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Foliar water uptake in Amazonian trees: evidence and consequences

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Abstract

The absorption of atmospheric water directly into leaves enables plants to alleviate the water stress caused by low soil moisture, hydraulic resistance in the xylem and the effect of gravity on the water column, whilst enabling plants to scavenge small inputs of water from leaf wetting events. By increasing the availability of water, and supplying it from the top of the canopy (in a direction facilitated by gravity), foliar uptake (FU) may be a significant process in determining how forests interact with climate, and could alter our interpretation of current metrics for hydraulic stress and sensitivity. FU has not been reported for lowland tropical rain forests; we test whether FU occurs in six common Amazonian tree genera in lowland Amazônia, and make a first estimation of its contribution to canopy-atmosphere water exchange. We demonstrate that FU occurs in all six genera and that dew-derived water may therefore be used to 'pay' for some morning transpiration in the dry season. Using meteorological and canopy wetness data, coupled with empirically-derived estimates of leaf conductance to FU (k_{fu}), we estimate that the contribution by FU to annual transpiration at this site has a median value of 8.2 % (103 mm yr^{-1}) and an interquartile range of 3.4 to 15.3 %, with the biggest sources of uncertainty being k_{fu} and the proportion of time the canopy is wet. Our results indicate that FU is likely to be a common strategy and may have significant implications for the Amazon carbon budget. The process of foliar water uptake may also have a profound impact on the drought tolerance of individual Amazonian trees and tree species, and on the cycling of water and carbon, regionally and globally.

Introduction

In the classic scheme of a soil-plant-atmosphere-continuum, water moves from the soil, through the plant, evaporates from the leaf surfaces, and precipitation from atmospheric moisture then replenishes soil water (Tyree *et al.*, 2002). However, where vegetation cover is dense, the water from some leaf-wetting events, such as dew, fog (so-called 'occult precipitation') and even light rainfall, is intercepted by foliage and most does not reach the soil. In the classical view, occult precipitation events do not contribute directly to plant water status. However, there is mounting evidence that water uptake by leaves, or foliar uptake (FU), plays a significant role in a wide range of ecosystems. Foliar uptake has been found to occur in desert ecosystems (Nadezhdina & Nadezhdin, 2017, Yan *et al.*, 2015), savanna (Oliveira *et al.*, 2005), the Mediterranean (Fernandez *et al.*, 2014, Gouvra & Grammatikopoulos, 2003), temperate forests (Anderegg *et al.*, 2013, Boucher *et al.*, 1995, McDowell *et al.*, 2008, Simonin *et al.*, 2009, Stone, 1957), tropical montane cloud forests (Eller *et al.*, 2013, Goldsmith *et al.*, 2013), and has been reported in conifers (Breshears *et al.*, 2008, Limm *et al.*, 2009), broadleaf trees (Fernandez *et al.*, 2014) and herbaceous vegetation (Gouvra & Grammatikopoulos, 2003), meaning that the large-scale effects and importance of occult precipitation may be greater than previously understood.

The occurrence of water entering leaves directly from the atmosphere has two major implications, the first being that it increases the total amount of water available to the plant, and by extension the amount of carbon assimilated (Berry *et al.*, 2014, Oliveira *et al.*, 2014). The second implication is that water entering at the top of the system can effectively act independently of the cohesion-tension theory; that is, it enables water pressure in the canopy xylem to be above the theoretical maximum pressure based on water supply from the soil (Goldsmith, 2013), and hypothetically even achieve positive pressures.

A consequence of the first point is that if, in a given system, FU is a common trait and quantitatively important, the representation of carbon-water relationships is likely to be incomplete in models if, as is almost universally the case, the water-supply component is based only on soil water or precipitation. Typically, water intercepted by the canopy is assumed to temporarily depress photosynthesis due to occlusion of stomata and the scattering and reflection of radiation by surface water (Gerlein-Safdi *et al.*, 2018, Pariyar *et al.*, 2017, Rosado & Holder, 2013) and, until recently, has not been thought to contribute significantly to the plant water budget (Dawson & Goldsmith, 2018). If, on the other hand, wet leaves become rehydrated, rather than reducing carbon assimilation, the additional water will effectively be offset or reversed enabling the plant to achieve higher stomatal conductance at some later point during the day.

The second consequence is more complex. According to the cohesion-tension theory, the evaporation of water from leaves generates tension in the water column, and water moves down a gradient of tension from higher to lower pressure, minus the effects of gravity (Dixon & Joly, 1895). Gravity results in a pressure drop in the water column proportional to height, so for flux to occur, the pressure difference must be greater than 0.1 MPa for every 10 vertical meters (Roderick, 2001). Any point above 10 m height in a tree, therefore, is expected to have a water potential (Ψ) lower than -0.1 MPa (a pressure equivalent to absolute vacuum), even if the roots are in a soil that is saturated. Hydraulic systems like tall trees are subject to a number of biophysical limitations, even under such conditions of maximum hydration: 1) upper leaves are always the driest part of the plant and require water to be transported from distant organs below, resulting in negative water potentials associated with resistance of the hydraulic pathway and the height difference between leaves and the storage organ; 2) assuming that woody tissue capacitance is similar throughout the plant, the relative water content i.e. stored water, will always be highest in organs most distant from leaves and decrease with proximity to the leaves where the water is required; and 3) low water potentials in the xylem cause conduits to cavitate, causing a reduction in hydraulic conductance which is costly to restore, if restoration is possible.

FU modifies these relationships. If water is absorbed directly into the leaves, the water potential can be higher than the theoretical maximum according to the cohesion-tension theory (Kangur *et al.*, 2017, Simonin *et al.*, 2009). This means that predawn water potential, a common metric for assessing drought stress in plants and soil water potential, does not accurately represent the system (plant and soil) when the leaves have been wet i.e., the leaves could theoretically have a higher tissue water potential, i.e. be 'wetter', than the soil. If a fraction of the water lost in transpiration comes from FU, less water is transported from distant organs, reducing the effect of resistance in the hydraulic pathway on the water potential of the leaves. A supply of water direct to the leaves reduces the impact of a loss of conductance in the stem xylem to the leaves and, hypothetically, water taken up by leaves could cause high enough xylem pressures to repair embolised conduits passively (Mayr *et al.*, 2014). These factors may alter the interpretation of existing metrics for assessing drought sensitivity, such as the P50 (Ψ at 50% loss of hydraulic conductance) and the hydraulic safety margin (the difference between a typical and the critical level of drought stress – this is always estimated without accounting for foliar water uptake).

An emergent consideration of foliar water uptake is the effect it could have on forest-climate interactions. If forests are gaining small inputs of water from precipitation events such as dew and fog, then this occult precipitation may supply small but essential quantities of water (and therefore carbon) throughout the dry season and other periods of drought stress. Dew formation is very sensitive to temperature and humidity, meaning that small changes in climate may have a large impact on this potentially crucial source of water and, therefore, on forest drought tolerance.

Given these considerations, it is important to assess how common foliar water uptake is in forests globally, and the impact of FU on ecosystem functioning. Foliar uptake has been shown to result in improvements in plant water status in multiple biomes (Eller *et al.*, 2013, Gouvra & Grammatikopoulos, 2003, Simonin *et al.*, 2009), but has not been investigated in terms of the quantitative impact it has on ecosystem-level water and carbon exchange. The Amazon accounts for over half of the world's rainforests (Fritz *et al.*, 2003), is considered to be a powerful regulator of the global carbon cycle (Le Quere *et al.*, 2013), and its biophysical functioning is known to be strongly sensitive to reductions in water availability (Gatti *et al.*, 2014, Meir & Woodward, 2010, Phillips *et al.*, 2009). To our knowledge, there are no reports yet addressing the occurrence of foliar water uptake in lowland tropical rain forests, the impact FU might have on large-scale fluxes of carbon and water, and whether or not FU may influence the response of forests to climate change.

We tested the central hypothesis that foliar water uptake exists in six hyper-dominant genera (ter Steege *et al.*, 2013) in lowland Amazon rainforest by using a range of both *in situ* and laboratory experiments including wetting experiments, predawn leaf water potentials, and sap flux to assess the occurrence and magnitude of FU at an eastern Amazon rainforest. This multi-method ecophysiological approach was coupled with 15 years of meteorological data and 1 year of canopy-profile leaf wetness data and used to address the following questions: (i) do Amazonian trees take up water directly from the atmospheric environment via their leaves?; and (ii) could water taken up via FU in Amazonian trees make an important contribution to the transpiration budget? We then discuss the implications of foliar uptake in the context of hydraulic vulnerability, carbon exchange and changing climate.

Materials and methods

Study Site

The study was undertaken in the Caxiuanã National Forest Reserve in the eastern Amazon (1º 43'S, 51º 27'W). The site is situated in lowland *terra firme* rainforest 10-15 m above river level. The site has a mean temperature of ca. 25 ºC, receives 2000 – 2500 mm of rainfall annually and has a dry season in which rainfall is <100 mm per month between June and November. The soil is a yellow oxisol of 3-4 m depth, below which is a narrow laterite layer 0.3-0.4 m thick (Fisher *et al.*, 2007, Meir *et al.*, 2015).

Meteorological data including temperature, relative humidity (aspirated psychrometer, WP1-UM2, Delta-T Devices, Cambridge, UK) and rainfall (tipping bucket rainfall gauge, Campbell Scientific, Loughborough, UK) have been recorded continuously from the top of a 40 m high above-canopy tower since 2001. Leaf wetness sensors (LWS, Decagon, Labcell Ltd., Four Marks, UK) were used to measure a two full vertical profiles of canopy (leaf) wetness at heights of 10, 20, 25, 30, 32, 34, 36, 38 and 40 m from the ground. The dataset from the leaf wetness sensors is from December 2016 to December 2017.

Study specimens

This study uses mature upper-canopy trees from six genera: *Manilkara, Eschweilera*, *Pouteria, Protium, Swartzia,* and *Licania.* Of the six, *Eschweilera*, *Protium*, *Pouteria* and *Licania* are ranked as the top four most abundant Amazonian genera; *Swartzia* is ranked 17th and *Manilkara* is ranked 73rd (ter Steege *et al.*, 2013). Where possible, a single species was used to represent a genus (*Pouteria anomala* (Pires) T.D. Penn., *Manilkara bidentata* (A.DC.) A.Chev., *Swartzia racemosa* (Benth.)), but more than one species was used where there were too few individuals in a species over the study area: *Eschweilera* is represented by the species *E. coriacea* (DC.) S.A.Mori, *E. grandiflora* (Aubl.) Sandwith, and *E. pedicellata* (Rich) S.A.Mori, *Licania* by *L. membranacea* (Sagot ex Laness) and *L.octandra* (Kuntze) and *Protium* by *P.tenuifolium* Engl. and *P. paniculatum* Engl. Sample leaves and branches were all collected from the upper-canopy where they would have been exposed to full sunlight for at least a proportion of the day. Because of the physical difficulty of sampling, high species diversity and consequent relatively low replication at the genus/species level, data from all trees were grouped for the statistical analyses to give plot-level results.

Experiments

The ingress of water to detached leaves was measured using a series of wetting experiments. The occurrence of FU *in situ* was determined by comparing predawn leaf water potentials with the theoretical maximum leaf water potential (Ψ_{max}) of all species, and by measuring reverse sap flux in terminal branches of *Manilkara*.

Wetting experiments

Artificial rainfall experiment

Leaves, collected at midday, were transported from the field into the laboratory in a sealed plastic bag that had been blown into to reduce further water loss. Leaf water potential was taken ($\Psi_{initial}$) using a Scholander pressure chamber (PMS Instruments Co., Corvallis, OR, USA), after which the open end of the petiole was sealed using cyanoacrylate adhesive ('superglue') to prevent non-lamina water uptake. Leaves were supported in a horizontal position by inserting the petiole into a small section of silicon tubing (approximately 20 mm long) which, in turn, was fastened to a freestanding wooden post. ‘Rain’ was created by drilling evenly spaced holes, 0.8 mm diameter and 20 mm apart, in the bottom of a bucket. The bucket was supported above the leaves while being continuously supplied with water to generate a constant flow rate. Leaves were subjected to 1 hour of artificial rain from the bucket arrangement, in shaded conditions at ambient temperature (26 – 28 ºC). Following the rain event the leaves were immediately patted dry with paper towels and placed in sealed plastic bags. The glued tip of the petiole was removed before measuring the final water potential (Ψ_{final}). Because the data were not normally distributed, and could not be adequately transformed into a normal distribution, paired Wilcoxon signed rank tests were used to test the hypotheses that $\Psi_{initial} < \Psi_{final}$ and $mass_{initial} < mass_{final}$, for significance.

Humidity and condensation experiment

Leaves were collected as in the artificial rainfall experiment, and their water potential and mass were measured before being put into a sealed chamber with over 98% relative humidity. Water potential and mass were taken again after 6 and 19 hours in the chamber. The humidity chamber consisted of a sealed plastic box in which leaves were placed on a mesh between free water (20 mm below) and a damp towel (100 mm above). The lid of the box was tightly fitting and was further sealed using thin-film low-density polyethylene (‘cling wrap’) to prevent gas exchange between the internal and external environments. The actual vapour pressure was calculated using the psychrometric equation and the temperature difference between the leaves (dry bulb) and whichever was cooler: the surface of the water or the damp towel (wet bulb), as measured with copper-constantan type T thermocouples connected to a CR1000 data logger (Campbell Scientific, Logan, USA). Leaf temperature was always between the temperature of the water surface and the damp towel, therefore creating the possibility of condensation on the leaf surface. As above, differences in water potential and mass before and after treatment were tested for significance using paired Wilcoxon signed rank tests.

Lamina rehydration experiment

To measure the rate of water potential change in response to FU, leaves, collected as above, were measured for water potential and mass before and after being submerged in water (with petioles remaining dry) for periods of three minutes. Following submersion, the leaves were dried with paper towel and allowed to equilibrate in sealed plastic bags for a minimum of five minutes before being remeasured. This was repeated four times on each leaf, on 72 leaves from the six study genera (three leaves per tree, minimum of three trees per genus, except for *Swartzia*, which is represented by only two trees). The nonlinear least squares function was used to test if the relationship between the final leaf water potential and the rehydration time was consistent with the equation describing the recharging of a capacitor (Brodribb & Holbrook, 2003).

In situ FU measurement

Leaf water potentials

Leaf water potentials were taken from branches collected from the top of the canopy between 05:30 and 07:00 ($\Psi_{predawn}$) and 12.00 and 14.00 (Ψ_{midday}). These measurements were made in October 2013, June 2014, October and November 2015, June 2016 and December 2016, where June is the end of the wet season and October to December is the end of the dry season. Water potential was taken on three leaves per tree (exceptionally two leaves per tree), and on three trees per genus per field campaign.

For the measurements taken in December 2016, the height of the sampled leaves was also measured using a Suunto Optical Reading Clinometer (Suunto, Sweden). The measured water potential values were compared with the theoretical maximum (least negative) water potential (Ψ_{t_max}) at the given height and soil water potential (Ψ_{soil}) as per the relationship: $\Psi_{t\_max} = \Psi_{soil} - \rho g h$ where ρ is the density of water, *g* is gravity, and *h* is the height of the sample. Because a genus-level separation was noticed in the relationship between $\Psi_{predawn}$ and height, a general linear model was used to test for a statistically significant difference between genera.

For $\Psi_{predawn}$ measurements taken prior to 2016, precise height measurements were not available for the sampled branches. To make sure we did not underestimate the Ψ_{t_max} (i.e., too negative, and hence overestimate the observed water potential disequilibrium at predawn), we assumed that branches were sampled at 15 m height which was the minimum height of any predawn water potential leaf sample. This provided a conservative estimate of the effect of height on leaf water potential.

Soil water potential, Ψ_{soil}

Volumetric soil water content ($m^3\ m^{-3}$) was measured at depths of 0, 0.5, 1 and 2.5 m using CS616 soil moisture sensors (Campbell Scientific, Logan, USA) in one soil pit and converted to Ψ_{soil} using the widely-applied Van Genuchten (1980) model:

$$\Psi_{soil} = \frac{\left(\left[\frac{\theta - \theta_r}{\theta_s - \theta_r}\right]^{-\left({n}/{n-1}\right)} - 1\right)^{1/n}}{\alpha}$$

where θ is volumetric water content, θ_r residual water content, θ_s saturated water content, *n* is a scaling factor which determines the curve shape, and α is a value proportional to the maximum pore size (kPa^{-1}). A pressure plate analysis was performed on four soil samples taken from each depth, from the same pit in which the water content sensors were installed, measuring θ at pressures of 0, 6, 10, 30, 100, 500 and 1500 kPa, where the θ at 0 kPa = θ_s (Richards & Fireman, 1943). The residual water content, θ_r, is taken to be the point at which the gradient of the slope between θ and pressure tends to 0. Here, it was taken to be the θ at which there was < 0.1 % change over 10 MPa difference in pressure. The parameters α and n were fitted using a non-linear least squares regression (Fig S1.1).

The soil water content sensors occasionally measured θ values < θ_r, posing a limitation on the model i.e. the model cannot function using negative percent saturation values. Moreover, an inflection point in the relationship between Ψ_{soil} and θ means that θ values close to θ_r generate excessively low water potentials e.g. < -100 MPa. We speculate that this is a limitation of using the van Genuchten model to derive water potential at such low water content given the precision of the sensors (+/- 2.5 % volumetric water content). Given this limitation, Ψ_{soil} < -5 MPa were excluded from the results, using instead a mean value from the other soil layers, which resulted in a more conservative outcome with respect to the analysis. The soil water potential measurements are listed in Table S1 together with the measurement periods and depths that were out of range.

A mean Ψ_{soil} of all soil depths, from 0 to 2.5 m, which should account for > 99.9 % of cumulative root fraction (Galbraith, 2010, Jackson *et al.*, 1996), was used to represent soil water potential for the purpose of calculating the maximum theoretical predawn leaf water potential. Soil moisture values intermittently fell outside the limit of calculation, as described above, thus not all mean Ψ_{soil} values have the same n. As there was no systematic failure of sensors at a particular depth, this was not thought to bias the soil water potential values.

Sap flux

Upper-canopy measurements of sap flux were limited by access and were made on two terminal branches of a single *Manilkara bidentata* tree that was fully accessible from a canopy tower. Because of the low replication of the sap flux data, these results are provided as auxiliary data in support of the findings of the other lines of evidence, although the data are not fundamental to the conclusions of the study. In 2015, sap flux sensors (ICT International, Armadale, Australia) were installed in two places on one branch, first at a position measuring 17.2 mm in diameter and then further upstream at 50.8 mm in diameter. In 2016, sensors were installed in another branch of the same tree <20 mm in diameter. Because the sensor probes (35 mm long) extended through the branches, blocks of closed-cell foam were used to insulate the exposed ends and the probes and branch segment were wrapped in aluminium foil to reduce the potential for radiative heating of the probes. Sap flux was measured for a period of seven days during the dry seasons of 2015 and 2016 and the branches were then removed to get an unequivocal zero value for sap flow. Sap flow velocity was calculated according to Burgess et al. (2001).

Leaf conductance to the uptake of surface water, k_{fu}

Here we treat k_{fu} as a purely physical process in which the flux, *F*, into the leaf is proportional to the water potential gradient between the surface water on the leaf, $\Psi_{surface}$, and the water potential in the leaf, Ψ_{inside}, such that $k_{fu} = F / (\Psi_{surface} - \Psi_{inside})$ consistent with Ohm's Law (Sack & Holbrook, 2006). Therefore, using a modified form of the equation that describes discharge of a capacitor, k_{fu} can be determined thus: $k_{fu} = - C\, ln[\Psi_{initial}/\Psi_{final}] / t$, where *C* is hydraulic capacitance (mol MPa^{-1}), $\Psi_{initial}$ and Ψ_{final} are the water potentials before and after wetting respectively, and *t* is duration of wetting (Brodribb & Holbrook, 2003). k_{fu} was calculated using the change in water potential ($\Delta\Psi$) and time (*t*) from the lamina rehydration experiment, and the leaf capacitance derived from pressure volume curves (Binks *et al.*, 2016).

We also used an alternative method of deriving k_{fu} using the mean value of 6 nights' reverse sap flux (V, g hr^{-1}) that occurred at 06:00 hrs, normalised by the leaf area of the branch (A_f) and predawn leaf water potential ($\Psi_{predawn}$): $K_{fu\_sf} = V / [A_f \, \Psi_{pd}]$.

The sap flux-derived term for k_{fu} is an underestimate because it does not take into account the storage of water between the leaves and the sensors and its calculation also assumes 100 % leaf wetness. Moreover, it is based only on the uptake by one species. For those reasons, the capacitance-derived term was used in the model of canopy-scale water uptake.

In this study, k_{fu} does not distinguish between the conductances of the abaxial and adaxial surfaces, and represents water taken up by the whole leaf surface area (e.g., both sides as per Guzman-Delgado et al. (2018)). See SI section '*S2. Determining leaf hydraulic conductance to foliar water uptake'* for a detailed explanation of the determination of k_{fu}.

Calculating canopy foliar water uptake (U_c)

The total annual water uptake of the canopy U_c (g H_2O m^{-2} ground area yr^{-1}) is calculated by the relationship

$$U_c = k_{fu} \, (\Psi_{surface} - \Psi_{canopy}) \, P_p \, L \, t_y$$

where k_{fu} is the conductance of the leaf cuticle to water (g MPa^{-1} s^{-1} m^{-2}), Ψ_{canopy} and $\Psi_{surface}$ are the mean water potential of the canopy and of the surface water (assumed to be 0, i.e. to have negligible solute concentration), respectively (MPa). P_p is the product of the proportion of leaf area index L ($m^2_{leaf\_area}$ $m^{-2}_{ground\_area}$) that is wet, and the proportion of the year that it is wet, as determined by the data from two through-canopy vertical profiles of leaf wetness sensors, and t_y (s yr^{-1}) is the number of seconds in a year. Because this is the first time that canopy-scale foliar water uptake has been calculated, there is inevitably some uncertainty in the true value of the parameters. To account for this, we use simulated data based on empirically-derived distributions of the parameter values to provide a statistical distribution of results. Hence, the output of the model is a distribution based on 10,000 iterations of the equation above using data which have been randomly generated to represent the measured parameter distributions explained below and in Table 1. See SI section '*S3. Canopy foliar uptake model parameters'* for a more detailed explanation of model parameter selection.

The distribution of canopy water potential, Ψ_{canopy}, was based on the range of predawn and midday water potentials measured in the wet and dry season (Fig S3.1). The mean wet season water potential (predawn and midday combined) was -0.66 MPa, and the mean dry season water potential was -1.11 MPa. In both seasons, the range between predawn and midday was around 1 MPa and, therefore, we used a mid-value of -0.89 MPa and a standard deviation (SD) of 0.5 to generate the distribution of canopy water potentials. This gave maximum and minimum values of 0 and -2.9 MPa respectively, thus accounting for a wide distribution of water potentials spatially (throughout the canopy) and temporally. Initially, estimates of Ψ_{leaf} were made temporally explicit by taking into account diurnal and seasonal fluctuations of Ψ. However, this made little difference to the model and so the simpler method was used. See SI section S3b. *Leaf water potential* for a detailed explanation of the temporally explicit leaf water potential calculation.

The cumulative duration of leaf wetness over a given time period is $P_p = D_d + D_r + N\overline{D}_e$, where D_d is the duration of dew events, D_r the duration of precipitation events, N the number of precipitation events, and $\overline{D}_e$ is the mean length of time for canopy drying following a rain event. The leaf wetness sensors give a continuous millivolt output in response to surface wetness and typically a clearly defined threshold is selected in which the sensor is either wet or dry

(Aparecido *et al.*, 2016). While the magnitude of the sensor output is a poor indicator of how wet the sensor is, dew events have a distinctive signal, characterised by a gradual increase in wetness overnight and abrupt drying at sunrise, which is easy to identify (Fig. S3.2). We used a script, in R, to identify rain events and dew events separately, based on their different signals.

Over the course of a year, the leaf wetness sensors detected 141 dew events which occurred on rainless nights, with a mean duration of 3.06 hrs. Thus, 3 hrs of dew were assumed to occur every rainless night in the dry season over the duration of the meteorological dataset from 2001 to 2015. The canopy drying time, in response to a rain event, was derived from the leaf wetness sensor drying time. The difference between the sum of the duration of rainfall and dew events ($D_d + D_r$,) and the duration of surface wetness of the sensors (D_{lws}) gives the total drying time of the sensors. Thus, the mean sensor drying time is given by $(D_{lws} - D_d - D_r) / N$, where N is the total number of precipitation events.

We suspected that the angle of the leaf wetness sensors would influence their drying time and did a further analysis to assess this affect. See SI '*S3 d. Sensor drying time versus leaf drying time*' for description of sensor analysis and derivation of correction factor, Fig. S3.3. In order to obtain a closer approximation of canopy drying time from the sensors we applied a correction to the sensor angle of 40^o to represent the mean leaf angle in the canopy (Bailey & Mahaffee, 2017, Kull *et al.*, 1999, Pisek *et al.*, 2013, Raabe *et al.*, 2015).

All statistical analyses were performed in R (R Core Team, 2015).

Results

Wetting experiments

Water taken up through leaves in a 1 hr artificial rainfall experiment significantly increased leaf water potential, Ψ_{leaf}, across all trees, from -1.31 ± 0.06 to -0.68 ± 0.04 MPa, (mean plus or minus standard error, $P < 0.001$, $n = 110$ leaves, minimum 14 leaves per genus, Fig. 1). The mass did not increase significantly in the rainfall experiment ($P = 0.18$), but this test was confounded by fragments of superglue breaking off the petioles while detaching the leaves from the silicon tubes. Leaves placed in an environment of > 98 % relative humidity for 16 hrs significantly increased water potential in all genera ($P < 0.001$, $n = 102$ leaves, minimum 15 leaves per genus), with *Eschweilera* having the greatest change and *Licania* the smallest, although there were no significant differences among genera (Fig. S4.1). Fresh mass per area also increased significantly in the humidity experiment ($P < 0.001$, Fig. S4.2). In both the artificial rainfall and humidity experiment there was a strong negative relationship between the change in Ψ ($\Psi_{final} - \Psi_{initial}$) and $\Psi_{initial}$ as determined by a linear regression ($R^2 = 0.59$ and 0.69 respectively, Fig. 2).

The lamina rehydration experiment showed that Ψ_{leaf} increased with each successive wetting event according to the relationship $\Psi_{leaf} = \Psi_{initial}\ e^{-t\ K/C}$ (voltage capacitance equation), where $\Psi_{initial}$ is Ψ_{leaf} before wetting, t is the duration of wetting, K is k_{fu}, and C is the hydraulic capacitance (Fig. 3). The relationship was significant at $P < 0.001$.See SI section '*S5. Rate dependence of dΨ on* $\Psi_{initial}$' for an explanation of the relevance of $d\Psi/\ \Psi_{initial}$ to k_{fu}. The results from the rainfall, humidity and lamina rehydration experiments all support the known analogue of leaf water uptake and the recharging of a capacitor (Brodribb & Holbrook, 2003).

Predawn water potentials and leaf height

Leaf predawn water potentials ($\Psi_{predawn}$) conducted in December 2016 revealed a divide between a group of genera that tended have higher $\Psi_{predawn}$ than the theoretical maximum Ψ_{t_max} (*Eschweilera*, *Licania* and *Swartzia,* Fig. 4) and a second group that had higher $\Psi_{predawn}$ than Ψ_{t_max} based on soil water potential only (*Manilkara*, *Pouteria* and *Protium*), however the genus-level replication was insufficient to test this relationship for significance. The mean soil water potential (Ψ_{soil}) of depths 0.5 and 1 m was -2.19 MPa over the duration of the $\Psi_{predawn}$ and height measurements (depths 0 and 2.5 were out of the calculable range of water potential during these measurements, Table S1).

Of the predawn water potential measurements taken from 2013 to 2016: (i) 25 out of 99 were higher than Ψ_{t_max} taking into account height alone, i.e., assuming Ψ_{soil} = 0 MPa (Fig. 5); (ii) 73 out of 86 measurements were higher than the soil, i.e., the leaves were wetter than the soil (Fig. 6); and (iii) 80 out of 86 were higher than the Ψ_{t_max}, assuming the combined effect of the minimum leaf sample height of 15 m and the mean soil water potential over the measurement period. The value of $\Psi_{predawn}$ - Ψ_{soil} of the dry season data was 1.86 +/- 0.11 MPa standard error, while the wet season was 0.29 +/- 0.05 MPa.

Sap flux

The sap flux data from both of the terminal branches (in 2015 and 2016) revealed that reverse sap flow occurred in *Manilkara bidentata* every night during the dry season in response to the deposition of dew, and rainfall that occurred on two of the eight nights in 2016 (Fig. S4.3 and S4.4). Installing two sensors at different positions on the same branch (performed in 2015) showed that negative flow occurred at a branch position measuring 17.2 mm in diameter, but not at a point more distal from the leaves with a 50.8 mm diameter. This indicated that the water taken up via the leaves was contributing to refilling the hydraulic capacitance of the terminal portion of the branches in this species (Fig. S4.3). The duration of measured nocturnal water uptake was typically around seven hours per night; however, the duration of dew deposition tended to be less than that, at around 3 to 4 hours. The disparity in results could be caused by dew forming on the leaves before detectable changes in sensor readings (possibly because of different rates of radiative cooling), or by the uptake of water vapour through open stomata prior to dew point. Data from both terminal branches demonstrate that the maximum rate of reverse sap flux tended to occur at around 06:00 hrs, just before dawn.

The cumulative amount of water taken up by the branch, which had a leaf area of 0.66 m^2, ranged from 2.3 to 12.0 g over the 8 nights of measurement in 2016, with a mean of 4.9 g +/- 1.0 standard error (Fig. S4.4). On one of the nights >55 mm of rain fell between 20:00 and 21:00 and over the course of the whole night the total amount of water taken up by the branch was 12.6 g, or 19.1 g per m^{-2} one-sided leaf area. The water taken up accounted for between 45 and 120 minutes of early morning transpiration, as determined from the time interval between the transition from negative to positive sap flux (Fig. 4.4) to the point where the water gained equalled water transpired.

Leaf conductance to foliar water uptake, k_{fu}

The mean +/- standard error k_{fu} for all genera, derived from the lamina rehydration experiment, was 2.24 +/- 0.28 mg m^{-2} s^{-1} MPa^{-1} (Fig. S2.1), which is of a similar magnitude to the values reported by Guzman-Delgado et al. (2018): 1.5 mg m^{-2} s^{-1} MPa^{-1} in *Prunus dulcis,* and 0.38 mg m^{-2} s^{-1} MPa^{-1} in *Quercus lobata*.

Canopy foliar water uptake

The median value for yearly canopy-scale foliar water uptake was 102.85 mm yr^{-1} with an interquartile range (IR) of 43.01 to 191.69 mm yr^{-1} (Fig. 7). This corresponds to a median contribution of 8.2 % of the annual transpiration budget with an IR of 3.4 to 15.3 %. Using the data from Fisher et al. (2007) on transpiration (E) and the value for gross primary productivity (GPP), from the same site, a plot-level value of water use efficiency (WUE) was calculated (GPP/E = WUE) in order to estimate a site-based carbon-gain value consistent with the amount of extra water taken up via FU at canopy scale. The median value for FU-dependent carbon uptake was 2.5 t ha^{-1} yr^{-1} (~8% of GPP) with an IR of 1.1 to 4.7 t ha^{-1} yr^{-1} (~4-16% of GPP).

Discussion

The results from the multiple experiments presented here consistently demonstrate that foliar water uptake (FU) occurred in all six hyper-dominant genera that were studied, and provide the first evidence that FU may be a common strategy among the dominant tree species of Amazonian rainforests. Combining these multi-taxa leaf hydraulics data from two years of wet and dry seasons with 14 years of meteorological data, and 1 full year of canopy profile leaf wetness measurements we estimate that the total FU-related water uptake by the canopy could account for a median value of 8.2 % (103 mm yr^{-1}) of annual transpiration and a potential contingent carbon assimilation of 2.5 t ha^{-1} yr^{-1} (~8% of GPP).

There are many uncertainties regarding how FU affects stand scale carbon and water dynamics, but in our simple model we offer a first estimate of what may be a globally significant flux. The impact of FU will vary depending on climatic conditions. It seems likely that in some years, conditions that favour dew formation in the dry season, e.g., comparatively high humidity and large diurnal temperature changes, will result in a substantial input of FU water together with a contingent carbon flux, and in other years perhaps the quantitative role of FU will be negligible. However, we will not be able to make a better-constrained assessment of this impact until we have an improved understanding of the relevant variables.

Significance and limitations of predawn WP measurements

Our data also demonstrate that predawn water potential in these species routinely overestimates the water status of the soil and particularly in the dry season (Fig. 4, 5, and 6). Measuring the soil water potential that plants are experiencing is challenging because of the uncertainty about rooting depth, and this uncertainty extends to the maximum theoretical water potential (Ψ_{t_max}) of the leaves. Our measurements of soil water content integrate the depths 0 to 2.5 m which should account for 99.99 % of the cumulative root fraction (Galbraith, Jackson *et al.*, 1996). However, this does not rule out the possibility that very deep roots are accessing wetter soil layers. Nevertheless, our analysis shows that even if the soil were saturated, i.e., Ψ_{soil} = 0 MPa, many of the predawn water potential values are still above the maximum theoretical value due to height alone (Fig. 4 and 5). Therefore, the results unambiguously demonstrate that foliar uptake elevates leaf water status above the highest value that could be achieved from the uptake of soil water alone in these Amazonian tree species. Assuming that our analysis of soil water potential represents plant-available water, then our results show that the effect of FU is far more substantial in the dry season (Fig. 6), meaning that small quantities of water moving directly into the leaves at regular intervals (often daily from dew) may sustain large upper-canopy trees throughout periods of low water availability. Calculations of the upper limit of leaf water potential can thus be modified to $\Psi_{t\_max} = \Psi_{soil} - \rho g h + \Delta\Psi_{FU}$, where $\Delta\Psi_{FU} = dt\, F_{FU} / C_{leaf}$, and F_{FU} is the flux into the leaf via FU; dt is the duration over which the flux occurs and C_{leaf} is the hydraulic capacitance of the leaf. This equation relates to the relationship set out in Simonin et al. (2009) describing a modified version of the soil-plant-atmosphere-continuum model which includes parameters for foliar water uptake.

The relevance of foliar uptake to drought sensitivity

The transpiration of water stored in the terminal branches (as observed in the sap flux data Fig S4.3 – 4.5) suggests a partial decoupling of canopy processes from soil water and functional stem xylem. This increases the potential for hydraulic recovery following drought periods, and suggests that hydraulic capacitance and water storage in the canopy could be fundamental traits in determining the ability of these species to cope with drought conditions. Furthermore, we suggest that our data change how predawn water potential measurements should be understood. Predawn leaf water potentials are not representative of whole-plant water stress, or soil water potential in these species (Fig. 4, 5 and 6), as tissue water potential is also determined by the duration of leaf wetness, lamina conductance to water (k_{fu}), the hydraulic conductance upstream of the leaf, and the capacitance and water storage of the rest of the plant.

The extent to which FU is purely a physical process, of water moving through a permeable barrier down a water potential gradient, versus being a trait which has been subject to selection pressure and thus given rise to physiological adaptations, is poorly understood. If the value of FU is as important as this study suggests it might be, then one would expect adaptations that increase the duration of leaf wetness, e.g., leaf surface morphology, or increase the rate at which water is taken up. The exact route by which water moves into the leaves of these genera is unknown, but studies on non-rainforest taxa have shown water uptake via trichomes (Fernandez *et al.*, 2014, Nguyen *et al.*, 2016), stomata (Burkhardt *et al.*, 2012, Eichert & Goldbach, 2008), directly through the cuticle (Eller *et al.*, 2013), and even adsorption onto the cuticle (Chamel *et al.*, 1991, Schönherr & Schmidt, 1979). Of the six genera in this study, only *Licania* has trichomes (on the abaxial leaf surface), suggesting that, instead, the cuticular pathway may be a more common means of water ingress amongst Amazonian taxa. This raises the possibility of a trade-off between traits favouring foliar water uptake and water loss, i.e. cuticular transpiration, due to cuticle permeability. If this trade-off exists, then future increases in vapour pressure deficit (VPD) may lead to a disproportionate rise in hydraulic vulnerability, because of both the loss of water inputs and the increase in water loss. Thus, whether or not the capacity for foliar uptake results in greater cuticular transpiration is a question of pressing importance in evaluating the sensitivity of Amazonian species to predicted future climates.

The potential impact of foliar uptake on carbon balance

The gross primary productivity at this site was calculated to be 30.94 t C ha^{-1} yr^{-1} (Fisher *et al.*, 2007). Thus, our median estimate of the possible contribution of FU to carbon gain, 2.5 t C ha^{-1} yr^{-1} equates to over 8 % of the gross primary productivity. This value is based on the potential photosynthesis afforded by the direct uptake of atmospheric water by leaves from all precipitation events throughout the year. However, we also found that dew could ‘pay’ for the first hour of transpiration (Fig S4.5), and this source of water, and its effects, are currently unaccounted for in the classical view of plant-atmosphere interactions. Whilst clearly a first estimate with a quantified but relatively wide uncertainty range, the potential impact of FU on water and carbon cycling in this region suggests the need for detailed further study of the effects of FU in lowland tropical rainforest.

Additionally, there may be indirect effects of FU on stand dynamics and ecosystem carbon storage due to the potential influence of FU on drought-induced tree mortality. Because the rate of FU is inversely proportional to leaf water potential (a more negative leaf water potential drives a higher flux), the gradient for water uptake increases in response to drought. This might mean that small precipitation events in the dry season, e.g. dew, are disproportionately important, ecophysiologically resulting in greater water uptake at a time that it is most needed. Indeed, this phenomenon may account for the surprisingly small hydraulic safety margin of many tree species globally (Choat *et al.*, 2012). Some of the modelled projections of future Amazonian climate predict increases in dry season length and strengthening of the seasonal cycle (Boisier *et al.*, 2015, Fu *et al.*, 2013, Jupp *et al.*, 2010), which could conceivably result in fewer minor precipitation events throughout the dry season. Moreover, higher temperatures are expected to cause elevated VPD in the future (Scheff & Frierson, 2014, Sherwood & Fu, 2014), reducing the likely frequency of dew formation. If many abundant forest tree species are dependent on small precipitation inputs for maintaining favourable water status and avoiding mortal hydraulic risk, such climate scenarios of reduced precipitation and high VPD could increase overall tree mortality risk purely through their impacts on FU-derived leaf water, with consequences for net carbon uptake and storage at large scale.

How can we more accurately quantify the contribution of FU to the forest water budget?

There are a number of challenges associated with getting accurate values of water uptake at the ecosystem-scale. Principally, these are obtaining a reliable mean for canopy k_{fu}, determining what proportion of the canopy is wet, and for how long. Relatively little is known about k_{fu} but it is likely to vary by canopy position, leaf side (Fernandez *et al.*, 2014), and species (Fig. S2.1 Eller *et al.*, 2016, Limm *et al.*, 2009). Canopy wetness has the potential to influence large-scale water uptake substantially because of the magnitude of variation over time and space. The study forest here, at Caxiuanã National Forest in the eastern Amazon has a leaf area index of approximately 5.5 m^2 m^{-2} (Fisher *et al.*, 2007) resulting in a maximum absorptive surface of 11 m^2 for every m^2 of ground surface if uptake occurs from both sides of the leaf, which may (Eller *et al.*, 2013) or may not (Fernandez *et al.*, 2014) be the case. These two factors might interact such that leaves that are wet for longer have higher rates of foliar uptake. Accordingly, future work must focus on quantifying these parameters.

The model we present lacks a feedback term. In reality, as the plant/canopy reaches saturation, the flux will decline. The factors that influence the rate of decline/saturation are the same that influence predawn water potential, namely, the hydraulic conductance of each part of the pathway, the capacitance and water storage capacity of the plant. Theoretically, if the conductance of the water away from the leaf is considerably higher than the conductance into the leaf, k_{fu}, and the capacitance is high, then the outcome will be something similar to our model. However, these parameters, particularly in the context of foliar uptake, and in tropical rain forests, are poorly known, so warrant further investigation.

Tropical rainforests present the additional challenge of high species diversity. Here we measured upper canopy trees as these account for a very high proportion of the total forest biomass and transpiration (Brum *et al.*, 2018). However, canopy wetness and k_{fu} may differ throughout the profile of the forest, and among species. In this study, we measured species from six different hyper-dominant genera, but unavoidable low species-level replication prevented us from accurately testing for inter-specific differences. In order to obtain a better-constrained value for the ecosystem-level impact of FU, the variance in FU across the forest, between individuals, species and canopy positions, must be quantified. The results of this study demonstrate that foliar water uptake is likely to be a common strategy across the Amazon, partially decoupling leaves from soil water conditions and allowing canopy water potential to be higher than is considered in classical and current soil-plant-atmosphere computational schemes. Our best estimates based on results from multiple independent measurement approaches suggest that water taken up directly into leaves may account for approximately 8 % of annual transpiration, with upper values potentially reaching 15 % (a value comparable to branch-level measurements by Gotsch et al. (2014)). Further, the uptake of dew during periods of substantial water shortage may be a critical mechanism allowing the trees to avoid potentially lethal hydraulic stress, and to maintain small but reliable supplies of water and carbon in the dry season. The carbon assimilation that is attributable to foliar water uptake is uncertain, but our first estimates suggest a range of 1.1 to 4.7 t C ha^{-1} yr^{-1} at our study site (4-16% of GPP). This could amount to a significant flux at the scale of the Amazon region which is potentially very sensitive to future changes in temperature and humidity. Foliar uptake of water may thus have a profound impact on the water and carbon cycles at small and large scales, and on the functioning and survival of Amazonian forest trees under future climate change.

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Tables

Table 1. Description of values and distributions used in the model to quantify the effects of canopy-scale foliar water uptake.

Variable	Distribution	Description
Ψ_{canopy}	Normal*, mean -0.89 MPa, SD 0.5	-0.89 MPa was the mean of the predawn and midday water potentials taken in dry season 2015 and wet season 2014. The range between predawn and midday water potentials were around 1 MPa in both seasons.
k	Uniform, range 0 to 3.8	A mean value for *k* (mg m^{-2} MPa^{-1} s^{-1}) was derived using the change in water potential from wetting experiments and capacitance measured from pressure-volume curves. The range of *K* represents the interquartile range, while the mean was 2.2 mg m^{-2} Mpa^{-1} s^{-1}.
L	Normal, mean 5.5, SD 1	Mean and range of leaf area index consistent with previous estimates. The value 5.5 is equivalent to 50% of the entire leaf surface area being wet, i.e., one side of all leaves being wet.
P_p	Normal*, mean 0.47, SD 0.05	The proportion of time leaves are wet. Value is a mean of the annual values taken from 15 years of meteorological data. Leaf wetness duration = $D_d + D_r + N\bar{D}_e$ where is D_d duration of dew events, D_r the duration of precipitation events, N the number of precipitation events, and $\bar{D}_e$ is the mean length of time for canopy drying following a rain event.

Normal* is a 'truncated normal' distribution, i.e., a normally distributed population of values from which impossible values have been removed e.g. values < 0 or > 1, as appropriate for a proportion. SD = standard deviation.

Figure Captions

Figure 1. Water potentials of detached leaves collected at midday before and after being exposed to experimental 'rain' for one hour. Water potential is significantly less negative in post-rain leaves ($P < 0.001$, one-tailed, paired Wilcoxon test).

Figure 2. The change in leaf water potential (Ψ) versus initial water potential of leaves which were separately exposed to: a) one hour of artificial rainfall; and b) 16 hours in a high humidity atmosphere (> 98 % RH) resulting in condensation on the leaves.

Figure 3. The water potential of leaves collected at midday and submerged in water for 3 minute intervals, with the petiole remaining out of the water (n = 72). The regression line shows a non-linear fit of the form $\Psi_{leaf} = \Psi_{initial}\, e^{-t/RC}$, where t is the rehydration time and RC is a fitted parameter equivalent to the time constant ($P < 0.001$, residual standard error = 0.4461). This equation is consistent with rehydration according to a charging capacitor (Brodribb & Holbrook, 2003) and assumes the final Ψ_{leaf} will tend towards 0 MPa; if the final Ψ_{leaf} is assumed to tend towards a non-zero negative value, the residual error is marginally smaller at 0.4284, $P < 0.001$.

Figure 4. The relationship between predawn leaf water potential ($\Psi_{predawn}$) and sample height. Data points in the white area are above the maximum theoretical Ψ values (Ψ_{t_max}) considering tree height only (and no soil moisture deficit). The points in the grey area are above the Ψ_{t_max} considering both tree height and soil water potential. Mean soil water potential at depths 0.5 and 1.0 m, at 05:00 hrs, over the course of the measurements, from 8 – 12/12/2016, was -2.19 MPa meaning that all of the leaf water potentials had less negative Ψ values (ie were 'wetter') than the soil to that depth. Symbols represent genera whereby the closed circles, squares and triangles are *Eschweilera, Licania* and *Swartzia*, respectively; and the open circles, squares and triangles are *Manilkara, Pouteria* and *Protium*, respectively. The genus-level replication is insufficient to determine if the difference between genera represented by closed and open symbols is significant. Each point represents a mean leaf water potential per tree from a minimum of 3

leaves per tree +/- standard error; one outlying point (*Pouteria*, 2.55 MPa) was removed for the sake of clarity, but was included in the calculation of the mean value.

Figure 5. Distribution of predawn leaf water potentials in the dry and wet season. All leaves were taken from a height of >15 m above the ground. All points above the dashed horizontal line (=25/99 points in total, 25% of all data) are higher (i.e. 'wetter') than the theoretical maximum possible leaf water potential, after accounting for the height of the leaves, and making the assumption that the soil water potential is always 0 MPa. Each point from which the box plots are derived represents the mean water potential of at least two leaves per tree per field campaign, dry season n = 60, wet season n = 39; one outlying point (*Pouteria*, 2.55 MPa) was removed for the sake of clarity.

Figure 6. The difference between mean leaf predawn and soil water potential ($\Psi_{predawn}$ - Ψ_{soil}). All points which are above 0, the horizontal dashed line, represent leaves with a water potential higher (less negative, or 'wetter') than the soil. The seasonal difference is significant at P < 0.001. Each point from which the box plots are derived represents the mean water potential of at least two leaves per tree per field campaign, dry season n = 38, wet season n = 43.

Figure 7. Probability distribution of the contribution of foliar water uptake to a) the total amount of water taken up annually by the forest canopy at Caxiuanã and b), the percent of annual transpiration. The bold vertical line indicates the median of the distribution of modelled outputs; the box indicates the first and third quartile; the lower whisker represents the lower range of the data while the upper whisker shows 1.5 times the interquartile range.

Foliar water uptake in Amazonian trees: evidence and consequences

Figures

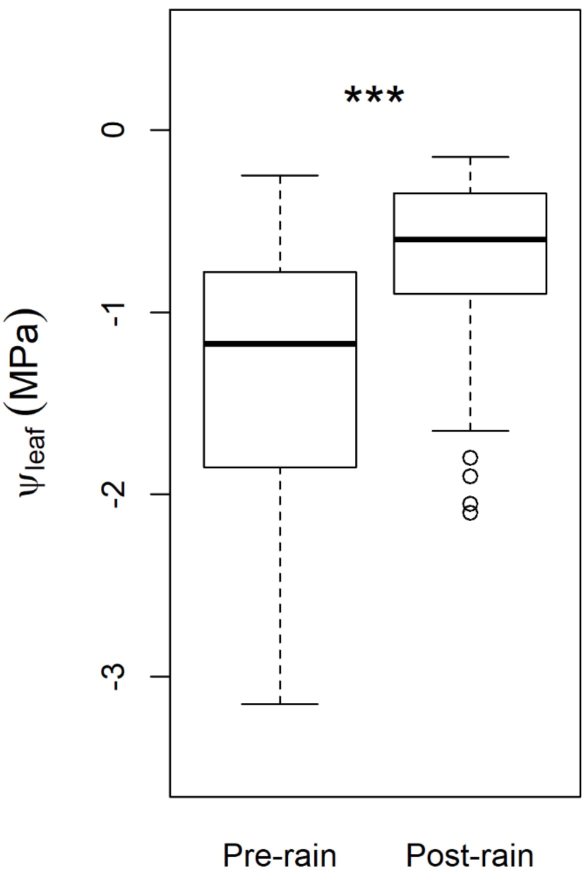
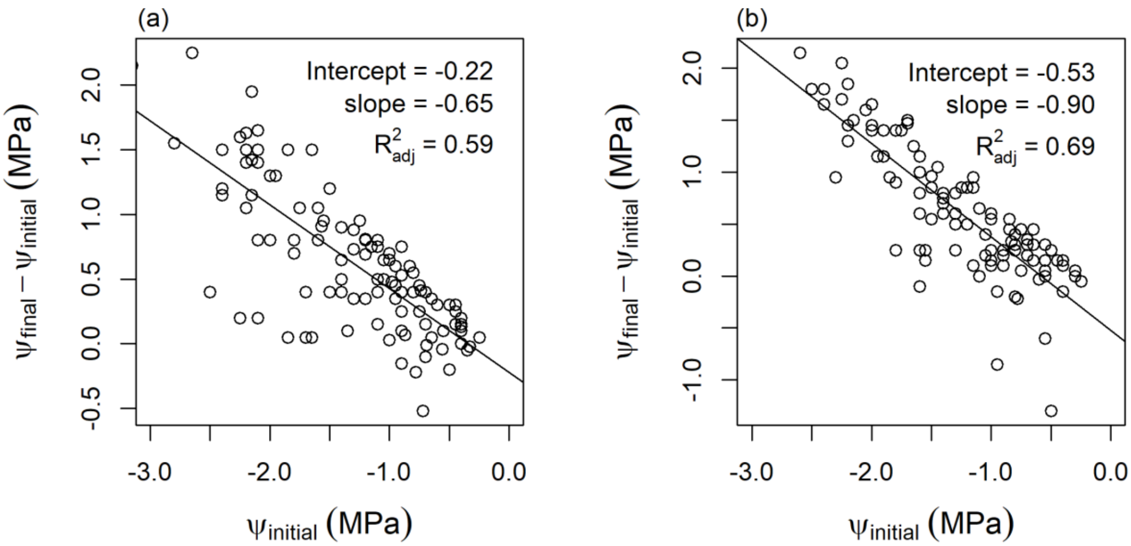


Figure 1. Water potentials of detached leaves collected at midday before and after being exposed to experimental ʹrainʹ for one hour. Water potential is significantly less negative in post-rain leaves ($P < 0.001$, one-tailed, paired Wilcoxon test).



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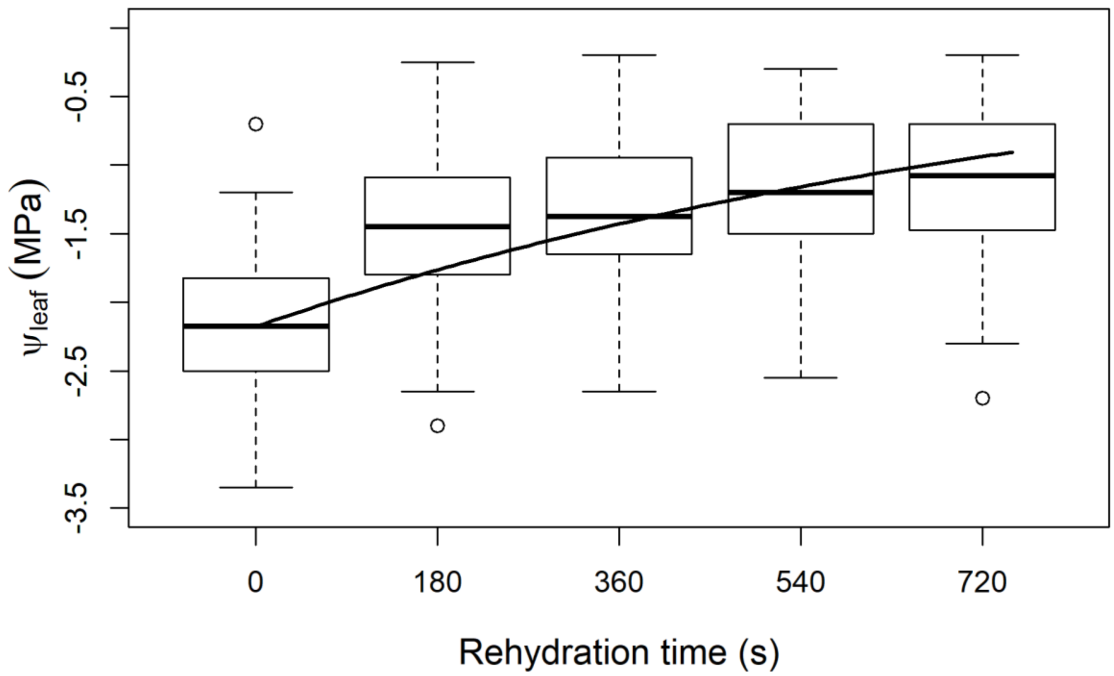

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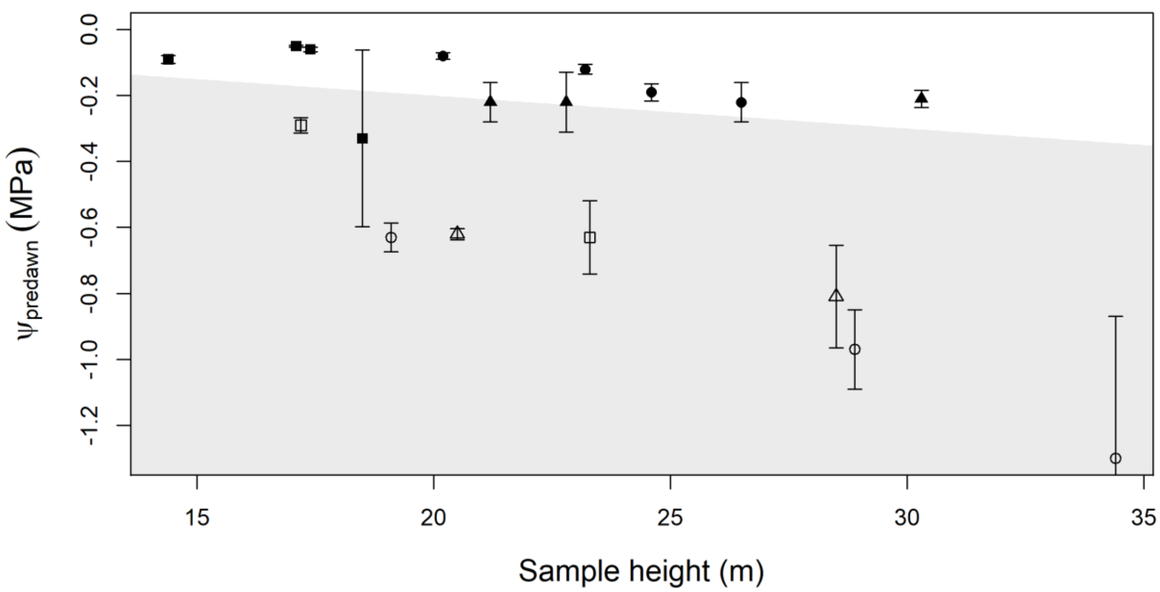

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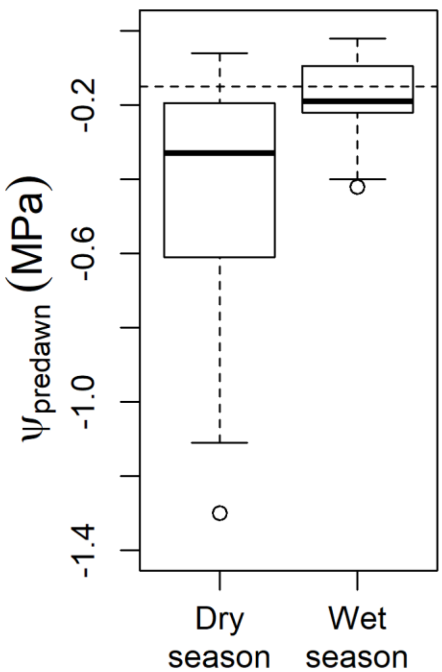

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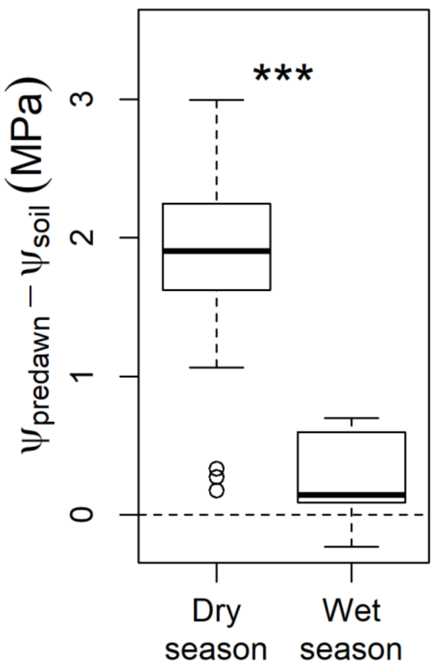

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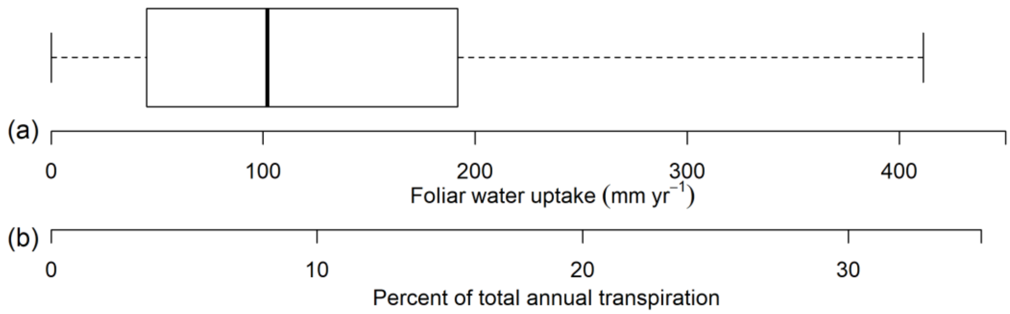

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