

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

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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 (1-5 and 7 in color)
No. of Tables	1
No. of Supporting Information files	3 figures (all color)

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

What hypotheses or questions does this work address?

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

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

The importance of non-meteoric water 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 $2.6 \pm 0.88\text{\textperthousand}$ in $\delta^{18}\text{O}$ (mean \pm SE) and $3.4 \pm 2.4\text{\textperthousand}$ in δD . These values are higher than the
189 average difference we observed between two halves of the same *Colocasia esculenta* leaf, both extracted
190 by cryogenic vacuum distillation and analyzed by IRIS ($0.3 \pm 0.2\text{\textperthousand}$ in $\delta^{18}\text{O}$ and $1.9 \pm 1.2\text{\textperthousand}$ in δD). The
191 observed error is therefore not attributable to the analysis on IM-CRDS and IRMS being conducted on
192 each half of the same leaf. Further testing is clearly necessary before using the IM-CRDS technique as an
193 absolute method. However, our goal in this paper is to compare strongly enriched waters and the order of the
194 differences presented in the next section are up to two orders of magnitude bigger than the error observed for
195 the IM-CRDS. We therefore believe that the IM-CRDS is an appropriate method here, as it allowed us to
196 quickly process many small samples, therefore increasing the spatial and temporal resolution of our analysis.

197 II.6 Statistical analysis

198 Responses for the different experiments were analyzed using a two-sample t-test (Welch's t-test) with a 5%
199 significance level. This test has been recognize as a better alternative to the Student's t-test when dealing with
200 groups of unequal sample size or variance [Ruxton, 2006]. The tests were all performed using Matlab v. 2014b
201 (Mathworks, Natick, MA, USA). When comparing the results of the different treatments in Experiments 1a
202 and 1b, we treated the multiple samples collected on each leaf as a single population.

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 a progressive enrichment [Cernusak and Kahmen, 2013] of leaf water when moving away from
210 the main stem towards the rims of the leaf (Average difference between the center and the rim of the leaf:
211 $\Delta^{18}\text{O} = 11.1 \pm 1.2\text{\textperthousand}$ (mean \pm SE) and $\Delta\text{D} = 23.9 \pm 3.3\text{\textperthousand}$). Comparing the results for both treatments at the
212 end of the experiment, we see that the dew treated plants exhibits a significantly higher d-excess values than
213 the control ones ($\Delta\text{d-excess} = 63.0\text{\textperthousand}$, two-sample t-test: $t = -9.3$, $P < 0.001$). The effect of the dew treatment
214 was not apparent for days 12/14 ($\Delta\text{d-excess} = 10.2\text{\textperthousand}$, two-sample t-test: $t = -1.6$, $P = 0.11$).

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

216 Similar maps were produced for Experiment 1b (Figure 4). In this case, the heat lamp artificially increased
217 the transpiration rate in both the control and the misted leaves, leading to significantly enriched $\delta^{18}\text{O}$ and δD

values and very low d-excess values for both treatments. The d-excess in the control case is a lot more negative (reaching values down to ~-800 ‰) than for the dew treated leaves (reaching values down to ~-300 ‰): $\Delta d\text{-excess} = 173.0 \text{ ‰}$, two-sample t-test: $t = 3.9$, $P < 0.001$). 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.

III.3 Effects of foliar shielding on leaf water potential

Experiment 2 was design to look at the temporal evolution of water potential in artificially drying leaves (see Figure 5). Strong differences in drying pattern are shown for the misted or drought leaves. In both the control and the the high heat & mist cases, the leaf water potential experiences a slow decline, which is best approximated by a linear function. However, the high heat treated leaves experience a faster decline and are best approximated by a parabola. Table 2 presents the average decline from initial to final leaf water potential for the three different treatments. All the data is normalized for leaf size and drying time. The misted leaves exhibit a much smaller decline in water potential than the leaves subjected to the same high heat treatment but that did not get sprayed (two-sample t-test: $t = 2.36$, $P < 0.05$). The decline observed for misted leaves is not statistically different to the one observed for naturally drying leaves (two-sample t-test: $t = -1.46$, $P = 0.19$).

IV. Discussion

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

IV.1 Linking d-excess and transpiration

[Allison et al., 1985] stomatal conductance $0.36 \text{ mmol.m}^{-2}.\text{s}^{-1}$ [Hughes et al., 2014] The enrichment is due to the progressive transpiration of the leaf water as it moves away from the source water that enters the leaf through the petiole. The lighter isotopologues are transpired first, leaving the heavier ones in the leaf [Farquhar et al., 2006]. This translates into a decrease in d-excess from the center of the leaf towards to the edges. Those results reinforced our confidence in the IM-CRDS method. 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.

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.

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

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

First, the deposited droplets increase the albedo of the leaf, allowing more of the radiations to be reflected away from the leaf. The albedo is the reflection coefficient for solar radiations of natural surfaces. Depending on the direction of the incoming solar radiations, 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 do dew deposition has been observed in the field many times [Pinter, 1986, Zhang et al., 2012]. By reflecting more radiations when there are wet, leaves will then decrease the incoming shortwave radiations and consequently keep their temperature 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 evaporated droplets allow to 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 increase 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. The leaf size dependency of this third mechanism is confirmed by the leaf size dependent behavior observed for the misted case of Experiment 2 (see Figure 5): if only the first two mechanisms were at play, one would not expect a difference between two leaves of different size receiving mist. However, bigger misted leaves will create a larger micro-climate, increasing the length of the boundary layer and therefore decreasing the VPD even further than a small leaf could [Defraeye et al., 2013]. This lower VPD then induces a decrease in transpiration and an increase in leaf water potential, as it is the case in Experiment 2. High water potential values are correlated with high leaf relative water content [Maxwell and Redmann, 1978]. Water potential is also positively correlated 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, foliar shielding will allow the leaf to maintain its water status and increase CO₂ assimilation.

IV.3 Implications for foliar uptake studies using stable isotopes of water as tracers

The three mechanisms described in section IV.2 will also decrease leaf water isotopic enrichment. Indeed, by decreasing evaporation, foliar shielding suppresses the isotopic enrichment associated with leaf water transpiration [Farquhar et al., 2006]. Therefore, leaves undergoing foliar shielding will have a bulk isotopic composition lower (more depleted) than leaves that do not experience it. The average δD enrichment between the first and last days of collection for Experiment 1A were -9.0 ‰ for the control leaf and -26.8 ‰ for the dew treated leaf. This corresponds to a -17.8 ‰ difference in enrichment between sprayed and control treatments. In the case of highly water stressed leaves (Figure 4), the difference in enrichment reaches -94.0 ‰. In both cases, the fog treated leaf was more depleted in heavy isotopes than the control.

Non-meteoric water is usually more enriched than rain and soil water by up to 30 ‰ in some parts of the world [Scholl et al., 2010]. If foliar uptake is indeed happening in a leaf, the uptake of heavy fog water will then enrich the leaf water, while foliar shielding depletes leaf water in heavy isotopes. [Limm et al., 2009] pointed out the tension between foliar uptake and nighttime suppression of respiration due to the saturated atmosphere during fog events. Transpiration is a much larger water loss for plants than respiration and the effects of foliar shielding during day time is expected to be have a even larger impact on leaf isotopes than that discussed by [Limm et al., 2009].

In order to look at the relative effects of foliar uptake and foliar shielding, we analyzed the results of three different studies that conducted similar experiments on different species. [Limm et al., 2009] looked at a ten different species from the coast redwood ecosystem of California (*Pseudotsuga menziesii* and *Se-*

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

341 Foliar uptake has the largest impact on conifers (see Figure 6), where the difference in enrichment between
342 treatment and control reaches up to 20 ‰. Foliar shielding for the non-water stressed case (Experiment 1a)
343 exhibits the opposite effect, with a magnitude similar to the largest foliar uptake case. In the water stressed
344 case (Experiment 1b), the depletion observed is as large as 94 ‰. While this second case is most likely not a
345 realistic one, the true effect of foliar shielding on leaves in the field during a drought is probably in between
346 the two cases shown here. The three foliar experiments presented here all used nighttime treatment, so foliar
347 shielding most likely did not impact the enrichment observed. However, the competing effects of foliar uptake
348 and foliar shielding are likely to be very important when analyzing field or day time foliar uptake experiment
349 data. For example, [Berry et al., 2014b] observed a significantly larger enrichment when fogging saplings in
350 the morning than in the afternoon or the evening. This results is perfectly explained if the effects of foliar
351 shielding on temperature and transpiration are taken into account. Our results point at a larger impact of foliar
352 shielding on leaf isotopes than does foliar uptake in the field, but the relative importance of foliar uptake VS
353 foliar shielding will depend on many factors, including the isotopic composition of the non-meteoric water,
354 the timing and length of the wetting event, the size of the leaf, the atmospheric conditions and of course,
355 the specie. In order to properly interpret isotope data, future studies on foliar uptake should include foliar
356 shielding into their isotope balance calculation.

357 The results of our study show a larger impact of foliar shielding in time of drought than in well-
358 watered conditions. While the concurrent occurrence of non-meteoric water deposition and drought is
359 rare, it is very common in drylands [Agam and Berliner, 2006], where many plants actually rely on non-
360 meteoric water as their primary source of water [Stanton and Horn, 2013]. Regular dew formation has also
361 been observed in the upper canopy of the Amazon forest during the dry season [Satake and Hanado, 2004,
362 Frolking et al., 2011]. In those cases, energy balance has been proved to be one of the main drivers of
363 leaf water isotopic composition, with a response much larger than to soil water availability for example
364 [Wayland, 2015]. The influence of the water droplets on the leaf energy balance will delay the time when
365 leaves will reach their maximum transpiration rate and attain isotopic steady state [Dubbert et al., 2014].
366 [Abtew and Melesse, 2012] calculated that dew evaporation from the surface of a leaf takes c. 75 min in
367 southern Florida, and [Garratt and Segal, 1988] estimated that the reduction in transpiration after sunrise due

368 to dewfall could reduce daily plant water use by almost 10%. Isotopic steady state is often assumed when
369 interpreting transpiration data, but [Dubbert et al., 2013] recently showed that this assumption is typically
370 unjustified and can lead to errors in estimated transpiration fluxes by up to 70% since steady state models
371 systematically overestimate the isotopic enrichment of leaf water. This results in agreement with the
372 decrease in leaf water enrichment that we observed in leaves experiencing foliar shielding. Isotopic steady
373 state depends highly on the leaf transpiration rate, which changes fast as the leaf energy incoming flux
374 changes, for example when the leaf goes from the shade to the sun. Because of this fast response, foliar
375 shielding will have a large impact at short time scales on both leaf transpiration and water isotopes.

376 In this paper, we used the highly hydrophobic leaves of *Colocasia esculenta* to study the impact of dew
377 water droplets deposition (called foliar shielding) on the leaf energy, water and isotope balance. Our results
378 show that foliar shielding decreases leaf transpiration, maintains leaf water potential and limits leaf water
379 isotopic enrichment. We highlighted the opposite effect of foliar uptake, which, in natural conditions, tends to
380 enrich leaf water in heavy isotopes, and foliar shielding, which depletes the leaf in heavy isotopes. Because
381 both effects are of similar magnitude, taking into accounts both processes is crucial to properly interpret
382 field data of foliar uptake. Our results are also in agreement with recent studies pointing at the importance
383 of non-isotopic steady state for the proper understanding of leaf water fluxes. More experiments are now
384 required to understand the effects of foliar shielding on different species and for a range of leaf shapes
385 and sizes. Introducing stable isotopes of water in a model of leaf energy and water balance could help to
386 interpret the competing effects of foliar uptake and foliar shielding, give a new insight into non-steady-state
387 transpiration, and improve the general understanding of the interaction of leaves with their environment.

388 Acknowledgments

389 The authors thank Todd Dawson and Wenbo Yang from the Center for Stable Isotope Biogeochemistry at the
390 University of California in Berkeley for the IRMS analysis and the fruitful discussions on isotope analysis
391 techniques. C.Gerlein-Safdi and K.K. Caylor acknowledge the financial support of NASA Headquarters under
392 the NASA Earth and Space Science Fellowship Program - Grant 14-EARTH14F-241 - and of the Science,
393 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.

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

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

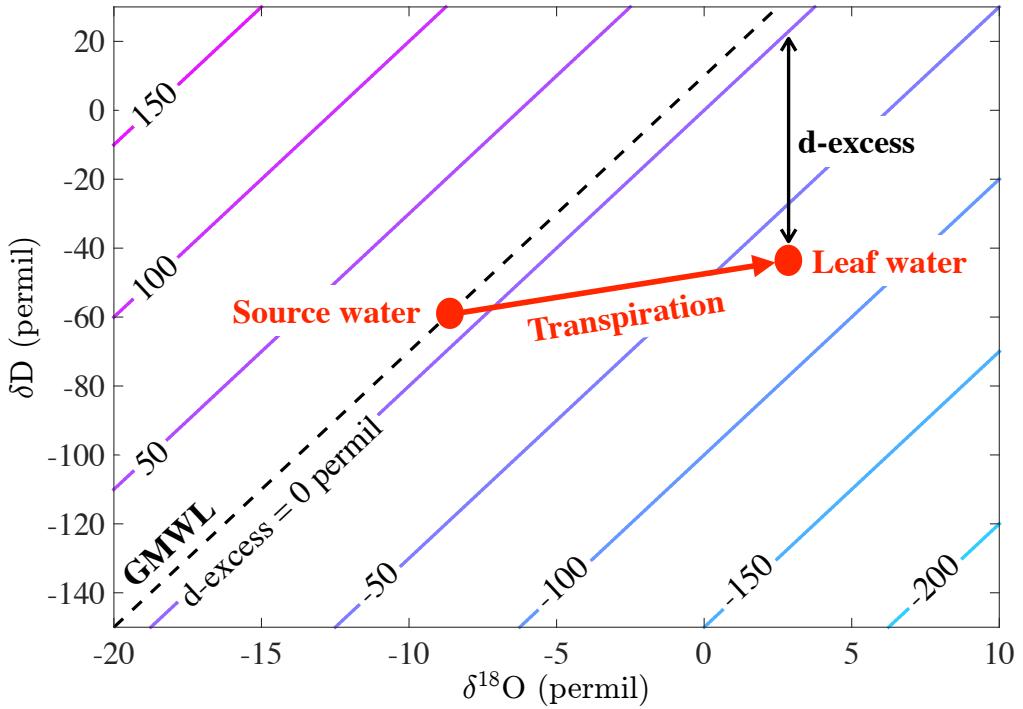


Figure 1: Adapted from [Voelker et al., 2014]: Conceptual figure showing the evaporative conditions controlling the evolution of $\delta^{18}\text{O}$ and δD in leaf water from source water located on the global meteoric water line (GMWL, dashed black line). The slope of the transpiration line depends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

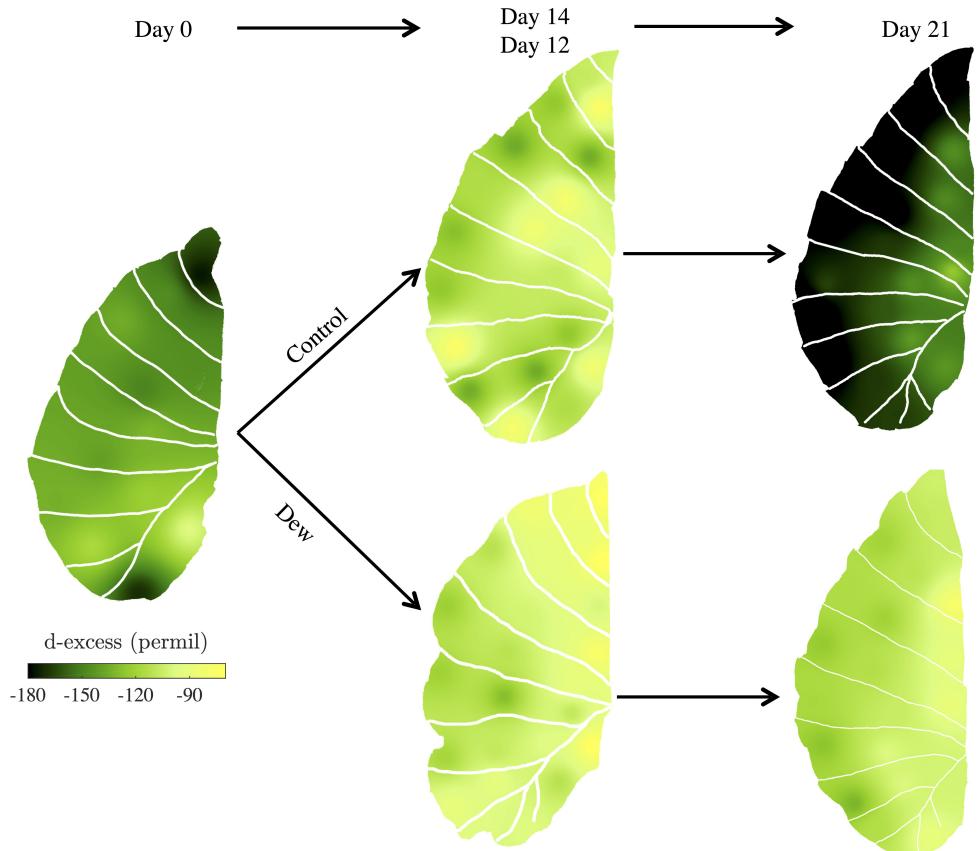


Figure 2: Maps of the spacial distribution of d-excess of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial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

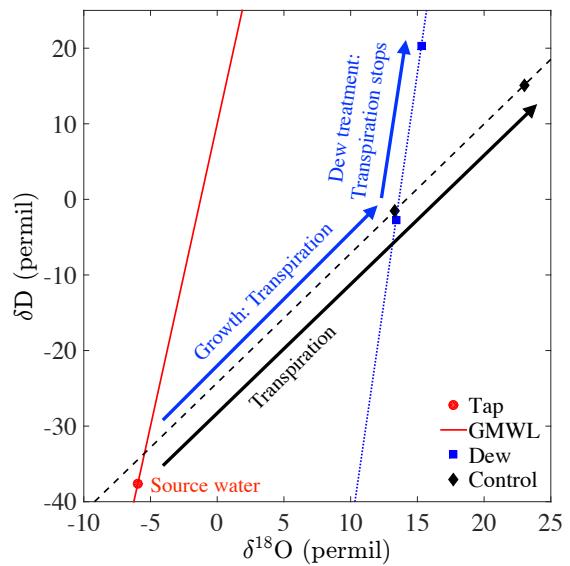


Figure 3: Average $\delta^{18}\text{O}$ and δD of four leaves analyzed in Experiment 1a. **Red circle:** Composition of the tap water used to water the plants during initial growth. **Red solid line:** Global meteoric water line (GMWL). **Blue squares:** Isotopic composition of leaves collected on days 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.

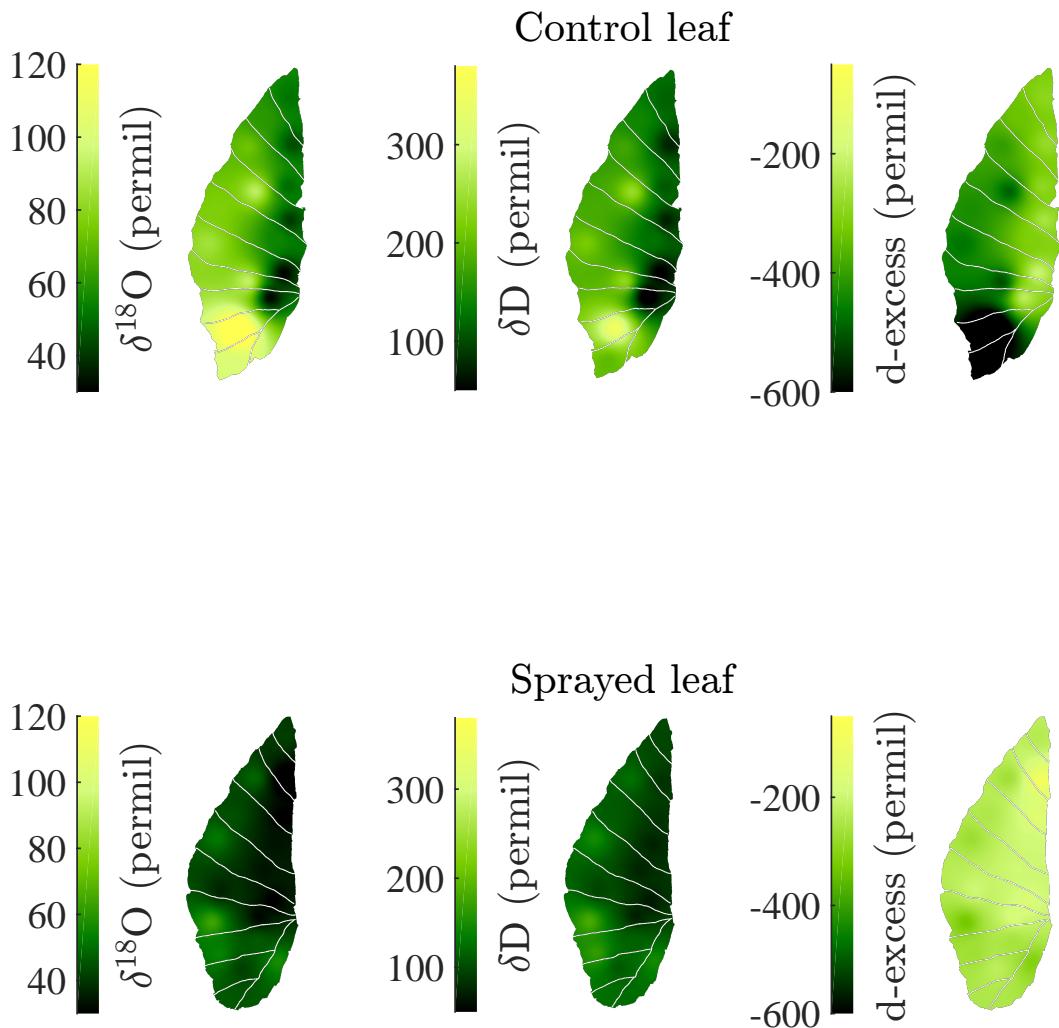


Figure 4: Maps of two leaves left to dry under a 500W blue light for four hours. **Top row:** $\delta^{18}\text{O}$, δD and d-excess of the control (not sprayed) leaf. **Bottom row:** $\delta^{18}\text{O}$, δD and d-excess of the leaf sprayed with isotopically enriched water ($\delta^{18}\text{O} = 8.85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

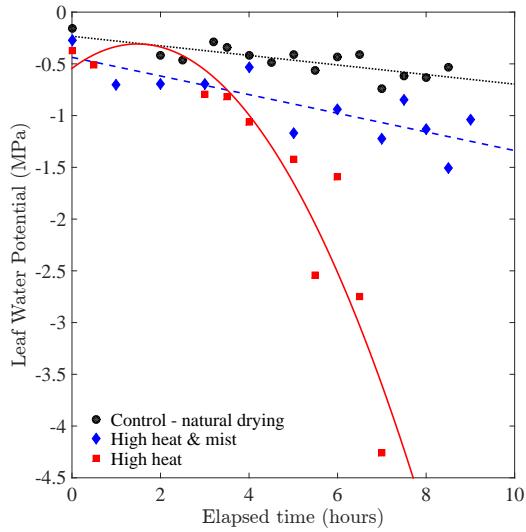


Figure 5: Typical examples of the temporal evolution of the leaf water potential of *Colocasia esculenta* leaves under three different treatments. All the leaves under the natural drying (black circles) and the high heat & mist (blue diamonds) treatments are best fitted by a linear relation (black dotted and blue dashed lines, respectively). All but one of the leaves under the high heat drying case (red squares) are best fitted by a parabola (red solid line). All the leaves shown here are c. 38 cm long.

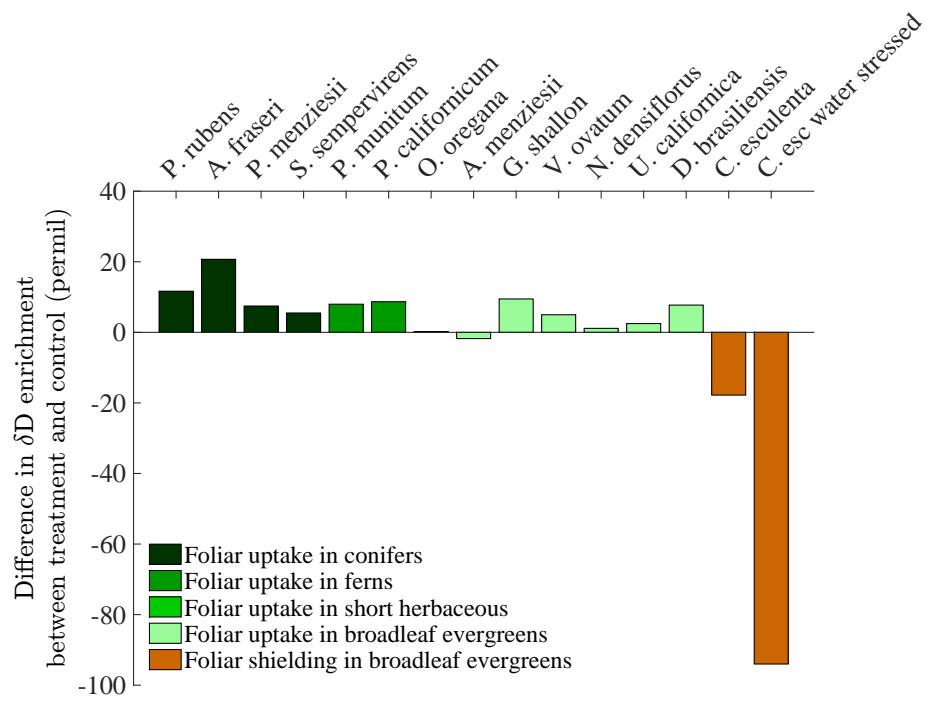


Figure 6: Comparing the impact of foliar uptake of nighttime fog in three studies [Limm et al., 2009, Eller et al., 2013, Berry and Smith, 2014] to foliar shielding in *Colocasia esculenta*. Bars represent the magnitude of the difference in enrichment between fogged/sprayed and control plants. Enrichment 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

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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.

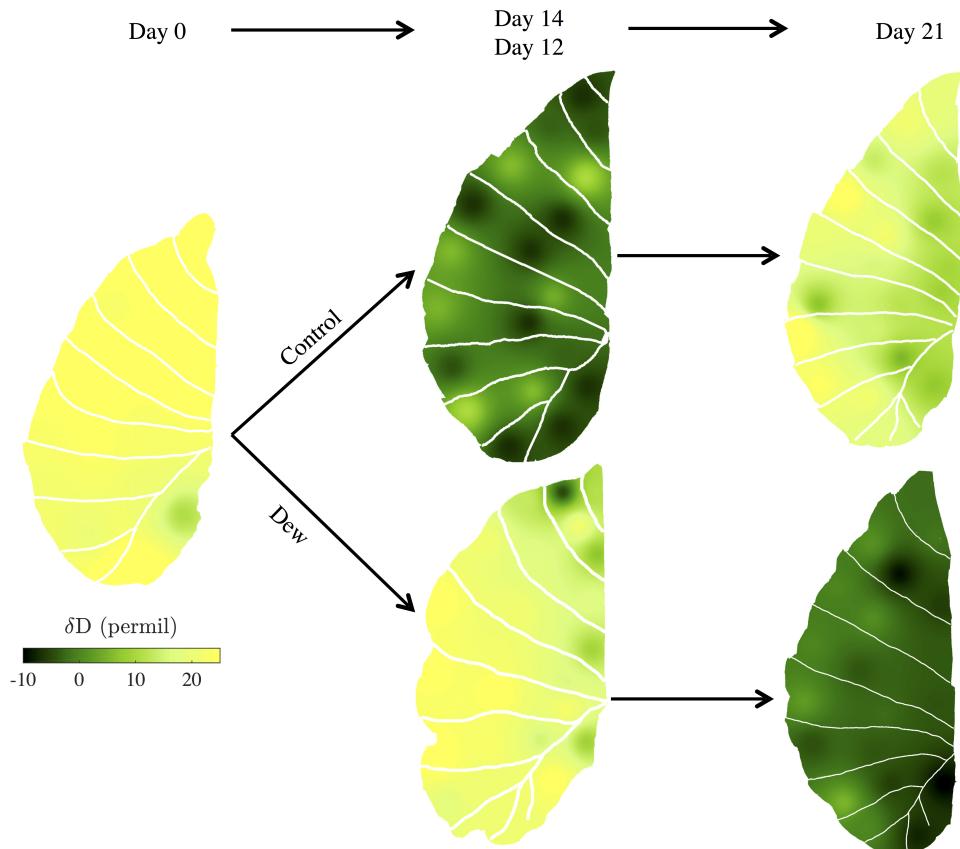


Figure S1: Maps of the spacial distribution of δD of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** initial leaf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

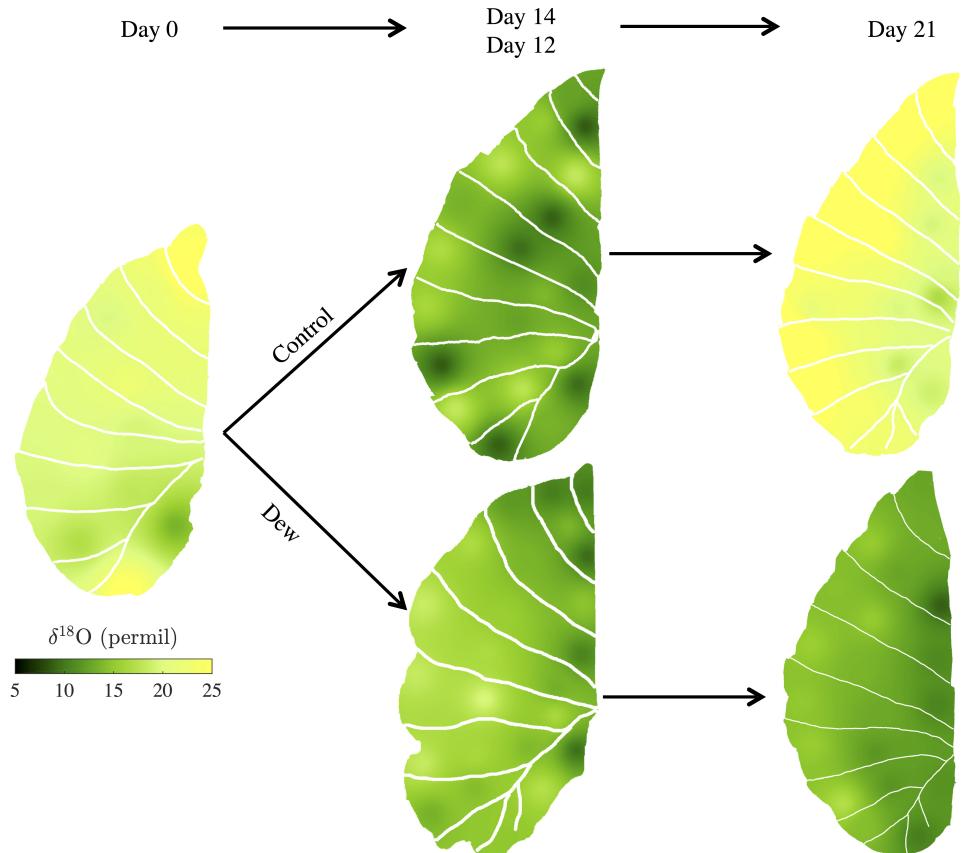


Figure S2: Maps of the spacial distribution of $\delta^{18}\text{O}$ of five *Colocasia esculenta* leaves collected throughout Experiment 1a. The maps were obtained by inverse distance interpolation of 12 to 25 sampling points analyzed on the Picarro Induction Module. All leaves are c. 38 cm long. **Left:** 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.

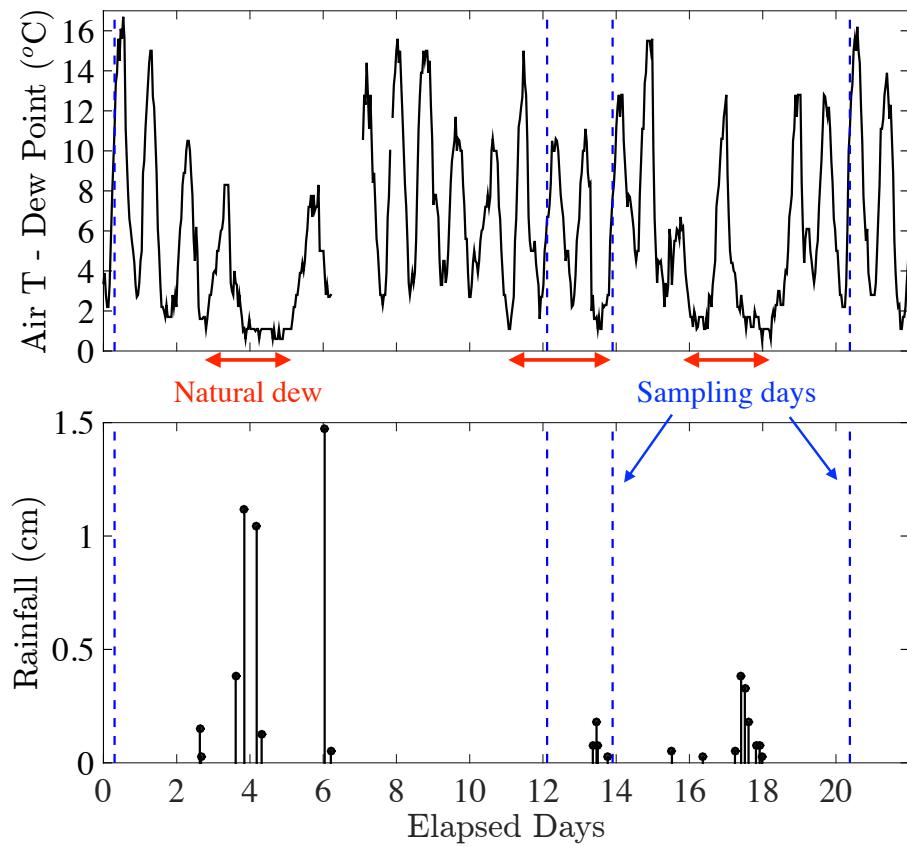


Figure S3: **Top panel:** Difference between the air and the dew point temperature over the course of the experiment ($^{\circ}\text{C}$). **Bottom panel:** Rainfall (cm) over the course of the experiment. The blue dashed vertical lines mark the days of collection: the initial leaf was collected on day 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.