

Water status of hydrophobic leaves improved by the impact of artificial dew deposition on leaf energy balance

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Abstract

Uptake of water from the surface of the leaves instead of the roots has been observed in many different species and many different ecosystems. This phenomenon, called foliar uptake, is common when rainfall is scarce and non-meteoric water (like dew or fog) is the only source of water. However, many species across the world have very water repellent leaves and none of the past studies have tried to differentiate between the uptake of deposited water droplets and the impact of those droplets on the energy balance of the leaf. We conducted three experiments on the highly hydrophobic *Colocasia esculenta* leaves that allowed us to investigate the impact of non-meteoric water deposition on the energy balance of the leaves, while ruling out any direct water uptake. We present evidence that the effect of the droplets on the energy intake of the leaves impacts its water balance. We conclude by presenting three possible mechanisms through which water droplets interact with the leaf energy balance.

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 been focusing 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., 2014] is adapted to using fog as its main source
¹¹ of water. Similarly, dew water has been shown to be a major source of water on islands where fresh water is
¹² scarce [Clus et al., 2008] or by species that have physical features allowing them to collect dew water, like
¹³ 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 actually have very water-repellent leaves [Neinhuis and Barthlott, 1997] and leaves that
¹⁷ are often exposed to dew tend to be even more hydrophobic [Aryal and Neuner, 2009]. Those hydrophobic
¹⁸ species are not adapted to uptake water from their leaves. For most plants, non-meteoric water deposition is
¹⁹ a source of nuisance as it may freeze and cause damages to the leaf in cold climate, or stagnate and cause
²⁰ rotting and pathogen infection in warm environments [Evans et al., 1992]. However, not all of them are as
²¹ water repellent as the iconic water lilies and micro-droplets of water will indeed form on the surface of even
²² very hydrophobic leaves. The interaction of those droplets on the leaf energy balance has not yet been studied,
²³ despite its potentially very large impact. Indeed, dew or fog formation impacts large areas at once and small
²⁴ changes in the energy balance of each single leaf could therefore have large a large impact at the ecosystem
²⁵ level.

²⁶ **Leaf energy balance** Because they are unable to move to the shade, leaves are very vulnerable to sun
²⁷ radiations, and leaves can often be warmer than the surrounding air. Leaf temperature will in turn affect
²⁸ saturation vapor pressure, isotope fractionation, respiration, photosynthesis and many other functions. Because
²⁹ their boundary layer is thinner, smaller leaves tend to be at a temperature closer to the ambient air. This is
³⁰ the reason why, on a single tree, sun leaves are usually smaller than shade ones. To stay cool, leaves use a
³¹ combination of re-radiation (transfer of energy to the surroundings), convection (heat loss as cool air moves
³² over the surface of the leaf) and evaporative cooling (evaporation of water inside the leaf into water vapor,
³³ which is an exothermic process) [Vogel, 2012]. During a drought, leaves have to preserve water to maintain
³⁴ turgor pressure, which competes with evaporative cooling. In this case, leaves are left with re-radiation and
³⁵ convection to cool themselves down, which is not enough to maintain a low temperature. If the duration of
³⁶ the drought extends for too long, it will often lead to plant mortality.

³⁷ By depositing a layer of small water droplets on the surface of the leaves, non-meteoric water can

38 provide the plants with a pool of water that will supplement the scarce leaf water and provide a form of
39 externalized evaporative cooling. Moreover, the presence of the droplets will both increase the albedo
40 of the leaves, allowing it to reflect more energy [Pinter, 1986], and increase surface roughness which
41 will increase the leaf boundary layer, therefore decreasing the vapor pressure deficit (VPD) and lowering
42 the evaporative demand. By affecting the leaf energy cycle, the deposition of non-meteoric water
43 droplets is therefore directly affecting the water status of the leaf. Depending on the location and climate,
44 dew deposition can take from 1.5 [Abtew and Melesse, 2012] to 6 hours [Monteith, 1957] after sunrise to
45 completely evaporate from the surface of the leaves. Dew and fog can also form in the late afternoon
46 before sunset [Wilson et al., 1999, Kabela et al., 2009]. Although neither dew nor fog is usually present
47 at the hottest hour of the day, they can effectively shorten the duration of the water-stressed part of the
48 day. This will significantly help the plant maintain its water status over an extended period of drought
49 [Madeira et al., 2002, Proctor, 2012]. Dew formation is usually included in global climate models (GCM)
50 as it merely involves tracking dry bulb temperatures going below the dew point temperature. However, its
51 interaction with vegetation is never taken into account. Because non-meteoric water deposition occurs all
52 around the world, even in dryland ecosystems and because its impact on the leaf energy, water and carbon
53 cycle are important at the leaf scale, including this interaction into GCM would allow modelers to better
54 understand vegetation response to climate change and its feedback on CO₂ atmospheric concentrations.

55
56 In this study, we present three experiments that focus on the effects of water droplets deposition at the
57 surface of *Colocasia esculenta* leaves. This specie is native from South East Asian tropical forests but has
58 been cultivated across the world for many centuries under the name of taro. With a contact angle of 164°
59 [Neinhuis and Barthlott, 1997], *Colocasia esculenta* is considered to have highly water-repellent leaves. Its
60 leaves can reach a size of up to 50 cm in length and 40 cm in width, allowing for spatially high-resolution
61 mapping of the leaf water properties. Using isotopically labelled water as well as traditional plant physiology
62 techniques, we confirm that the *Colocasia esculenta* leaves do not uptake water from the surface of the leaves.
63 We also show that water droplets deposition decreases leaf transpiration and increases water potential. We
64 conclude by presenting three mechanisms that explain the influence of water deposition on water-repellent
65 leaves and that could have large impacts on plant water and carbon cycles.

66 **II. Methods**

67 **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 H₂¹⁸O and HD¹⁶O, where D symbolizes deuterium. 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

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

of isotope ratios [Mook, 2006], where δ_i is expressed in ‰ and the index i stands for ^{18}O or D. $R_{^{18}\text{O}} = [\text{H}_2^{18}\text{O}] / [\text{H}_2^{16}\text{O}]$ and $R_D = [\text{HD}^{16}\text{O}] / [\text{H}_2^{16}\text{O}]$ are the isotope ratios, while the R_{r_i} are the ratios of the corresponding standard. For water, the reference is the Vienna Standard Mean Ocean Water (VSMOW). Because precipitation condenses under conditions of equilibrium fractionation, $\delta^{18}\text{O}$ and δD in precipitation evolve along a line with slope 8, the global meteoric water line (GMWL) [Voelker et al., 2014]. However, kinetic isotope effects associated with the difference in diffusivity of the different isotopologues of water can lead to deviation from the GMWL [Farquhar et al., 2006]. For example, since HD ^{16}O diffusivity is greater than that of H $_2^{18}\text{O}$, the water of a leaf that has undergone heavy transpiration will be more depleted in D than in ^{18}O (see Figure 1). Deuterium excess (d-excess) is a widely used measure of how evaporated a pool of water (ocean, lake, leaf) is and is defined as:

$$\text{d-excess} = \delta\text{D} - 8 \times \delta^{18}\text{O}.$$

68 The average d-excess for precipitation is 10. Lower d-excess values generally indicate that the pool undergone
69 some evaporation [Brooks et al., 2014] (see Figure 1). Stable isotopes are also very efficient in helping
70 identify different water sources in plants [Ehleringer and Dawson, 1992]. Simple mixing models allow one
71 to separate the composition and the fluxes coming from different sources. For this reason, stable isotopes are
72 great natural labels that can be used to track pathways of water within plants without harming them.

73 **II.2 Experiment 1a: Effects of dew deposition on *Colocasia esculenta* water isotopes in natural con-
74 ditions**

75 This first experiment examines leaf scale spatial and temporal patterns of water isotopes induced by the
76 presence or the absence of dew under drought condition. Six bulbs of *Colocasia esculenta* were planted in
77 separate pots. All pots were placed outside and received full sun for four weeks. During this time, all plants
78 were heavily watered with tap water ($\delta^{18}\text{O} = -5.96\text{ ‰}$, $\delta\text{D} = -37.63\text{ ‰}$) to allow plant growth. Once the six
79 plants reached maturity, watering stopped and the plants were moved to a shaded area to remove any sun
80 exposition difference between the plants. The area was very protected and temperature was usually lower
81 than outside of it. Similarly, relative humidity was usually slightly higher. Three of the six pots were left
82 to dry and did not receive any water for the rest of the experiment. The upper surface of the leaves of the
83 other three pots were misted with isotopically enriched water ($\delta^{18}\text{O} = 8.85\text{ ‰}$, $\delta\text{D} = 737.64\text{ ‰}$) every two
84 days using a spray bottle. Any extra water would run off the leaves, leaving them covered in submillimeter
85 size droplets, which is a realistic size for dew deposition drops [Defraeye et al., 2013]. The misting simulated
86 dew and occurred as early as possible in the morning. In order to avoid contact between the misted water and
87 the soil in the pots, the surface of all pots was covered in wrapping plastic. Six leaves were collected between
88 the beginning of the drought/dew treatments and the end of the experiments, three weeks later. The sampling
89 and the analysis are described in Section II.5.

90 **II.3 Experiment 1b: Effects of water droplets deposition on *Colocasia esculenta* leaf water isotope
91 under high water stress conditions**

92 This second experiment was designed to artificially increase the contrast between the drought and misted
93 treatments from Experiment 1a. The plants from this former experiment were moved into the laboratory and
94 well-watered for multiple weeks to offset any effects from the first experiment. Two leaves of similar size and
95 of the same *Colocasia esculenta* plant were cut at the junction of the petiole and the rachis and left to dry
96 80 cm under a blue light (Eiko 1960 EBW, 500 W, 10500 lumens, color temperature of 4800 K). One leaf
97 was misted with isotopically labelled water ($\delta^{18}\text{O} = 8.85$ permil, $\delta\text{D} = 737.64$ permil) every half-hour. The
98 other leaf was left to dry without any intervention. After four hours, samples were collected from both leaves
99 as described in Section II.5.

100 **II.4 Experiment 2: Effects of dew deposition on *Colocasia esculenta* leaf water potential under high
101 water stress conditions**

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

111 **II.5 Sampling and processing methods for the isotopic analysis**

112 For the water isotope analysis, each analyzed leaf was sampled in 12 to 25 different locations depending on
113 the size of the leaf. All the sampling points were located on the same half of the leaf and consisted in four
114 holes (6 mm diameter) punched next to each other forming a square. Each hole was punched as quickly as
115 possible to avoid evaporation, which would influence the isotopic composition of the neighboring holes. Each
116 leaf disk was then secured in an aluminum foil and inserted in a sealed vial. The entire leaf was sampled in
117 one go and as fast as possible. The prepared vials were then stored in the fridge until being analyzed. The
118 leaf samples were analyzed using an Induction Module (IM) combined to a Cavity Ring Down Spectrometer
119 (CRDS) L2103-i from Picarro Inc. (Sunnyvale, CA, USA). The IM was set on the "normal leaf" setting: the
120 leaf disks did not appear carbonized and after being dried in the oven at 60°C for 48 hours, they show no
121 decline in weight, proving that this setting dried the leaf samples completely. The IM was equipped with a
122 micro-combustion module (MCM). The MCM has been proven to efficiently reduce the interferences due to
123 the presence of organics in water samples extracted from plants (Kate Dennis, private communication). The
124 entire sampling and IM analysis process lasted from 1.5 to 2 days per leaf depending on the size of the leaf.

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

136 **IRIS and IRMS analysis** Ten samples were sent to the Center for Stable Isotope Biogeochemistry at the
137 University of California in Berkeley for IRMS analysis. For the IRMS method, δD was obtained by chromium
138 combustion using an H/Device (labelled as HDEV; Thermo Finnigan, Bremen). Microliters of water were
139 injected in the HDEV and reduced to H_2 gas. The ratio of D/H was then measured on a Thermo Delta Plus
140 mass spectrometer. For the $\delta^{18}\text{O}$ analysis, water from standards and samples were pipetted into glass vials
141 and quickly sealed. The vials were then purged with 0.2% CO_2 in Helium and allowed to equilibrate at room
142 temperature for at least 48 hours. The ^{18}O in the CO_2 was then analyzed by continuous flow using a Thermo
143 Gas Bench II interfaced to a Thermo Delta Plus XL mass spectrometer. In this $\text{H}_2\text{O}-\text{CO}_2$ equilibration method,
144 the dissolved components (organic and/or inorganic) do not affect the values of $\delta^{18}\text{O}$. For the IRIS analysis,
145 1.8 μL of water were injected into a vaporizer and the vapor pushed through a MCM. The concentrations of
146 H_2^{18}O and HD^{16}O were measured on a water isotope analyzer (L2103-i) from Picarro Inc. (Sunnyvale, CA,
147 USA).

148 The ten samples analyzed both by IRMS and IRIS were used to calculate the offset between the two
149 techniques. All the samples that had been run exclusively by IRIS or IM-CRDS (and had not been analyzed
150 by IRMS) were then corrected for this offset. The IM-CRDS method has not been widely used yet and
151 protocols and precision analysis are still absent from the scientific literature. In order to justify the results
152 from the IM-CRDS, we compared the values obtained from the extracted water of the half-leaf analyzed by
153 IRIS to the average leaf water composition obtained using a nearest neighbor interpolation on the half-leaf
154 analyzed by IM-CRDS. For the seven leaves analyzed by IM-CRDS, the average difference between those
155 two methods was 2.6‰ in $\delta^{18}\text{O}$ and 3.4‰ in δD . These values are higher than the average difference we
156 observed between two halves of the same *Colocasia esculenta* leaf, both extracted by cryogenic vacuum
157 distillation and analyzed by IRIS (0.3‰ in $\delta^{18}\text{O}$ and 1.9‰ in δD). The observed error is therefore not
158 attributable to the analysis on IM-CRDS and IRMS being conducted on each half of the same leaf. Further
159 testing is clearly necessary before using the IM-CRDS technique as an absolute method. However, our goal in
160 this paper is to compare strongly enriched waters and the order of the differences presented in the next section
161 are up to two orders of magnitude bigger than the error observed for the IM-CRDS. We therefore believe
162 that the IM-CRDS is an appropriate method here, as it allowed us to quickly process many small samples,

163 therefore increasing the spatial and temporal resolution of our analysis.

164 III. Results

165 **Effects of dew deposition in natural conditions** The results of Experiments 1a are presented as maps
166 of the analyzed half leaves (Figure 2). The maps were obtained using an inverse distance interpolation in
167 Matlab® and show the evolution of the d-excess of leaves from the drought and misted treatments collected at
168 0, 12 (dew), 14 (drought) and 21 (dew and drought) days from the beginning of the experiment. All the maps
169 of $\delta^{18}\text{O}$ and δD (not presented here) show the expected progressive enrichment of leaf water when moving
170 away from the main stem towards the rims of the leaf [Cernusak and Kahmen, 2013]. This enrichment is
171 due to the progressive transpiration of the leaf water as it moves away from the source water that enters the
172 leaf through the petiole. The lighter isotopologues are transpired first, leaving the heavier ones in the leaf
173 [Farquhar et al., 2006]. This translates into a decrease in d-excess from the center of the leaf towards to the
174 edges. Those results reinforced our confidence in the IM-CRDS method. Comparing same day results for
175 both treatments, we see that the dew treated plants systematically exhibit higher d-excess values than the
176 drought treated ones. The lower (more negative) d-excess values are associated with higher transpiration rate.
177 On the other hand, the misted leaves had a lower rate of transpiration, which led to higher values of d-excess.
178 The leaf average isotopic composition of the dew and drought treated leaves (see Figure 3. Figure 1 provides
179 an explanation on how to interpret this figure.) shows that the isotopic composition of the drought treated
180 leaves evolved directly from evaporated source water (tap water), while the dew treated leaves are evolving
181 on a line parallel to the GMWL. Before the treatment started the water in the dew treated leaves most likely
182 followed an evaporation line similar to that of the drought treated leaves. However, after the treatment started,
183 transpiration in the dew treated leaves stopped and the water in those leaves followed a line parallel to the
184 GMWL. For the samples to evolve on such a line, only equilibrium isotopic fractionation is happening within
185 the leaf. Indeed, any kinetic fractionation would induce a slope of less than 8. In terms of leaf physiology,
186 this is the sign that water vapor is not diffusing out of the leaf, i.e. that little transpiration is occurring.

187 Leaves collected from both treatments on day 12 or 14 present results that disagree with the trends formed
188 by the results of day 0 and 21 (Figure 2). In the drought treatment case, d-excess is generally decreasing
189 between day 0 and day 21, showing increased evaporation. However, the drought treatment leaf collected on
190 day 14 shows values of d-excess higher than expected, signaling a low evaporation rate. In the dew treatment
191 case, the general trend is reverse and d-excess at the end of the experiment (day 21) is much higher than on
192 day 0. But the dew treated leaf collected on day 12 presents lower values of d-excess than expected from this
193 general trend. One must recall that the plants were kept outside throughout the experiment and were therefore
194 subjected to the daily variations of temperature and relative humidity, which both influence the transpiration
195 rate as well as the isotopic composition. The dew treated leaf collected on day 12 was sampled after a
196 prolonged period of dry and hot weather that might have enhanced the transpiration despite the artificial dew
197 treatment. This explains why this leaf presents lower d-excess values than expected. During the experiment,
198 the plants were kept in a shaded, protected area below a building where the temperature is often lower and the
199 relative humidity higher than outside of the shelter. During the four days preceding the collection of the first

200 drought treated leaf (day 14), the air temperature came within 1°C from the dew point temperature every night
201 (see Figure 4). Because of the locally lower temperature and higher relative humidity under the sheltered area,
202 natural dew probably formed at the surface of the leaves. Indeed, natural dew formation was observed on the
203 leaves multiple times. Moreover, a series of small rain events happened on the day preceding the collection,
204 which would have greatly affected the transpiration rate and the resulting isotopic composition of the leaf.

205 **Effects of dew deposition in high water stress conditions** Similar maps were produced for Experiment
206 1b (Figure 5). In this case, the heat lamp artificially increased the transpiration rate in both the drought
207 and the misted leaves, leading to highly enriched $\delta^{18}\text{O}$ and δD values and very low d-excess values for
208 both treatments. However, the d-excess in the drought case is a lot more negative (reaching values down to
209 ~-800‰) than for the dew treated leaves (reaching values down to ~-300‰). This experiment was merely an
210 extreme version of Experiment 1a, with the objective of accentuating the contrast between the two treatments.
211 While the high heat treatment led to a strong drying of some areas of the leaf, in particular those far away from
212 the central vein, the large differences observed between the drought and the misted treatments do confirm the
213 results of Experiment 1a.

214 **Effects of dew deposition on leaf water potential** Experiment 2 was designed to look at the temporal
215 evolution of water potential in artificially drying leaves (see Figure 6). Strong differences in drying pattern
216 are shown for the misted or drought leaves. In both the natural drying and the high heat & mist cases, the
217 leaf water potential experiences a slow decline, which is best approximated by a linear function. However,
218 the high heat treated leaves experience a faster decline and are best approximated by a parabola. Without the
219 results of Experiments 1 and 2, that confirmed the leaves' high hydrophobicity, this results could easily be
220 mistaken for a foliar uptake process.

221 Large differences in water potential patterns were also observed as a function of leaf size for the high
222 heat treatment: smaller leaves had a stronger decline in water potential than big leaves did. This difference
223 disappears when the leaf is misted. In order to verify that this leaf size difference was not related to a
224 difference in water repartition within the leaf (on a short time scale, evaporation occurs mainly in the lamina),
225 eight *Colocasia esculenta* leaves of length ranging from 14 to 64 cm were weighted, their veins and lamina
226 (inter-vein tissues) separated and re-weighted before being oven-dried for 48 hours and weighted one last
227 time. On average, veins accounted for 39% and the lamina for 41% of the total leaf water. These values are
228 uncorrelated with leaf size (Figure 7), showing that the size dependent change in water potential in the high
229 heat treatment is due to the process of the drying itself, and not due to pre-existing differences in water
230 distribution.

231 IV. Discussion

232 Dew and fog have been shown to have a direct impact on plants water status through direct uptake of water
233 from the leaves or needles [Stanton and Horn, 2013, Eller et al., 2013, Clus et al., 2008, Lakatos et al., 2012,
234 Berry et al., 2014, Berry and Smith, 2014]. As mentioned before, *Colocasia esculenta* is native to tropical
235 wetlands and possesses highly hydrophobic leaves [Neinhuis 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 drought treated leaves. This is the sign that none of the highly enriched sprayed water is being taken up by the leaves, even in artificially dry and hot conditions. However, 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 these water droplets is triple.

First, the 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 around 0.2 for visible light. The increase of vegetation albedo due to dew deposition has been observed in the field many times [Pinter, 1986, Zhang et al., 2012]. By reflecting more 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 6): 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, dew droplets deposition will allow the leaf to maintain its water status and increase CO₂ assimilation.

275 Water droplets from rain interception will have a similar effect as non-meteoric water deposition. However
276 in the first case the soil water would also be replenished, making the gain in water obtain by lowering
277 transpiration less necessary than in the case of dew or fog droplets forming during a drought. Many
278 studies have indeed demonstrated that dew or fog deposition had little impact on well watered plants
279 [Andrade, 2003, Eller et al., 2013]. Dew and fog commonly occur all around the world and in a wide range
280 of ecosystems, from drylands [Agam and Berliner, 2006] to tropical forests [Lakatos et al., 2012]. Indeed,
281 regular dew formation has been observed by scatterometer in the upper canopy of the Amazon forest, even
282 during the dry season [Satake and Hanado, 2004, Frolking et al., 2011].

283 [Frolking et al., 2011] observed a sharp decrease in morning backscatter over the Amazon forest for the
284 summer months of 2005, which they associated with a lack of morning dew formation. This summer was
285 known as a mega-drought for the Amazon forest and led to a high tree mortality [Zeng et al., 2008]. However,
286 the accumulating water deficit anomaly for that year was just as high as that of the year 2002, which did not
287 experience the same tree mortality. The main difference in water resources between the two years appears to
288 be the presence or absence of dew.

289 The results of our study hint at a large impact of water droplets deposition on hydrophobic leaves in time
290 of drought. The influence of the water droplets on the leaf energy balance will delay the time when leaves
291 will reach their maximum transpiration rate. [Abtew and Melesse, 2012] calculated that dew evaporation
292 from the surface of a leaf takes about 75 min in southern Florida. Many parameters, including leaf size,
293 relative humidity or shading could potentially prolong this time. In the context of climate change and with an
294 increasing number of drought in some tropical forests, and in particular the Amazon forest [Cook et al., 2014],
295 even a small delay in the beginning of the transpiration in the morning could have a huge impact when
296 spanning over the whole dry season and, for example, the entire Amazon forest. While tropical forests are
297 usually carbon neutral, [Gatti et al., 2015] calculated that during the 2010 mega-drought in the Amazon, the
298 basin lost 0.48 PgC.yr^{-1} . This corresponds to about 10% of the amount of anthropogenic carbon released in
299 the atmosphere for that year. Understanding all the aspects of plant functions in topical forests is therefore
300 crucial if we want to better anticipate future climate. Despite its potentially large impact, dew and fog
301 deposition on plants is yet to be include in climate models. Further investigation is now necessary to quantify
302 the transpiration decrease associated with water droplets deposition, as well as the impact on leaf carbon
303 uptake. Combining a process-based model with flux tower and satellite data could help better quantify
304 regional scale carbon uptake.

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Figure Legends

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 Picasso Induction Module. All leaves are about 38 cm long. **Left:** initial leaf collected on day 0. **Top row:** leaves collected on day 14 (center) and 21 (far right) from the drought treatment. **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 ($\delta^{18}\text{O} = 8.85 \text{ ‰}$, $\delta\text{D} = 737.64 \text{ ‰}$) every two days. The color scheme is the same for all rows and the values are expressed in permil.

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 drought treatment. The black dashed line shows the linear regression. The drought treated 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: **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 drought treatment 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 dew treated leaf happened right after a series a small rain events and four nights in a row of temperatures close to the dew point temperature.

Figure 5: 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 non-sprayed leaf. **Bottom row:** $\delta^{18}\text{O}$, δD and d-excess of the leaf sprayed with iso-

topically enriched water ($\delta^{18}\text{O} = 8.85\ \text{\textperthousand}$, $\delta\text{D} = 737.64\ \text{\textperthousand}$) every half-hour. The non-sprayed leaf shows higher enrichment and lower d-excess values that are associated with increased transpiration compared to the sprayed leaf.

Figure 6: Five examples of the temporal evolution of leaf water potential of *Colocasia esculenta* leaves. The red diamonds are 38 cm long leaves. All other leaves are 45 cm long (black and blue). On the left, natural drying (black dotted line) and both sizes leaf in the high heat & mist (red dashed and blue solid lines) case are best fitted by a linear relation. On the right, the high heat drying case is best fitted by a parabola for both 38 (red dashed line) and 45 cm (blue solid line) leaves.

Figure 7: Percent water from veins and lamina for eight leaves of *Colocasia esculenta* with lengths ranging from 14 to 64 cm. **Red squares:** % water from the lamina (dashed red line represents the mean value). **Black circles:** % water from the veins (solid black line represents the mean value). On average, veins accounted for 39% and the lamina for 41% of the total water content of the leaves. The repartition of leaf water between the veins and the lamina shows no significant correlation with leaf size.

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, DEST and HERA are intermediate waters. DEST is the drift monitoring reference water whereas HERA is treated as a sample for quality control. All reference waters except HERA are used for memory correction.

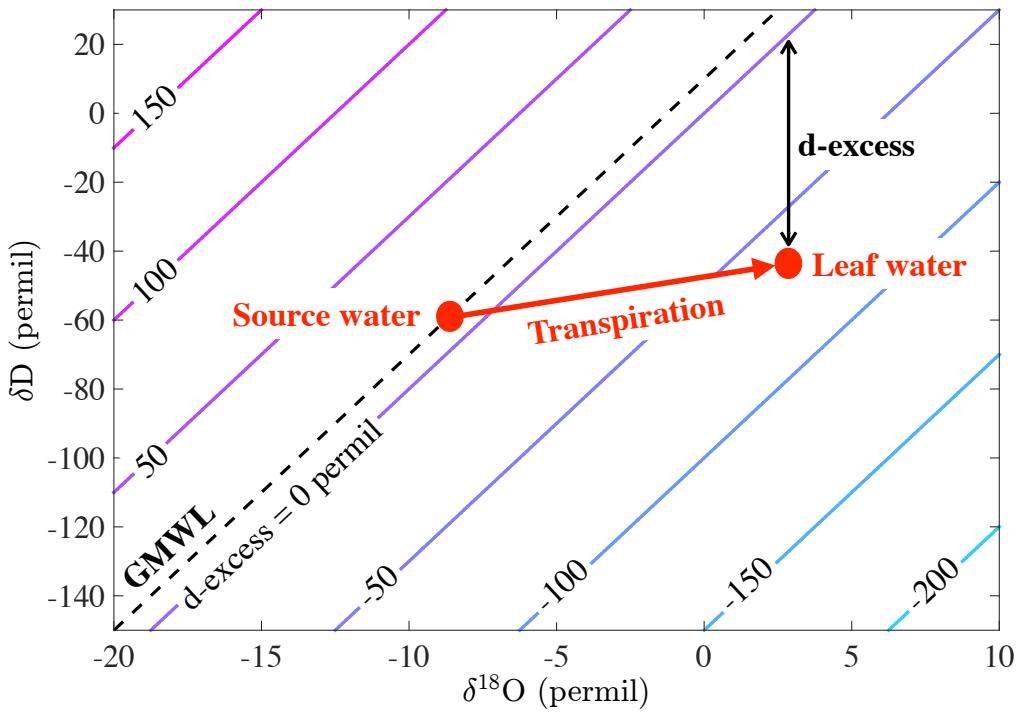


Figure 1: Adapted from [Voelker et al., 2014]: Conceptual figure showing the evaporative conditions controlling the evolution of $\delta^{18}\text{O}$ and δD in leaf water from source water located on the global meteoric water line (GMWL, dashed black line). The slope of the transpiration line depends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

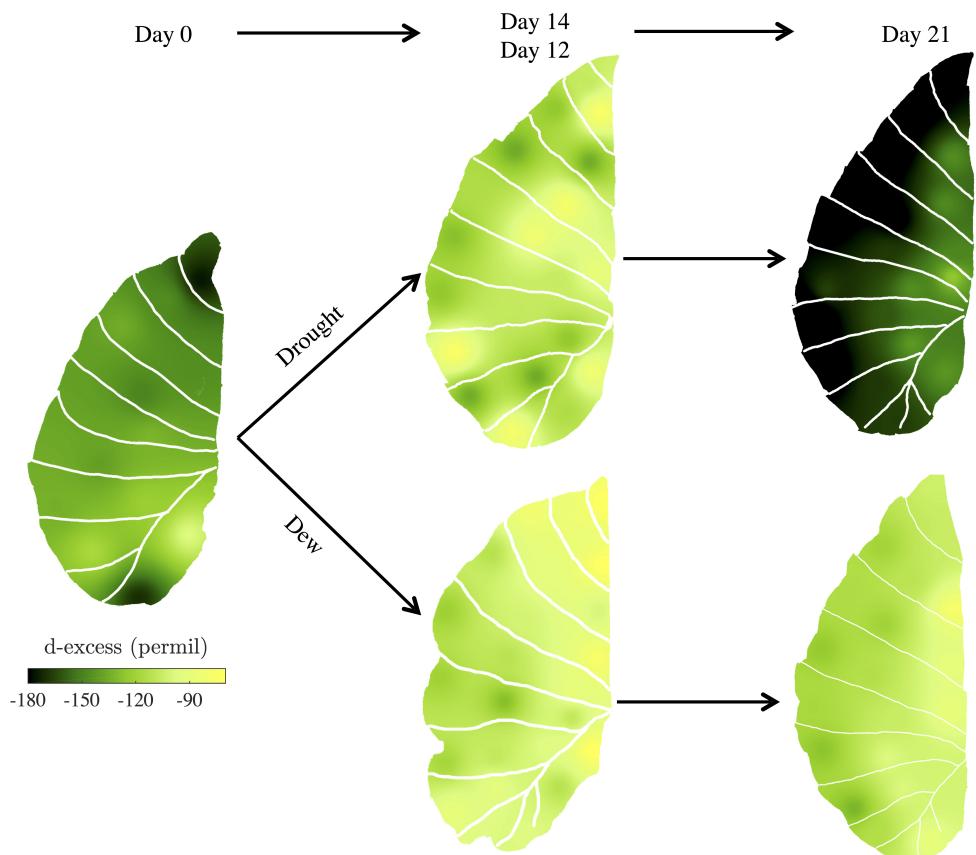


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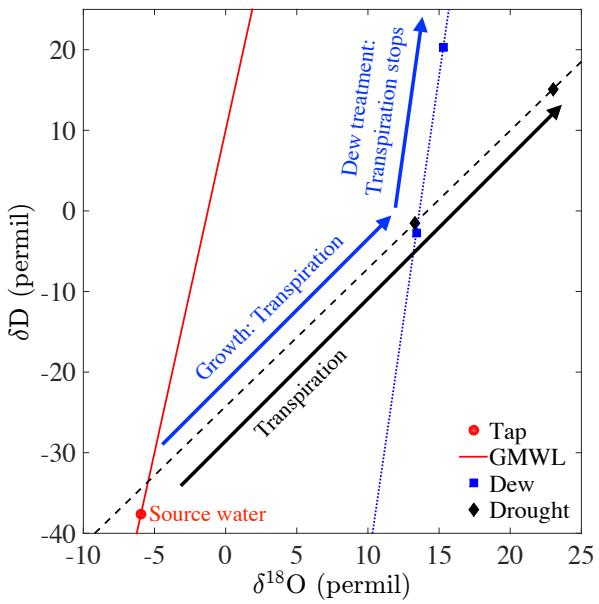


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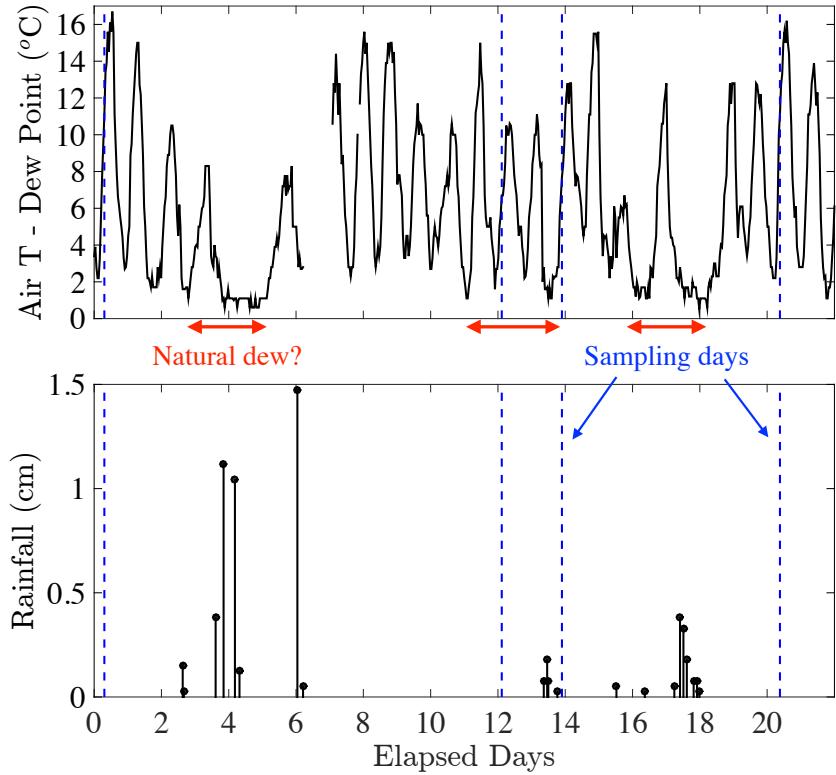


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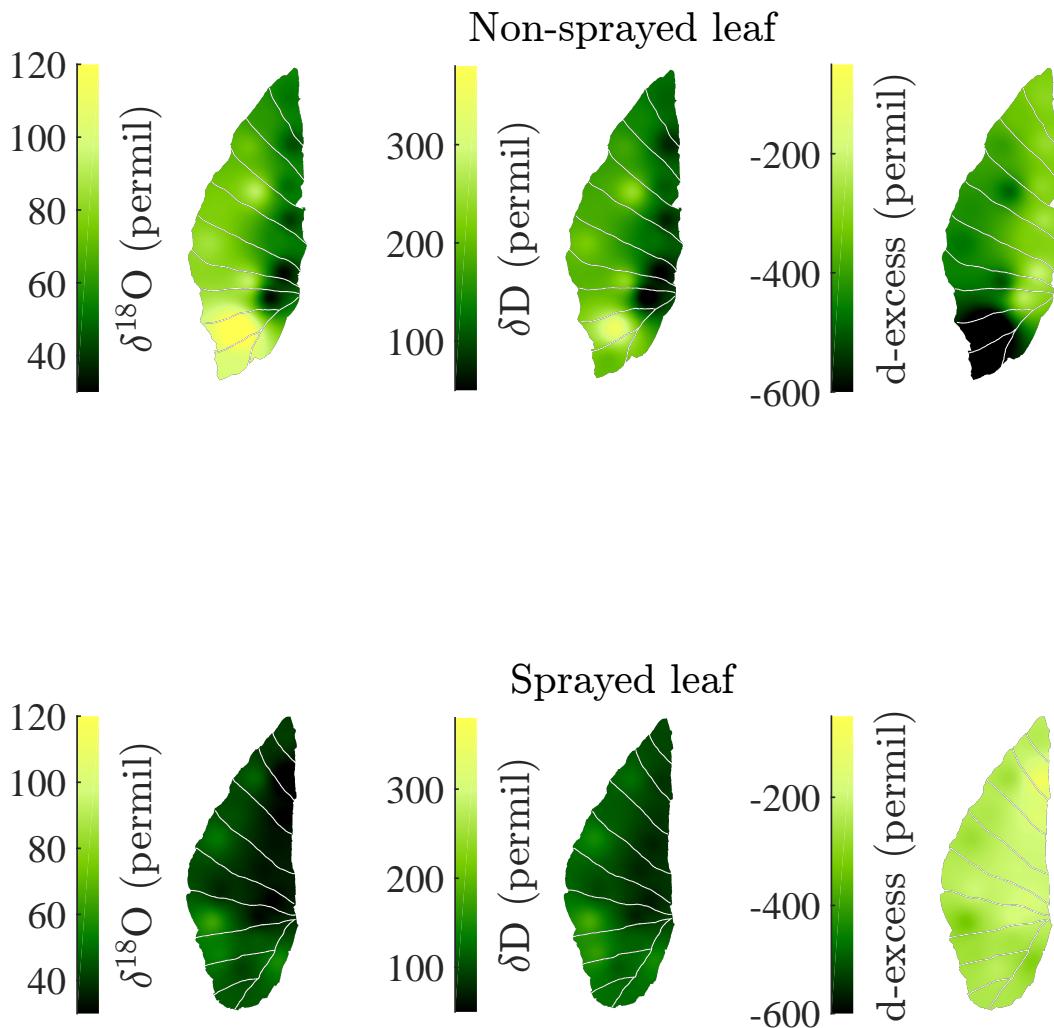


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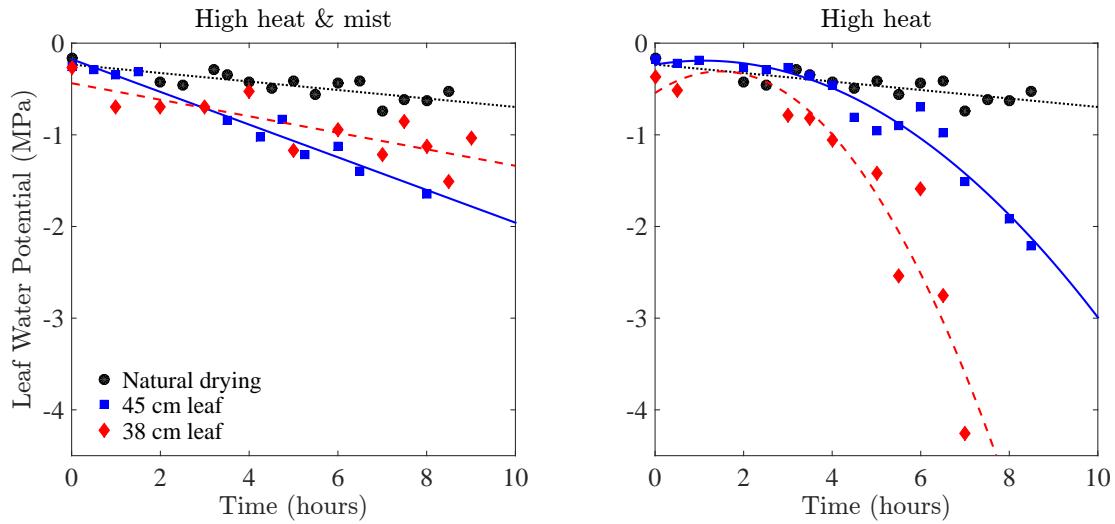


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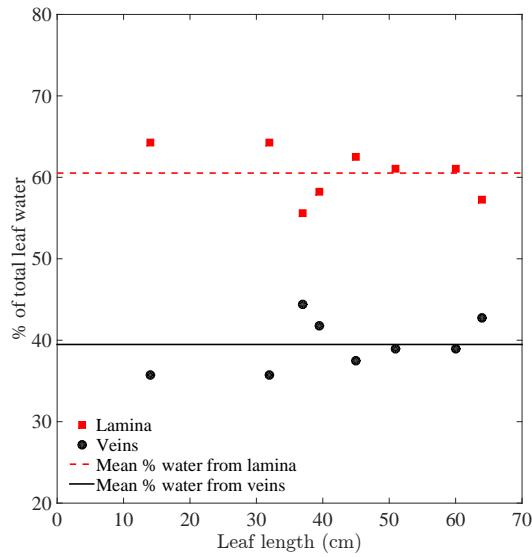


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