Chapter I: Late Summer Fog Use in the Drought Deciduous Shrub, *Artemisia californica* (Asteraceae)

ABSTRACT

Coastal fog affects many California plant species and can be critically important to species that experience periodic drought. Drought-deciduous species in particular rely on water availability to maintain their leaves during the summer. To determine fog water use in drought-deciduous plants, this study manipulated access to fog drip and measured the water relations of the common shrub, *Artemisia californica*, near Santa Barbara, CA. Measuring the stable isotope ratio of hydrogen and oxygen, this study found that *A. californica* uses fog water in the late summer months when fog is present. This additional water increased plant water content but had no effect on pre-dawn xylem pressure potential. While climatic variability inhibits reliable fog input to *A. californica* in Santa Barbara, this species can use fog water opportunistically and benefits from large fog events during the summer drought.

INTRODUCTION

In arid ecosystems, water is often the most limiting factor for plant survival and growth. This water generally comes in the form of rainfall; however, in coastal regions fog water can act as a strong influence on plants (Klemm et al. 2012). Fog provides a significant amount of water to plants in regions as distinct as the Atacama Desert of Chile (Cereceda et al. 1999) and Coastal Redwoods of California (Limm et al. 2009). Ecological studies of fog have explored the response of many plant types to fog water inputs (Corbin et al. 2005, Fischer et al. 2009, Limm et al. 2009, Berry and Smith 2012, Vasey et al. 2012, West et al. 2012). However, research has largely ignored drought-deciduous species, whose leaf phenology responds directly to seasonal water availability. Drought-deciduous plants drop their leaves during seasonal periods of drought as a means of conserving water (Harrison et al. 1971). In coastal California, fog tends to occur in the summer months during peak drought (Williams 2009). This additional water could provide significant physiological benefits for drought-deciduous shrubs along the California coast.

The most common drought-deciduous species along the California coast is *Artemisia californica* Less. (Harrison et al. 1971). This shrub species has high transpiration rates due to weak stomatal control and a thin cuticle (Harrison et al. 1971, Poole and Miller 1975). During periods of summer drought, *A. californica* will shed leaves as a means of reducing water loss. Previous research suggests that the rooting systems of *A. californica* are shallow compared to evergreen species that grow in the same environment (O'Leary 1990). This enables *A. californica* to respond rapidly to rainfall events but also reduces drought tolerance (Poole and Miller 1975). Considering the weak transpirational control and shallow rooting system of *A. californica*, the acquisition of late summer fog could provide significant physiological benefits if the plants are capable of taking up the fog water.

Fog can affect the water budget of *A. californica* through foliar uptake or through fog drip. Fog drip occurs when water vapor from a low-lying cloud condenses on plant material and then drips into the soil where it can be taken up by the roots. Foliar uptake, or the absorption of water into the plant directly through the leaves, can also provide some physiological benefits (Limm et al. 2009), but appears to be short-lived and has yet to be effectively quantified. As *A. californica* is drought-deciduous in the late summer, foliar uptake is unlikely to affect the shrub as there are few leaves for water to enter. However, the shallow rooting system of *A. californica* may allow this species to take advantage of fog drip that collects in the top layer of soil. In this study, we address the question: Can *Artemisia californica* access fog water and if so, does it affect plant water relations? We used the natural abundances of stable isotopes of water extracted from the xylem of the shrubs before and after fog events to evaluate whether plants could take up fog. Simultaneously, we experimentally excluded fog drip from one set of shrubs using careful placement of tarps. We hypothesized that *A. californica* shrubs exposed to fog drip would experience an increase in their water content and water potential compared to plants from which fog drip was excluded.

METHODS

Study Site

This study was conducted at Coal Oil Point Reserve (COPR), a part of the University of California Natural Reserve System, located approximately two miles west of the University of California Santa Barbara campus in Santa Barbara County, California (34 24'N, 119 52'W). Mean precipitation is 441±8 mm of rain per year with rainfall typically occurring between October and May. Mean temperatures fall between 6°C in January to 24°C in August (UCNRS 2014). This study took place from May to October in 2011 and August to September in 2012. Precipitation data were obtained from the COPR meteorological station (Roberts et al. 2010). Precipitation during the 2010–2011 rain year was higher than average (654 mm of rain), whereas 2012 was a drier year than average (282 mm of rain). Fog was quantified using fog collectors modified from a previous design (Fischer and Still 2007). This study took place in an area with interspersed patches of California sage scrub and grassland. The soil is Concepcion fine sandy loam with intrusions of clay.

Field Sampling

To quantify the effects of fog drip, fog water was excluded from the soil below shrub canopies using plastic tarps in the summers of 2011 and 2012. Fog drip exclusion was done in a manner similar to the precipitation exclusion experiments described in Breshears et al. (2008). In 2011, six adjacent A. californica shrubs were treated by placing tarps from the base of the stems to several feet beyond the edge of the canopies. The tarps were sealed together with waterproof adhesive tape to form a large rectangular matted area below the six treatment shrubs. The large tarps were removed prior to the first fall rain event in another six adjacent shrubs were left without tarp as control plants. We measured xylem pressure potential (XPP) and plant water content (WC) for each individual shrub. Xylem pressure potential measurements were taken before dawn, between 3:00 and 4:00 a.m. (pre-dawn) and between 1:00 and 3:00 p.m. the next day (midday) on each sampling date. Stem samples were bagged, placed in a cooler and within the hour, measured for XPP in the lab using a Scholander-type pressure chamber (Model 1000, PMS Instrument Comp., Corvallis, OR). Midday XPP stem samples were weighed prior to the XPP measurement and subsequently placed in a drying oven for 48 hours at 80°C. Plant water content was calculated as the water weight divided by the dry weight of the plant tissue. WC samples averaged 2.1 g dry weight (60.58 g). Data was collected monthly from May through October, for a total of six sampling dates.

In 2012, to avoid the problem of pseudoreplication, we selected eight treatment and eight control shrubs that were isolated (.5 m apart) and interspersed with one another in the same area. Tarps were laid underneath treatment shrubs from the stem base to several feet beyond the canopy. Measurements of all plants were taken every two weeks from August through September, for a total of five sampling dates. As in 2011, measurements included XPP and WC. All samples were collected at midday, between 1:00 and 3:00 p.m. At the end of the 2012 field season, 5 cm deep soil samples were taken from below both treatment and control A. californica plants. Cores were collected 5 cm from the base of the plant to measure gravimetric soil moisture content in the lab.

Only adult shrub individuals were selected for the experiment. All shrubs were 0.75–1 m in height and had a large canopy to withstand destructive sampling over a summer season.

Stable Isotopes

To track fog water into xylem tissue, we measured the stable isotopic ratios of hydrogen and oxygen (Dawson et al. 2010). In 2011, we collected water samples from rain, fog and groundwater to characterize the water sources available to A. californica. Each rain event was captured in a small Nalgene container at a location five miles east of the field site. Fog water was collected from a harp-string collector design modified from Fischer et al. (2007) every few weeks during the summer months. Rain and fog water were collected with a 2–3cm layer of mineral oil in the container to prevent evaporation. Ground water samples were taken from nearby wells established by the Cheadle Center for Biological and Ecological Restoration. All water samples were run through a cellulose filter to remove particulate matter before analysis on a Los Gatos Research Liquid Water Isotope Analyzer (Model LWIA-24EP) at the California Institute of Technology.

Multiple fog (44) and rain (19) samples from 2011–2013 were used to construct a local meteoric water line (LMWL). The LMWL for Coal Oil Point Reserve is $\delta D = 7.456\delta^{18}O + 6.4349$, $R^2 = 0.94$. The line differs from the global meteoric water line (Gat 1996); however, this is expected as the line includes water from fog and rain (Gonfiantini and Longinelli 1962). Plant water samples consisted of suberized stem tissue from several of the A. californica shrubs. Once a month in July, August, and September of 2011, plant tissue samples were collected midday in sealed scintillation vials and placed on ice until they were brought back to the lab freezer (-25°C).

Plant water samples were extracted using a cryogenic vacuum extraction line (Ehleringer et al. 2000) at UC Santa Barbara. These water samples were then shipped to the Stable Isotope Biogeochemistry Lab at UC Berkeley where they were analyzed on an Isotope Ratio Mass Spectrometer. Plant water samples were collected in 2012 but were not analyzed, as there was insufficient fog deposition during the summer of 2012.

We corrected all plant water samples for soil evaporation using the correction method developed by Corbin et al. (2005) in Northern California. Use of an evaporation correction is necessary for studies in semi-arid ecosystems, as the water used by plants has experienced evaporative fractionation prior to uptake. Plant samples were corrected back to the local meteoric water line for COPR. We then used a mixing model analysis with two isotopes and three sources (rain, groundwater and fog) for all plant water samples to determine the proportion of fog water used by plants (Phillips and Gregg 2001).

Analysis

Data were analyzed using JMP® Pro 11 (SAS Institute). We conducted a repeated measures analysis for plant water content and predawn XPP over time to compare the effects of the matting treatment within each year. For WC we used a residual error covariance structure as it had the lowest value for the AICc criteria, for five of the six sampling dates (excluding October). For XPP we used an AR(1) covariance structure as it had the lowest value for the AICc criteria. We used a one-way ANOVA to analyze the difference in soil moisture between treatment and control. Differences in fog proportion by date were compared with a pairwise Student's *t* test.

RESULTS

Fog and Rain Inputs

Quantities of rainfall and fog water collected were both greater during 2011 than 2012 (Fig. 1). In 2011, a total of 1693 ml of fog water was collected from 5/6/2011 through 10/25/2011, whereas only 188 ml was collected from 7/1/ 2012 through 9/27/2012. In 2012, fog data collection began two months later than in 2011; however, there was much less late summer fog in 2012. In 2011, total fog collected was more than nine times greater than that of 2012. The only rain event to occur during the treatment period was a 30 mm rain event on 6/6/2011. There was rain on 10/5/2011; however, the tarps had been removed just prior to this event.

The isotopic signature of fog water at Coal Oil Point Reserve was more enriched in the heavy isotopes of Hydrogen and Oxygen compared to both rain and groundwater (Fig. 2) as is typical of fog water in other ecosystems (Scholl et al. 2010). Rain and groundwater were not significantly different from one another.

Fog Water Isotope Analysis

The isotopic signature of A. californica stem water varied across the summer of 2011; it was initially depleted of heavy isotopes in the midsummer and became enriched in September. Both treatment and control plants experienced an increase in the proportion of fog water present in their stem tissue in September. There is a significant difference between September and both July and August (July: $p = 0.0093^*$, August: $p = 0.0008^*$) when treatment and control plants are combined (Fig. 3).

Plant Water Status

In 2011 the plant water content (WC) of both control and fog drip exclusion plants decreased during the summer, and increased after the first fall rain (Fig. 4). A small rain event on June 6th temporarily increased WC of both control and fog drip exclusion plants. A repeated measures analysis of WC for the five sampling dates between June and October found that there was a significant effect of time ($p < 0.0001$*) with WC generally decreasing throughout the dry season. The treatment effect alone was not significant ($p = 0.4258$), but there was an interaction effect of treatment*time ($p = 0.0004$*). In 2012 the difference in WC between treatment and control was non-significant ($p = 0.2786$) and there was no interaction effect with time ($p = 0.8677$).

The 2011 pre-dawn xylem pressure potential (XPP) of both groups decreased during the summer and increased after the first fall rain event (Fig. 5). A repeated measures analysis of XPP yielded a significant effect of time ($p < 0.0001$*) but no significant effect of treatment ($p = 0.597$). There was no significant interaction effect of the treatment over time ($p = 0.193$). For midday XPP, there was a significant effect of treatment ($p = 0.028$*) as the control plants had slightly higher water potential at each sampling date. This slight difference was observed from the beginning of the experiment as the difference between treatment and control values did not change over time ($p = 0.975$). This indicates that the difference observed was an artifact of the individual plants selected for the experiment, not an effect of the treatment. In 2012 there was no effect of treatment ($p = 0.902$) or treatment over time ($p = 0.340$).

The soil moisture beneath the fog drip exclusion and control plants was significantly different at the end of the 2012 treatment ($p = 0.011$*), with the fog drip exclusion plants having an average soil moisture of 4.66% (±0.66%) and the control plants an average 4.08% (±0.56%).

DISCUSSION

The results presented here support the hypothesis that Artemisia californica uses fog water in the late summer. This additional water appears to increase plant water content for individual A. californica shrubs.

A significant fog event (128 ml over four days) before the September sampling date likely caused the observed difference in WC in September of 2011 (Fig. 4). No rain occurred from August to September, further supporting the idea that the increase in WC of control plants was due to the large fog event that occurred in early September (Fig. 1). While control and treatment plants differed in their WC, the water isotopes in their stem tissue both reflected a higher proportion of fog water in September of 2011 (Fig. 3). This suggests that the treatment plants, despite the attempted exclusion of fog drip, were incorporating fog water into their stem tissue betweenAugust and September of 2011. This presence of fog water in treatment plants, if not through root uptake, may be due to foliar uptake. Foliar uptake of fog has been found in numerous plant species, including California shrub species (Limm et al. 2009). If this is the case, foliar uptake of fog was not enough to alter WC in the treatment plants, but was detected in the water isotopes of all shrubs. For control plants, root access to fog water may have increased WC in September, but it had little effect on the pre-dawn XPP (Fig. 5). These results suggest that although A. californica could acquire fog through multiple mechanisms, root uptake of fog drip can improve the water budget of this drought-deciduous shrub during periods of significant fog deposition.

The similarity in pre-dawn XPP between control and treatment plants may be explained by a difference in soil water content below the tarps. The soil moisture data from 2012 suggests that the tarps had the unintentional effect of reducing soil evaporation, as the control plants had significantly lower soil moisture than the treatment plants. In 2011, this would explain thelack of difference between the XPP of the treatment and control individuals (Fig. 5). If reduction in soil water evaporation increased the amount of water available to treatment plants, it could result in no observable difference in pre-dawn XPP. Alternatively, by the late summer both treatment and control plants may no longer have the ability to effectively conduct water. The late summer XPP observed in this study is similar to the values observed in Jacobson et al. (2007) where there was 75% loss of hydraulic conductivity in A. californica during the dry season. It is possible that although A. californica can take up fog water, hydraulic conductivity is too low to alter pre-dawn water potential inside stems.

Overall, this study provides the first evidence of fog water use by a drought-deciduous shrub, and attempts to understand the importance of fog drip during the seasonal drought period in coastal southern California. Dropping leaves in the summer is costly for plants and is likely triggered by water availability (Harrison et al. 1971). Fog inputs could prolong leaf lifespan and enablegreater carbon assimilation for species such as A. californica. Our results suggest that fog increases A. californica water content through roots and possibly foliar uptake. However, the effects of fog appear to be temporary and do not provide a consistent summer water resource for coastal California’s drought-deciduous shrub species.

The interannual variability of fog deposition observed in this study (Fig. 1) is consistent with long-term cloud records (Williams 2009). In coastal California regions with consistent and large quantities of fog deposition, fog can contribute greatly to plant water relations (Burgess and Dawson 2004, Fischer et al. 2009, Vasey et al. 2012). Plant species in the Santa Barbara region are unlikely to depend on summer fog as a water source, though some may opportunistically use fog water during the summer drought. With predictions of a warmer climate in California (Cayan et al. 2008), the results from this study may provide a window into future climate-plant interactions for more northern shrub-dominated ecosystems along the California coast.

ACKNOWLEDGMENTS

We thank the University of California Natural Reserve System for access to Coal Oil Point Reserve. Funding is thanks to the University of California, Santa Barbara Undergraduate Research and Creative Activities Grant, the Worster Award and C. H. Muller Award. Thank you to Dr. Alex Session's lab at the California Institute of Technology, Dr. Chris Still, and University of California, Santa Barbara's D'Antonio Lab and the Life Science Biology Workshop for their support.

TABLES AND FIGURES

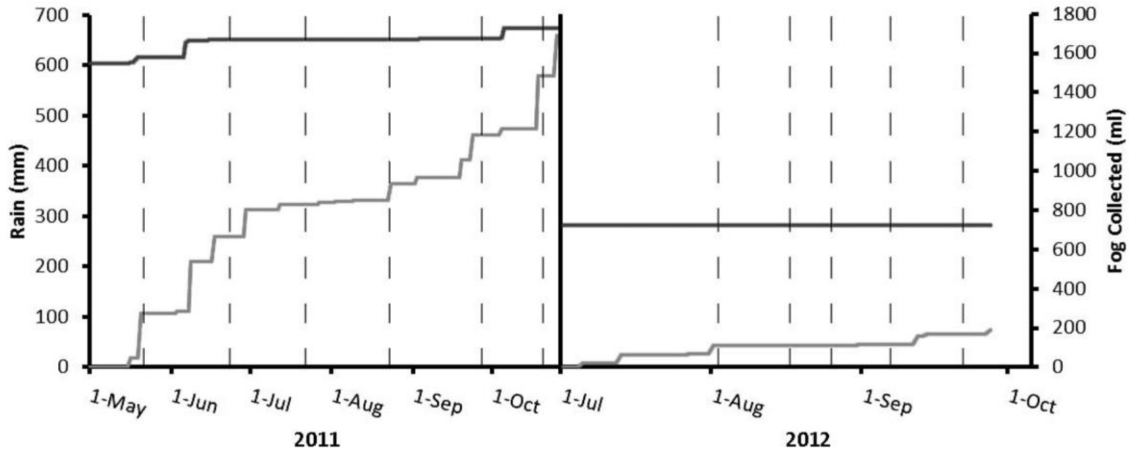

Figure 1. Rain and fog accumulation for 2011 and 2012. The dark gray line represents rain and the light gray line represents fog water. The vertical dashed lines represent the dates of vegetation sampling for each year.

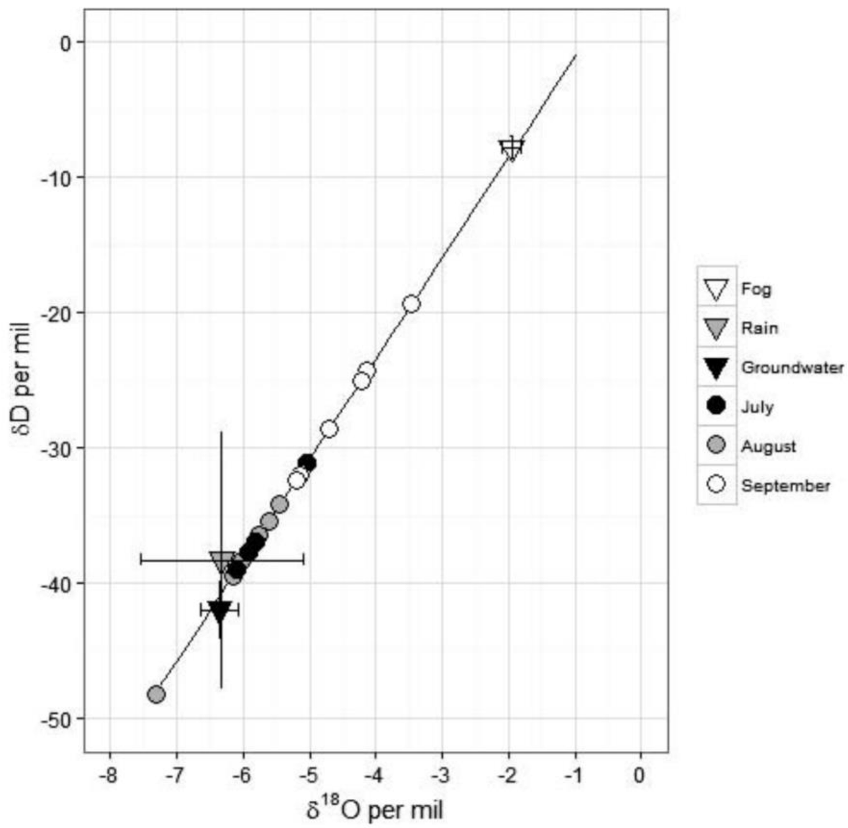

Figure 2. The isotopic signatures of water and *A. californica* stem tissue at Coal Oil Point Reserve. Fog is isotopically enriched in the hydrogen and oxygen isotopes (white triangle). Rain and groundwater are depleted (gray and black triangle, respectively). Plant water samples were corrected to the local meteoric water line (black line). Error bars are the standard error associated with source water isotopic values.

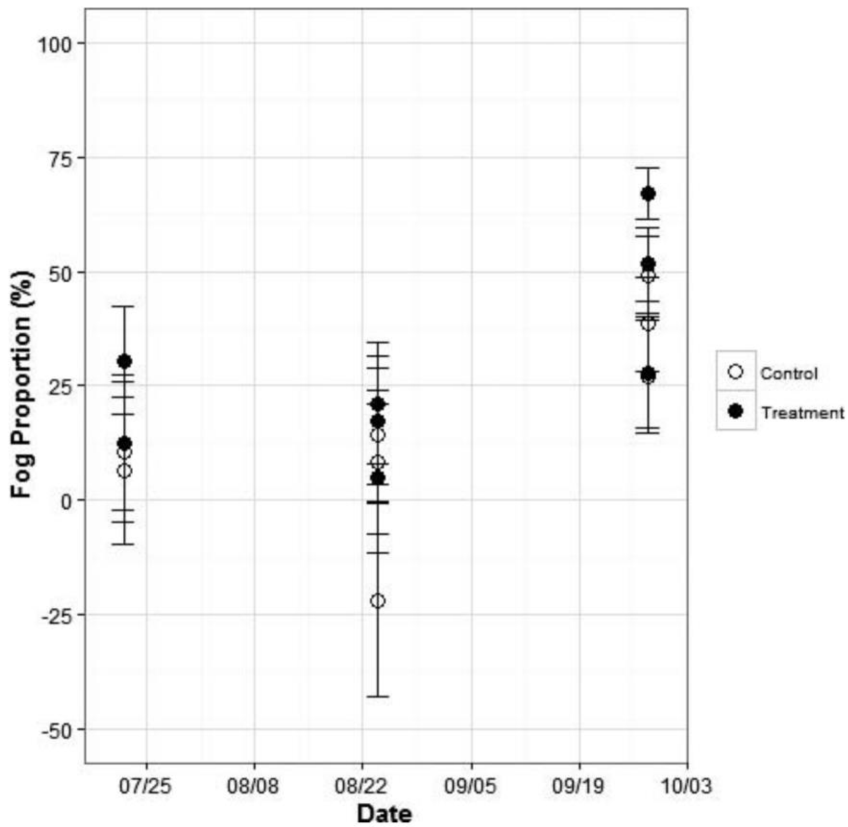

Figure 3. Phillips and Gregg's (2001) mixing model results for fog proportion in stem water for 2011. Both treatment and controls plants shifted towards fog in September. Each point with bars is an individual plant with the mean and standard error of fog proportion according to the model.

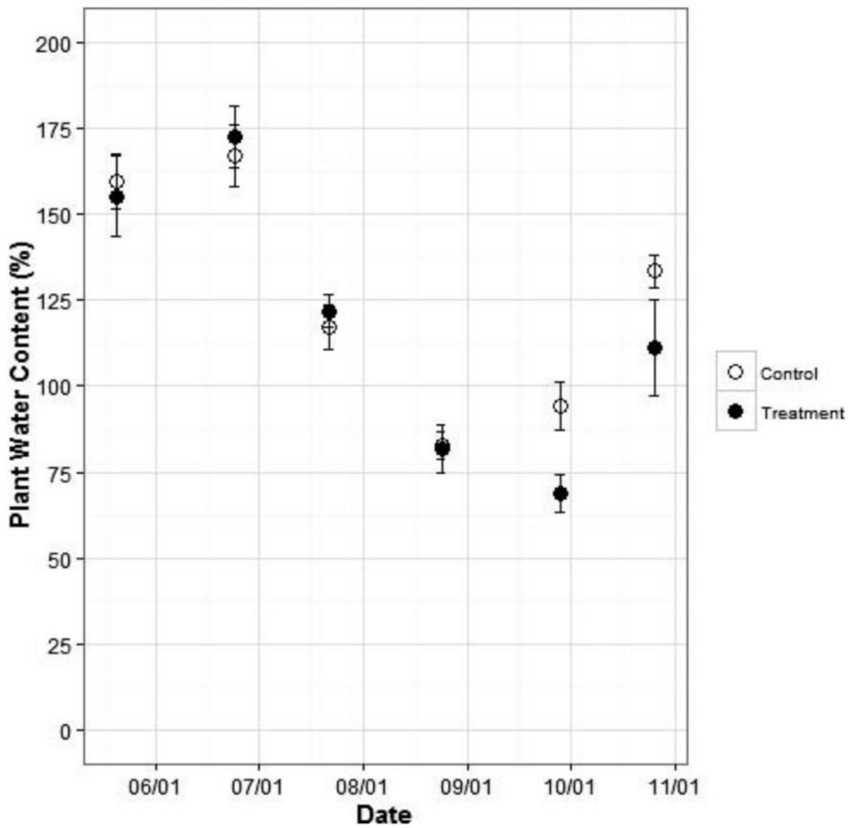

Figure 4. Plant water content (%) of *A. californica* during the 2011 summer sampling period. Error bars represent plus/minus one standard error.

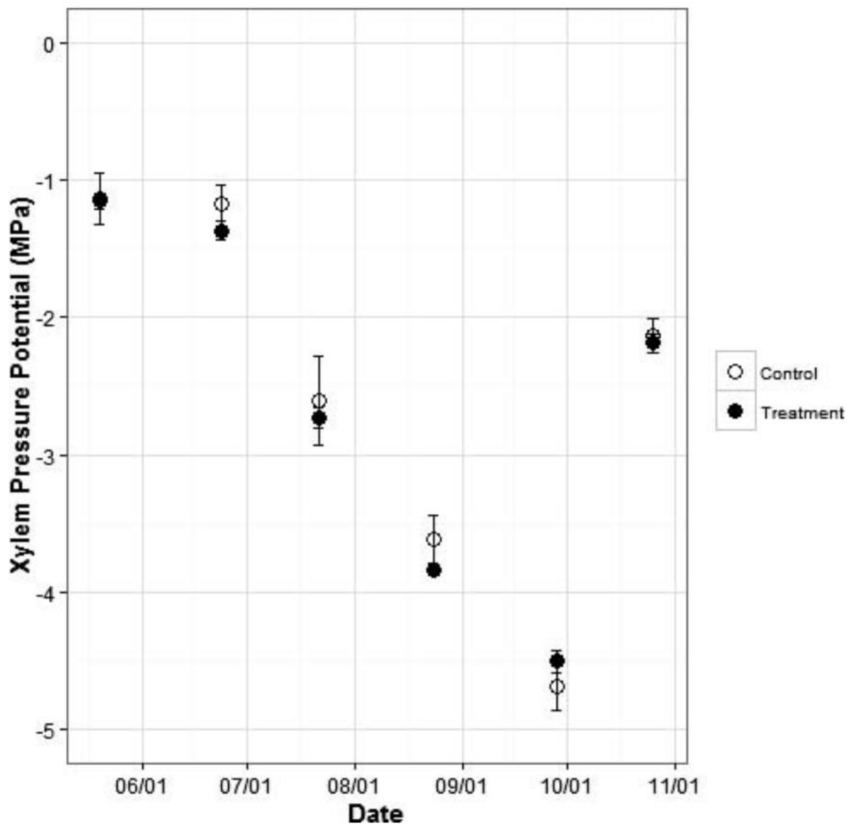

Figure 5. Pre-dawn xylem pressure potential of *A. californica* during the 2011 summer sampling period. Values represent means of the six plants per treatment. Error bars represent plus/minus one standard error.

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Chapter II: Foliar Uptake of Fog in Coastal California Shrub Species

ABSTRACT

Understanding plant water uptake is important in ecosystems that experience periodic drought. In many Mediterranean-type climates like coastal California, plants are subject to significant drought and wildfire disturbance. During the dry summer months, coastal shrub species are often exposed to leaf wetting from overnight fog events. This study sought to determine whether foliar uptake of fog occurs in shrub species and how this uptake affects physiology and fuel condition. In a controlled greenhouse experiment, dominant California shrub species were exposed to isotopically labeled fog water and plant responses were measured. Potted plants were covered at the base to prevent root uptake. The deuterium label was detected in the leaves of four out of five species and in the stems of two of the species. While there was a minimal effect of foliar water uptake on live fuel moisture, several species had lower xylem tension and greater photosynthetic rates after overnight fog treatments, especially *Salvia leucophylla*. Coastal fog may provide a moisture source for many species during the summer drought, but the utilization of this water source may vary based on foliar morphology, phenology and plant water balance. From this study, it appears that drought-deciduous species (*Artemisia californica* and *Salvia leucophylla*) benefit more from overnight fog events than evergreen species (*Adenostoma fasciculatum, Baccharis pilularis* and *Ceanothus megacarpus*). This differential response to fog exposure among California shrub species may affect species distributions and physiological tolerances under future climate scenarios.

INTRODUCTION

Our understanding of plant water uptake has shifted significantly in recent decades. Traditionally, plant physiologists have focused on passive root uptake as the primary means of water acquisition in plants. The Soil-Plant-Air Continuum (SPAC) framework has dominated the scientific discussion of plant-water movement for many years (Philip 1966). Despite early evidence of water uptake in leaves (Stone 1957), only relatively recently have researchers uncovered the physiological effects and ecological importance of foliar water uptake in plant species (Martin and von Willert 2000, Burgess and Dawson 2004, Breshears et al. 2008, Limm and Dawson 2009, Limm and Dawson 2010, Eller et al. 2013, Berry and Smith 2014, Gotsch et al. 2014). While the mechanism of foliar uptake is not well known, studies have shown uptake through the cuticle (Eller et al. 2013), leaf hydathodes (Martin and von Willert 2000) and stomata (Burkhardt et al. 2012). This uptake can improve water status (Gouvra and Grammatikopoulos 2003, Breshears et al. 2008, Limm et al. 2009, Berry and Smith 2014) and enhance plant survival under drought conditions (Eller et al. 2013). Foliar water uptake influences plant species in a number of ecosystems, and is particularly influential in plant communities with pronounced dry periods (Munné-Bosch 2010, Goldsmith 2013) and episodic leaf wetness (Burgess and Dawson 2004, Breshears et al. 2008, Ewing et al. 2009).

Mediterranean-type climate regions (MTC) are typified by cool, wet winters and hot, dry summers. In addition to seasonal drought, MTCs are influenced by coastal weather patterns. In coastal California, fog forms offshore and is advected onto land by a pressure differential between the coast and the interior of California (Filonczuk et al. 1995). In several coastal California plant communities, fog ameliorates drought stress (Corbin et al. 2005, Fischer et al. 2009, Carbone et al. 2013, Baguskas et al. 2014) and maintains soil water availability (Vasey et al. 2012). Fog events tend to occur overnight and dissipate by mid-morning, exposing plants to foliar wetting that potentially creates a reverse water potential gradient between the atmosphere and the inside of plant leaves. If water enters the leaves, it could improve plant water status.

For four of the five MTC regions, there are natural fire disturbance regimes that shape plant communities (Edwards 1984, Pausas and Vallejo 1999, Keely and Fotheringham 2001, Bradstock et al. 2002). These fire regimes are characterized by the seasonality, frequency, size, and intensity of fire disturbances within an ecosystem (Whelan 1995). While many climatic and biotic factors affect fire patterns, live fuel moisture, a measure of water content in live plant tissue, is important for ignitability, fire spread, intensity and fire size (Countryman and Dean 1979, Anderson 1982, Dennison and Moritz 2009). While spring rainfall influences LFM patterns in southern California (Dennison and Moritz 2009), it is unknown as to how foliar uptake of summer fog affects live fuel moisture. Foliar water uptake could decrease plant flammability and potentially alter fire patterns. Of the species known to demonstrate foliar water uptake, only 31% of them are from MTC regions and of those found in California, all have been discovered in the last ten years (Emery unpublished). There is a pressing need for understanding the influence of foliar water uptake on the water balance of species in coastal California shrublands, a region that experiences a warmer and drier climate than all other MTCs (Cody and Mooney 1978) and where fire is considered an important structuring force (Keeley and Fotheringham 2001, Franklin et al. 2005).

Previous studies of foliar uptake from around the world have measured water status and gas exchange the morning after a night of fog exposure (Cole 2005, Limm et al. 2009, Eller and Oliveira 2013, Berry and Smith 2014). Yet in many MTC regions overnight fog events are followed by dry, sunny conditions during the day. Additionally, multiple nights of fog inundation may be necessary to alleviate drought stress in MTC species. While the effects of multiple foggy nights have been explored previously (Simonin et al. 2009), few studies have examined MTC shrub species. This study sought to characterize the accumulation of fog effects on shrub species over several days and whether the influence of overnight foliar wetting lasts through mid-afternoon, when air temperatures peak.

In this study I address the following questions: (1) How do shrub species respond physiologically to overnight foliar wetting, and does this response differ based on foliar morphology and life history traits? (2) Which species demonstrate direct foliar uptake? And (3) How do plant responses change with several consecutive nights of fog exposure? To understand the physiological impacts of overnight fog and presence of foliar uptake, individual potted plants were exposed to artificial fog over the course of four sequential nighttime treatments. During the experiment, midday xylem pressure potential, live fuel moisture and morning photosynthesis were measured for control and treatment plants. To determine if foliar uptake of fog occurred, fog was labeled with deuterium-enriched water and plant samples evaluated for the δD ratio before and after the first night of fog treatment.

METHODS

Study Species

This study investigates how fog and foliar uptake affects the physiology and flammability of five coastal California shrub species. The study species were selected based on several criteria: a widespread distribution along the California coast, likelihood of experiencing fog inundation in wild populations, different leaf habit (evergreen or drought-deciduous), and variation in leaf morphology. Two of the study species are dominants in the local chaparral community, a sclerophyllous shrub-dominated plant community found at mid-elevations in California (Hanes 1977). In the Santa Barbara region, this plant community receives higher annual rainfall than lower elevations and summer fog tends to occur primarily in May and June (Fischer et al. 2009, Emery unpublished). *Adenostoma fasciculatum* is found throughout California, has small tough needle-like leaves and variable rooting depth (Kummerow et al. 1977). The second chaparral species, *Ceanothus megacarpus*, is found on south-facing slopes of coastal chaparral in southern California. It has small sclerophyllous leaves and tends to have shallow roots (Hellmers et al. 1955, Schlesinger et al. 1982). Both species are considered to be strongly drought tolerant (Jacobsen et al. 2007) and as part of the coastal chaparral ecosystem, experience occasional summer fog (Leipper 1994, Fischer et al. 2009).

The three other shrub species are primarily found in California sage scrub (CSS), a plant community at lower elevations near the coast of central and southern California (Westman 1981), although they can also occur as an early successional plant community within chaparral (Hanes 1971). *Salvia leucophylla* and *Artemisia californica* are drought-deciduous, shallow-rooted shrubs that comprise CSS (Kirkpatrick and Hutchinson 1977). In contrast, *Baccharis pilularis*, is a fast growing, generally deep-rooted shrub with evergreen glabrous leaves (Wright 1928, Ackerly et al. 2002) that commonly occurs within CSS, open grasslands and areas of recent disturbance within chaparral (Kirkpatrick and Hutchinson 1977).

This study sought out genotypes from the Southern California coast, a region that experiences wildfires (Keely and Fotheringham 2001) and summer fog events (Leipper 1994) as foliar water uptake can vary within a species across their geographic range (Limm and Dawson 2010). Individual plants of *Salvia leucophylla* (n=11), *Artemisia californica* (n=12), *Baccharis pilularis* (n=11) and *Ceanothus megacarpus* (n=10) used in the experiment were local genotypes of the Santa Barbara Region purchased in 2011 from Santa Barbara Natives Nursery (Santa Barbara, CA). *Adenostoma fasciculatum* (n=10) individuals were from the Southern California coast and purchased from El Nativo Growers, Inc (Somis, CA) in 2011. *Adenostoma fasciculatum*, *Baccharis pilularis* and *Ceanothus megacarpus* were repotted to 5 gallon pots with Sunshine® Mix #5 (Sungro). *Salvia leucophylla* and *Artemisia californica* were repotted with 2/3 Sunshine® Mix #5 (Sungro), 1/3 sand as advised by the Santa Barbara Natives Nursery. The plants were kept outdoors on greenhouse benches for over a year prior to the experiment to allow for acclimatization to the local climate. All individuals were potted at the same time and any effects of becoming root bound in the pots are likely to have affected all plants equally. During this acclimatization period, plants were well watered every 1-1.5 weeks to encourage growth of the plant canopy.

Fog chamber construction

To expose shrubs to a controlled fog treatment, a chamber was constructed out of PVC piping and Tyvek sheeting. The box-shaped chamber had an intake and exit hole so that there was sufficient airflow and fog could move through the chamber. The dimensions were 1.25m by 1.25m by 2m. To generate fog, an ultrasonic fog-generating humidifier with an internal fan system was used to direct fog into the chamber (MH10 Industrial Ultrasonic Humidifier, Mainland Mart Corp., El Monte, CA). The machine volatilizes water with vibrating ceramic discs without chemicals or heat (similar to Limm et al. 2009, Berry and Smith 2014). Approximately one liter of water was volatilized per hour and passed through the chamber. To ensure constant supply of water to the machine, a reservoir was constructed to allow water to passively flow into the machine for the duration of the overnight treatments. The flow of water from the reservoir to the machine was controlled by a float valve.

Experimental setup

This study was conducted in the fall of 2013 at the UC Santa Barbara greenhouse facilities on the UC Santa Barbara campus at approximately 30m elevation and within 1km of the coast. Because the size of the fog chamber could only fit one species at a time, each species was tested in sequence. All plant species not undergoing the experiment were housed outside of the greenhouse on benches. The dates of treatment were different for each species in the fall of 2013: 10/13-10/17 *B. pilularis*, 10/20-10/24 *S. leucophylla*, 10/27-10/31 *C. megacarpus*, 11/3-11/7 *A. fasciculatum*, 11/12-11/16 *A. californica*. From October to mid-November in Santa Barbara, outside temperatures ranged from 22°-9°C with an average temperature of 16°C. For the duration of each experiment, all plants being tested were kept inside a climate-controlled greenhouse. Every evening for four nights, experimental plants were placed in the fog chamber and taken out every morning. Control plants were located in the same greenhouse as the treatment plants to experience similar ambient conditions but they stayed in that greenhouse overnight while the treatment plants were in the fog chamber. Temperature, relative humidity and leaf wetness were recorded using Decagon sensors (Decagon Devices, Pullman, Washington) placed inside the fog chamber and in the greenhouse adjacent to the control plants for the duration of the experimental period.

Fog treatment and ambient conditions

The greenhouse ambient conditions mimicked fall weather conditions and were allowed to fluctuate between 15°-27°C from 7:00 to 17:00 and 10°-15° C with 99% RH (or approaching 99%) from 17:00 to 7:00 the next morning. Fog treatments consisted of the fog machine running from 0:00 to 6:00 each day. This period of time is typically when Santa Barbara experiences nighttime fog (personal observations, Fischer et al. 2009). Maintaining constant fog inside the chamber was difficult after sunrise so the treatments were ended just prior to sunrise at 6:00. There were four consecutive nights of fog treatment with the first night consisting of isotopically labeled water followed by three nights of unlabeled water supplied by the greenhouse. For the first night of fog, greenhouse water was labeled with D_2O in order to increase the δD ratio to 100 per mil above the background greenhouse water level used in fog treatments. To prevent contamination, control plants were moved to a nearby greenhouse with the same controlled conditions only for the first night of fog treatment. Labeled fog was only used for one night for each species to reduce isotopic contamination of the water vapor in the greenhouse. For the subsequent three nights of fog treatment, water from the greenhouse was used and the control plants were kept in the same greenhouse as the fog chamber.

Plant preparation

After purchase and repotting in 2011, shrubs were well watered for over a year prior to the experiment. Exactly 14 days prior to the beginning of the experimental period for each species, individual plants were given a single watering of 600ml. This study attempted to mimic summer drought conditions by withholding water from potted shrubs for two weeks prior to experimental treatment. Pre-treatment TDR (Time-Domain Reflectrometry) of soil water for all species averaged 4.6% ±2.5 (SD) soil water content. In order to prevent fog water absorption by roots, the soil surface was isolated from fog drip. During the afternoon prior to the experimental period, pots were placed in an autoclave bag and wrapped to the base of the plant stem. A 2’x2’ square piece of polyurethane tarp was placed on top of the bag at the base of the plant and sealed to the base with waterproof adhesive tape and Smartbond® Landscape Construction Adhesive (DAP Products Inc). The tarp was draped over the pot and secured to it with cord. This process closed off the base of the plant to prevent water entering the soil without permanently sealing the pot off from air. The overnight bagging and securing procedure was performed on both control and treatment plants for each night of the experiment. Every morning the tarp was untied and autoclave bag removed, exposing the soil surface to the surrounding atmosphere. During daylight hours, the tarps remained on top of the pots for both control and treatment plants as the seal at the base of the stem was permanently fixed.

Measurements

Soil Moisture

To determine if water from the treatment leaked into the soil, soil moisture was measured using a 10cm MiniTrase TDR soil moisture probe (Model #: 6050X2, SoilMoisture Inc, Goleta, California). Measurements were taken the night before (18:00), the first morning after treatment (8:00) and the morning after the 4th night of treatment (8:00). To take a measurement, the tarp was lifted slightly to allow the TDR probes to enter the top 10cm of soil at the base of the stem. Two measurements on opposite sides of the main stem were averaged to produce a measurement for soil moisture. While relative error in TDR measurements increases when soil water content is low (Skierucha 2000), a 10cm probe is still accurate for measuring absolute soil water content (Noborio 2001). Soil water isotope samples were also collected before and after the first night of fog treatment and were scheduled for analysis if there was a difference in soil moisture. Based on soil moisture results from the TDR probe, soil water isotope samples were not analyzed.

Xylem Pressure Potential and Live Fuel Moisture

Xylem pressure potential (XPP) was measured with a Scholander-type pressure chamber (Model 1000, PMS Instrument Comp., Corvallis, OR). To measure XPP, a terminal segment of suberized stem with several leaves was clipped, sealed in a plastic bag and placed in a dark cooler until measurements could be made in the laboratory. Less than 30 minutes elapsed between clipping stems and measurements on the pressure chamber. Midday (15:00-

16:30) XPP measurements were taken the day prior, day 1 and day 5 of the experiment. Individual plants were designated treatment or control based on their pre-treatment xylem pressure potential. The lowest XPP was designated as a control, second lowest as treatment and alternated henceforth. This was done to prevent accidental bias of initial plant condition. For some species, the control and treatment groups differed in sample size by one individual. The sample sizes for all species and treatments were constrained by the size of the fog chamber. XPP was measured at midday to reduce measurement error from leaf wetness, to observe potential lagged effects of nighttime foliar wetting, and to coincide with live fuel moisture measurements. Immediately before measuring XPP, each stem sample was weighed ("Wet Weight"). After measuring XPP in the laboratory, the sample was placed in a drying oven at 80^{0}C for 48 hours to obtain the "Dry Weight." Live fuel moisture (LFM) was calculated according to the United States Forest Service as

$LFM = \frac{Wet\ Weight - Dry\ Weight}{Dry\ Weight}$ (Countryman and Dean 1979). After clipping of any plant tissue on the potted plant, the plant stem was sealed with a thermosetting adhesive to prevent water uptake through cut stems during subsequent nights of fog treatment.

Photosynthesis

Photosynthesis, stomatal conductance and transpiration were measured with a LI-6400 (LI-COR, Lincoln, Nebraska) the morning (9:00-10:00) before fog treatments began and the morning (9:00-10:00) after the 4th night of fog exposure. Fog exposure ended at 6:00 and the chamber was opened between 7:00-8:00. The 9:00 timing was sufficiently long enough to allow for water on leaves to be absorbed or evaporate from the overnight fog treatment. Two groups of leaves per plant (1-3 leaves depending on the species) were measured with the LI-6400 and then removed to quantify leaf area. This study used ImageJ software (NIH, USA, http://rsb.info.nih.gov/ij/) to calculate leaf area and adjust the LI-6400 measurements.

Stable Isotopes

Leaves and suberized stem tissue adjacent to selected leaves were sampled the evening before (18:00) the first night of fog using procedures from Limm et al. (2009). This method consists of spraying leaf tissue with DI water and patting dry before collecting and freezing tissue for later analysis. This same sampling procedure was conducted approximately an hour after the first fog treatment ended (7:00) to wash off any labeled water from the surface. Plant samples were separated into leaves and stems, sealed in scintillation vials with Parafilm and placed in a -10*C freezer. To determine the δD ratio for each sample, water was extracted at the Center for Stable Isotope Biogeochemistry, University of California Berkeley using cryogenic vacuum extraction (Ehleringer et al. 2000) and analyzed with an Isotope Ratio Mass Spectrometer (model Delta plus XL; Finnigan MAT, Breman, Germany).

Analysis

To test for and remove outliers, the Dixon test was performed for each set of data and species (Dixon 1950). For each analysis, the Brown-Forsythe test for equal variance (Brown and Forsythe 1974) was used for control and treatment plants for each species. For the measurements with equal variance a Student's t-test was performed and subsequently a sequential bonferroni to correct for multiple tests across the five species. If the variance was unequal, the Alexander Govern test (Alexander and Govern 1994) was used and p-values corrected using a sequential bonferroni. All p-values reported are corrected family-wide p-values at the 0.05 alpha level. All analyses were conducted using JMP Pro 11 (SAS Institute, Cary, North Carolina). Plant species could not directly be compared because they were tested on separate dates.

Leaf surface images

Leaves from all five species were selected for surface imaging to examine foliar surface morphology. Environmental scanning electron microscopy (ESEM) was performed in the Micro-Environmental Imaging and Analysis Facility at the University of California at Santa Barbara (https://www.bren.ucsb.edu/facilities/MEIAF/) under NSF Awards BES-9977772 and DBI-0216480. Images were taken in May, 2015 and April, 2016. Leaves were destructively sampled from the plants used in this study (Fig 1).

RESULTS

Environmental conditions and soil moisture

The environmental sensors indicated that greenhouse conditions (where the control plants resided) were broadly similar to the fog chamber in both temperature and relative humidity (Fig 2). During the period of fog exposure, temperatures were 6^0C higher inside the fog chamber. This is likely due to the ultrasonic volatilization process heating up the fog water. Relative humidity was also higher due to the presence of fog throughout the experimental chamber.

The leaf wetness sensor detected higher condensation inside the fog chamber compared to the surrounding greenhouse (Fig 2), indicating fog saturation in the overnight treatment. Treatment plants generally had wet leaves until 8:00-9:00 the morning after fog exposure as can be observed with the leaf wetness sensor (Fig 2). Between 8:00-9:00 is when the chamber was opened and treatment plants placed in the open area of the greenhouse.

For soil moisture, there was no significant difference between treatment and control individuals for any of the five shrub species after one night or four nights of fog treatment (Table 1). Average soil moisture across all species increased slightly for treatment individuals from 4.22% ±0.9 (SD) to 4.31% ±1.1 (SD). Average soil moisture across all species decreased slightly for control individuals from 4.39% ±0.9 (SD) to 4.24% ±0.9 (SD). The non-significant differences in soil moisture between treatment and control individuals for all species indicate that roots and soil were effectively isolated from fog water during overnight treatments.

Plant water isotopes

The δD ratio for the leaves of treatment plants was significantly enriched compared to the control (Fig 3) for *A. fasciculatum* (p=0.0028), *A. californica* (p=0.0005), *B. pilularis* (p=0.0039),) and *S. leucophylla* (p=0.007). Only *C. megacarpus* showed no significant enrichment compared to the control (p=0.3318).

The δD ratio for stems of treatment plants was significantly enriched compared to the control (Fig 3) for two of the species: *B. pilularis* (p=0.003) and *S. leucophylla* (p=0.023). There was no significant difference between control and treatment for *C. megacarpus* (p=0.4459). While *A. fasciculatum* (p=0.4459) and *A. californica* (p=0.2149) were also not significantly different, treatment plant average was slightly enriched by 8.37 and 6.8 δD per mil respectively compared to the control plant average.

Live fuel moisture

A single night of fog treatment had little effect on live fuel moisture for treatment plants across all species (Table 2). While there was no significant difference in LFM change between control and treatment after four nights of fog treatment, treatment plants of all species tended to have increased LFM compared to the controls (Table 2). The average difference between treatment and control across all species was a 14% (SE ±4.8%) increase in LFM for plants exposed to overnight fog treatments.

Xylem pressure potential

After one night of fog, midday XPP was marginally higher in the treatment plants for *A. fasciculatum* (p=0.09, Table 3). *C. megacarpus*, *B. pilularis*, *S. leucophylla* and *A. californica* showed no significant difference in XPP after one night of fog treatment. After four nights of fog exposure, four of the five shrub species showed no significant difference in midday XPP between control and treatment (Table 3). *Salvia leucophylla* was the only species with significantly higher XPP in treatment plants compared to control individuals (p=0.0445).

Photosynthesis & stomatal conductance

For the evergreen species, *C. megacarpus*, *A. fasciculatum* and *B. pilularis*, both treatment and control individuals experienced a decrease in photosynthetic rates during the experimental period, likely due to lack of watering (Table 4). The two drought-deciduous shrubs, *A. californica* and *S. leucophylla*, maintained photosynthetic rates under the fog treatment with *S. leucophylla* treatment plants having marginally higher rates than control plants (p=0.0885). Photosynthetically active radiation was maintained at 1800 µmol mol^{-1}. Across all species, leaf temperature averaged 26.09^{0}C ± 0.12 (SE) and vapor pressure deficit derived from leaf surface temperature averaged 2.25 kPa ± 0.02 (SE). There was improved stomatal conductance for *A. fasciculatum* treatment plants compared to the control (p=0.043, Table 5). *A. californica*, *B. pilularis* and *S. leucophylla* tended to have improved stomatal conductance after four nights of fog compared to the controls. Ci/Ca was also evaluated and no significant trends or differences were found for all species.

DISCUSSION

Species differences in foliar water uptake

Four of the five shrub species demonstrated foliar water uptake based on the δD isotopic ratios (Fig 3). The only species without an isotopic signal of fog in leaf or stem tissue was *C.*

megacarpus. While the leaves of this species are small and sclerophyllous, these foliar characteristics are also shared by *A. fasciculatum* and *B. pilularis*. *C. megacarpus* is a member of the subgenus *Cerastes* which is known to have stomatal crypts (Nobs 1963). This recessed stomatal anatomy is thought to reduce transpiration (Turner 1994) and enhance gas exchange (Hassiotou et. al. 2009). It is possible that stomatal crypts in *C. megacarpus* reduce contact between stomates and condensed water droplets on the leaves thus making it difficult for plants to take up water. Stomatal uptake of water has been observed previously (Burkhardt et al. 2012) and foliar water uptake capacity decreases with increased leaf hydrophobicity (Lekson et al. 2015). In addition to stomatal crypts, *C. megacarpus* has trichomes (Fig 1) which may increase hydrophobicity and the distance between water droplet and leaf interior. While stomatal crypts and trichomes may have affected FWU for *C. megacarpus*, the general mechanism of FWU is still under debate (Qiu et al. 2010).

Evidence suggests that foliar water can enter through the cuticle (Yates and Hutley 1995, Kersteins 1996, Eller et al. 2013), leaf epidermal hydathodes (Martin and von Willert 2000) and stomata (Burgess and Dawson 2004, Burkhardt et al. 2012). The four shrub species in this experiment that demonstrated foliar water uptake have very different leaf morphologies, phenologies and stomatal control. Although *A. fasciculatum* and *B. pilularis* are both evergreen, *A. fasciculatum* has small sclerophyllous needle-like leaves while *B. pilularis* has glabrous leaves with a relatively thick cuticle. In contrast, the drought-deciduous species *A. californica* and *S. leucophylla* have “softer” leaves that curl and turn brown during the summer, weak stomatal control, and high transpiration rates compared to evergreen chaparral species (Harrison et al. 1971). A notable anatomical difference is the shape of their leaves; *S. leucophylla* has broad elliptical leaves while *A. californica* has feather-like leaves with a high surface area to volume ratio. Atmospheric water may enter through thin cuticles or through the stomata in these species. Both *A. californica* and *S. leucophylla* have a dense layer of trichomes that cover both sides of a leaf (Fig 1). These structures may enhance FWU as trichomes in other species have been shown to facilitate water uptake in leaves (Benzing and Burt 1970, Martin and von Willert 2000). Additionally, circadian rhythms of stomatal conductance (Resco de Dios et al. 2013) may affect the relative uptake of water through stomata during different times of day or night. Foliar water uptake occurred in four plant species in this study, despite large differences in leaf morphology, suggesting that there may be multiple mechanisms operating simultaneously to facilitate foliar water uptake in these Mediterranean type shrub species.

In two of the shrub species, *S. leucophylla* and *B. pilularis*, isotopically enriched water was also evident in stem tissue (Fig 3). Previous isotopic research has focused on detecting foliar water uptake in leaf tissue alone (Limm et al. 2009, Berry and Smith 2014). Evidence for water transport in xylem through foliar absorption has been detected with reversal of sap flow in several tree species that experience regular fog inundation (Burgess and Dawson 2004, Eller et al. 2013). Alternatively, the enriched water may have been taken up through bark. Recent work has demonstrated bark water uptake in Coastal redwoods (*Sequoia sempervirens*; Earles et al. 2015). For *S. leucophylla* and *B. pilularis* fog water present in stem tissue indicates reversal of sap flow and/or bark water uptake. Either mechanism suggests that these two species can benefit from foliar uptake of fog water.

Plant Water Content

Although all five shrub species periodically experience fire disturbance, they are distributed across different fire regimes along the California coast. An important correlate of fire size in the shrub-dominated ecosystems of coastal California is live fuel moisture (Dennison and Moritz 2009), which is likewise a key component of plant flammability

(Anderson 1970, Martin et al. 1994). For all five shrub species in the Santa Barbara region, LFM tends to decrease during the summer drought until the first fall rains occur (LACFD 2015, Emery unpublished). Summer fog may affect plant water relations for these species as there is evidence of fog water use for *A. californica* in late summer (Emery and Lesage 2015). From the evidence presented by this study, FWU alone appears to slightly increase LFM after several nights of fog exposure (Table 2). Due to the short timescale of this study, the slight increase is likely due to water uptake and not from changes in dry matter content (Jolly et al. 2014). It is possible that FWU might contribute to water conservation, reducing loss of plant water content during the summer months. Coastal fog influence on plant flammability is likely dependent on the quantity of fog present and the ability for shrubs to take up fog water through surface roots, a means of water uptake that was excluded in this study.

Previous work on FWU has shown that taking up water through leaves improves water status (Gouvra and Grammatikopoulos 2003, Breshears et al. 2008, Limm et al. 2009, Berry and Smith 2014). In this study, fog effects on midday XPP were minimal except for *S. leucophylla* (Table 3). This species has high transpiration rates under drought conditions (Harrison et al. 1971) suggesting the possibility of stomatal water uptake. FWU in *S. leucophylla* may improve hydraulic functioning and reduce tension in xylem tissue. For the remaining three species that demonstrated FWU, it is possible that any difference in plant water status between control and treatment is lost by midday. While foliar wetting of *A. california* leaves increases pre-dawn XPP (Cole 2005), this study found no difference between control and treatment plants for *A. californica* (Table 3). Treatment plants for all five species tended to have higher stomatal conductance in the morning (Table 5), meaning more transpiration and water loss. This could result in similar XPP for control and treatment plants by midday. This is particularly relevant to Mediterranean-type climate regions which can experience overnight fog events followed by hot, dry weather the following afternoon. The results of this study suggest that FWU has temporary benefits to plant physiology, and the improvements may not be easily detected by the afternoon following fog immersion.

It is also possible that the experimental conditions inhibited the improvement of overall water status as measured by XPP. Drought conditions stimulate abscisic acid accumulation, limiting stomatal response in many plant species (Zhang et. al. 2006). Initial XPP measurements indicate that all species had relatively low water potentials prior to the experimental period (Table 3). Despite exposure to fog for several nights, foliar uptake may have been inhibited by biochemically mediated limitations in stomatal response. For *Sequoia sempervirens*, well-watered leaves absorbed more fog water than water-stressed leaves (Burgess and Dawson 2004). Although conditions were meant to reflect a summer drought typical of the Santa Barbara region, low levels of leaf hydration in this experiment could have reduced the effects FWU on plant water status.

Photosynthesis

Foliar water uptake of fog may supplement water availability in leaves, enhancing morning photosynthesis during the dry summer months. Treatment individuals for the two drought-deciduous species had increased photosynthetic rates and the species with FWU tended to have improved rates compared to the controls (Table 4). Compared with chaparral species, *A. californica* and *S. leucophylla* have rapid physiological responses to rain events (Gray 1982, Cole 2005). These two species may be more responsive to foliar wetting during summer droughts, allowing for more summertime CO_2 assimilation. Additional carbon resources during drought could then enhance hydraulic function by providing resources for repair and maintenance (McDowell 2011). This summertime carbon gain may also prolong leaf lifespan for drought-deciduous species that likely drop leaves due to water availability (Harrison et al. 1971). Despite an overall reduction in photosynthetic rates over the course of the experiment for evergreen species (*B. pilularis*, *C. megacarpus* and *A. fasciculatum*), the treatment plants for the two species with FWU (*B. pilularis* and *A. fasciculatum*) tended to have higher photosynthetic rates with fog exposure than controls (Table 4). Overnight wetting of leaves for *A. fasciculatum* and *B. pilularis* may provide a small boost in photosynthesis during the early morning hours of the day. The results of this study suggest that FWU can maintain photosynthetic activity in drought-deciduous species and buffer the loss of CO_2 assimilation in evergreen species with thicker, more sclerophyllous leaves.

Conclusions

Fog influences on plant water relations are well established in regions with consistent, high quantities of fog deposition such as montane cloud forests (Scholl et al. 2011, Goldsmith et al. 2013, Eller et al. 2013, Gotsch et al. 2014), the redwood forests of Northern California (Burgess and Dawson 2004) and bishop pines on the Channel Islands (Fischer et al. 2009, Baguskas et al. 2016). Much less is known about semi-arid ecosystems with highly variable fog deposition such as the shrublands of coastal California. While fog can be variable across years (Williams 2009), it can provide significant moisture during the summer drought (Hiatt et al. 2012, Vasey et al. 2012). This study found that for many species, overnight foliar wetting of leaves can result in water uptake. In the species with foliar water uptake, fog treatment plants tended to have higher stomatal conductance and photosynthetic rates. Few plants reacted to a single night of fog treatment suggesting that several consecutive nights of fog exposure may be necessary to significantly affect shrub physiology.

California shrublands, like many Mediterranean-type climates, experience seasonal drought and periodic wildfires. While coastal fog in California provides shading and water for several woody species (Burgess and Dawson 2004, Fischer et al. 2009, Vasey et al. 2012, Carbone et al. 2013, Baguskas et al. 2016), fog patterns may be changing (Johnstone and Dawson 2010, Williams et al. 2015). For plant communities in arid regions, foliar absorption of atmospheric water may provide a critical supplement during periods of drought. From this study, it appears that drought-deciduous species (*A. californica* and *S. leucophylla*) benefit more from overnight fog events than evergreen species (*A. fasciculatum, B. pilularis* and *C. megacarpus*). This differential response to fog exposure in California shrub species may affect how plant communities and ecological interactions change under future climate scenarios.

ACKNOWLEDGMENTS

Many thanks to Dr. Carla D'Antonio and the UCSB Greenhouse for logistical and financial support, Dr. Carla D'Antonio, Dr. Max Moritz, Dr. Chris Still and Dr. Dar Roberts for helpful comments on an earlier version of this manuscript, and Dr. Todd Dawson, Dr. Stefania Mambelli and the Center for Stable Isotope Biogeochemistry at UC Berkeley for guidance and facilities. This project was funded by National Science Foundation Doctoral Dissertation Improvement Grant Award #1311605 and supported by the Isotope Inter-University Training for Continental-scale Ecology Fellowship, University of Utah.