

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

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One-sentence summary

Non-meteoric water deposition on hydrophobic *Colocasia esculenta* leaves relieves leaf water stress by modifying the leaf energy balance.

Abstract

1 I. Introduction

2 The uptake of carbon dioxide by vegetation is a major sink of CO₂ and a factor that will determine future
3 climate. Some studies predict a decrease in carbon uptake from vegetation [Raupach et al., 2013] because
4 of a general drying of the southern hemisphere, including some tropical areas [Zhao and Running, 2010].
5 A mechanistic understanding of land-atmosphere carbon exchanges at the individual and regional scales is
6 necessary to build a comprehensive carbon budget at the global scale and determine whether one can already
7 observe this decline [Ballantyne et al., 2012].

8 Because they have optimal temperature and rainfall conditions for vegetation growth, the tropics play
9 a major role in carbon uptake [Osborne, 2012]. However, their future is subject to more debate than any
10 other part of the planet [Cox et al., 2013, Huntingford et al., 2013]. The difficulty in assessing the response
11 of tropical wet forests to climate change comes from the proximity of the mean annual precipitation (MAP)
12 of these areas to 2000 mm/year. If the MAP is above ~2000 mm/y, the vegetation growth is limited by the
13 lack of sunlight (radiation-controlled ecosystems), while if the MAP is below this level, it is limited by water
14 scarcity (water-controlled ecosystems). The predicted climate changes will bring the MAP in some of these
15 areas from above to below this threshold [Guan et al., 2015]. It is therefore crucial for the global modeling
16 effort to assess which areas will be transitioning to water-controlled ecosystems and what implications this
17 will have on their carbon uptake rate.

18 At the global scale, climate models predict an increase in the number of drought events in some part of the
19 globe, including in the tropics [Neelin et al., 2003]. Plants absorb CO₂ through their stomata, which are small
20 openings on their leaves. In the process, water vapor may escape through the opened stomata [Buckley, 2005].
21 Measuring this flux of water vapor, called transpiration, is therefore an effective method for estimating carbon
22 uptake by vegetation. Severe droughts in tropical areas impact global levels of CO₂ not only because of the
23 resulting tree loss, but also because trees shut down their stomata to limit water vapor losses that may induce
24 cavitation and permanent damage. This shutdown results in a decrease in carbon uptake. Only a precise
25 knowledge of the water sources that plants have access to would allow one to predict this shut down with
26 accuracy. However, water sources in the tropics vary significantly between the wet and dry seasons and are
27 poorly understood. For example, vegetation in tropical forests have been known for a long time to be using
28 fog [Stanton and Horn, 2013, Eller et al., 2013], dew [Andrade, 2003, Clus et al., 2008, Lakatos et al., 2012]
29 and other non-meteoric atmospheric water sources through foliar uptake. The literature suggesting this
30 importance of this mechanism is growing [Berry et al., 2014, Berry and Smith, 2014] and includes a wide
31 range of plant species. However, many tropical species are known for having very hydrophobic leaves
32 [Neinhuis and Barthlott, 1997]. In areas where the relative humidity is high, for example in the understory,
33 preventing water from stagnating at the surface of the leaf helps to prevent it from rotting or the developing
34 armful fungus. Those species are most likely not adapted to uptake water from the leaves.

35 In this study, we present three experiments that focus on the effects of water droplets deposition at the
36 surface of *Colocasia esculenta* leaves. This specie is native from South East Asian tropical forests but
37 has been cultivated across the world, including Brazil, for many centuries. With a contact angle of 164°
38 [Neinhuis and Barthlott, 1997], *Colocasia esc.* is considered to have highly water-repellent leaves. Its leaves

39 can reach a size of up to 50 cm in length and 40 cm in width, allowing for high-resolution mapping of the
40 leaf water properties. Using isotopically labelled water as well as traditional plant physiology techniques,
41 we confirm that the *Colocasia esc.* leaves do not uptake water from the surface of the leaves. We also show
42 that water droplets deposition decreases leaf transpiration and increases water potential. We conclude by
43 presenting three mechanisms that explain the influence of water deposition on water-repellent leaves.

44 **II. Methods**

45 **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 $HD^{16}O$, 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. $R_{^{18}O} = [H_2^{18}O]/[H_2^{16}O]$ and $R_D = [HDO]/[H_2O]$ 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). Deuterium excess (d-excess) is a widely used measure of how evaporated a pool of water (ocean, lake, leaf) is and is defined as:

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

46 The average d-excess for precipitation is 10. Lower d-excess values generally indicate that the pool un-
47 dergone some evaporation [Brooks et al., 2014]. Stable isotopes are also very efficient in helping identify
48 different water sources in plants [Ehleringer and Dawson, 1992]. Kinetic isotope effects associated with the
49 difference in diffusivity of the different isotopologues of water can lead to different isotopic composition
50 [Farquhar et al., 2006]. Simple mixing models allow one to separate the composition and the fluxes coming
51 from different sources. For this reason, stable isotopes are great natural labels that can be used to track
52 pathways of water within plants without harming them.

53 **II.2 Experiment 1a: Effects of dew deposition on *Colocasia esc.* water isotopes in natural conditions**

54 This first experiment examines leaf scale spatial and temporal patterns of water isotopes induced by the
55 presence or the absence of dew under drought condition. Six bulbs of *Colocasia esculenta* were planted in
56 separate pots. All pots were placed outside and received full sun for four weeks. During this time, all plants
57 were heavily watered with tap water to allow plant growth. Once the six plants reached maturity, watering
58 stopped and the plants were moved to a shaded area to remove any sun exposition difference between the

59 plants. Three of the six pots were left to dry and did not receive any water for the rest of the experiment.
60 The upper surface of the leaves of the other three pots were misted with isotopically enriched water ($\delta^{18}\text{O}$
61 = 8.85 ‰, δD = 737.64 ‰) every two days using a spray bottle. All of the extra water would run off the
62 leaves, leaving them covered in submillimeter size droplets, which is a realistic size for dew deposition drops
63 [Defraeye et al., 2013]. The misting simulated dew and occurred as early as possible in the morning. In order
64 to avoid contact between the misted water and the soil in the pots, the surface of all pots was covered in
65 wrapping plastic. Six leaves were collected between the beginning of the drought/dew treatments and the end
66 of the experiments, three weeks later. The sampling and the analysis are described in Section II.5.

67 **II.3 Experiment 1b: Effects of water droplets deposition on *Colocasia esc.* leaf water isotope under
68 high water stress conditions**

69 This second experiment was designed to artificially increase the contrast between the drought and misted
70 treatments from Experiment 1. Two leaves of similar size and of the same *Colocasia esc.* plant were cut
71 at the junction of the petiole and the rachis and left to dry 80 cm under a blue light (Eiko 1960 EBW,
72 500 W, 10500 lumens, color temperature of 4800 K). One leaf was misted with isotopically labelled water
73 ($\delta^{18}\text{O}$ = 8.85 permil, δD = 737.64 permil) every half-hour. The other leaf was left to dry without any
74 intervention. After four hours, samples were collected from both leaves as described in Section II.5.

75 **II.4 Experiment 2: Effects of dew deposition on *Colocasia esc.* leaf water potential under high water
76 stress conditions**

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

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

87 For the water isotope analysis, each analyzed leaf was sampled in 12 to 25 different locations depending on
88 the size of the leaf. All the sampling points were located on the same half of the leaf and consisted in four
89 holes (6 mm diameter) punched next to each other forming a square. Each hole was punched as quickly as
90 possible to avoid evaporation, which would influence the isotopic composition of the neighboring holes. Each
91 leaf disk was then secured in an aluminum foil and inserted in a sealed vial. The entire leaf was sampled in
92 one go and as fast as possible. The prepared vials were then stored in the fridge until being analyzed. The
93 leaf samples were analyzed using an Induction Module (IM) combined to a Cavity Ring Down Spectrometer

94 (CRDS) L2103-i from Picarro Inc. (Sunnyvale, CA, USA). The IM was set on the "normal leaf" setting: the
95 leaf disks did not appear carbonized and after being dried in the oven at 60°C for 48 hours, they show no
96 decline in weight, proving that this setting dried the leaf samples completely. The IM was equipped with a
97 micro-combustion module (MCM). The MCM has been proven to efficiently reduce the interferences due to
98 the presence of organics in water samples extracted from plants (Kate Dennis, private communication).

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

110 **IRIS and IRMS analysis** Ten samples were sent to the Center for Stable Isotope Biogeochemistry at the
111 University of California in Berkeley for IRMS analysis. For the IRMS method, δD was obtained by chromium
112 combustion using an H/Device (labelled as HDEV; Thermo Finnigan, Bremen). Microliters of water were
113 injected in the HDEV and reduced to H_2 gas. The ratio of D/H was then measured on a Thermo Delta Plus
114 mass spectrometer. For the $\delta^{18}\text{O}$ analysis, water for both standards and samples were pipetted into glass vials
115 and quickly sealed. The vials were then purged with 0.2% CO_2 in Helium and allowed to equilibrate at room
116 temperature for at least 48 hours. The ^{18}O in the CO_2 was then analyzed by continuous flow using a Thermo
117 Gas Bench II interfaced to a Thermo Delta Plus XL mass spectrometer. In this $\text{H}_2\text{O}-\text{CO}_2$ equilibration method,
118 the dissolved components (organic and/or inorganic) do not affect the values of $\delta^{18}\text{O}$. For the IRIS analysis,
119 1.8 μL of water were injected into a vaporizer and the vapor pushed through a MCM. The concentrations of
120 H_2^{18}O and HD^{16}O were measured on a water isotope analyzer (L2103-i) from Picarro Inc. (Sunnyvale, CA,
121 USA).

122 The ten samples analyzed both by IRMS and IRIS were used to calculate the offset between both analysis
123 methods. All the samples that had been run exclusively by IRIS or IM-CRDS were then corrected for this
124 offset. The IM-CRDS method has not been widely used yet and protocols and precision analysis are still
125 absent from the scientific literature. In order to justify the values obtained using the IM-CRDS, we compared
126 the values obtained from the extracted water of the half-leaf analyzed by IRIS to the average leaf water
127 composition obtained using a nearest neighbor interpolation on the half-leaf analyzed by IM-CRDS. For
128 the seven leaves analyzed by IM-CRDS, the average difference between those two methods was 2.6‰ in
129 $\delta^{18}\text{O}$ and 3.4‰ in δD . These values are higher than the average difference we observed between two halves
130 of the same *Colocasia esc.* leaf, both extracted by cryogenic vacuum distillation and analyzed by IRIS

131 (0.3‰ in $\delta^{18}\text{O}$ and 1.9‰ in δD). Further testing is clearly necessary before using the IM-CRDS technique
132 as an absolute method. However, our goal here is to compare strongly enriched waters and the order of the
133 differences presented in the next section are up to two orders of magnitude bigger than the error observed for
134 the IM-CRDS. We therefore believe that the IM-CRDS is an appropriate method here, as it allowed us to
135 quickly process many small samples, therefore increasing the spatial resolution of our analysis.

136 III. Results

137 Figure 1 presents the evolution of the isotopic composition of leaves from the drought and misted plants in
138 Experiment 1a. All the maps of both $\delta^{18}\text{O}$ and δD show the expected progressive enrichment of leaf water
139 when moving away from the main stem towards the rims of the leaf [Cernusak and Kahmen, 2013]. This
140 enrichment is due to the progressive evaporation of the leaf water as it moves away from the source water that
141 enters the leaf through the petiole. The lighter isotopologues are evaporated first, leaving the heavier ones
142 in the leaf [Farquhar et al., 2006]. The third column of Figure 1 shows the corresponding d-excess. Again,
143 the increase in evaporation at the rims, characterized by lower d-excess values, is apparent. Those results
144 reinforced our confidence in the IM-CRDS method. The average composition of each leaf is summarized in
145 Table 2. Because the plants were kept outside during the experiment, the day to day variations in temperature
146 and relative humidity both influenced the transpiration rate as well as the isotopic composition. However,
147 comparing same day results for both treatments, we see that the dew treated plants systematically exhibit
148 higher d-excess values than the drought treated ones. The lower d-excess values are associated with higher
149 transpiration rate. On the other hand, the misted leaves had a lower rate of transpiration, which led to higher
150 values of d-excess.

151 Similar maps were produced for Experiment 1b (Figure 2). In this case, the heat lamp artificially increased
152 the transpiration rate in both leaves, leading to highly enriched $\delta^{18}\text{O}$ and δD values and very low d-excess
153 values for both treatments. However, the d-excess in the drought case is a lot more negative (reaching values
154 down to ~-800 ‰) than for the dew treated leaves (reaching values down to ~-300 ‰). This experiment was
155 merely an extreme version of Experiment 1a, with the objective of accentuating the contrast between the two
156 treatments. While the high heat treatment led to a strong dry out of some areas of the leaf, in particular those
157 far away from the central vein, the large differences observed between the drought and the misted treatments
158 do confirm the results of Experiment 1a.

159 Finally, Experiment 2 was design to look at the temporal evolution of water potential in artificially drying
160 leaves (see Figure 3). Strong differences in drying pattern are shown for the misted or non misted leaves.
161 In both the natural drying and the the high heat & mist cases, the leaf water potential experiences a slow
162 decline, which is best approximated by a linear function. However, the high heat treated leaves experience
163 a faster decline and are best approximated by a parabola. Without the results of Experiments 1 and 2, that
164 confirmed the leaves high hydrophobicity, this results could easily be mistaken for a foliar uptake process.
165 Large differences in water potential patterns were also observed as a function of leaf size: both the high heat
166 and the high heat & mist treatments had a stronger decline in water potential for small leaves than for big
167 leaves.

168 IV. Discussion

169 Dew and fog have been shown to have a direct impact on plants water status through direct uptake of water
170 from the leaves or needles [Stanton and Horn, 2013, Eller et al., 2013, Clus et al., 2008, Lakatos et al., 2012,
171 Berry et al., 2014, Berry and Smith, 2014]. As mentioned before, *Colocasia esculenta* is native to tropical
172 wetlands and posses highly hydrophobic leaves [Nehuis and Barthlott, 1997] that allow the plant to prevent
173 the development of fungus. This is confirmed by Experiments 1a and 1b in which the misted leaves all exhibit
174 lower isotopic enrichment in ^{18}O and D as the drought treated leaves. This is the sign that non of the highly
175 enriched sprayed water is being uptaken by the leaves, even in artificially dry and hot conditions. However,
176 despite the leaf's hydrophobicity and the absence of foliar uptake, submillimeter size droplets of water do
177 stay attached to the surface of the leaf and allow it to decrease its transpiration rate and maintain its water
178 potential. The water balance of the leaf is therefore influenced by the change in energy balance associated
179 with the water droplets deposited at the surface. The influence of these water droplets is triple. First, the
180 droplets increase the albedo of the leaf, allowing more of the radiations to be reflected away from the leaf.
181 Second, part of the oncoming energy will be dissipated through the evaporation of the droplets, which also
182 provides evaporative cooling to the surface of the plant. Finally, the evaporated droplets allow to increase the
183 boundary layer [Defraeye et al., 2013] and locally decrease vapor pressure deficit (VPD), creating a moister
184 environment around the leaf.

185 While the first two mechanisms will have a homogenous impact on all leaves, the third mechanism
186 proposed will be leaf size dependent. This is confirmed by the leaf size dependent behavior observed for
187 the misted case of Experiment 2 (see Figure 3): if only the first two mechanisms were at play, one would
188 not expect a difference between two leaves of different size receiving mist. However, bigger misted leaves
189 will create a larger micro-climate, increasing the length of the boundary layer and therefore decreasing the
190 VPD even further than a small leaf could [Defraeye et al., 2013]. This lower VPD then induces a decrease in
191 transpiration and an increase in water potential, as it is the case in Experiment 2.

192 Water droplets from rain interception will have a similar effect. However in this case the soil water would
193 also be replenished, making the gain in water obtain by lowering transpiration less necessary than in the case of
194 dew or fog droplets forming during a drought. Many studies have indeed demonstrated that dew or fog deposition
195 had little impact on well watered plants [Andrade, 2003, Eller et al., 2013]. Dew and fog commonly occur
196 all around the world and in a wide range of ecosystems, from drylands [Agam and Berliner, 2006] to tropical
197 forests [Lakatos et al., 2012]. Indeed, regular dew formation has been observed by scatterometer in the upper
198 canopy of the Amazon forest, even during the dry season [Satake and Hanado, 2004, Frolking et al., 2011].
199 [Frolking et al., 2011] observed a sharp decrease in morning backscatter over the Amazon forest for the
200 summer months of 2005, which they associated with a lack of morning dew formation. This summer was
201 known as a mega-drought for the Amazon forest and led to a high tree mortality [Zeng et al., 2008]. However,
202 the accumulating water deficit anomaly for that year was just as high as that of the year 2002, which did not
203 experience the same tree mortality. The main difference in water resources between the two years appears to
204 be the presence or absence of dew.

205 The results of our study hint at a large impact of water droplets deposition on hydrophobic leaves in time

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

REFERENCES

- [Abtew and Melesse, 2012] Abtew, W. and Melesse, A. (2012). *Evaporation and Evapotranspiration. Measurements and Estimations*. Springer Science & Business Media.
- [Agam and Berliner, 2006] Agam, N. and Berliner, P. R. (2006). Dew formation and water vapor adsorption in semi-arid environments—A review. *Journal of Arid Environments*, 65(4):572–590.
- [Andrade, 2003] Andrade, J. L. (2003). Dew deposition on epiphytic bromeliad leaves: an important event in a Mexican tropical dry deciduous forest. *Journal of Tropical Ecology*, 19(5):479–488.
- [Ballantyne et al., 2012] Ballantyne, A. P., Alden, C. B., Miller, J. B., Tans, P. P., and White, J. W. C. (2012). Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature*, 488(7409):70–72.
- [Berry et al., 2014] Berry, Z. C., Hughes, N. M., and Smith, W. K. (2014). Cloud immersion: an important water source for spruce and fir saplings in the southern Appalachian Mountains. *Oecologia*, 174(2):319–326.
- [Berry and Smith, 2014] Berry, Z. C. and Smith, W. K. (2014). Experimental cloud immersion and foliar water uptake in saplings of *Abies fraseri* and *Picea rubens*. *Trees*, 28(1):115–123.
- [Brooks et al., 2014] Brooks, J. R., Gibson, J. J., Birks, S. J., Weber, M. H., Rodecap, K. D., and Stoddard, J. L. (2014). Stable isotope estimates of evaporation : inflow and water residence time for lakes across the United States as a tool for national lake water quality assessments. *Limnology and Oceanography*, 59(6):2150–2165.
- [Buckley, 2005] Buckley, T. N. (2005). The control of stomata by water balance. *New Phytologist*, 168(2):275–292.
- [Cernusak and Kahmen, 2013] Cernusak, L. A. and Kahmen, A. (2013). The multifaceted relationship between leaf water ^{18}O enrichment and transpiration rate. *Plant, Cell & Environment*, 36(7):1239–1241.
- [Clus et al., 2008] Clus, O., Ortega, P., Muselli, M., Milimouk, I., and Beysens, D. (2008). Study of dew water collection in humid tropical islands. *Journal of Hydrology*, 361(1-2):159–171.
- [Cook et al., 2014] Cook, B. I., Smerdon, J. E., Seager, R., and Coats, S. (2014). Global warming and 21st century drying. *Climate Dynamics*.
- [Cox et al., 2013] Cox, P. M., Pearson, D., Booth, B. B., Friedlingstein, P., Huntingford, C., Jones, C. D., and Luke, C. M. (2013). Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature*, 494(7437):341–344.
- [Defraeye et al., 2013] Defraeye, T., Verboven, P., Derome, D., Carmeliet, J., and Nicolai, B. (2013). International Journal of Heat and Mass Transfer. *International Journal of Heat and Mass Transfer*, 65(C):180–191.

- [Ehleringer and Dawson, 1992] Ehleringer, J. R. and Dawson, T. E. (1992). Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell & Environment*, 15(9):1073–1082.
- [Eller et al., 2013] Eller, C. B., Lima, A. L., and Oliveira, R. S. (2013). Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis*(Winteraceae). *New Phytologist*, 199(1):151–162.
- [Farquhar et al., 2006] Farquhar, G. D., Cernusak, L. A., and Barnes, B. (2006). Heavy Water Fractionation during Transpiration. *Plant Physiology*, 143(1):11–18.
- [Frolking et al., 2011] Frolking, S., Milliman, T., Palace, M., Wisser, D., Lammers, R., and Fahnestock, M. (2011). Tropical forest backscatter anomaly evident in SeaWinds scatterometer morning overpass data during 2005 drought in Amazonia. *Remote Sensing of Environment*, 115(3):897–907.
- [Gatti et al., 2015] Gatti, L. V., Gloor, M., Miller, J. B., Doughty, C. E., Malhi, Y., Domingues, L. G., Basso, L. S., Martinewski, A., Correia, C. S. C., Borges, V. F., Freitas, S., Braz, R., Anderson, L. O., Rocha, H., Grace, J., Phillips, O. L., and Lloyd, J. (2015). Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature*, 506(7486):76–80.
- [Griffis et al., 2010] Griffis, T. J., Sargent, S. D., Lee, X., Baker, J. M., Greene, J., Erickson, M., Zhang, X., Billmark, K., Schultz, N., Xiao, W., and Hu, N. (2010). Determining the Oxygen Isotope Composition of Evapotranspiration Using Eddy Covariance. *Boundary-Layer Meteorology*, 137(2):307–326.
- [Guan et al., 2015] Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., Taylor, K. K., Sheffield, J., Wood, E. F., Malhi, Y., Liang, M., Kimball, J. S., Saleska, S. R., Berry, J., Joiner, J., and Lyapustin, A. I. (2015). Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience*.
- [Huntingford et al., 2013] Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L. M., Sitch, S., Fisher, R., Lomas, M., Walker, A. P., Jones, C. D., Booth, B. B. B., Malhi, Y., Hemming, D., Kay, G., Good, P., Lewis, S. L., Phillips, O. L., Atkin, O. K., Lloyd, J., Gloor, E., Zaragoza-Castells, J., Meir, P., Betts, R., Harris, P. P., Nobre, C., Marengo, J., and Cox, P. M. (2013). Simulated resilience of tropical rainforests to CO₂. *Nature Geoscience*, 6(4):268–273.
- [Lakatos et al., 2012] Lakatos, M., Obregón, A., Büdel, B., and Bendix, J. (2012). Midday dew - an overlooked factor enhancing photosynthetic activity of corticolous epiphytes in a wet tropical rain forest. *New Phytologist*, 194(1):245–253.
- [Mook, 2006] Mook, W. G. (2006). *Introduction to Isotope Hydrology Stable and Radioactive Isotopes of Hydrogen, Carbon and Oxygen*. London: Taylor & Francis.
- [Neelin et al., 2003] Neelin, J. D., Chou, C., and Su, H. (2003). Tropical drought regions in global warming and El Niño teleconnections. *Geophysical Research Letters*, 30(24):2275.

- [Neinhuis and Barthlott, 1997] Neinhuis, C. and Barthlott, W. (1997). Characterization and distribution of water-repellent, self-cleaning plant surfaces. *Annals of Botany*, 79(6):667–677.
- [Osborne, 2012] Osborne, P. L. (2012). *Tropical Ecosystems and Ecological Concepts*. Cambridge University Press.
- [Raupach et al., 2013] Raupach, M. R., Gloor, M., Sarmiento, J. L., Canadell, J. G., Frölicher, T. L., Gasser, T., Houghton, R. A., Le Quéré, C., and Trudinger, C. M. (2013). The declining uptake rate of atmospheric CO₂ by land and ocean sinks. *Biogeosciences Discussions*, 10(11):18407–18454.
- [Rothfuss et al., 2012] Rothfuss, Y., Braud, I., Le Moine, N., Biron, P., Durand, J.-L., Vauclin, M., and Bariac, T. (2012). Factors controlling the isotopic partitioning between soil evaporation and plant transpiration: Assessment using a multi-objective calibration of SiSPAT-Isotope under controlled conditions. *Journal of Hydrology*, 442-443:75–88.
- [Satake and Hanado, 2004] Satake, M. and Hanado, H. (2004). Diurnal change of Amazon rain forest σ^0 observed by Ku-band spaceborne radar. *IEEE Transactions on Geoscience and Remote Sensing*, 42(6):1127–1134.
- [Stanton and Horn, 2013] Stanton, D. E. and Horn, H. S. (2013). Epiphytes as “filter-drinkers”: life-form changes across a fog gradient. *The Bryologist*, 116(1):34–42.
- [van Geldern and Barth, 2012] van Geldern, R. and Barth, J. A. C. (2012). Optimization of instrument setup and post-run corrections for oxygen and hydrogen stable isotope measurements of water by isotope ratio infrared spectroscopy (IRIS). *Limnology and Oceanography: Methods*, 10:1024–1036.
- [Wang et al., 2013] Wang, L., Niu, S., Good, S. P., Soderberg, K., McCabe, M. F., Sherry, R. A., Luo, Y., Zhou, X., Xia, J., and Caylor, K. K. (2013). The effect of warming on grassland evapotranspiration partitioning using laser-based isotope monitoring techniques. *Geochimica et Cosmochimica Acta*, 111:28–38.
- [Zeng et al., 2008] Zeng, N., Yoon, J.-H., Marengo, J. A., Subramaniam, A., Nobre, C. A., Mariotti, A., and Neelin, J. D. (2008). Causes and impacts of the 2005 Amazon drought. *Environmental Research Letters*, 3(1):014002.
- [Zhao and Running, 2010] Zhao, M. and Running, S. W. (2010). Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 Through 2009. *Science*, 329(5994):940–943.

Identifiers		
ID	Type	Injections
Blank 1 to	Empty vial	1
Blank 6	Empty vial	1
DEST	Drift ref. water	10
HIS	High ref. water	10
ANTA	Low ref. water	10
DEST	Drift ref. water	10
HERA	QC ref. water	4
Sample 1 to	Sample	4
Sample 10	Sample	4
DEST	Drift ref. water	6
Sample 11 to	Sample	4
Sample 20	Sample	4
DEST	Drift ref. water	6

Table 1: Typical sequence layout of an IM-CRDS run with four reference waters. Following [van Geldern and Barth, 2012], HIS and ANTA are the names of the reference waters with high and low delta values, DEST and HERA are intermediate waters. DEST is the drift monitoring reference water whereas HERA is treated as a sample for quality control. All reference waters except HERA are used for memory correction.

Day	Treatment	$\delta^{18}\text{O}$ (‰)	δD (‰)	d-excess (‰)
0		20.0	24.1	-136.1
14	Drought	13.3	-1.5	-108.0
14	Dew	15.3	20.32	-102.4
20	Drought	23.0	15.1	-169.0
20	Dew	13.4	-2.7	-109.6

Table 2: Average leaf isotopic composition obtained by nearest neighbor interpolation for each of the leaves presented in Figure 1.

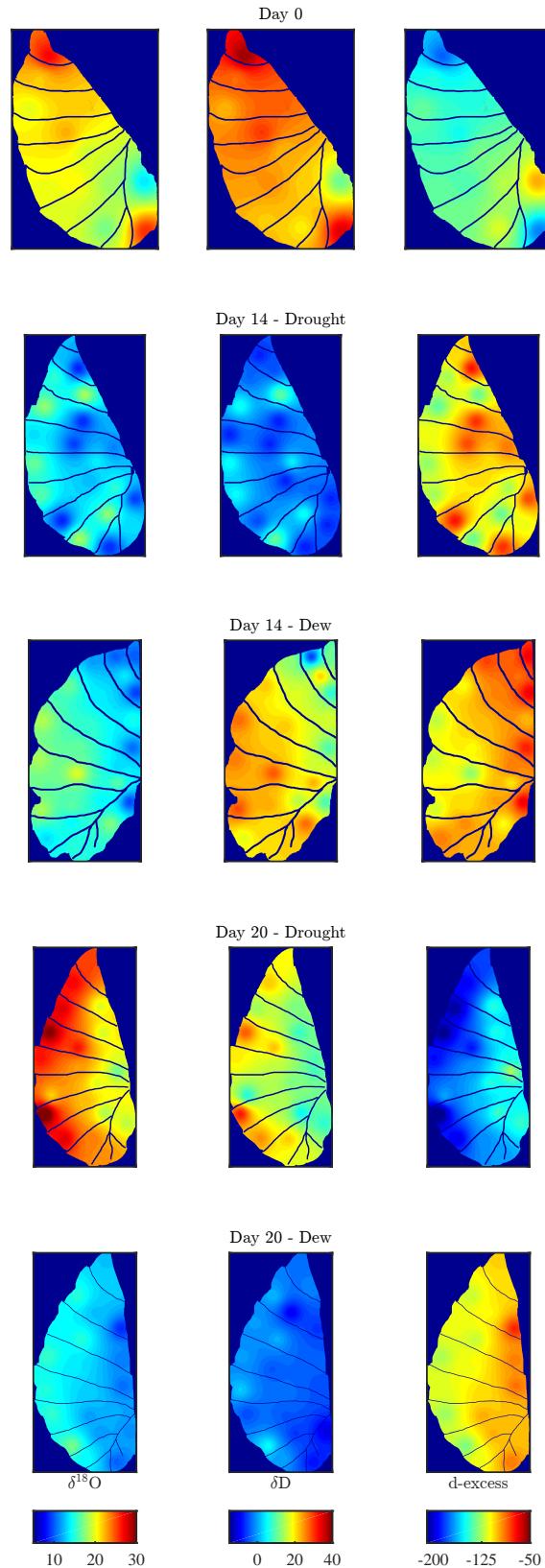


Figure 1: Maps of five *Colocasia esc.* leaves collected throughout Experiment 1. All leaves are about 38 cm long. The first column shows $\delta^{18}\text{O}$, the second δD and the last column shows d-excess. Row 1 shows the isotopic composition of a leaf on day 0. Rows 2 and 4 shows leaves from the drought treatment collected at days 14 and 20, respectively. Rows 3 and 5 show leaves collected on similar days but 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.

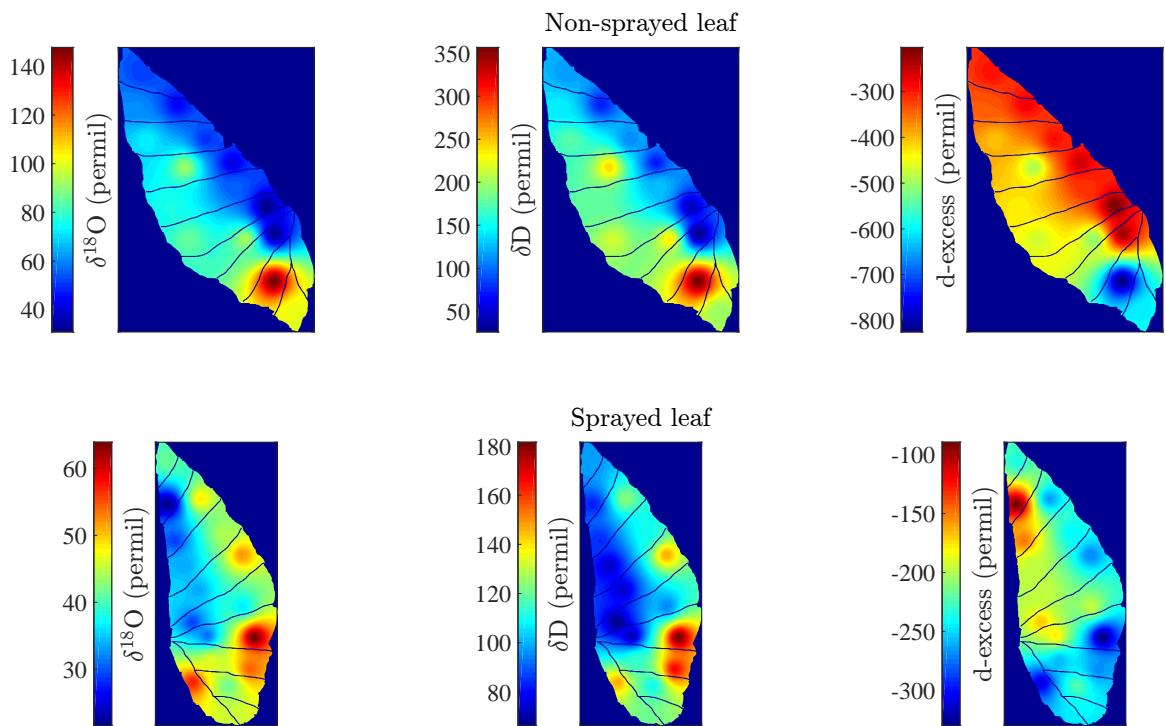


Figure 2: Maps of two leaves left to dry under a 500W blue light. The top row shows $\delta^{18}\text{O}$, δD and d-excess of the non-sprayed leaf. Bottom row shows the same for a leaf sprayed with isotopically enriched water ($\delta^{18}\text{O} = 8.85 \text{ ‰}$, $\delta\text{D} = 737.64 \text{ ‰}$) every half-hour.

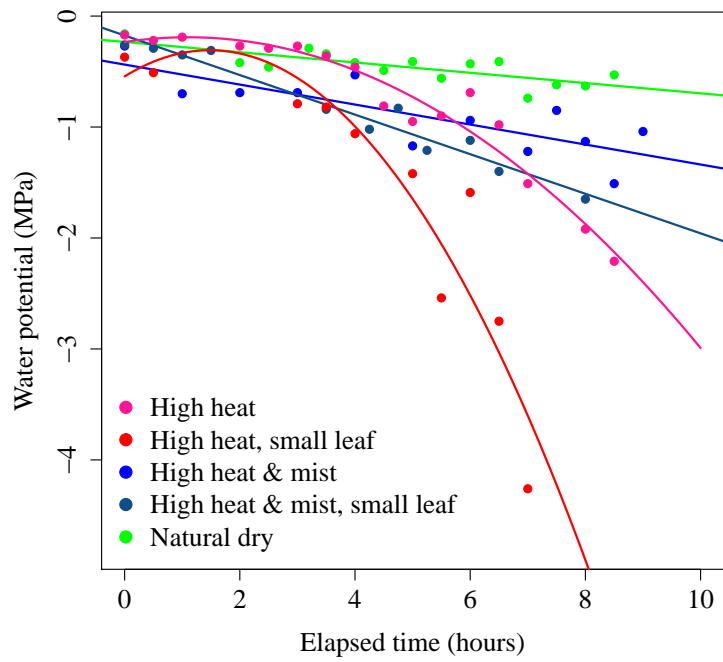


Figure 3: Five examples of the temporal evolution of leaf water potential of *Colocasia esc.* leaves. Natural dryout (green) and high heat & dew (blue and charcoal) cases are best fitted by a linear relation. The high heat drying (red and pink) cases are best fitted by a parabola. “Small leaf” refers to 38 cm long leaves. All other leaves are 45 cm long.