The impact of leaf anatomy and drought on foliar water uptake and whole-plant rehydration

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Abstract

Fog and low lying clouds can impact ecosystems through increases in water inputs, changes in microclimate and direct impacts on plant water cycling. The interception of cloud water by vegetation leads to an increase in precipitation inputs resulting in increases in soil moisture content. Fog also directly impacts evapotranspiration via a reduction in evaporative demand. The absorption of fog directly by leaf surfaces (i.e. foliar uptake) alters plant water relations via an increase in water storage or relaxation of the tension in the xylem. Foliar uptake may therefore be an essential water source to plants that are experiencing both extended periods of drought and periods of fog or cloud immersion. Foliar uptake capacity has been measured in a number of different species although variation in the degree of rehydration is substantial and the reason for such variation has not been investigated. To determine whether leaf anatomy affects variation in foliar uptake, I completed a comparative survey of 16 species of plants in 13 different families. I quantified foliar uptake capacity and measured cuticle thickness, mesophyll thickness, hydrenchyma thickness, and overall leaf thickness. All species demonstrated a capacity for foliar uptake. I observed a four-fold variation in foliar uptake capacity between species. I found a significant negative correlation between the capacity for foliar uptake and average leaf thickness. In contrast, foliar uptake capacity was not correlated with any other anatomical measures. I then performed a greenhouse experiment with *Jatropha curcas* to investigate whether foliar uptake capacity is affected by exposure to drought. Heat-ratio sap flow sensors, which detect reversals in the transpiration stream of plants, were placed on plants that underwent drought and well-watered conditions. Following a three or five-day period of drought, all plants were placed in experimental fog chambers for a 24-hour period to examine patterns of transpiration and foliar uptake. In addition, water potential and relative water content of leaves were measured before and after the fogging event. I concluded from this experiment that plants under drought stress take up more water through their leaves than well-watered plants. These results indicate that changes that occur to leaf cells during drought in *J. curcas* alter their ability to absorb fog water.
**Introduction**

Moisture from low lying clouds and fog play a critical role in both the water balance of plants and the hydrologic cycle of watersheds (Oberlander 1956, Dawson et al. 1998). Fog water input is particularly important in areas that experience fog during seasons when there is little precipitation (Dawson 1998, Johnstone and Dawson 2010, Bruijnzeel et al. 2011 Gotsch et al. 2014, Berry et al. 2014). For example, seasonal fog water inputs in the coastal redwood forests of California account for 34% of annual water input and occur primarily in the summer months when it is dry (Dawson 1998). In some habitats, fog water is the primary source of water to the ecosystem. In the Atacama Desert in Chile, semi-arid forests experience annual fog water inputs of approximately 200 mm, which is double the amount of annual rainfall (de-Val et al. 2006). In general, fog and low lying clouds have a significant effect on the total water input to cloud forest environments and can also allow plants to thrive when there is little precipitation (Dawson 1998, Berry and Smith 2013, Gotsch et al. 2014, Berry et al. 2014).

Fog immersion has been shown to reduce the evaporative demand on plants through a reduction of the vapor pressure deficit (VPD; Goldsmith et al. 2012, Gotsch et al. 2014). A high VPD results in high levels of transpiration while a low VPD, which is characteristic of fog events, reduces transpiration (Gotsch et al. 2014, Goldsmith et al. 2012). In a temperate montane cloud forest, Berry and Smith (2014) detected a 3 to 4-fold decrease in transpiration levels during cloud immersion for *Picea rubens* and *Abies fraseri*. In a tropical montane cloud forest in Veracruz Mexico, fog events also resulted in a decrease in VPD and a reduction in transpiration of >83% (Alvarado-Barrientos et al. 2014). Decreased VPD can relieve plants of dehydration resulting from transpiration.
Fog water interception may also affect water relations via the absorption of water directly into the leaves (Munné-Bosch et al. 1999, Martin and von Wilbert 2000, Burgess and Dawson 2004, Limm et al. 2009, Simonin et al. 2009, Gotsch et al. 2014, Berry and Smith 2014). This process has been described as foliar uptake, or FU. Plants that demonstrate the capacity for FU are able to recover water lost during transpiration events. Gotsch and colleagues (2014) determined that Quercus lanceifolia in central Veracruz, Mexico, was able to recover 9.3%, 24 L on average, of transpired water throughout the dry season. FU has also been observed to increase plant hydration enough in Sequoia sempervirens to compensate for the drought stress trees experience from the soil water deficit during experienced during the dry season (Simonin et al. 2009). Foliar uptake may therefore be vital to the survival of many plants in cloud forests (Burgess and Dawson 2004, Simonin et al. 2009, Breshears 2008, Limm et al. 2009, Goldsmith 2012, Berry et al. 2014, Gotsch et al. 2014).

Although foliar uptake has been observed to have drastic effects on the water balance of plants, little is known about the pathway for foliar uptake and how plants take advantage of it during periods of stress. One observed mechanism for foliar uptake is the diffusion of water through the cuticle of plants via specialized channels such as hydathodes or specialized trichomes (Benzing et al. 1978, Yates and Hutley 1995, Martin and von Willert 2000, Olivera et al. 2005). In the absence of specialized structures, water may still diffuse via the cuticle into the mesophyll and increase leaf water content (Yates and Hutley 1995). If cuticular reabsorption is possible, then more water should be absorbed into dehydrated, drought stressed leaves than into fully hydrated leaves (Breshears 2008). This would occur because the difference in water potential would be greater in the dehydrated
leaves than in the hydrated leaves causing more water to diffuse into the dehydrated leaf. This assumption coincides with the observations of Simonin and colleagues (2009) who observed *Sequoia sempervirens* saplings that were experiencing drought stress and nightly fog periods maintained a water potential above -0.07 MPa, while sapling that were not experiencing regular fog periods had water potential measurements that dropped below -1.1 MPa. Plants experiencing regular fog periods can compensate for the detrimental effects of drought, but how FU changes in drought stressed plants compared to well water plants is still unknown.

Recent studies that have examined the capacity for foliar uptake suggest that interspecific variation may be substantial. Goldsmith and colleagues (2012) observed a difference in foliar uptake capacity, measured by the improvement in water potential of 12 species found in the understory of Monteverde, Costa Rica. They found a difference of 0.67 MPa in montane species and 0.55 MPa in pre-montane species. Foliar uptake capacity has also been measured as the increase in leaf water content. In these studies the percent increase in leaf water content ranged from a <1% increase to an 11% increase (Limm et al. 2009). In the summer of 2014, our lab group studied the relationships between FU and functional traits in canopy species in the Tropical Montane Cloud Forests of Costa Rica. We found a negative relationship between overall leaf thickness and foliar uptake capacity (Gotsch *unpublished data*). While our results from Costa Rica provide evidence that leaf anatomy may play a role in the capacity for FU, we did not measure specific components of the cross-section of the leaf such as cuticle thickness. The cuticle is a protective structure that limits leaf water loss and may therefore limit foliar absorption as well (Reiderer and Schreiber 2001). Plants with thick cuticles maybe more resistant to drought stress but
foliar uptake may also be limited (Shepherd and Wynne Griffiths 2006). To fully understand the role of foliar uptake in plant water balance, an understanding of how plants benefit from FU during periods of drought and the influence of leaf anatomy on FU must be considered.

To explore the effects of drought and leaf anatomy on patterns of FU, I conducted a two-part study. The first part consisted of a comparative analysis of foliar uptake capacity and leaf anatomy for 16 species of plants outside the cloud forest ecosystem. The second part of my research project consisted of a manipulative experiment exploring the role of drought stress on patterns of foliar uptake when *Jatropha curcus*, a crop plant that is fast growing, demonstrates high levels of transpiration are placed in fog chambers. I hypothesized that thick leaves and specifically a thick cuticle would negatively impact the ability of leaves to reabsorb water. To determine how foliar uptake (FU) is affected by drought stress, I conducted a manipulative greenhouse experiment. I subjected plants to a series of drought periods and then placed plants in fog chambers. Transpiration and other water relations measures were determined before and after fogging. I predicted that drought stressed individuals would absorb more water through their leaves than plants experiencing well-watered conditions. I also predicted that FU and improvement in water potential would be greater in plants experiencing drought than in plants that were well-watered.

**Materials and Methods**

**Foliar Uptake Capacity**

Foliar uptake capacity (FUC) was determined for 16 species, 8 of which were taken from the collections module of the Plant Growth Facility at Franklin and Marshall College
(no grow lights, natural light cycles, temperatures ranging from 23-26°C, and a relative humidity at 60%) while the other 8 species were grown in a separate module (14-hour light cycle, temperature at 23°C, and relative humidity at 65%, Table 1). The different growing environments ensured that plants were in species-specific ideal growing conditions. For each species, three to four leaves were measured, one leaf per individual available.

Determination of FUC was accomplished through the following methods, which were similar to those described by Goldsmith and colleagues (2013). Branchlets of each sample were cut under water and then stored in water under black plastic overnight to ensure full rehydration. One leaf was removed from the fully hydrated sample, and an initial leaf water potential (WP) measurement was taken to ensure that rehydration was successful. Samples were then dehydrated by applying 60 seconds of 1.0 MPa of pressure to the leaf (Goldsmith et al. 2013). A paper towel was held to the exposed petiole or stem to remove water that was expelled from the cut surface. After dehydration, another water potential measurement was taken to determine post stress water potential. The exposed petiole or stem was wrapped in parafilm to prevent water from evaporating or entering the leaf through the petiole. Cuttings were then immediately submerged in water. After an hour of submersion, leaves were removed and dried thoroughly and a post-soak water potential was measured. Foliar uptake capacity (FUC) was calculated as the improvement in leaf water potential (WP) post submersion. All water potential measurements were obtained using a PMS Pressure Chamber (Model 1505D-EXP, PMS instrument Company, Albany, OR USA).

Anatomical leaf measurements

Leaves were hand-sectioned and stained using safranin dye to improve contrast. Leaf cross-sections were observed under 400x magnification on a Nikon Microscope.
(Alphaphot-2 YS2-H, Nikon instruments Inc, Melville, NY). The width of tissue layers was determined with an optical micrometer which was calibrated at 400x, 100x and 4x with a stage micrometer. Mesophyll thickness, cuticle thickness, hydrenchyma (water storage layer) thickness and overall leaf thickness were measured on the youngest mature leaf of one leaf per plant and three plants per species. Choosing the youngest mature leaf ensured that anatomical measurements were accurate because the cuticle would be fully developed and not degraded from weathering or age. The highest power magnification (400x) was used whenever the whole anatomical feature could be viewed at that magnification. For species that had thicker mesophyll (e.g. the succulents), lower powered magnifications were used.

**Fog experiment**

To determine the influence of drought on foliar fog water uptake, 24 individuals of *Jatropha curcus* were separated into either a drought treatment or a control group. All plants experienced a 14-hour light cycle from 600h to 2000h, 23°C, and a relative humidity of 65%. Plants in the drought treatment experienced three consecutive periods of water limitation (2 days, 4 days and another 4 days). After each drought period, plants were placed in the fog chambers for 24 hours. Following the fog treatment, drought plants were rehydrated with 1 L of water added to the soil twice within a 24 hour period prior to the subsequent round of drought. The control plants were well-watered throughout the period and were also placed in the fog chambers at the same time as the plants in the drought treatment. While inside the fog chambers, all plant soil containers were enclosed in two white plastic bags, which were sealed at the stem with parafilm to ensure that the fog water was not entering the leaves via the soil-root-leaf pathway. Soil moisture sensors were
placed in the soil of the potted plants to measure soil moisture content before and after
periods of fog. Water exclusion from the pots was successful because a paired samples t-
test indicated no significant difference between soil moisture content before and after
fogging periods ($t_4=-0.06 \ P=0.95$). The plants in the drought treatment were subjected to
three rounds of fog. Three periods of drought were used to determine if extended periods
of drought cause changes in foliar uptake. Round one of fog occurred on the third day of the
initial drought period, round two occurred on the fifth day of a second drought period and
round three occurred on the fifth day of a third drought period. Between fog events and
drought periods, plants had a recovery period consisting of 1L of water delivered to soil
over a 30-minute period at 1700h and 900h before they were subject to the next drought
period. The control group was watered with 1L of water delivered over 30 minutes, twice a
day (900h and 1700h) when they were not in the fog chamber. Plants in the control
entered the fog chambers on the same days as drought treatment plants. A leaf wetness
sensor (Decagon Devices, Pullman, Washington) was placed in fog chambers to record
when leaf wetness occurred. Temperature was measure by a air/soil temperature probe
(Decagon Devices, Pullman, Washington) inside the chamber. Temperature within the
chamber was greater that the temperature in the plant growth module by 1 to 3°C, which
would not likely have been high enough stress the plants.

*Water balance and stomatal conductance*

Leaf water potential and relative water content were measured on nine plants per
treatment before and after the plants were subjected to the fogging periods. Water
potential (WP) and relative water content (RWC) were measured on one leaf per plant
before and after individuals entered the fog chamber. In each round of drought, three
different plants in the two treatments were measured for WP and RWC before and after fogging. Different plants were measured in each round because the Jatropha were small and did not have enough leaves to measure WP and RWC before and after each round of fog.

**Sap Flow**

To characterize transpiration in *Jatropha curcas*, I measured sap flow using the heat ratio method, which allows bidirectional flow to be measured (Burgess et al. 2001). Sensors were constructed at Franklin and Marshall according to Clearwater et al. (2009). This method calls for a small heater constructed of a 47 Ω chip resistor, 3.2 mm long, 1.6 mm wide and 0.55 mm high (Kamaya RMC1/8K470FTP, Part no. 421-9034, RS Components, Auckland, New Zealand) with 0.2-mm-diameter enameled copper soldered at each end. The resistor was placed centrally in a custom-made silicon block. Two copper-constantan thermocouples, 0.13-mm-diameter single-stranded Teflon-insulated thermocouple wires (TFCC-005 and TFCP-005, Omega Engineering, Manchester, UK) were approximately placed 6 mm above and below the heater. Sap flow uses a heat tracer to measure transpiration. The heat pulse is produced by the flow of electricity through the resistor, which slows electrons and releases heat, and then dissipates into the xylem water of the shoot. The heat then moves up or down with the movement of the water in the xylem and the thermocouples measure the temperature above and below the resistor. The ratio of the temperature between the top thermocouple to the bottom thermocouple is stored by a datalogger (CR1000, Campbell Scientific Inc., Logan Utah, USA) every 10 minutes.

Sap flow sensors were attached to the stems by wrapping layers of parafilm around
the stem and the sensor, which ensured contact between the sensor and the stem and also prevent water from affecting the sensors. Sap flow sensors were placed on three individuals in each treatment. Heating elements and thermocouples were connected in series to a datalogger, that was attached to a 12V battery. The datalogger was used to run a program that sent a 6 sec heat pulse every 10 minutes to the heater. After a 2-minute period that allowed for thermal diffusion, the datalogger recorded thermocouple temperatures both upstream and downstream of the heater for 30 seconds. An average ratio was calculated for this 30-second period and this value was stored in the datalogger. A 6-second heat pulse was chosen as the appropriate pulse time to avoid excessive heating of the tissue next to the sensor. Data were periodically collected from the datalogger, and the ratio of temperature from the top thermocouple to the bottom thermocouple (\( \delta T_1/\delta T_2 \)), was screened for electrical errors common in sap flow systems. Negative values and peaks of data orders of magnitude greater or lesser than surrounding values are due to electrical noise and were manually removed from the dataset (Burgess et al. 2001). The dataset was then corrected for smaller errors resulting in variation in sensor construction (Burgess et al. 2001). Baseline values were often shifted slightly above or below one because the sensors are made by hand, which may cause some error in the ratio of \( \delta T_1/\delta T_2 \) recorded by the datalogger (Burgess et al. 2001). To adjust the baseline, a period of zero transpiration must be determined to evaluate the ratio output of the sensors. To evaluate each sensor, I compared the datalogger output during a time when transpiration should have been zero (nighttime, temperature was set to 15.5°C, and relative humidity to 60%). To ensure that there was zero transpiration, plants were covered with black plastic over night. There was no water on the leaves when the bags were removed in the morning.
which ensures that foliar uptake did not occur either. The average ratio during these periods was assumed to be representative of the “true zero” and the average ratio output from the datalogger was adjusted up or down based on the value of the “true zero”. This process is referred to as “met-zero-ing” and has been employed previously when severing xylem has not been a viable option to confirm sensor values during times with zero flow (Ambrose, Sillett & Dawson 2009, Ambrose et al. 2010, Gotsch et al. 2014). After initial corrections were made, heat pulse velocity, \( V_h \) (cm/hr), could then be determined from the following equation:

\[
V_h = \frac{k}{x} \ln \left( \frac{\delta T_1}{\delta T_2} \right)
\]

where \( x \) is the distance between the heater and the thermocouple (0.5 cm), \( \delta T_1 \) and \( \delta T_2 \) are the downstream and upstream temperature (°C), and \( k \) represents the thermal diffusivity constant \( 2.83 \times 10^{-3} \text{cm}^2 \text{sec}^{-1} \) (Clearwater et al. 2009, Goldsmith et al. 2013). Hourly averages were then calculated for each sample. Values were then averaged for individuals in each treatment. Sap flow velocity (cm/hr) was then determine by the following equation:

\[
V_s = \frac{V_h \ p_b (c_w + m_c c_s)}{p_s c_s}
\]

where \( p_b \) is the wood density, \( c_w \) is the specific heat capacity of the wood matrix (1200 Jkg\(^{-1}\) °C\(^{-1}\) at 20 °C), \( c_s \) is the specific heat capacity of water (4182 J kg\(^{-1}\) °C\(^{-1}\) at 20 °C), \( m_c \) is the water content of the xylem and \( p_s \) is the density of water (Burgess et al. 2001). Total foliar uptake was calculated as the total amount of water absorbed (mL) within each 24-hour period of fog. Data collected from the second round of fog were not used because the sap flow sensors became wet and stopped working.
Data Analysis

A Shapiro-Wilk test was used to test the normal distribution of all data used in statistical analyses. The anatomical leaf measurements did not have normal distributions and were transformed using the natural log prior to performing a statistical analysis. A linear regression was run between the mean species thickness for every anatomical feature measured and the transformed mean species FUC. An independent samples t-test was run between treatments for the improvement in water potential. Stomatal conductance was compared between treatments and before and after fogging events with a paired samples t-test. The improvement in RWC was compared between treatments with an independent samples t-test.

Results

Foliar Uptake Capacity and Leaf Anatomy

All 16 species had the capacity for foliar fog uptake (Figure 1). In general, the succulent species including the Kalanchoe disagremontiana (Mother of thousands), Kalanchoe pinnata (Cathedral bells), and Pepperomia sp (Peperomia) had lower foliar uptake capacities. However, the plant with the lowest foliar uptake capacity (0.14 MPa) was the Hedera canariesis variegate (Algerian ivy), which is not a succulent. Plants that had higher foliar uptake capacity were Viburnum pragense (Prague viburnum), Viburnum dentatum (Arrowood viburnum), and Hibiscus moscheutos (Hibiscus), which had the highest foliar uptake capacity (0.548 MPa). There was a four-fold difference in foliar uptake capacity between species.

I found a significant relationship between foliar uptake capacity and leaf thickness. (Figure 2, \( r^2=0.349, P=0.026, \text{s.e.}=0.06 \)). As leaves increased in thickness, the capacity for
foliar uptake decreased. I did not find a significant relationship between foliar uptake capacity and cuticle thickness, mesophyll thickness or hydrenchyma thickness.

*Sap flow*

During the period before the first round of fog, normal diurnal transpiration patterns were observed (Figure 3). Transpiration rates peaked at 1500h with a rate of 66.96 mL/hour (Figure 3a). Foliar uptake occurred at night during this period and was greater in the drought treatment (45.38 mL/hour at 2000h). During the drought period before the third round of fog, plants experienced similar diurnal patterns (Figure 3b). The maximum transpiration rates were as high as 28.64 mL/hour at 1900h for the drought treatment and 23.37 at 1500h for the control. Some foliar uptake did occur at night in absence of fog with maximum rates of 8.01 mL/hour at 2200h for the drought treatment and 15.5 mL/hour at 2100h for the control treatment.

During fogging periods, reverse sap flow was observed within an hour of being placed in the fog chambers (Figure 3). Leaf wetness occurred 20 to 40 minutes after entering the chambers. In the first round of fog, the average maximum foliar uptake rate was 95.47 mL/hour in the drought treatment and 41.29 mL/hour in the control treatment. In the third round of fog, FU uptake rates were lower with a maximum of 50.96 mL/hour in the control and 45.17 mL/hour in the drought. The total amount of water absorbed during the 24-hour fogging period was 368.46 mL for the drought treatment and 254.56 mL for the control treatment.

To quantify any changes in water status, leaf water potential was measured before and after plants were exposed to fog. After fogging, plants in the drought treatment experienced a significantly greater improvement in water potential when compared with
the control treatment (Figure 4, $t_{4} = -6.141$, $P = 0.004$). The drought treatment had an average water potential improvement of 0.032 MPa while the average improvement in water potential for the control was 0.004 MPa. This represents a seven-fold difference in water potential improvement between the treatment groups. I did not find a significant relationship for stomatal conductance between treatments before and after fog periods or in the improvement in the RWC between treatments.

**Discussion**

The purpose of this study was to determine whether the capacity for foliar uptake (FU) exists across a wide range of taxa outside the cloud forest ecosystem. In addition I explored whether drought affects the degree to which foliar uptake or FU is performed by plants. Here I present the first dataset that explores the variation in foliar uptake as a function of leaf anatomy in species from outside cloud forest habitats. In addition, my work builds upon other research that examines the role that drought has on foliar uptake (Limm et al. 2009).

*Foliar Uptake Variation*

I found that the capacity for FU is prevalent in species outside of the cloud forest ecosystem. While all species in this study were able to reabsorb foliar water, the degree of leaf water potential improvement in this study (0.33MPa) was lower than terrestrial species in the tropical montane cloud forest (0.67 MPa) but similar to values found in the canopy (0.22 MPa; Gotsch *unpublished data*). Variation in foliar uptake has also been observed in studies that have used leaf-water content to quantify foliar uptake capacity (Limm et al. 2009).

In this study, FUC was negatively correlated with overall leaf thickness but not with
the other leaf anatomy traits, such as mesophyll thickness, cuticle thickness and hydrenchyma thickness. This result means that the cuticle may not be a barrier for foliar uptake, as was previously hypothesized (Yates and Hutley 1995, Limm and Dawson 2010). This result was surprising since researchers have suggested a mechanism for foliar uptake via diffusion through the cuticle (Yates and Hutley 1995, Limm and Dawson 2010). Olivera and colleagues (2005) suggest that water uptake occurs through the pseudostem of *Vellozia flavicans*, which have specialized structure *velamen radicum* to absorb water from the air. Since the species I quantified for FUC do not have these specialized structures, foliar uptake is hypothesized to occur through the cuticle. If diffusion does occur through the cuticle, cuticle thickness would be expected to be correlated with foliar uptake capacity.

I propose two possible reasons why we did not find a significant relationship between cuticle thickness and FUC. One possible explanation is that the diffusion of water through the cuticle is not the main source of foliar uptake and that some other leaf features facilitate foliar uptake, such as stomatal density. However, this explanation may not be plausible since it has been shown that a film of water cannot enter the leaf through the stomata as a result of surface tension (Schönherr and Bukovac 1972). Another possibility is that the method to quantify foliar uptake capacity in this experiment is flawed and the pathway that water must take to be measured causes an error in the determination of FUC. For FUC to be measured, water must travel from the outside of the leaf, through the cellular matrix and into the vascular tissue (Lambers et al. 2008). Any water that moves into the hydrenchyma or mesophyll cells, instead of moving into the xylem would decrease the observable FUC. Such movement of water into non-xylem elements may underestimate foliar uptake in species that have adaptations to store water in the leaves. Regardless of the
potential errors associated with the method employed in my study, the data presented still indicate an ability for a wide range of plants to absorb water through their leaves. 

The importance of fog in the water balance of plants experiencing drought stress

The Jatropha experiencing drought absorbed 44% more water while immersed in fog than the control plants. In addition, the relative humidity was 70%, high enough for plants in the drought treatment to absorb water even prior to placement in the fog chambers, as relative humidity was higher during this period of the experiment than when we were calibrating the sensors. Drought plants demonstrated reverse flow rates that were twice those of the control plants the night before they were placed in the fog chamber. The reverse flow rates as well as the difference observed in water absorption were likely the result of a greater difference in the leaf-to-air vapor pressure deficit (VPD) in the plants experiencing drought. These findings are consistent with those of Limm and colleagues (2009) who suggest that foliar uptake will increase as a result of an increase in the driving force for the process, the leaf-to-air VPD. The significant 7-fold difference between treatments in the improvement of water potential also demonstrates that foliar uptake improves water status following drought. These results indicate a substantial decrease in drought stress resulting from the 24-hour period of fog.

While a number of studies have addressed the impact of soil water deficit on foliar uptake, results have been inconsistent (Burgess and Dawson 2004, Breshears 2008, Limm et al. 2009). A decrease in foliar uptake was observed in Sequoia sempervirens during severe drought due to the contraction of the epidermis and cuticle from leaf dehydration (Burgess and Dawson 2004, Limm et al. 2009). Breshears (2008) found improvements in WP of 1.0 MPa from foliar uptake in Juniperus sp. that were experiencing an increase in soil
water deficit. The aforementioned study examines species under high levels of water limitation (WP≤-2.1 MPa), which are generally found in drier climates. From these studies, the patterns of foliar uptake would seem to be determined by the plants’ response to drought in general. In this experiment, Jatropha plants undergoing water limitation took advantage of fog and absorbed 50% more water than the control plants during the 24-hour fog period. In previous studies and in this experiment with Jatropha plants experiencing drought were able to use fog as a means of rehydration.

The reversal of midday transpiration occurred within an hour of plants entering the fog chamber. In central Veracruz, Mexico, there was a lag time ranging from four to ten hours during fog events and foliar uptake while a decreased lag time of a few hours is experienced during rain events (Gotsch et al. 2014). Gotsch and colleagues (2014) suggest that the lag time between the beginning of the fog event and the wetting up of the canopy of the *Quecus lanceifolia* causes the delay in foliar uptake to occur. Shorter lag times have been observed in plants with needle like leaves (Burgess and Dawson 2004). My results indicate the fog chamber environment allows for leaf wetness to occur quickly, within an hour of entering the chambers, as well as a short wetting up period that resulted in foliar uptake.

Future directions for this research should include an investigation into the pathway of water from the outside of the leaf to the vascular tissue to determine the specific pathway of absorbed water. In addition, the experimental component of my study should be expanded to determine how patterns of FU in different types of plants are affected by drought. A different method to evaluate foliar uptake capacity may also be needed in order to accurately assess the total water absorbed by the leaf.

**Conclusion**
The capacity for foliar uptake is a prevalent process amongst species that are not in cloud forest ecosystems. This suggested that foliar uptake might be a crucial mechanism for water absorption. Foliar uptake may be crucial to plants in areas that experience seasonal fog input during dry season condition. If drought periods are complemented with periods of fog, plants that are experiencing drought stress will be able to take better advantage of the intercepted fog water. The ability to recover more water during drought may result in the survival of plants in areas where increases in drought stress would otherwise result in plant death. For instance, in the tropical montane cloud forest, there has been a documented increase in the period of time without precipitation (Pounds et al. 1999, Pounds pers comm). However, this may not be detrimental to plant communities if they can recover large amounts of water during foggy periods.

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Works Cited


Table 1 Scientific and common names for plants used in this study

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<td>Succulent</td>
<td>Cathedral bells</td>
</tr>
<tr>
<td>Crassulaceae</td>
<td>Sedum sp</td>
<td>Succulent</td>
<td>Sedum</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Jatropha curcas</td>
<td>Crop</td>
<td>Jatropha</td>
</tr>
<tr>
<td>Hydrangeaceae</td>
<td>Hydrangea macrophylla</td>
<td>Temperate shrub</td>
<td>Hydrangea</td>
</tr>
<tr>
<td>Malvaceae</td>
<td>Hibiscus moscheutos</td>
<td>Temperate shrub</td>
<td>Hibiscus</td>
</tr>
<tr>
<td>Piperaceae</td>
<td>Pepperomia sp</td>
<td>Succulent</td>
<td>Peperomia</td>
</tr>
<tr>
<td>Salicaceae</td>
<td>Salix caprea</td>
<td>Temperate shrub</td>
<td>French pussy willow</td>
</tr>
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Figure 1. Foliar uptake capacity (MPa, ± 1 s.d.) of 16 different species. Foliar uptake capacity was measured as the improvement in water potential following dehydration and 60 minutes of leaf submersion.
Figure 2. Foliar uptake capacity (MPa, n=16) as a function of overall leaf thickness (mm). Foliar uptake capacity was measured as the improvement in WP. Overall leaf thickness was measured using an optical micrometer calibrated with a stage micrometer.
Figure 3A and B. Volumetric sap flow through stems during the first round of fog (A) and the third round of fog (B). Dashed lines and blue boxes indicate periods of fog. Plants were subjected to a 14-hour light cycle with light period from 600h to 2000h (grey boxes).
Figure 4A and B. Total water absorbed by each treatment during 24 hours of fog (A) and the improvement in WP (± 1 s.d., n=3) observed before and after fogging Periods of fog (B). Total water absorbed was calculated as an average of the total water absorbed in the first round of fog and the third round of fog. Say that they were similar which is why they were averaged. * p≤0.05