foliar shielding on the leaf energy cycle**

281 Despite the leaf's hydrophobicity and the absence of foliar uptake, submillimeter size droplets of water do
282 stay attached to the surface of the leaf and allow it to decrease its transpiration rate and maintain its water
283 potential. The water balance of the leaf is therefore influenced by the change in energy balance associated
284 with the water droplets deposited at the surface. The influence of foliar shielding is triple.

285 First, the deposited droplets increase the albedo of the leaf, allowing more of the radiations to be reflected
286 away from the leaf. The albedo is the reflection coefficient for solar radiations of natural surfaces. Depending
287 on the direction of the incoming solar radiations, water can have an albedo as high as 1 (perfect reflector)
288 whereas typical values for leaves are c. 0.2 for visible light. The increase of vegetation albedo due do dew
289 deposition has been observed in the field many times [Pinter, 1986, Zhang et al., 2012]. By reflecting more

290 radiations when there are wet, leaves will then decrease the incoming shortwave radiations and consequently
291 keep their temperature lower. This will in turn reduce the evaporative demand and the leaf transpiration.

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

298 Finally, the evaporated droplets allow to increase the boundary layer [Defraeye et al., 2013] and locally
299 decrease the VPD, creating a moister environment around the leaf. The increase in surface roughness
300 associated with the presence of the droplets at the surface of the leaf will also contribute to increase the size
301 of the boundary layer. The evaporation of the droplets will cause the air close to the leaf to have a higher
302 relative humidity than the surrounding air, creating a moist micro-climate around the leaf [Jones, 1992]. This
303 will decrease the difference between the interstitial and the air vapor pressures. This decrease in gradient
304 will therefore reduce the flux of water vapor out of the leaf, namely transpiration. By decreasing the outward
305 flow of water vapor, more CO₂ will be able to enter the leaf, increasing interstitial CO₂ concentration,
306 photosynthesis and water use efficiency. The leaf size dependency of this third mechanism is confirmed by
307 the leaf size dependent behavior observed for the misted case of Experiment 2 (see Figure 5): if only the
308 first two mechanisms were at play, one would not expect a difference between two leaves of different size
309 receiving mist. However, bigger misted leaves will create a larger micro-climate, increasing the length of the
310 boundary layer and therefore decreasing the VPD even further than a small leaf could [Defraeye et al., 2013].
311 This lower VPD then induces a decrease in transpiration and an increase in leaf water potential, as it is
312 the case in Experiment 2. High water potential values are correlated with high leaf relative water content
313 [Maxwell and Redmann, 1978]. Water potential is also positively correlated with stomatal conductance
314 [Lhomme et al., 1998]: by maintaining a higher water potential, the leaf will be able to open its stomata
315 wider. CO₂ assimilation is in turn linearly correlated to stomatal conductance [Lambers et al., 2008]. As a
316 result, by affecting the leaf energy cycle, foliar shielding will allow the leaf to maintain its water status and
317 increase CO₂ assimilation.

318 **IV.2 Implications for foliar uptake studies using stable isotopes of water as tracers**

319 The three mechanisms described in section IV.1 will also decrease leaf water isotopic enrichment. Indeed,
320 by decreasing evaporation, foliar shielding suppresses the isotopic enrichment associated with leaf water
321 transpiration [Farquhar et al., 2006]. Therefore, leaves undergoing foliar shielding will have a bulk isotopic
322 composition lower (more depleted) than leaves that do not experience it. The average δD enrichment between
323 the first and last days of collection for Experiment 1A were -9.0 ‰ for the control leaf and -26.8 ‰ for the dew
324 treated leaf. This corresponds to a -17.8 ‰ difference in enrichment between sprayed and control treatments.
325 In the case of highly water stressed leaves (Figure 4), the difference in enrichment reaches -94.0 ‰. In both
326 cases, the fog treated leaf was more depleted in heavy isotopes than the control.

327 Non-meteoric water is usually more enriched than rain and soil water by up to 30 ‰ in some parts of the

328 world [Scholl et al., 2010]. If foliar uptake is indeed happening in a leaf, the uptake of heavy fog water will
329 then enrich the leaf water, while foliar shielding depletes leaf water in heavy isotopes. [Limm et al., 2009]
330 pointed out the tension between foliar uptake and nighttime suppression of respiration due to the saturated
331 atmosphere during fog events. Transpiration is a much larger water loss for plants than respiration and the
332 effects of foliar shielding during day time is expected to be have a even larger impact on leaf isotopes than
333 that discussed by [Limm et al., 2009].

334 In order to look at the relative effects of foliar uptake and foliar shielding, we analyzed the results of
335 three different studies that conducted similar experiments on different species. [Limm et al., 2009] looked
336 at a ten different species from the coast redwood ecosystem of California (*Pseudotsuga menziesii* and *Se-*
337 *quoia sempervirens* (two conifers), *Polystichum munitum* and *Polystichum californicum* (two types of fern),
338 *Oxalis oregana* (a short herbaceous), *Arbutus menziesii*, *Gaultheria shallon*, *Vaccinium ovatum*, *Notholitho-*
339 *carpus densiflorus* and *Umbellularia californica* (all evergreen broadleaf)), while [Eller et al., 2013] fo-
340 cused on *Drimys brasiliensis*, a woody broadleaf evergreen native from Central and South America, and
341 [Berry and Smith, 2014] concentrated on *Abies fraseri* and *Picea rubens*, two montane conifers found in the
342 Appalachian Mountains. All the studies conducted glasshouse experiments in which the samples experienced
343 nighttime fog. Leaf samples were collected in the evening before the fogging treatment and in the morning,
344 right after the treatment. All studies used isotopically labeled fog, but the isotopic composition of the fog
345 differed between studies ($\delta D_{\text{fog}} - \delta D_{\text{soil}} = 16 \text{ ‰}$ in [Berry and Smith, 2014], 78 ‰ in [Limm et al., 2009]
346 and 712 ‰ in [Eller et al., 2013]). In order to compare the different experiments, we normalized the results
347 to reflect the leaf water enrichment that would have been observed if the fog water had been 20 ‰ heavier
348 than soil water, since this is within the range of natural values [Scholl et al., 2010].

349 Foliar uptake has the largest impact on conifers (see Figure 7), where the difference in enrichment between
350 treatment and control reaches up to 20 ‰. Foliar shielding for the non-water stressed case (Experiment 1a)
351 exhibits the opposite effect, with a magnitude similar to the largest foliar uptake case. In the water stressed
352 case (Experiment 1b), the depletion observed is as large as 94 ‰. While this second case is most likely not a
353 realistic one, the true effect of foliar shielding on leaves in the field during a drought is probably in between
354 the two cases shown here. The three foliar experiments presented here all used nighttime treatment, so foliar
355 shielding most likely did not impact the enrichment observed. However, the competing effects of foliar uptake
356 and foliar shielding are likely to be very important when analyzing field or day time foliar uptake experiment
357 data. For example, [Berry et al., 2014b] observed a significantly larger enrichment when fogging saplings in
358 the morning than in the afternoon or the evening. This results is perfectly explained if the effects of foliar
359 shielding on temperature and transpiration are taken into account. Our results point at a larger impact of foliar
360 shielding on leaf isotopes than does foliar uptake in the field, but the relative importance of foliar uptake VS
361 foliar shielding will depend on many factors, including the isotopic composition of the non-meteoric water,
362 the timing and length of the wetting event, the size of the leaf, the atmospheric conditions and of course,
363 the specie. In order to properly interpret isotope data, future studies on foliar uptake should include foliar
364 shielding into their isotope balance calculation.

365 The results of our study show a larger impact of foliar shielding in time of drought than in well-
366 watered conditions. While the concurrent occurrence of non-meteoric water deposition and drought is

rare, it is very common in drylands [Agam and Berliner, 2006], where many plants actually 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 has been proved to be one of the main drivers of leaf water isotopic composition, with a response much larger than to soil water availability for example [Wayland, 2015]. The influence of the water droplets on the leaf energy balance will delay the time when leaves will reach their maximum transpiration rate and attain isotopic steady state [Dubbert et al., 2014]. [Abtew and Melesse, 2012] calculated that dew evaporation from the surface of a leaf takes c. 75 min in southern Florida, and [Garratt and Segal, 1988] estimated that the reduction in transpiration after sunrise due to dewfall could reduce daily plant water use by almost 10%. 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. This results in agreement with the decrease in leaf water enrichment that we observed in leaves experiencing foliar shielding. Isotopic steady state depends highly on the leaf transpiration rate, which changes fast as the leaf energy incoming flux changes, for example when the leaf goes from the shade to the sun. Because of this fast response, foliar shielding will have a large impact at short time scales on both leaf transpiration and water isotopes.

In this paper, we used the highly hydrophobic leaves of *Colocasia esculenta* to study the impact of dew water droplets deposition (called foliar shielding) on the leaf energy, water and isotope balance. Our results show that foliar shielding decreases leaf transpiration, maintains leaf water potential and limits leaf water isotopic enrichment. We highlighted the opposite effect of foliar uptake, which, in natural conditions, tends to enrich leaf water in heavy isotopes, and foliar shielding, which depletes the leaf in heavy isotopes. 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.

Acknowledgments

The authors thank Todd Dawson and Wenbo Yang from the Center for Stable Isotope Biogeochemistry at the University of California in Berkeley for the IRMS analysis and the fruitful discussions on isotope analysis techniques. C.Gerlein-Safdi and K.K. Caylor acknowledge the financial support of NASA Headquarters under the NASA Earth and Space Science Fellowship Program - Grant 14-EARTH14F-241 - and of the Science, Technology, and Environmental Policy Fellowship from the Princeton Environmental Institute.

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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 $\delta^{18}O$ of the leaves analyzed in Experiment 1a.

Fig. S3: Rainfall amount, air and dew point temperatures for the course of 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.

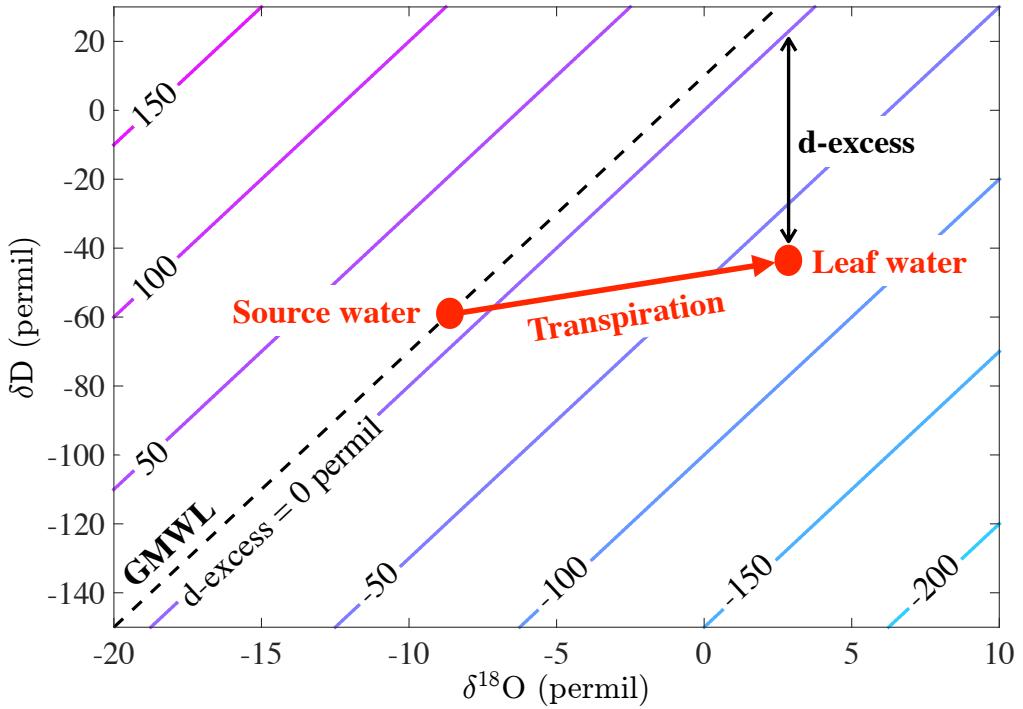


Figure 1: Adapted from [Voelker et al., 2014]: Conceptual figure showing the evaporative conditions controlling the evolution of $\delta^{18}\text{O}$ and δD in leaf water from source water located on the global meteoric water line (GMWL, dashed black line). The slope of the transpiration line depends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

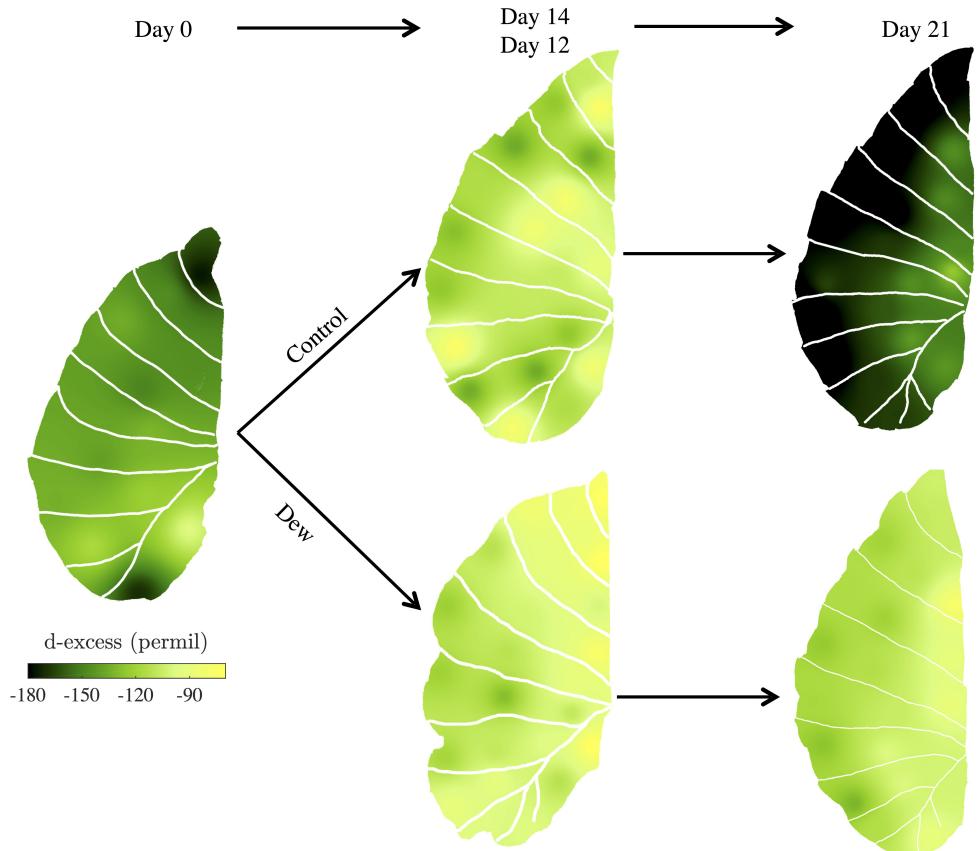


Figure 2: Maps of the spacial distribution of d-excess of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial 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 ($\delta^{18}\text{O} = 8.85\text{\textperthousand}$, $\delta D = 737.64\text{\textperthousand}$) every two days. The color scheme is the same for all rows.

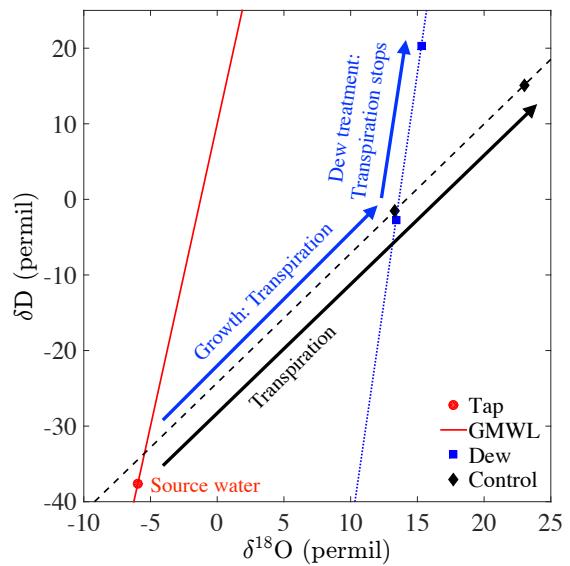


Figure 3: Average $\delta^{18}\text{O}$ and δD of four leaves analyzed in Experiment 1a. **Red circle:** Composition of the tap water used to water the plants during initial growth. **Red solid line:** Global meteoric water line (GMWL). **Blue squares:** Isotopic composition of leaves collected on days 12 and 21 from the dew treatment, where the leaves were sprayed with isotopically enriched water ($\delta^{18}\text{O} = 8.85 \text{ ‰}$, $\delta\text{D} = 737.64 \text{ ‰}$) every two days. The blue dotted line shows the linear regression. **Black diamonds:** Isotopic composition of leaves collected on days 14 and 21 from the control pots. The black dashed line shows the linear regression. The control leaves have a composition that corresponds to that of evaporated tap water, which was used to water the plants until maturation. The dew treated leaves are evolving on a line parallel to the GMWL, showing that transpiration almost completely stopped after the treatment began.

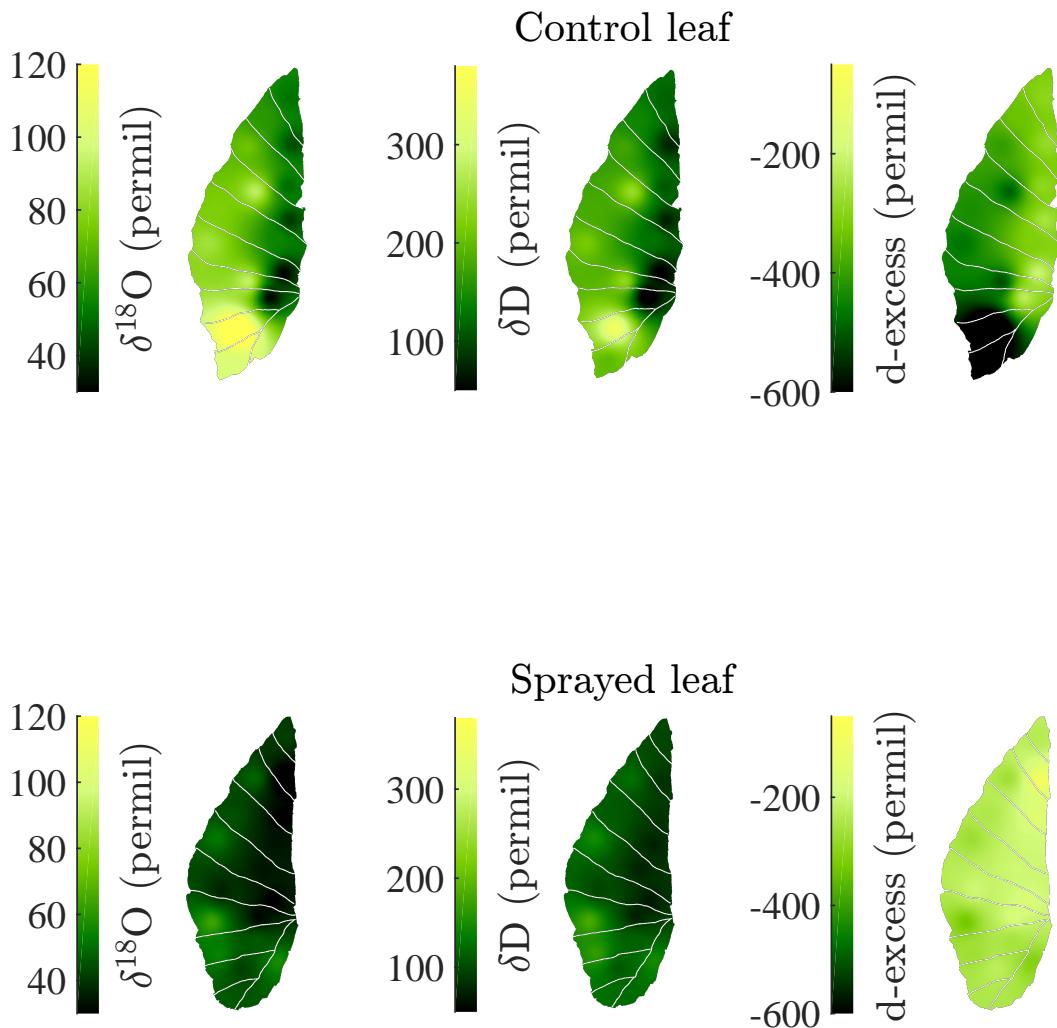


Figure 4: Maps of two leaves left to dry under a 500W blue light for four hours. **Top row:** $\delta^{18}\text{O}$, δD and d-excess of the control (not sprayed) leaf. **Bottom row:** $\delta^{18}\text{O}$, δD and d-excess of the leaf sprayed with isotopically enriched water ($\delta^{18}\text{O} = 8.85 \text{ ‰}$, $\delta\text{D} = 737.64 \text{ ‰}$) 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.

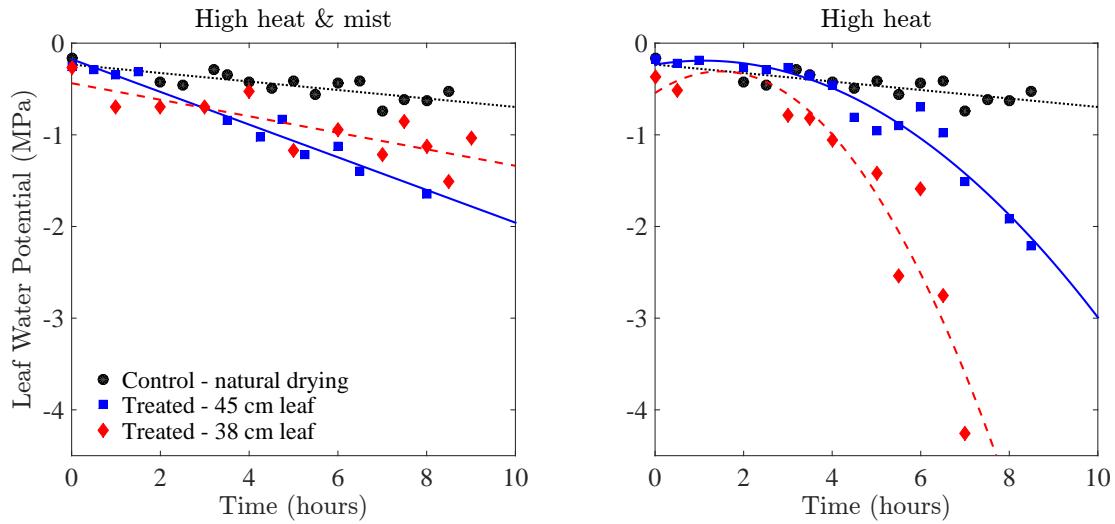


Figure 5: Five examples of the temporal evolution of leaf water potential of *Colocasia esculenta* leaves. The red diamonds are 38 cm long leaves. All other leaves are 45 cm long (black and blue). On the left, natural drying (black dotted line) and both sizes leaf in the high heat & mist (red dashed and blue solid lines) case are best fitted by a linear relation. On the right, the high heat drying case is best fitted by a parabola for both 38 (red dashed line) and 45 cm (blue solid line) leaves.

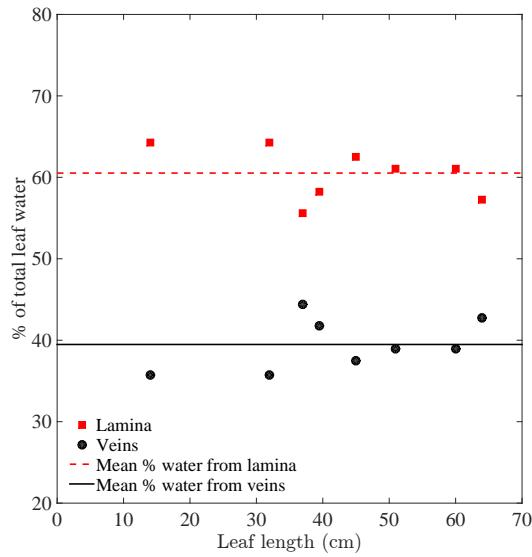


Figure 6: Percent water from veins and lamina for eight leaves of *Colocasia esculenta* with lengths ranging from 14 to 64 cm. **Red squares:** % water from the lamina (dashed red line represents the mean value). **Black circles:** % water from the veins (solid black line represents the mean value). On average, veins accounted for 39% and the lamina for 41% of the total water content of the leaves. The repartition of leaf water between the veins and the lamina shows no significant correlation with leaf size.

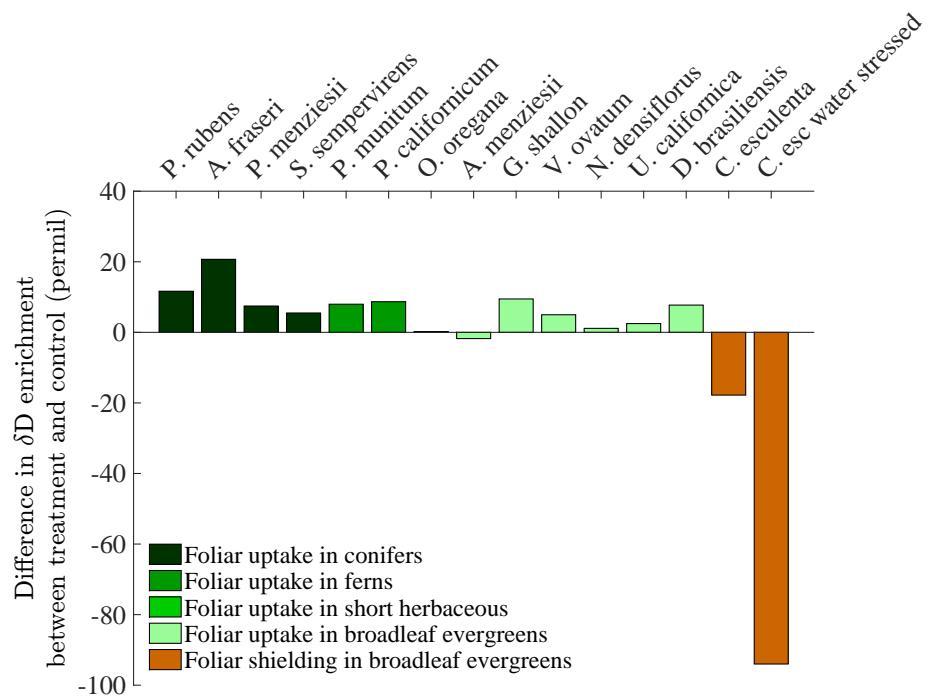


Figure 7: Comparing the impact of foliar uptake of nighttime fog in three studies [Limm et al., 2009, Eller et al., 2013, Berry and Smith, 2014] to foliar shielding in *Colocasia esculenta*. Bars represent the magnitude of the difference in enrichment between fogged/sprayed and control plants. Enrichment is the difference between pre- and post-treatment leaves. All the foliar uptake data was normalized to reflect enrichment corresponding to a realistic difference of 20 % between rain and fog water [Scholl et al., 2010].

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.

Fig. S3: Rainfall amount, air and dew point temperatures for the course of Experiment 1a.

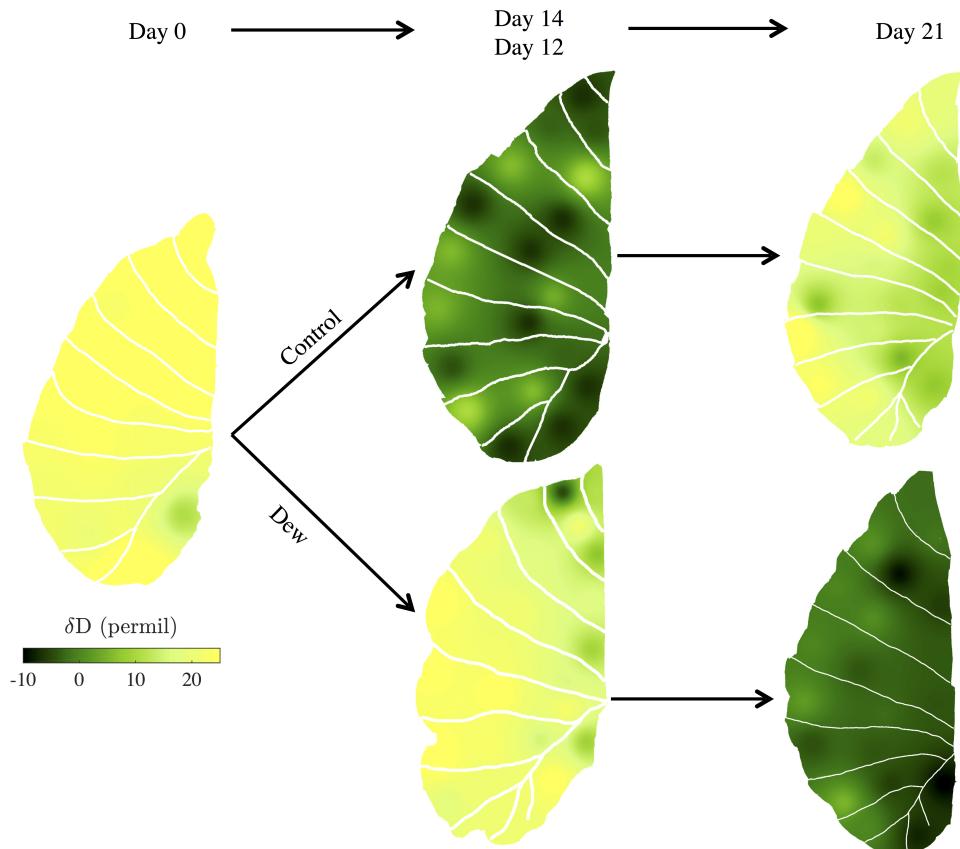


Figure S1: Maps of the spacial distribution of δD of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial leaf 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 ($\delta^{18}O = 8.85 \text{ ‰}$, $\delta D = 737.64 \text{ ‰}$) every two days. The color scheme is the same for all rows.

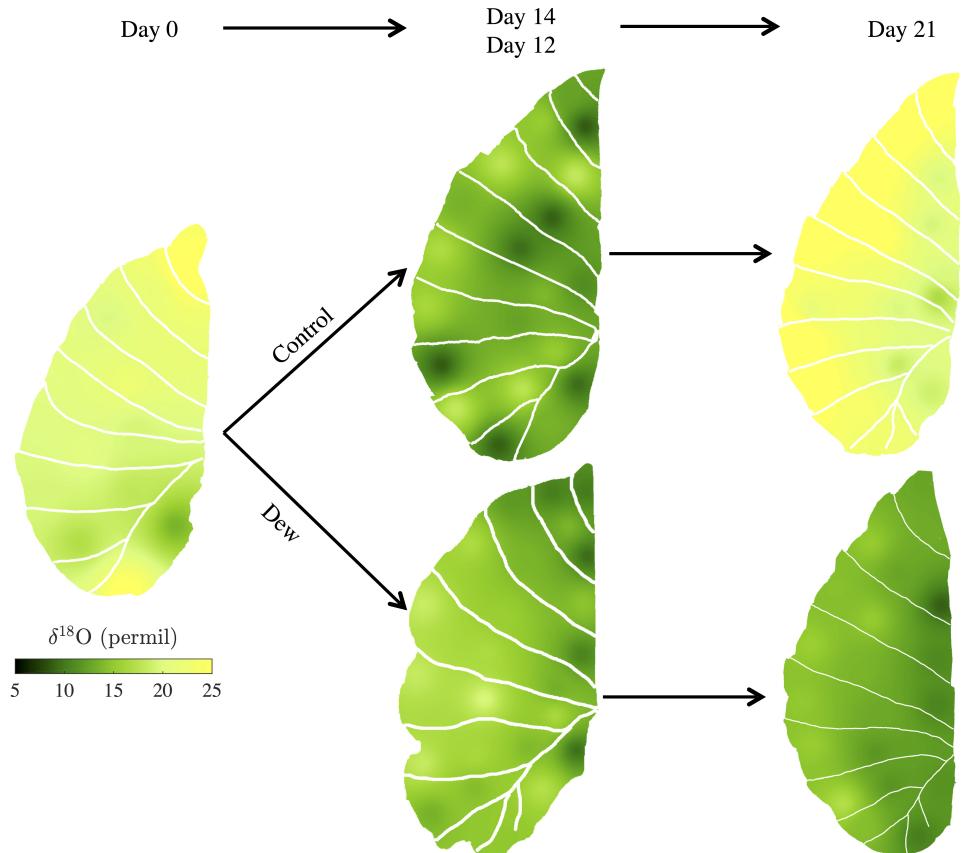


Figure S2: Maps of the spacial distribution of $\delta^{18}\text{O}$ of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:**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

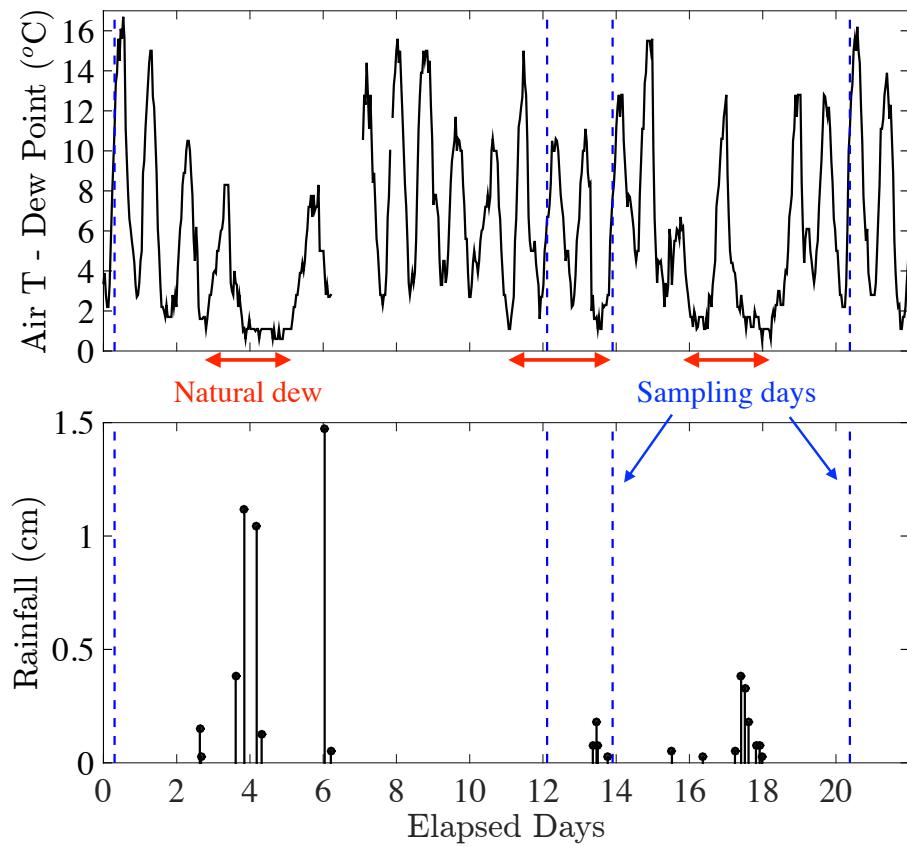


Figure S3: **Top panel:** Difference between the air and the dew point temperature over the course of the experiment ($^{\circ}\text{C}$). **Bottom panel:** Rainfall (cm) over the course of the experiment. The blue dashed vertical lines mark the days of collection: the initial leaf was collected on day 0, leaves from the dew treatment were collected on days 12 and 21 and leaves from the control were collected on days 14 and 21. Red horizontal arrows indicate days when the leaves most likely experienced natural dew deposition because of the local air temperature and relative humidity under the sheltered area. The collection of the first control leaf happened after a series of small rain events and four nights of natural dew formation.