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

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Summary

- The uptake of water from the surface of the leaves, called foliar uptake, is common when rainfall is scarce and non-meteoric water (dew or fog) is the only water source. However, many species have very water repellent leaves. Past studies have not differentiated between the uptake of water and the impact of the droplets on the energy balance of the leaf, which we call 'foliar shielding'.

- Leaves of the hydrophobic *Colocasia esculenta* were sprayed with isotopically enriched water. We developed a protocol using a laser spectrometer and an induction module for the rapid analysis of leaf samples. The leaf water potential and water isotopes were monitored for different water-stress conditions.

- Dew-treated leaves exhibited a higher leaf water potential ($P < 0.05$) and c. 30% decrease in transpiration rate ($P < 0.001$) compared to the control. The dew treated leaves also had a depleted water isotopic composition compared to the control ($P < 0.001$). Three possible mechanisms are proposed for the interaction of water droplets with the leaf energy and water balance.

- Comparing three previous foliar uptake studies to our results, we conclude that foliar shielding has a comparable yet opposite effect to foliar uptake on leaf water isotopes.

I.   Introduction

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

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

In the present study, we will focus on the interaction of non-meteoric water droplets on the leaf energy balance, which we call 'foliar shielding'. It is known that many species have water-repellent leaves [Neinhuis and Barthlott, 1997] which are not adapted to uptake water. For most plants, non-meteoric water deposition is a source of nuisance as it may freeze and cause damages to the leaf in cold climate, or stagnate and cause rotting and pathogen infection in warm environments [Evans et al., 1992]. Leaves that are repeatedly exposed to dew have even been shown to become more water-repellent [Aryal and Neuner, 2009]. However, micro-droplets of water will indeed form on the surface of even very hydrophobic leaves. The interaction of these droplets on the leaf energy balance (foliar shielding) has been mentioned in previous work [Limm et al., 2009, Berkelhammer et al., 2013], but this study is the first to quantify the impact of this process on leaf water balance and leaf water isotopes.

Leaf energy balance —   Because they are unable to move to the shade, leaves are vulnerable to sun radiation, and they can often be warmer than the surrounding air. The leaf temperature will in turn affect the saturation vapor pressure, isotope fractionation, transpiration, and photosynthesis. Smaller leaves tend to be at a temperature closer to the ambient air, since their boundary layer is thinner. This is the reason why, on a single tree, leaves exposed to the sun are usually smaller than shaded ones. To stay cool, leaves use a combination of re-radiation (transfer of energy to the surroundings), convection (heat loss as cool air moves over the surface of the leaf) and evaporative cooling (evaporation of water inside the leaf into water vapor, which is an exothermic process) [Vogel, 2012]. During a drought, leaves have to preserve water to maintain

turgor pressure, which competes with evaporative cooling. In this case, leaves are left with re-radiation and convection to cool themselves down. This is sometimes not enough to maintain a low temperature. If its duration extends for too long, a drought might lead to plant mortality.

Non-meteoric water can supply the plants with a pool of water that will supplement the scarce leaf water by depositing a layer of small water droplets on the surface of the leaves. This provides a form of externalized evaporative cooling. Moreover, the presence of the droplets will both increase the albedo of the leaves, allowing it to reflect more energy [Pinter, 1986], and increase surface roughness, which increases the leaf boundary layer, therefore decreasing the vapor pressure deficit (VPD) and lowering the evaporative demand. This later mechanism was proposed by [Limm et al., 2009] to explain how fog suppresses nighttime respiration in redwoods.

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

Dew formation is usually included in global climate models (GCMs) as it merely involves tracking dry bulb temperatures going below the dewpoint temperature. However, its interaction with vegetation is not commonly taken into account. Non-meteoric water deposition events occur around the world, even in dryland ecosystems [Agam and Berliner, 2006], and may affect large areas at the same time. The small changes in the energy, water and carbon balance of each single leaf can therefore have a large cumulative impact at the ecosystem level. Including this interaction into GCMs would allow modelers to better understand the response of vegetation to climate change and the feedback on CO_2 atmospheric concentrations.

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

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In this study, we present three experiments that focus on the effects of water droplets deposition at the surface of *Colocasia esculenta* leaves. This specie is native to South East Asian tropical forests but has been cultivated across the world for many centuries under the name of taro. With a contact angle of ~164° [Neinhuis and Barthlott, 1997], *Colocasia esculenta* is considered to have highly water-repellent leaves. Its leaves can reach a size of up to c. 50 cm in length and c. 40 cm in width. We present the first protocol for the fast analysis of small sized leaf samples, allowing for spatial and temporal high-resolution mapping of the leaf-water properties. Using isotopically-labelled water as well as traditional plant physiology techniques, we confirm that the *Colocasia esculenta* leaves do not uptake water from the surface of the leaves. So far, few studies have attempted to map leaf isotopes because it is both time and labor intensive. While the number of replica presented in this study was limited by the novelty of the protocol, c. 550 plant samples were analyzed. This number largely exceeds the number of samples analyzed by previous studies focused on spatial patterns of leaf-water isotopes [Gan et al., 2002, Šantrůček et al., 2007]. We analyze the spatial patterns of leaf water isotopic enrichment and compare them to three different models. In addition, we show that foliar shielding decreases leaf transpiration and increases water potential, and we present three mechanisms that explain the influence of water droplet deposition on the energy and water cycles of water-repellent leaves. Finally, we compare our results to multiple foliar uptake studies. We conclude that foliar shielding has an opposite and larger effect on leaf isotopes than foliar uptake. It is therefore crucial to include foliar shielding in leaf isotope models to properly interpret isotope data of foliar uptake.

II. Materials and Methods

II.1 The added value of stable isotopes

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

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

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

96 Because precipitation condenses under conditions of equilibrium fractionation, δ^{18}O and δD in precip-

97 itation evolve along a line with slope c. 8, the global meteoric water line (GMWL) [Voelker et al., 2014].

98 However, kinetic isotope effects associated with differences in diffusivity among the different isotopologues of

99 water can lead to deviations from the GMWL [Farquhar et al., 2006]. For example, since HD^{16}O diffusivity

100 is greater than that of H$_2$^{18}O, the water of a leaf that has undergone heavy transpiration will be more depleted

101 in D than in ^{18}O (Fig. 1). Deuterium excess (d-excess) is a widely used measure of how evaporated a pool

102 of water (ocean, lake, leaf) is and is defined as d-excess = δD $- 8 \times \delta^{18}$O. The average d-excess for precipi-

103 tation is c. 10‰. Lower d-excess values generally indicate that the pool has undergone some evaporation

104 [Brooks et al., 2014] (Fig. 1).

105 Stable isotopes are also very efficient to identify different water sources in plants [Ehleringer and Dawson, 1992].

106 Indeed, simple mixing models allow one to separate the composition and the fluxes coming from differ-

107 ent sources [Phillips and Gregg, 2001]. For this reason, stable isotopes are great natural labels that can

108 be used to track pathways of water within plants without harming them; they have been the method of

109 choice for many studies looking at foliar uptake [Breshears et al., 2008, Limm et al., 2009, Eller et al., 2013,

110 Berry et al., 2014b]. Indeed, non-meteoric water is usually enriched in heavy isotopes [Scholl et al., 2010],

111 making it easy to trace even after entering the leaf.

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

113 Our first experiment examines leaf scale spatial and temporal patterns of water isotopes induced by the

114 presence or the absence of dew under natural conditions. Six bulbs of *Colocasia esculenta* were planted in

115 separate pots. All pots were placed outside and received full sun for four weeks. During this time, all plants

116 were heavily watered with tap water (δ^{18}O $\simeq$ -5.96 ‰, δD $\simeq$ -37.63 ‰) to allow plant growth. Once the six

117 plants reached maturity, watering stopped and the plants were moved to a shaded area to remove any sun

118 exposure differences between the plants.

119 Watering stopped two days before the beginning of the treatment. The upper-leaf surfaces in three of

120 the six pots were misted with isotopically-enriched water (δ^{18}O $\simeq$ 8.85 ‰, δD $\simeq$ 737.64 ‰) every two days

121 using a spray bottle. Any extra water would run off the leaves, leaving them covered in submillimeter-size

122 droplets, which is approximately the natural size for dew-deposition drops [Defraeye et al., 2013]. The

123 misting simulated dew and was always performed around 08:00h.

124 The three control pots were not watered and did not receive any mist. To avoid contact between the misted

125 water and the soil in the pots, the surfaces of all pots were covered in wrapping plastic. Six leaves were

126 collected between the beginning of the control/dew treatments and the end of the experiments, three weeks

127 later. The sampling and the analysis are described in Section II.5.

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

Our 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 c. 80 cm under a blue light (Eiko 1960 EBW, 500 W, 10500 lumens, color temperature of 4800 K). The entire experiment lasted four hours. During that time, the treated leaf was misted with isotopically-labelled water (δ^{18}O $\simeq$ 8.85 ‰, δD $\simeq$ 737.64 ‰) 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 leaf water potential

In this final experiment, we focused on the effect of water droplet 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 and 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 between 8 and up to 10 hours. In the high heat and 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 Isotope analysis

For the water isotope analysis, each leaf was sampled in 12 to 25 different locations depending on the size of the leaf. All of the sampling points were located on the same half of the leaf and each point consisted of 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. 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 showed no decline in weight, proving that this setting dried the leaf samples completely. The IM was

equipped with a micro-combustion module, which has been proven to efficiently reduce the interferences due to the presence of organics (Kate Dennis, private communication) in water samples extracted from plants [West et al., 2010]. On average, each half-leaf was sampled in c. 18 different locations, which corresponds to c. 73 punched holes.

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

IM-CRDS analysis sequence   The IM has only been available commercially for a few years and the number of published studies making use of it is still very limited [Berkelhammer et al., 2013]. Here we present the first detailed protocol for the analysis of leaf samples.

The IM-CRDS analysis sequence was adapted from a protocol developed in [van Geldern and Barth, 2012] for liquid water samples. 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, δ^{18}O, and δD for the six vials were 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 filter paper 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 was necessary to reproduce the amount of water contained by one punch hole of *Colocasia esculenta*. The data was corrected for drift and memory effects, and it was also rescaled back to VSMOW.

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 (Thermo Finnigan, Bremen). Microliters of water were injected in the H/Device and reduced to H_2 gas. The ratio of D/H was then measured on a Thermo Delta Plus mass spectrometer. For the δ^{18}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 (Wenbo Yang, private communication).

In this H_2O-CO_2 equilibration method, the dissolved components (organic and/or inorganic) do not affect the values of $\delta^{18}O$ [West et al., 2010]. For the IRIS analysis, 1.8 μl of water was injected into a vaporizer and the vapor was pushed through a MCM with dry air. The concentrations of $H_2^{16}O$, $H_2^{18}O$ and $HD^{16}O$ were measured on a laser spectrometer (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 protocols and precision analyses are still absent from the scientific literature. To justify the results from the IM-CRDS, we compared the values obtained from the extracted water of the half-leaf analyzed by IRIS to the average leaf water composition obtained using a nearest neighbor interpolation on the half-leaf analyzed by IM-CRDS. For the seven leaves analyzed by IM-CRDS, the average difference between those two methods was 2.6±0.88‰ in $\delta^{18}O$ (mean ± SE) and 3.4±2.4‰ in δD. One potential source of error comes from the IM-CRDS analyses being conducted on a different half of a leaf than the IRMS analyses. However, the average difference we observed between two halves of the same *Colocasia esculenta* leaf was 0.3±0.2‰ in $\delta^{18}O$ and 1.9±1.2‰ in δD. The differences between the results obtained with the IM-CRDS and the IRMS are therefore not attributable to the analyses being conducted on different halves of the same leaf. The number of studies making use of the fast analyzing capacity of the IM-CRDS is slowly growing [Berkelhammer et al., 2013], but further testing is still clearly necessary before using the IM-CRDS technique as an absolute method. However, our goal in this present study is to compare strongly enriched water samples and the order of the differences presented in the next section are up to two orders of magnitude greater than the error observed for the IM-CRDS. We therefore believe that the IM-CRDS is an appropriate method for our applications.

II.6 Linking d-excess and transpiration

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

$$\Delta_E \;=\; (1+\epsilon^*)\big[(1+\epsilon_k)(1-h)+h(1+\Delta_v)\big]-1 \tag{2}$$

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

$$\epsilon_k^{H_2^{18}O} = \frac{28.5 r_s + 18.9 r_b}{r_b + r_s} \quad \text{and} \quad \epsilon_k^{HDO} = \frac{16 r_s + 10 r_b}{r_b + r_s} \tag{3}$$

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

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

$$\Delta_i = \frac{R_i}{R_{\text{source}}} - 1. \tag{4}$$

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

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

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

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

Here, P is the atmospheric pressure taken to be 101.3 kPa and g_s (in mmol m^{-2} s^{-1}) is the stomatal conductance equal to $1/r_s$. e_i^* (in kPa) is the saturated vapor pressure calculated for a leaf temperature of 25°C. e_{air}^* (in kPa) is the saturated vapor pressure at air temperature, which is also taken to be 25°C. In our analysis, we compare the transpiration rates of dew treated leaves, E_{dew}, and that of control leaves, E_{control}.

II.7   Spatial patterns

Leaf water isotopic composition is often compared to the isotopic composition of freely evaporating water as described by the Craig-Gordon (CG) model [Craig and Gordon, 1965]. In this model, the fractionation is driven by the difference of saturation vapor pressure between the interior of the leaf and the atmosphere, and by the difference of diffusivity of the isotopologues. However, this simplistic model has been shown to largely

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underestimate the actual isotopic enrichment. Two main models have since then been proposed to better describe the complexity of leaf water isotopes patterns. The effect of the backward diffusion of enriched water, a form of Péclet effect [Farquhar and Lloyd, 1993, Barbour et al., 2004], has been shown to improve the prediction of bulk water enrichment, as well as the progressive enrichment of leaf water between the xylem and the sites of evaporation [Gan et al., 2002]. The string-of-lakes effect takes into account the progressive enrichment of leaf water along the path of water flow [Yakir et al., 1990, Helliker and Ehleringer, 2000] and improves the modeling of large scale variations of leaf water enrichment.

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

$$\Delta_{\text{CG}} \ = \ \epsilon_k + \epsilon^* + (\Delta_v - \epsilon_k) \, \frac{h \, e^*_{\text{air}}}{e_i{}^*}, \tag{7}$$

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

II.8   Competing effects of foliar uptake and foliar shielding

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

II.9   Statistical analysis

272 Responses for the different experiments were analyzed using a two-sample t-test (Welch's t-test) with a 5%

273 significance level. This test has been recognized as a better alternative to the Student's t-test when dealing

274 with groups of unequal sample size or variance [Ruxton, 2006]. In the following, we will report the p-value,

275 P, the test statistics, t, and the degrees of freedom of the test, ν. When comparing the results of the different

276 treatments in Experiments 1A and 1B, we treated the multiple samples collected on each leaf as a single

277 population. *stat* and *syst* refer to the statistical and the systematic errors, respectively.

III.   Results

III.1   Water isotopes

280 The results of Experiments 1A are presented as maps of the analyzed half leaves (Fig. 2). The maps were

281 obtained using an inverse distance interpolation and show the evolution of the d-excess of leaves from the

282 control and misted treatments collected at 0, 12 (dew), 14 (control) and 21 (dew and control) days from

283 the beginning of the experiment. All the maps of δD and $\delta^{18}O$ (Supporting Information, Fig.s S1 and S2)

284 show a progressive enrichment [Cernusak and Kahmen, 2013] of leaf water when moving away from the

285 main stem towards the rims of the leaf. The average difference between the center and the rim of the leaf for

286 the five leaves presented is $\Delta^{18}O = 11.1\pm1.2$ ‰ (mean ± SE) and $\Delta D = 23.9\pm3.3$ ‰. When comparing the

287 composition of the bulk water at the end of the experiment, the dew-treated leaf exhibits a d-excess higher by c.

288 63.0‰ than the control one (two-sample t-test: t = -9.4, $\nu = 29$, P < 0.001). There is no statistical difference

289 between the treated and control leaves collected on days 12/14 (difference in mean d-excess $\simeq 10.2$ ‰ ,

290 two-sample t-test: t = -1.6, $\nu = 35$, P = 0.11).

291 Similar maps were produced for Experiment 1B (Fig. 3). In this case, the heat lamp artificially increased

292 the transpiration rate in both the control and the misted leaves, leading to significantly enriched $\delta^{18}O$ and

293 δD values and low d-excess values for both treatments. The d-excess in the control case is c. 173.0 ‰ more

294 negative than for the dew treated leaves (two-sample t-test: t = 3.9, $\nu = 29$, P < 0.001). This experiment was

295 merely an extreme version of Experiment 1A, with the objective of accentuating the contrast between the

296 two treatments. While the high heat treatment led to a strong drying of some areas of the leaf, in particular

297 those far away from the central vein, the significant difference observed between the control and the misted

298 treatments do confirm the results of Experiment 1A.

III.2 Leaf water potential

Experiment 2 looks at the temporal evolution of water potential in artificially drying leaves (Fig. 4). Strong differences in drying pattern are shown for the misted and drought leaves. In both the control and the high heat and mist cases, the leaf water potential experiences a slow decline, which is well approximated by a linear function. However, the high heat treated leaves experience a faster decline and are better 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 decline in water potential was c. 64% smaller in the misted leaves than in the leaves subjected to the same high heat treatment but that did not get sprayed (two-sample t-test: t = 2.37, $\nu = 7$, 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, $\nu = 6$, P = 0.19).

IV.   Discussion

IV.1 Foliar shielding-induced decrease in transpiration

Treated leaves in Experiments 1A and 1B are all less enriched in heavy isotopes than control ones, despite being sprayed with highly enriched water ($\delta^{18}O \simeq 8.85$ ‰, $\delta D \simeq 737.64$ ‰), which is consistent with a lack of foliar uptake. Foliar shielding is then the only phenomenon inducing differences in leaf water d-excess composition between treated and control leaves. We apply the model described in Section II.6 to interpret our results in terms of the transpiration rate, E.

The use of a constant stomatal conductance and leaf temperature are most likely the largest sources of systematic error in this model. To calculate the systematic error associated with our choices for those parameters, we calculate $E_{dew}/E_{control}$ for a range of leaf temperatures from 10° to 40^oC and for a stomatal conductance g_s from 0.1 to 0.8 mmol m^{-2} s^{-1}. We find that the systematic error associated with our choice of g_s is negligible, while that associated with the choice of T_{leaf} is important for Experiment 1A, but nor for Experiment 1B.

For Experiment 1A, the transpiration rate obtained for the dew treated leaf is significantly lower than that of the control (t = -9.4, $\mu = 38$, P < 0.0001) by 29.9 ±2.6 (stat) ±1.1 (syst) %. Similar results were found for Experiment 1B, where the dew treatment significantly (t = -3.9, $\mu = 29$, P < 0.0001) decreased transpiration by 29.9 ±9.1 (stat) %. These values are consistent with [Garratt and Segal, 1988], who estimated that the reduction in transpiration due to dewfall could reduce daily plant water use by c. 10%. This value was obtained for wheat plants associated with a low transpiration rate. Since *Colocasia esculenta* leaves are larger and have a higher transpiration rate, we expect the reduction to be larger in our case (see Section IV.2).

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

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

Temporal patterns Leaves collected from both treatments on day 12 or 14 present results that disagree with the trends formed by the results of day 0 and 21 (Fig. 2). It is important to note that the plants were kept outside throughout the experiment and were therefore subjected to the daily variations of temperature and relative humidity, which both influence the transpiration rate as well as the isotopic composition. The dew-treated leaf collected on day 12 was sampled after a prolonged period of dry and hot weather that might have enhanced the transpiration despite the artificial dew treatment. This may explain why this leaf presents lower d-excess values than expected. A series of small rain events happened on the day preceding the collection of the first control leaf on day 14, which may have decreased the transpiration rate and increased the d-excess composition of the leaf.

IV.2 Leaf energy cycle

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

First, the deposited droplets increase the albedo of the leaf, allowing more of the radiation to be reflected away from the leaf. Depending on the direction of the incoming solar radiation, water can have an albedo as

high as 1 (perfect reflector) whereas typical values for leaves are c. 0.2 for visible light. The increase of vegetation albedo due do dew deposition has been observed in the field many times [Pinter, 1986, Zhang et al., 2012]. By reflecting more radiation when they are wet, leaves will decrease the incoming shortwave radiation and consequently keep their temperatures lower. This will in turn reduce the evaporative demand and the leaf transpiration.

Second, the energy that is not reflected will be dissipated through the evaporation of the droplets. The dissipated energy 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 evaporation of the droplets will cause the air close to the leaf to have a higher relative humidity than the surrounding air [Defraeye et al., 2013], creating a moist micro-climate around the leaf [Jones, 1992]. This will decrease the difference between the interstitial and the air vapor pressures, and reduce the flux of water vapor out of the leaf, namely transpiration. By decreasing the outward flow of water vapor, more CO_2 will be able to enter the leaf, increasing interstitial CO_2 concentration, photosynthesis, and water use efficiency. The increase in surface roughness associated with the presence of the droplets at the surface of the leaf will also contribute to increasing the size of the boundary layer. Water potential values are correlated with leaf relative water content [Maxwell and Redmann, 1978] and with stomatal conductance [Lhomme et al., 1998]; by maintaining a higher water potential, the leaf will be able to open its stomata wider. CO_2 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 CO_2 assimilation through multiple mechanisms.

IV.3 Implications for foliar uptake studies

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 -9.1±3.7 ‰ (mean ± SE) for the control leaf and -27.9±2.9 ‰ for the dew treated leaf. This corresponds to a -18.8±6.6 ‰ difference in enrichment between sprayed and control treatments. In the case of highly water stressed leaves (Experiment 1B, Fig. 3), the difference in enrichment reaches -45.2±35.8 ‰.

Non-meteoric water is usually more enriched in deuterium than rain and soil water by up to 50 ‰ [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

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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].

Using previous studies on foliar uptake (described in Section II.8), we were able to compare the relative impact of both processes. Foliar uptake has the largest impact on conifers (Fig. 7), where the difference in enrichment between treatment and control reaches up to c. 20 ‰. Foliar shielding for the non-water stressed case (Experiment 1A) exhibits the opposite effect, with a magnitude similar to the largest foliar uptake case. In the water stressed case (Experiment 1B), the depletion observed is as large as c. 45.2 ‰. The three foliar experiments presented here all used nighttime treatment, so foliar shielding did not impact the enrichment observed. However, the competing effects of foliar uptake and foliar shielding are likely to be very important when analyzing field or day time foliar uptake experiment data. For example, [Berry et al., 2014b] observed a significantly larger enrichment when fogging saplings in the morning than in the afternoon. This results is well explained if foliar shielding is taken into account, since foliar shielding will have a larger effect in the afternoon, when leaves are hotter and radiations stronger. Our results suggest that, in the field, foliar shielding might have a larger impact on leaf isotopes than foliar uptake.

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

IV.4 Conclusion

In this study, we used the highly hydrophobic leaves of *Colocasia esculenta* to look at the impacts of dew water droplets deposition (called foliar shielding) on the leaf energy, water and isotope balance. We show that

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the spatial patterns of enrichment are consistent with the string-of-lakes model, which is common in monocots. Our results show that foliar shielding significantly decreases leaf transpiration by c. 30%, maintains leaf water potential, and limits leaf water isotopic enrichment. We highlight the opposite effects of foliar uptake, which enriches leaf water in heavy isotopes, and foliar shielding, which depletes it. Because both effects are of similar magnitude, taking both processes into accounts is crucial to properly interpret field data of foliar uptake.

Acknowledgments

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Figure Legends

Figure 1: Adapted from [Voelker et al., 2014]: Conceptual figure showing the evaporative conditions controlling the evolution of δ^{18}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 (δ^{18}O $\simeq$ 8.85 ‰, δD $\simeq$ 737.64 ‰) every two days. The color scheme is the same for all rows.

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

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

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

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

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

Supporting Information

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

Figure S1: Interpolated maps showing the δD of the leaves analyzed in Experiment 1A.

Figure S2: Interpolated maps showing the δ^{18}O of the leaves analyzed in Experiment 1A.

Identifiers		
ID	Type	Injections
Blank 1	Empty vial	1
to		
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	Sample	4
to		
Sample 10	Sample	4
DEST	Drift ref. water	6
Sample 11	Sample	4
to		
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, respectively. 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 and VSMOW 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 and mist' and 'High heat'. Third column shows one standard error. All the data was normalized to reflect the drop in water potential for a 40 cm long leaf over 8 hours.*