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Foliar water uptake by coastal wetland plants: A novel water acquisition mechanism in arid and humid subtropical mangroves

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Abstract

1. Climate change alters freshwater availability in many ecosystems leading to shifts in distributions for many plants. Despite living exclusively in intertidal, saline environments, mangroves rely on non-saline water to maintain plant productivity. However, several mangrove species persist in arid environments where non-saline water from rain and groundwater sources are limited. Under these conditions, foliar water uptake from fog and mist may be an important water acquisition strategy.
2. We conducted a field experiment in arid Baja California Sur, Mexico along with a controlled mist chamber experiment (using seedlings sourced from humid subtropical region, Florida, USA) to show that three co-occurring, neotropical mangrove species, *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*, growing in both arid and humid environments can access water condensed on their leaves.
3. Foliar water uptake was greatest in *A. germinans* and lowest in *R. mangle*, possibly reflecting leaf traits associated with species-specific water balance strategies. In our field misting experiment, the contribution of foliar water uptake was higher in *A. germinans* (32 ± 2%) than *L. racemosa* (26 ± 2%) and *R. mangle* (16 ± 1%). Foliar water uptake also varied across locations for *L. racemosa* and *R. mangle*, with declining uptake towards both species' northern range limits in Baja California Sur, suggesting the distribution patterns of arid-zone mangroves may be affected by species-specific spatial variation in foliar water use. Within species, foliar water use was comparable across field and controlled experiments irrespective of source population (Baja California Sur vs. Florida), suggesting foliar water uptake is not an arid-zone adaptation, and is instead used as a supplemental water balance strategy in arid and humid neotropical mangroves.
4. *Synthesis*. Our findings indicate mangroves have the potential to access atmospheric water, such as rain, dew and sea fog, through their leaves to offset soil water deficits. Variation in foliar water use across these three neotropical mangrove species may influence mangrove species distributions across arid-zone and pseudo-drought (highly saline) environments, with implications for mangrove response to climate change.

KEYWORDS
foliar, global change, isotopes, mangrove, plant–climate interactions, range limit, stress, water use

1 | INTRODUCTION

Although mangroves live in a saline environment and possess adaptations to use saline water sources, they preferentially use freshwater over saltwater sources (Ewe, Sternberg, & Childers, 2007; Reef, Markham, Santini, & Lovelock, 2015), and freshwater availability is an important driver of mangrove productivity and distribution (Gabler et al., 2017; Hayes et al., 2019; Osland et al., 2018). Mangrove size is positively correlated with precipitation, indicating the importance of freshwater to maintain plant productivity (Gabler et al., 2017; Méndez-Alonzo, López-Portillo, & Rivera-Monroy, 2008; Simard et al., 2019). Moreover, intraspecific variation in mangrove leaf anatomy and morphology is correlated with rainfall gradients, further implicating the acquisition of freshwater as a driving force of mangrove life-history traits (Méndez-Alonzo et al., 2008). To date, however, the ecophysiology of arid-zone mangroves, and their ability to persist in very low precipitation environments through novel water acquisition strategies, remains poorly explored.

Rainfall in arid regions is often too low to meet the physiological demands for growth and reproduction of many plant species living in these habitats. Plants endemic to arid environments often have specialized water-saving adaptations, such as sunken stomata, low stomatal density, increased leaf succulence, leaf pubescence and small leaf size (Mulroy & Rundel, 1977). Some plants can also access water sources such as dew, mist and rain water through foliar water uptake (Li, Xiao, Zhao, Zhou, & Wang, 2014; Martin & von Willert, 2000; Yan et al., 2015). Foliar water uptake occurs when water droplets condense on plant leaves and move along a water potential gradient from the outside of leaves into internal leaf tissues (Rundel, 1982). When the atmosphere becomes fully hydrated through rain, mist or fog events, the leaf–atmosphere interface experiences a water potential higher than the soil water potential, which changes the direction of water flow through the plant, lowering the leaf water potential and drawing water from the leaf further down into the plant towards the soil. A recent review of foliar water uptake found that up to 85% of plant species is able to absorb water through their leaves (Berry, Emery, Gotsch, & Goldsmith, 2019). However, significant knowledge gaps still remain in regard to different systems as well as across habitats and wet/dry intervals (Berry et al., 2019). For example, foliar water uptake may impact species distributions, enabling plants to persist in areas without sufficient supply of soil water, such as plants growing in desert locations, on steep slopes or in saline conditions (Schreel & Steppe, 2019).

Along arid coastlines, such as south-east Texas, USA, and Baja California Sur, Mexico, mangroves are likely limited by the arid and hypersaline conditions resulting from very low rainfall (<500 mm/year; Osland et al., 2017). Plants living in these marginal environments are likely to be especially sensitive to environmental change. As a result, interspecific variability in foliar water uptake could influence the composition of mangrove communities at these range limits. Furthermore, future changes in the amount of freshwater, and the form in which it is delivered (i.e. rain, mist, fog), may have a significant impact on mangrove distributions in these regions.

Despite increased understanding of the importance of precipitation and other non-saline water sources to mangrove productivity (Hayes et al., 2019; Lovelock, Reef, & Ball, 2017; Osland et al., 2018), research into foliar water uptake in mangroves has been limited. However, Steppe et al. (2018) used measurements of stem diameter variation, sap flow and stem water potential to develop a mechanistic model that predicted foliar water uptake in *Avicennia marina*. Furthermore, Schreel, Wal, Hervé-Fernandez, Boeckx, and Steppe (2019) used stable isotopes to definitively demonstrate foliar water uptake in *A. marina*. However, this study was performed on *A. marina* seedlings under controlled conditions and thus could not indicate whether foliar water use occurs in the field or in adult plants. No studies have examined foliar water use across multiple co-occurring mangrove species, in an arid environment, or across a latitudinal gradient, where the use of foliar water uptake is likely to be an important mechanism to meet the physiological demands of living in a dry, low-rain environment.

Here, we coupled field experiments in Baja California Sur, Mexico with controlled mist chamber experiments using plants sourced from a humid subtropical region in Florida, USA, to investigate the potential for foliar water uptake in three co-occurring neotropical mangrove species, *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia germinans*. We hypothesized that mangroves can take in water through their leaves to increase non-saline water availability, and that this may be an important water acquisition mechanism for mangroves to improve plant water status. We also hypothesized that foliar water use would differ interspecifically across mangrove species due to conserved differences in leaf anatomy. However, we expected that the chronic pseudo-drought conditions imposed by highly saline environments might select for similar intraspecific foliar water use across populations sourced from arid versus subtropical regions (Baja California Sur, Mexico vs. Florida, USA). We chose to use a two-scale approach to investigate foliar water uptake in mangroves by coupling a field and controlled greenhouse experiment. This allowed us to first test, under controlled conditions (greenhouse mist chambers) eliminating other possible water sources, if foliar water uptake was physically possible in mangroves. Second, in situ experiments allowed us to confirm whether foliar water uptake occurs under uncontrolled field conditions, and across sites over different latitudinal gradients. Our novel coupling of field and greenhouse-based measurements of foliar uptake in the three dominant mangrove species in North America can improve our understanding of an alternative water-use strategy for coastal wetland plants that chronically experience pseudo-drought conditions that might select for supplemental water-uptake strategies.

2 | MATERIALS AND METHODS

Our investigation of foliar water uptake in mangroves consisted of three separate but related experiments. Prior to conducting isotope experiments, we first investigated potential foliar water uptake in our study species by performing a simple experiment monitoring leaf water content (LWC) change following submergence in water (*Experiment* 1: *Foliar water capacity experiment*), whereby an increase in leaf mass following submergence indicates the potential for foliar water uptake (Limm, Simonin, Bothman, & Dawson, 2009). Second, we performed a field experiment (*Experiment* 2: *Field misting experiment*) across three locations in an arid region to investigate foliar water uptake by mangroves living in a rain-limited environment. We conducted this experiment in Baja California Sur, Mexico, as this arid location experiences sea fogging along the west coast of the peninsula which may offer an alternative water source (Table S1). We also selected three locations across a latitudinal gradient as we were interested in the potential of foliar water uptake as a mechanism to explain mangrove species distributions across Baja California Sur. Finally, we coupled our field experiment with a controlled greenhouse experiment (*Experiment* 3: *Controlled mist chamber experiment*) using plants from humid, subtropical Florida, USA, to investigate if foliar water uptake in mangroves is an arid-zone adaptation, or if foliar water uptake can be utilized irrespective of drought conditioning or evolutionary history.

Leaves for the initial leaf water submergence experiment were collected in Santispac, Baja California Sur (26°45′46.64″N, 111°53′35.17″W) in October 2018. Field experiments were conducted concurrently at three sites in Baja California Sur, Mexico: Magdalena Bay (24°47′45.64″N, 112°6′57.38″W), Santispac and Campo Rene (26°48′26.45″N, 113°28′45.55″W; Figure 1). All three species were present at Magdalena Bay and Santispac, but only *R. mangle* and *L. racemosa* were present at Campo Rene. Baja California Sur was an ideal location for our experiment due to its hot, arid environment with low annual rainfall and occasional fog (Table S1). Finally, the plants used in the controlled experiment were harvested from St Augustine, Florida, USA (29°43′41.63″N, 81°14′30.87″W).

2.1 | Experiment 1: Foliar water capacity

We harvested leaves from *A. germinans*, *L. racemosa* and *R. mangle* (four trees of each species) at Santispac, Baja California Sur, Mexico, pre-dawn and at dusk, to compare differences in LWC following water exposure across species and time (day vs. night). We collected samples at different time periods to test if leaves collected before and after sun exposure had different water content, which may influence the water content before foliar submergence. At each sampling period, we randomly selected four stems on each plant, from which we collected four sunlit, fully formed leaves closest to the terminal ends of each stem (n = 16 from each species at each time period). We then followed protocols adapted from Limm et al. (2009), and measured the potential for foliar water absorption by soaking leaves in water for a period of 6 hr and measuring change in leaf mass after submergence. We first weighed the harvested leaves before sealing the leaf petioles with thermosetting adhesive to minimize evaporation from leaf petioles to the air, and then pinned the leaves with the petioles above the water line to ensure any water entering leaves could only enter through the leaf. After soaking for 6 hr, we removed the leaves and dried them with paper

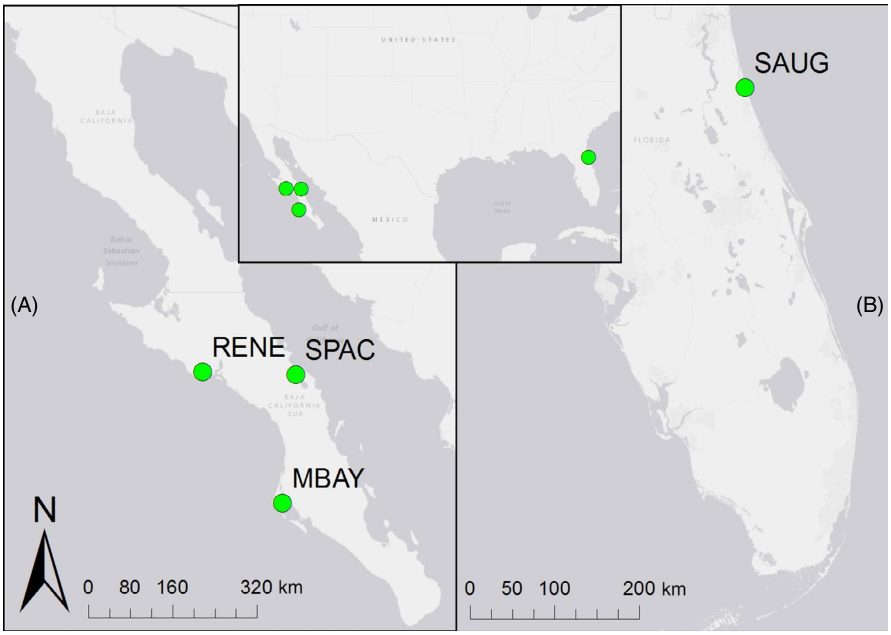

FIGURE 1 Map showing locations of experimental locations (circles) within Baja, Mexico (A). Experimental locations were at Magdalena Bay (MBAY), Santispac (SPAC) and Campo Rene (RENE). Plants used in the controlled experiment were collected from St Augustine, Florida, USA (B; SAUG)

towels and individually weighed each leaf. To ensure that any mass accumulated in the post-submergence mass was due to foliar water uptake and did not include surface water, we briefly re-submerged the leaves for one second after weighing, dried again on paper towel and reweighed each leaf (time insufficient to absorb any more water; Limm et al., 2009). We then averaged the two masses.

We measured the foliar water-uptake capacity as the difference between the masses (mg) of the leaves before and after being submerged. We calculated the per cent increase in (% LWC) for each leaf to measure the potential for foliar water uptake as follows:

$$\%\,\mathrm{LWC} = \frac{(((\mathrm{Mass2} + \mathrm{Mass3})/2) - \mathrm{Mass}_{\mathrm{dry}})}{(\mathrm{Mass1} - \mathrm{Mass}_{\mathrm{dry}})} - 1.$$

$\mathrm{Mass}_{\mathrm{dry}}$ is the dried leaf mass after drying in an oven at 60°C for 72 hr, Mass1 is the mass before any wetting, Mass2 is the mass after brief drying after 6 hr submergence and Mass3 is the mass after brief re-submergence and re-drying (Limm et al., 2009). We also compared foliar water uptake per unit area (A; mg cm^{-2}), to compare the difference in LWC before and after submergence (Limm et al., 2009). We calculated foliar water-uptake capacity per unit area (LWC mg cm^{-2}) as follows:

$$\mathrm{LWC}(\mathrm{mg\ cm}^{-2}) = \frac{(((\mathrm{Mass2} + \mathrm{Mass3})/2) - \mathrm{Mass1})}{A}.$$

2.2 | Foliar misting of stable isotopes

Next, to determine whether mangroves can access water that condenses on their leaves through fog or high dewpoints, we misted plants with isotopically labelled water and measured uptake in the leaf sap. We performed this experiment both in the field (Baja California Sur, Mexico; *field misting experiment*) and in a controlled environment (*controlled mist chamber experiment*), but with different source populations (arid- vs. humid-zone mangroves). This comparison allowed us to test the potential for local adaptation in the species' ability to access water through foliar uptake. We followed similar protocols for both the field misting experiment and controlled mist chamber experiment; leaves from *A. germinans*, *L. racemosa* and *R. mangle* were misted with isotopically labelled water, then measured for isotope abundance within leaves to investigate the extent of foliar water uptake across each species following a misting event. For labelled mist water, we used ^{18}O-enriched and D-enriched water. These oxygen and deuterium isotopes are heavier than the most abundant ^{16}O and ^{1}H isotopes of these elements, thereby making them an ideal tracer as the level of depletion or enrichment varies based on source water (seawater, porewater, atmospheric water or reference mist water; Table S2).

Although misting protocols for field and greenhouse experiments were similar, we used different isotope enrichments for each experiment. For the field misting experiment, we used isotopically labelled water with δD and δ^{18}O values of −41.61 ± 0.39‰ and 73.28 ± 0.03‰ respectively. For the controlled mist chamber experiment, we used isotopically labelled water with δD and δ^{18}O values of −47.46 ± 0.41‰ and 25.08 ± 0.03‰ respectively. From previous research (Hayes et al., 2019), we estimated mangrove isotopic leaf values (pre-treatment) would range between 0 and −30‰ for δD and between 0 and −6‰ for δ^{18}O. Thus, after application with our labelled mist water, if leaves accumulated labelled mist water following foliar mist exposure, we would expect internal leaf water values of δD to become more depleted and δ^{18}O to become more enriched.

2.3 | Experiment 2: Field misting experiment

We conducted the field experiment in October 2018 at three locations in Baja California Sur, Mexico: Magdalena Bay, Santispac and Campo Rene. At each location, we selected four trees from each species (approximately 2.0 m in height), ensuring all plants were within close proximity (~50 m distance between all trees). To capture any available atmospheric water at each location, we erected a mist catching net constructed of a 9-m^2 shade cloth (2-mm mesh size) with a water trapping container positioned below the net. There were no atmospheric watering events (rain, sea fog or dew) at any location during the sampling periods.

At dusk, we collected a mature, fully formed leaf from sunlit terminal stems from each tree (four trees from each species; 12 leaves in total). These excised leaves were used to measure baseline isotope values of the leaves prior to performing the labelled water experiments on the opposite intact leaves. The leaves were cut by hand and immediately stored in airtight tubes sealed with parafilm wax, before being frozen and stored at −20°C until analysis. We then placed polyethylene bags over the stem from where we had removed the pre-exposure leaf sample, sealing the bag around the stem using masking tape and parafilm wax. We made a small incision in the bag and sprayed 50 ml of isotopically labelled water inside the bag, ensuring the leaves were well saturated to replicate the effects of a rain or misting event saturating the leaves. We then placed a humidity and temperature sensor within each bag and sealed the bag incision using masking tape and parafilm wax.

After approximately 8 hr and before dawn, we removed the plastic bags, sprayed the leaves with DI water to remove the labelled treatment water, then carefully removed the opposite leaf (or closest leaf), to the pre-exposure leaf we had collected prior to labelled water application. We immediately dried the leaves on absorbent paper to remove external leaf water, stored in airtight tubes sealed with parafilm wax, before freezing and storing at −20°C until analysis. For control treatments, we used the same trees as the treatment group and followed the same protocols but without the application of labelled mist water.

2.4 | Experiment 3: Controlled mist chamber experiment

To assess whether foliar water uptake capacity was related to drought conditioning or differences in source populations, we repeated the mist exposure experiment under controlled conditions using plants sourced from a humid, subtropical region. We collected seedlings of *A. germinans*, *L. racemosa* and *R. mangle* in October 2018, from St Augustine, Florida, and grew them for a period of 3 months in a climate-controlled greenhouse at Villanova University, Pennsylvania. Following established protocols described in Hayes et al. (2017), we grew seedlings in cylindrical pots (175 mm diameter, 175 mm height and 2.7 L volume) filled with a soil mix of 50% Canadian peat moss (Sun Gro Horticulture Distribution Inc.) and 50% sand. We grew the plants in a growth pond containing a saline nutrient stock solution of 0.21 mM NH_4NO_3, 0.6 mM KNO_3, 0.35 mM Ca $(NO_3)_2$, 0.05 mM NaH_2PO_4, 0.025 mM Fe-EDTA and 500 mM NaCl (seawater salinity). The water level in the growth pond was kept to a depth of approximately 10 cm. We showered the plants daily with fresh water (approximately 50 ml) to simulate a rain event washing salt from their leaves. Salinity was monitored every second day and was adjusted with fresh water to maintain a consistent salinity concentration. Pond water was changed weekly. The plants were maintained in the greenhouse at a mean temperature of 23.6 ± 2.2°C *SD* and a mean humidity of 61.04 ± 10.5% *SD*, until being used in the mist chamber experiment in January 2018.

We constructed misting chambers of ½ inch PVC (1 m^3) surrounded by polyethylene sheeting to create airtight seals (reinforced with duct tape). Within each chamber, we installed a 6-inch circulation fan (BHRS Group) to circulate the water vapour, an ultrasonic cool-mist humidifier (TaoTronics) to create a mist atmosphere, and temperature and humidity monitors (HOBO MX2302) to monitor atmospheric conditions within the chambers.

To ensure that all labelled water detected in the leaves was the result of foliar water uptake, we sealed the plant pots and soil with plastic bags around the stems using masking tape and parafilm wax. We then collected pre-mist exposure leaves from each plant before placing the plants in the misting chambers. The harvested pre-mist exposure leaves were used to measure baseline isotope values of the leaves prior to performing the labelled water experiments on the opposite intact leaves. Leaves were immediately dried on absorbent paper, stored in airtight tubes sealed with parafilm wax, before being frozen and stored at −20°C until analysis. We randomly selected seven plants from each of the three study species before placing one plant of each species into each of the chambers. Over the course of a 6-hr exposure period (after dusk), we diffused 1.25 L of isotopically labelled water into the chambers. The mist chambers maintained a mean temperature of 20.8 ± 0.9°C and a mean relative humidity of 96.9 ± 1.8 *SD* over the 6-hr mist exposure period.

Following mist exposure, we removed plants from the chambers and sprayed them with deionized water to remove any labelled mist water from the plant surfaces. We then harvested the opposite leaf (or closest leaf), to the pre-exposure leaf we had collected prior to labelled water application. Each leaf was carefully dried with absorbent paper to ensure that any water detected by stable isotope analysis was the result of foliar water uptake and not residual foliar surface water. The leaves were then stored in airtight tubes sealed with parafilm wax, before being frozen and stored at −20°C until analysis.

2.5 | Measurements of δ^{18}O and δ^2D

Foliar water was extracted by cryogenic vacuum distillation prior to analysis of δ^{18}O and δD isotopes using a Picarro L2120-i Analyser (Picarro). Additional reference source water samples for stable isotope analysis were collected in Baja California Sur from adjacent ocean waters and from porewater at 50 cm depth below sample trees (Table S2). Rainfall is rare in Baja, Mexico and there were no rainfall, fog or misting events during the 4-week period of sampling in October 2018.

2.6 | Data analysis

Summarized data throughout the manuscript are reported with the standard error of the mean. All statistical analyses were performed using the R statistical BASE package 3.3.2 (R Foundation for Statistical Computing). Individual tests are described below. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality in any of our analyses. See Table S3 for additional information in regard to the statistical analyses used and corresponding results.

2.7 | Experiment 1: Foliar water capacity

To test whether leaf weights increased following foliar water exposure, we compared leaf mass pre- and post-submergence with a Student's *t* test. Within each model, foliar water content (%) was the response variable, and time point (pre- and post-exposure) was the independent factor in the model (water content ~ time point). We compared post-foliar water increase (%) across species, collection time point (dusk or dawn) and their interaction using a two-way ANOVA. Within the model, post-exposure foliar water increase (%) was the response variable, with plant species and collection (dusk or dawn) as independent and interactive effects in the model (post-exposure water content ~ species × collection time).

2.8 | Experiment 2: Change in foliar isotope composition pre- and post-mist exposure

To assess whether foliar water increased following external water exposure for each species in the field misting experiment, we compared foliar water composition (δD and δ^{18}O values) pre- and post-mist exposure (where pre = control leaf taken from the stem prior to labelled water exposure). We used a Student's *t* test to compare foliar water composition (foliar δD and $\delta^{18}O$ values) and time point (pre- and post-mist exposure; foliar water ~ time point). Within each model, foliar water composition (foliar δD and $\delta^{18}O$ values) was the response variable, and time point (pre- and post-exposure) was the independent factor in the model.

2.9 | Changes in foliar isotope composition post-mist exposure (absolute change in foliar isotopes)

To assess whether foliar water accumulation differed across species, we compared absolute change in foliar water isotope values (foliar δD and $\delta^{18}O$) following post-mist exposure across each of the mangrove species (post-mist minus pre-mist exposure). Within the model, foliar water change (foliar δD and $\delta^{18}O$) was the response variable and species were the independent factor in the model (foliar water ~ species). We used a Student's t test to assess whether leaf water accumulation in *A. germinans* differed across locations, and ANOVA models for *L. racemosa* and *R. mangle*. Within each model, foliar water change was the response variable and location was the independent factor (foliar water ~ location).

2.10 | Experiment 3: Controlled mist chamber experiment data analysis

Following foliar water extraction and measuring isotope values in the extracted water, we found the pre-mist exposure leaves had a $\delta^{18}O$ range (6.45–32.91‰) encompassing the enrichment value of the labelled water for our controlled mist treatment (25.08 ± 0.03‰). Thus, for the controlled mist chamber experiment, we only used D for our analysis. To assess whether foliar water increased following external water exposure for each species, foliar water composition (δD values) was compared pre- and post-mist exposure using the same methods as explained for the field misting experiment. We also followed the same field misting experiment methods to assess if foliar water accumulation within the greenhouse experiment varied across each of the three mangrove species.

2.11 | MixSiar isotope mixing model

We used the MixSiar package (Stock & Semmens, 2016) to determine the proportion of saline water and non-saline mist water that comprised the mangrove leaf water post-mist exposure in the field misting experiment. MixSiar is a Bayesian mixing model that uses biotracer data to estimate the proportions of source contributions to a mixture (consumer). In our case, we used the MixSiar package to determine the proportion of water contributions to foliar water following a misting event. To establish the mix of water sources within the post-misting leaf samples, we assumed that the possible water sources available to the leaves were the pre-mist exposure leaf water (water within leaves before mist water application) and labelled mist water (mist water taken up by the leaf following application to the leaf surface). Source water reference samples (pre-misting leaf water and labelled misting water) were used in the MixSiar package to establish a source water baseline (Figure S1; Table S2).

3 | RESULTS

3.1 | Experiment 1: Foliar water capacity

Leaf water content (%) increased significantly in all three species following soaking in water for 6 hr ($t_{(31)} = 14.05$, $p < 0.001$; $t_{(31)} = 10.65$, $p < 0.001$; and $t_{(31)} = 6.38$, $p < 0.001$ for *A. germinans*, *L. racemosa* and *R. mangle* respectively; Figure 2A; Table S2). There was also a significant difference in LWC post-treatment across species ($F_{2,90} = 9.89$, $p < 0.001$; Figure 2A; Table S2), where

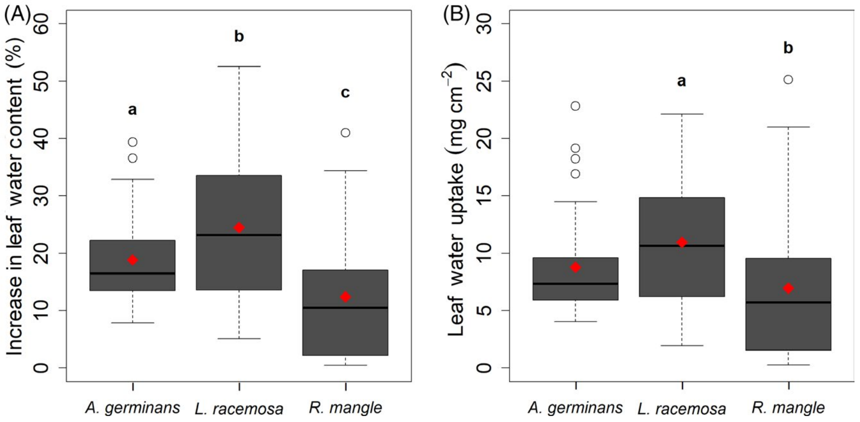

FIGURE 2 Increase in leaf water content (LWC; A; %) and leaf water uptake (B; mg cm^2) by excised leaves of each species during submergence in deionized water for 6 hr. LWC (%) and leaf water uptake (mg cm^2) increased significantly across all species after submergence ($p < 0.001$). Post-LWC (%) and leaf water uptake (mg cm^2) also varied significantly between each of the species ($p < 0.001$). Letters 'a', 'b' and 'c' indicate a significant difference ($p < 0.05$) between species. The solid line is the sample median, diamond is the mean, dashed lines are the minimum and maximum distribution

leaf water increase was significantly higher ($p < 0.05$) in *L. racemosa* (24.50 ± 2.29%) than either *A. germinans* (18.87 ± 1.34%) or *R. mangle* (12.45 ± 1.95%), which had a significantly lower foliar water increase than the other two species ($p < 0.05$). There was no significant difference in foliar water increase across collection time (dusk or dawn; $F_{1,90} = 0.76$, $p = 0.39$; Table S2), or with collection time and species interaction ($F_{2,90} = 0.62$, $p = 0.54$; Table S2). Taking leaf area into account, we found LWC (mg cm^2) increased in all three species ($t_{(31)} = 10.69$, $p < 0.001$; $t_{(31)} = 11.19$, $p < 0.001$; and $t_{(29)} = 6.02$, $p < 0.001$ for *A. germinans*, *L. racemosa* and *R. mangle* respectively; Figure 2B; Table S2). There was a significant difference in LWC (mg cm^2) across species ($F_{2,88} = 4.09$, $p < 0.001$; Figure 2B; Table S2). LWC (mg cm^2) was significantly higher ($p < 0.05$) in *L. racemosa* (10.99 ± 0.98 mg cm^2) than in *R. mangle* (6.96 ± 1.16 mg cm^2). However, there was no difference in LWC (mg cm^2) of *A. germinans* (8.8 ± 0.82 mg cm^2) with the other two species ($p < 0.05$). These observations indicate the potential for foliar water uptake within each of the mangrove species, and indicate foliar water-uptake capacity varies across species.

3.2 | Experiment 2: Change in foliar isotope composition pre- and post-mist exposure

In the field misting experiment, differences in foliar δD and δ^{18}O values following mist exposure were observed for all three species (*A. germinans:* $t_{(13.52)} = -10.82$, $p < 0.001$; and $t_{(12.25)} = 6.90$, $p < 0.001$ for foliar D and ^{18}O respectively; Figure 3A; *L. racemosa:* $t_{(20.90)} = -6.71$, $p < 0.001$; and $t_{(16.75)} = 5.95$, $p < 0.001$ for foliar D and ^{18}O respectively; Figure 3B; *R. mangle:* $t_{(20.36)} = -2.31$, $p < 0.05$; and $t_{(22)} = 7.33$, $p < 0.001$ for foliar D and ^{18}O respectively; Figure 3C; Table S2). There were no significant differences in foliar δD and δ^{18}O values in control samples (no labelled water application) for any of the species ($p > 0.05$; Table S2). Changes in foliar water composition in arid-zone *A. germinans*, *L. racemosa* and *R. mangle* after mist exposure indicate the capability of these species to use foliar water uptake.

In the controlled mist chamber experiment, change in foliar δD values following labelled mist exposure was highly variable across each of the three mangrove species. There was a significant difference in foliar δD values in *A. germinans* post-mist exposure ($t_{(9.75)} = 7.70$, $p < 0.01$; Figure 3A; Table S2), a weakly significant difference in foliar δD values in *L. racemosa* ($t_{(8.28)} = -2.18$, $p = 0.06$; Figure 3B; Table S2), and no significant difference in foliar δD values in *R. mangle* ($t_{(11.56)} = -0.53$, $p = 0.61$; Figure 3C; Table S2).

3.3 | Experiment 3: Changes in foliar isotope accumulation post-mist exposure (absolute change in foliar isotopes)

In the field misting experiment, the change in foliar δD and δ^{18}O (post-mist minus pre-mist exposure) differed significantly across each of the three species ($F_{2,29} = 17.37$, $p < 0.001$ and $F_{2,29} = 7.77$, $p < 0.001$ respectively; Figure 4A,B; Table S2). Changes in foliar δD and δ^{18}O were lower in *R. mangle* (7.90 ± 1.51‰ and 6.65 ± 0.78‰ respectively) than either *L. racemosa* ($p < 0.05$; 18.99 ± 2.14‰ and 11.45 ± 1.45‰ respectively) or *A. germinans* ($p < 0.05$; 22.58 ± 1.52‰ and 12.91 ± 1.09‰ respectively). There was no difference in change of foliar δD and δ^{18}O between *A. germinans* and *L. racemosa* ($p > 0.05$).

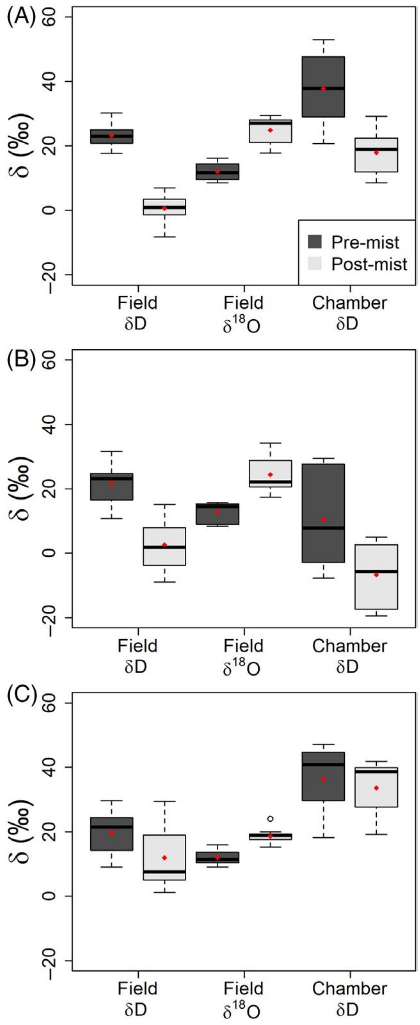

FIGURE 3 Changes in foliar isotope composition for *Avicennia germinans* (A), *Laguncularia racemosa* (B) and *Rhizophora mangle* (C) in Baja California Sur (field misting experiment) and controlled greenhouse (controlled mist chamber experiment) following exposure to labelled mist water. In the field misting experiment, following exposure with labelled water, foliar δD became more depleted across all species ($p < 0.05$), while foliar δ^{18}O became more enriched across all three species ($p < 0.05$). In the controlled mist chamber experiment, foliar δD became more depleted in *A. germinans* and *L. racemosa* ($p < 0.05$ and $p = 0.06$ respectively). The solid line is the sample median, diamond is the mean, dashed lines are the minimum and maximum distribution

In our controlled mist chamber experiment, we observed a similar pattern to that in the field misting experiment, where change in foliar δD (post-mist minus pre-mist application) differed significantly across each of the three species ($F_{2,17} = 10.42$, $p < 0.01$; Figure 4C;

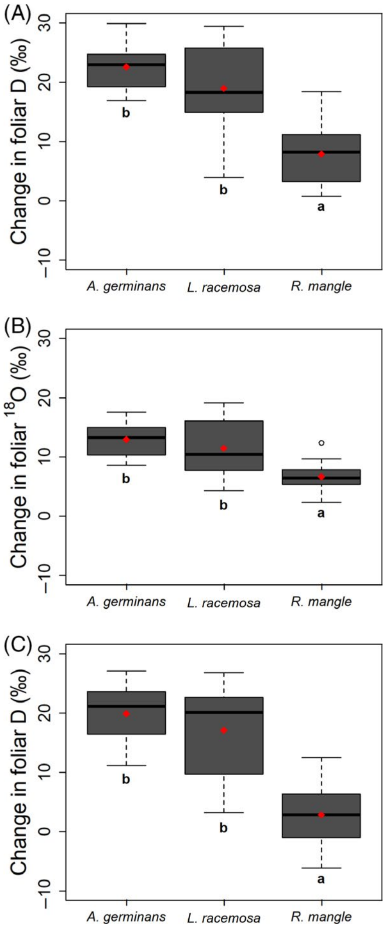

FIGURE 4 Absolute change in foliar δD (A and C) and $\delta^{18}O$ (B; post-mist minus pre-mist application) across each of the mangrove species in Baja California Sur field misting experiment (A and B) and controlled mist chamber experiments (C). Change in foliar δD and $\delta^{18}O$ differed significantly across each of the three species for both the field misting experiment and controlled mist chamber experiment ($p < 0.01$). *Rhizophora mangle* had significantly less change in foliar δD and $\delta^{18}O$ than *Laguncularia racemosa* ($p < 0.05$) or *Avicennia germinans* ($p < 0.05$). Letters 'a' and 'b' indicate a significant difference ($p < 0.05$) between species. The solid line is the sample median, diamond is the mean, dashed lines are the minimum and maximum distribution

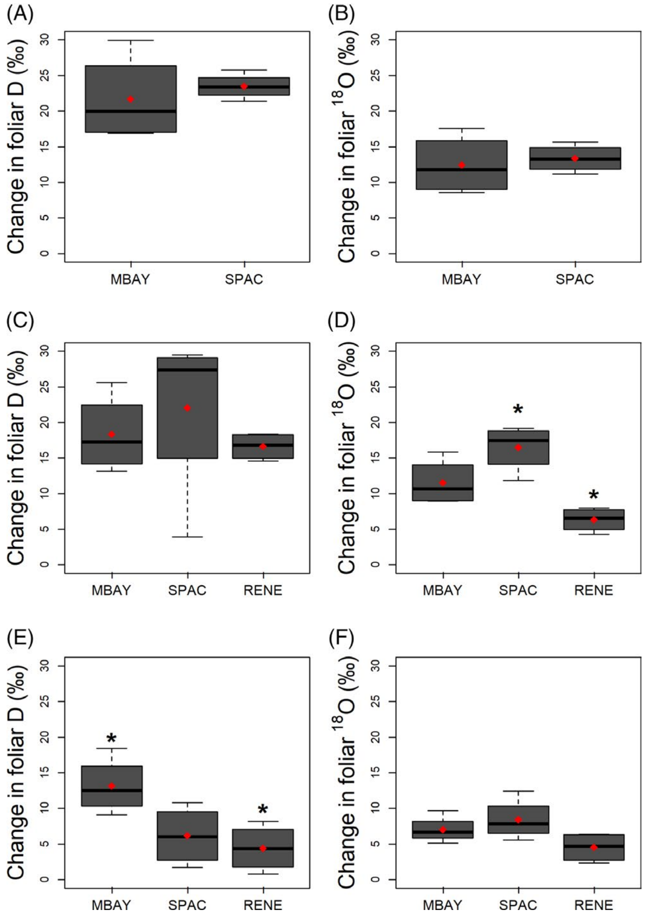

FIGURE 5 Absolute change in foliar ^{2}D ‰ and ^{18}O ‰ (post-mist minus pre-mist application) for *Avicennia germinans* (panels A and B), *Laguncularia racemosa* (panels C and D) and *Rhizophora mangle* (panels E and F) across each of the three mist exposure locations in Baja California Sur, Mexico. Change in foliar ^{18}O ‰ differed significantly across locations for *L. racemosa* ($p < 0.01$), while change in foliar ^{2}D ‰ differed significantly across locations for *R. mangle* ($p < 0.05$). Treatment locations are abbreviated as Magdalena Bay (MBAY), Santispac (SPEC) and Campo Rene (RENE). The solid line is the sample median, diamond is the mean, dashed lines are the minimum and maximum distribution. The asterisk indicates significant differences between locations

Table S2). Change in foliar δD was lowest in *R. mangle* (5.16 ± 1.55‰) than either *L. racemosa* ($p < 0.05$; 17.11 ± 3.65‰) or *A. germinans* ($p < 0.05$; 19.93 ± 2.14‰). There was no difference in change of foliar δD between *A. germinans* and *L. racemosa* ($p > 0.05$).

Change in foliar δD and $\delta^{18}O$ did not differ significantly across Baja California Sur treatment locations for *A. germinans* ($t_{(3.53)} = 0.56$, $p = 0.61$; and $t_{(4.24)} = 0.40$, $p = 0.71$ respectively; Figure 5A,B; Table S2). There was no significant interaction in change in foliar δD and treatment location for *L. racemosa* ($F_{2,9} = 0.50$, $p = 0.62$; Figure 5C). However, there was a significant interaction in change of foliar $\delta^{18}O$ for *L. racemosa* across treatment locations ($F_{2,9} = 12.57$, $p < 0.01$; Figure 5D). The most significant difference in change of foliar $\delta^{18}O$ was between Campo Rene and Santispac ($p < 0.01$), with only a weak nonsignificant difference between Magdalena Bay and Santispac ($p = 0.09$) or Campo Rene ($p = 0.07$). Conversely, there was a significant interaction in change in foliar δD in *R. mangle* across treatment locations ($F_{2,9} = 5.88$, $p < 0.05$; Figure 5E) with the largest difference observed between Magdalena Bay and Campo Rene ($p < 0.05$), and a weak difference between Magdalena Bay and Santispac ($p = 0.07$). There was no significant difference in change in foliar δD between Santispac and Campo Rene locations ($p = 0.81$). There was no significant change in foliar $\delta^{18}O$ for *R. mangle* across treatment locations ($F_{2,9} = 2.85$, $p = 0.11$; Figure 5F).

3.4 | Proportional use of water sources

The MixSIAR isotope mixing model for foliar water following labelled mist exposure indicated that the mean proportion of mist water within leaves following a misting event (in the field misting experiment) was highest in *A. germinans* (32 ± 2%), with mist water making up 26 ± 2% and 16 ± 1% for *L. racemosa* and *R. mangle* respectively. The mean proportion of mist water within leaves was highest for all species sampled in Santispac (28 ± 3%, 24 ± 2% and 13 ± 2% for *L. racemosa*, *A. germinans* and *R. mangle* respectively) followed by Magdalena Bay (19 ± 2%, 22 ± 3% and 12 ± 2% for *L. racemosa*, *A. germinans* and *R. mangle* respectively) and lowest in Campo Rene (12 ± 2% and 8 ± 2% for *L. racemosa* and *R. mangle* respectively).

4 | DISCUSSION

4.1 | Foliar water uptake increases plant water availability in mangroves

Changes in foliar δD and $\delta^{18}O$ following isotopically labelled mist exposure suggests *A. germinans*, *L. racemosa* and *R. mangle* all have the ability to use foliar uptake as a freshwater acquisition strategy. This finding supports our initial hypothesis that foliar water uptake will increase plant water availability. This is the first observation of foliar water use in three co-occurring mangrove species in an arid zone where foliar water uptake might be critical to relieving water stress, although the grey mangrove *A. marina*, a close relative of *A. germinans*, can also utilize foliar water (Schreel et al., 2019).

In our foliar water capacity experiment, we showed that LWC significantly increased in all three mangrove species after freshwater exposure. These findings demonstrate leaf surface permeability to water and the capacity to absorb water directly into photosynthetic leaf tissues in three species from three different families. In a similar foliar water capacity experiment in redwood forest species, Limm et al. (2009) found that 80% of dominant redwood forest species exhibited leaf surface permeability to water, and that LWC increased by up to 11% in some species. In our experiment, LWC increased by 18%, 13% and 8% for *A. germinans*, *L. racemosa* and *R. mangle* respectively. The larger increase in LWC for *A. germinans* and *L. racemosa* may have been due to the hydration condition of the plants from which the leaves were harvested at the time of sampling, or may reflect an inherent water deficit in mangroves due to these plants living in a more saline environment than redwood forests, which places the plants in a pseudo-drought condition at the root–plant interface (Reef & Lovelock, 2015). Thus, our LWC experiment, in conjunction with our observed changes in foliar δD and $\delta^{18}O$ values across all three mangrove species, suggests freshwater coalesced on leaf surfaces through rain, fog or mist events may play an important role in increasing leaf water hydration in mangroves. This mechanism may be particularly important in regions such as the Pacific coast of Baja California Sur and Northwest Australia that are characterized by low rainfall but regular occurrences of fog.

4.2 | Variations in foliar water uptake across co-occurring mangrove species

We also hypothesized that foliar water uptake would differ across co-occurring mangrove species. In our study, we found significant variation in foliar water accumulation across all three species, with the largest foliar water accumulation in *A. germinans*, and the lowest in *R. mangle*. This large difference in foliar water uptake across species may be indicative of species-specific water balance strategies adopted by different mangrove species. For example, leaf anatomical traits such as sunken stomata, stomata density, leaf succulence, leaf angle relative to the sun, leaf pubescence and leaf size all play a significant role in reducing plant water loss and vary broadly across mangrove species (Lovelock & Clough, 1992; Reef & Lovelock, 2015). Although we did not identify the specific pathway for water entry into leaves in our study, research into water-uptake pathways has shown that plant stomata, in addition to other possible water entry points, is an important pathway for foliar water uptake in plant tissues (Eichert, Kurtz, Steiner, & Goldbach, 2008). Thus, the density of stomata on leaf surfaces may also play an important role in limiting the ability of plants to access foliar water sources. However, these same water-saving adaptations may also reduce the ability of plants to access foliar water. For example, in a study of leaf gas exchange characteristics of our three study species, Krauss, Twilley, Doyle, and Gardiner (2006) found *A. germinans* had lower mean water-use efficiencies (WUEs) than either *R. mangle* or *L. racemosa*. Here, we report that *A. germinans* had higher foliar water uptake than *R. mangle* or *L. racemosa*. Similarly, Rodríguez-Rodríguez, Mancera Pineda, Melgarejo, and Medina Calderón (2018) identified a similar pattern across the same three species, with *R. mangle* having higher WUEs than either *A. germinans* or *L. racemosa*. Furthermore, they found stomatal density was lower in *R. mangle* compared to both *L. racemosa* and *A. germinans*, which may play an important function in reducing water loss to the atmosphere. Taken together, the results of Krauss et al. (2006) and Rodríguez-Rodríguez et al. (2018) and our results may suggest that *A. germinans* utilizes increased foliar water uptake to compensate for lower WUE. Additionally, *R. mangle* may have a lower ability to access foliar water because of water-saving adaptations, such as reduced stomatal density, that increase that particular species WUE. Thus, differences in foliar water-uptake capacity may be indicative of species-specific adaptations to avoid water deficits, and may explain the distribution patterns observed in these species across Baja California Sur.

Along the Pacific coastline of Baja California Sur, Magdalena Bay represents the northernmost distribution of *A. germinans*, whereas *L. racemosa* and *R. mangle* persist to 26°N, at Campo Rene. Interestingly, Campo Rene receives considerably fewer fog days (2.6 days/year; Table S1) than Magdalena Bay (10.7 days/year), and less precipitation (~50 mm/year; Table S1) than either Magdalena Bay (~94 mm/year) or Santispac (~189 mm/year). Thus, although relatively high rates of foliar water uptake may confer a competitive advantage to *A. germinans* in arid environments where atmospheric water is available, the relative rarity of fog and rainfall at the northernmost range limits for mangroves on the Pacific Baja coastline may preclude survival and growth of *A. germinans*. Although *L. racemosa* and *R. mangle* had lower capacity for foliar water uptake, their higher WUEs would likely reduce the necessity, and possibly the ability, to access foliar water to meet plant water demands, and in doing so, allowing their persistence in more arid climates.

4.3 | Foliar water use in plants sourced from arid or subtropical regions

The observed change in foliar δD following labelled mist exposure followed a near identical pattern across all three mangrove species in both our field misting experiment and controlled mist chamber experiment, suggesting that species-specific differences rather than environmental conditions dictate the extent of foliar water uptake. Although the change in foliar δD for *R. mangle* in the controlled mist exposure experiment was not significant, there was still some small increase in foliar δD and the variability in the amount of foliar δD was quite high across individuals. In the field misting experiment, there was clear uptake of foliar δD in *R. mangle*, which suggests that the water balance strategies and utilization of foliar water uptake across species and individuals may be complex and is likely driven by a range of external environmental factors that influence the capacity for a plant to access foliar water.

Interestingly, the mangrove populations used in our field misting experiment and controlled mist chamber experiment were from opposite sides of the North American continent and have been genetically isolated since the creation of the Panamanian Isthmus some three million years ago (Ochoa-Zavala, Jaramillo-Correa, Piñero, Nettel-Hernanz, & Núñez-Farfán, 2019; O'Dea et al., 2016; Sandoval-Castro et al., 2014). This observation across genetically isolated populations indicates that foliar water utilization by these mangrove species is likely not a water acquisition adaptation by range limit populations in dry, arid environments, or by populations in humid, subtropical environments, and that foliar water can be utilized irrespective of drought conditioning or genetic disposition in these three mangrove species. Thus, foliar water uptake in *A. germinans*, *L. racemosa*, and to a lesser extent by *R. mangle*, may be used as a water acquisition strategy by these plants across a large range of environmental conditions, and may be a key reason for these species' abilities to survive across large salinity and aridity gradients.

Changes in foliar water uptake across field misting experiment locations were highly variable across species and isotope signatures. Foliar water uptake did not vary across exposure locations for *A. germinans*, but there was a significant difference across exposure locations for both *L. racemosa* and *R. mangle* depending on isotope and environmental variability across locations. However, for both of these species, the general trend pointed towards reduced foliar water accumulation at Campo Rene, which is the northern most range limit for *L. racemosa* and *R. mangle* on the west coast of the Baja peninsula. Consequently, although we propose that foliar water uptake does vary significantly across exposure locations with a general pattern of declining foliar water accumulation towards the range limit of *L. racemosa* and *R. mangle*, where there is less freshwater availability, it is difficult to determine what the particular environmental factor, or combination of factors, that drives this change in foliar water accumulation across locations.

Proportional water sources, as indicated by the MixSiar isotope mixing model, suggest the importance of foliar water uptake for mangroves, in particular for *A. germinans*, where we observed mean proportional use of foliar water in leaves made up nearly a third of the water extracted from the leaves. Interestingly, the relative differences in foliar water uptake observed in the mixing model were similar across the three species as those observed in the foliar water capacity experiment, with foliar water uptake highest in *A. germinans* and lowest in *R. mangle*. However, the modelling results suggested a larger foliar water uptake than the foliar water capacity experiment. This is likely due to the intact plant–soil water potential gradient within intact leaves in the field misting experiment, drawing water from the external leaf surface into the leaf, and also simultaneously drawing internal foliar water into the plant stem towards the roots (Schreel et al., 2019; Steppe et al., 2018). For the foliar water capacity experiment, we used detached leaves which would not have a plant to soil water potential gradient and was therefore indicating change in water content within the leaves rather than a proportional change in foliar water sources following mist exposure. This observation highlights the importance of water potential gradients across the soil to plant and plant to atmosphere interfaces to facilitate foliar water uptake into plant leaf tissue, and then further down into plant stems towards the soil. The reverse flow of sap from the leaf surface down to the roots of the plant requires a directional change in the water potential gradient within the soil–plant–atmosphere gradient. A reverse sap flow has been reported in mangroves at night (Hao et al., 2009), and more recently as a result of foliar water uptake driven by rainfall events (Schreel et al., 2019), indicating the importance of atmospheric water coalescing on leaf surfaces, which increases atmospheric humidity high enough to alter the water potential gradient and drive foliar water uptake by reverse sap flow through the plant.

The pre-mist exposure isotope composition of leaves for each of the three species in the field misting experiment was highly enriched in comparison to source water, indicating possible fractionation and enrichment of source water during water uptake and transpiration processes. Isotopic discrimination of water has been shown to occur at the plant root to soil interface during water uptake (Ellsworth & Williams, 2007), and in proximity to leaf photosynthetic tissues (Flanagan & Ehleringer, 1991). In coastal habitats, hydrogen isotope fractionation has been shown to take place during water uptake (Lin & Sternberg, 1993; Sternberg & Swart, 1987). Plants living in arid, desert environments, in addition to plants living in saline habitats, experience isotope fractionation and enrichment as a result of plant adaptations and water balance strategies to reduce water loss to the atmosphere (Gat et al., 2007). This observation further supports our earlier suggestion that species-specific water balance strategies adopted by different mangrove species may be driving foliar water-use capabilities across species. In our results, there is a general observational trend towards higher isotope enrichment with higher latitude in pre-exposure leaf water composition, suggesting plants at higher, drier, latitudes (towards species range limits) are adopting more conservative water-saving strategies than plants in lower latitudes with higher incidence of fog and precipitation events (Table S1).

There was also a general trend for a decrease in isotopic change in foliar water composition post-mist exposure, suggesting plants at higher latitudes, which experience drier conditions, may be losing less water to the atmosphere as a result of water-saving strategies, and as a result, are also accessing less atmospheric water. To address this possible link between plant water balance strategies and foliar water uptake in mangroves, and to advance our understanding of the importance of foliar water use in all plants, we recommend more controlled studies, including further research into the influence of environmental factors on foliar water use, and any possible links between plant water-saving mechanisms such as leaf size, succulence, stomata density and size, and WUE on a plant's ability to access foliar water. We also recommend further research into how sea fog, and sea fog salinity, might affect foliar water uptake in mangroves. Although many types of arid-zone plants have been shown to access sea fog through foliar water uptake, to date there are no studies investigating how salinity concentrations within sea fog might vary and affect foliar water uptake.

4.4 | Broad ecological implications of foliar water uptake

Over the past few decades, annual minimum and maximum temperatures have increased at a faster rate than mean temperatures, with consequent increases in the incidence and severity of extreme weather events such as heat waves and drought (Hansen, Sato, & Ruedy, 2012; Kim et al., 2016; Krakauer, 2018; Wuebbles et al., 2017). The increased occurrence of extreme warming events is having a dramatic effect on many coastal wetland systems, such as increased fire frequency (Beckage, Platt, Slocum, & Panko, 2003) and mass mortality events (Lovelock, Feller, Reef, Hickey, & Ball, 2017). In arid regions such as Baja California, the west coast of South America, the Middle East, and Western Australia, where freshwater inputs are already low and limit the growth of mangroves at the edge of their current distribution, changes in water availability will likely have an important influence on mangrove distribution patterns (Lovelock, Krauss, Osland, Reef, & Ball, 2016; Record, Charney, Zakaria, & Ellison, 2013). Changes to non-saline water availability will negatively affect plant productivity and persistence of many coastal wetland ecosystems (Lovelock, Feller, et al., 2017). The ecological implications from loss of mangrove habitat include shifts in the geographical range limit of species (Cavanaugh et al., 2019; Osland et al., 2017), changes in species composition within communities (Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014), and changes in the structure and functioning of adjoining coastal ecosystems (Pittman, 2017; Sheaves, 2005). Thus, as the incidence of extreme weather events continues to rise, foliar water uptake may become an increasingly important mechanism for mangroves to maintain water balance during periods of water deficiency (Schreel & Steppe, 2020). However, we also need to better understand the impacts of climate change on foliar water sources such as fog and mist. Increases in temperate may act to reduce relative humidity, thereby limiting foliar water sources and negatively impacting species that currently depend on foliar water uptake.

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AUTHORS' CONTRIBUTIONS

M.A.H., K.C.C., S.C. and J.A.L. conceived and designed the experiments; M.A.H., A.J., J.D.P., E.O. and K.C.C. performed the experiments; M.A.H. and A.J. created the figures; M.A.H. wrote the manuscript with editorial support from all authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qv9s4mwbf (Hayes et al., 2020).

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REFERENCES

Beckage, B., Platt, W. J., Slocum, M. G., & Panko, B. (2003). Influence of the El Nino southern oscillation on fire regimes in the Florida everglades. *Ecology*, *84*, 3124–3130. https://doi.org/10.1890/02-0183

Berry, Z. C., Emery, N. C., Gotsch, S. G., & Goldsmith, G. R. (2019). Foliar water uptake: Processes, pathways, and integration into plant water budgets. *Plant, Cell & Environment*, *42*, 410–423. https://doi.org/10.1111/pce.13439

Cavanaugh, K. C., Dangremond, E. M., Doughty, C. L., Williams, A. P., Parker, J. D., Hayes, M. A., … Feller, I. C. (2019). Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 21602–21608. https://doi.org/10.1073/pnas.1902181116

Eichert, T., Kurtz, A., Steiner, U., & Goldbach, H. E. (2008). Size exclusion limits and lateral heterogeneity of the stomatal foliar uptake pathway for aqueous solutes and water-suspended nanoparticles. *Physiologia Plantarum*, *134*, 151–160. https://doi.org/10.1111/j.1399-3054.2008.01135.x

Ellsworth, P. Z., & Williams, D. G. (2007). Hydrogen isotope fractionation during water uptake by woody xerophytes. *Plant and Soil*, *291*, 93–107. https://doi.org/10.1007/s11104-006-9177-1

Ewe, S. M. L., Sternberg, L. D. S. L., & Childers, D. L. (2007). Seasonal plant water uptake patterns in the saline southeast Everglades ecotone. *Oecologia*, *152*, 607–616. https://doi.org/10.1007/s00442-007-0699-x

Flanagan, L. B., & Ehleringer, J. R. (1991). Effects of mild water stress and diurnal changes in temperature and humidity on the stable oxygen and hydrogen isotopic composition of leaf water in *Cornus stolonifera*. *Plant Physiology*, *97*, 298–305. https://doi.org/10.1104/pp.97.1.298

Gabler, C. A., Osland, M. J., Grace, J. B., Stagg, C. L., Day, R. H., Hartley, S. B., … McLeod, J. L. (2017). Macroclimatic change expected to transform coastal wetland ecosystems this century. *Nature Climate Change*, *7*, 142–147. https://doi.org/10.1038/nclimate3203

Gat, J. R., Yakir, D., Goodfriend, G., Fritz, P., Trimborn, P., Lipp, J., … Waisel, Y. (2007). Stable isotope composition of water in desert plants. *Plant and Soil*, *298*, 31–45. https://doi.org/10.1007/s11104-007-9321-6

Hansen, J., Sato, M., & Ruedy, R. (2012). Perception of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 2415–2423. https://doi.org/10.1073/pnas.1205276109

Hao, G.-Y., Jones, T. J., Luton, C., Zhang, Y.-J., Manzane, E., Scholz, F. G., … Goldstein, G. (2009). Hydraulic redistribution in dwarf *Rhizophora mangle* trees driven by interstitial soil water salinity gradients: Impacts on hydraulic architecture and gas exchange. *Tree Physiology*, *29*, 697–705. https://doi.org/10.1093/treephys/tpp005

Hayes, M. A., Chapman, S., Jesse, A., O'Brien, E., Langley, A. J., Bardou, R., … Cavanaugh, K. C. (2020). Data from: Foliar water uptake by coastal wetland plants: A novel water acquisition mechanism in arid and humid subtropical mangroves. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.qv9s4mwbf

Hayes, M. A., Jesse, A., Tabet, B., Reef, R., Keuskamp, J. A., & Lovelock, C. E. (2017). The contrasting effects of nutrient enrichment on growth, biomass allocation and decomposition of plant tissue in coastal wetlands. *Plant and Soil*, *416*, 193–204. https://doi.org/10.1007/s11104-017-3206-0

Hayes, M. A., Jesse, A., Welti, N., Tabet, B., Lockington, D., & Lovelock, C. E. (2019). Groundwater enhances above-ground growth in mangroves. *Journal of Ecology*, *107*, 1120–1128. https://doi.org/10.1111/1365-2745.13105

Kim, Y.-H., Min, S.-K., Zhang, X., Zwiers, F., Alexander, L. V., Donat, M. G., & Tung, Y.-S. (2016). Attribution of extreme temperature changes during 1951–2010. *Climate Dynamics*, *46*, 1769–1782. https://doi.org/10.1007/s00382-015-2674-2

Krakauer, N. Y. (2018). Shifting hardiness zones: Trends in annual minimum temperature. *Climate*, *6*, 15. https://doi.org/10.3390/cli6010015

Krauss, K. W., Twilley, R. R., Doyle, T. W., & Gardiner, E. S. (2006). Leaf gas exchange characteristics of three neotropical mangrove species in response to varying hydroperiod. *Tree Physiology*, *26*, 959–968. https://doi.org/10.1093/treephys/26.7.959

Li, S., Xiao, H.-L., Zhao, L., Zhou, M.-X., & Wang, F. (2014). Foliar water uptake of *Tamarix ramosissima* from an atmosphere of high humidity. *The Scientific World Journal*, *2014*, 1–10. https://doi.org/10.1155/2014/529308

Limm, E. B., Simonin, K. A., Bothman, A. G., & Dawson, T. E. (2009). Foliar water uptake: A common water acquisition strategy for plants of the redwood forest. *Oecologia*, *161*, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Lin, G., & Sternberg, L. (1993). Hydrogen isotopic fractionation during water uptake in coastal wetland plants. In J. Ehleringer, A. Hall, & G. Farquhar (Eds.), *Stable isotopes and plant carbon-water relations* (pp. 497–510). San Diego, CA: Academic Press.

Lovelock, C. E., & Clough, B. F. (1992). Influence of solar radiation and leaf angle on leaf xanthophyll concentrations in mangroves. *Oecologia*, *91*, 518–525. https://doi.org/10.1007/BF00650325

Lovelock, C. E., Feller, I. C., Reef, R., Hickey, S., & Ball, M. C. (2017). Mangrove dieback during fluctuating sea levels. *Scientific Reports*, *7*, 1680. https://doi.org/10.1038/s41598-017-01927-6

Lovelock, C. E., Krauss, K. W., Osland, M. J., Reef, R., & Ball, M. C. (2016). The physiology of mangrove trees with changing climate. In G. Goldstein & L. S. Santiago (Eds.), *Tropical tree physiology: Adaptations and responses in a changing environment* (pp. 149–179). Cham: Springer International Publishing.

Lovelock, C. E., Reef, R., & Ball, M. C. (2017). Isotopic signatures of stem water reveal differences in water sources accessed by mangrove tree species. *Hydrobiologia*, *803*, 133–145. https://doi.org/10.1007/s10750-017-3149-8

Martin, C. E., & von Willert, D. J. (2000). Leaf epidermal hydathodes and the ecophysiological consequences of foliar water uptake in species of crassula from the Namib Desert in Southern Africa. *Plant Biology*, *2*, 229–242. https://doi.org/10.1055/s-2000-9163

Méndez-Alonzo, R., López-Portillo, J., & Rivera-Monroy, V. H. (2008). Latitudinal variation in leaf and tree traits of the mangrove *Avicennia germinans* (Avicenniaceae) in the central region of the Gulf of Mexico. *Biotropica*, *40*, 449–456. https://doi.org/10.1111/j.1744-7429.2008.00397.x

Mulroy, T. W., & Rundel, P. W. (1977). Annual plants: Adaptations to desert environments. *BioScience*, *27*, 109–114. https://doi.org/10.2307/1297607

Ochoa-Zavala, M., Jaramillo-Correa, J. P., Piñero, D., Nettel-Hernanz, A., & Núñez-Farfán, J. (2019). Contrasting colonization patterns of black mangrove (*Avicennia germinans* (L.) L.) gene pools along the Mexican coasts. *Journal of Biogeography*, *46*, 884–898. https://doi.org/10.1111/jbi.13536

O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., … Jackson, J. B. C. (2016). Formation of the Isthmus of Panama. *Science Advances*, *2*, 1–11. https://doi.org/10.1126/sciadv.1600883

Osland, M. J., Feher, L. C., Griffith, K. T., Cavanaugh, K. C., Enwright, N. M., Day, R. H., … Rogers, K. (2017). Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs*, *87*(2), 341–359. https://doi.org/10.1002/ecm.1248

Osland, M. J., Gabler, C. A., Grace, J. B., Day, R. H., McCoy, M. L., McLeod, J. L., … Hartley, S. B. (2018). Climate and plant controls on soil organic matter in coastal wetlands. *Global Change Biology*, *24*, 5361–5379. https://doi.org/10.1111/gcb.14376

Pittman, S. J. (2017). *Seascape ecology*. Hoboken, NJ: John Wiley and Sons Ltd.

Record, S., Charney, N. D., Zakaria, R. M., & Ellison, A. M. (2013). Projecting global mangrove species and community distributions under climate change. *Ecosphere*, *4*, art34. https://doi.org/10.1890/ES12-00296.1

Reef, R., & Lovelock, C. E. (2015). Regulation of water balance in mangroves. *Annals of Botany*, *115*, 385–395. https://doi.org/10.1093/aob/mcu174

Reef, R., Markham, H. L., Santini, N. S., & Lovelock, C. E. (2015). The response of the mangrove *Avicennia marina* to heterogeneous salinity measured using a split-root approach. *Plant and Soil*, *393*, 297–305. https://doi.org/10.1007/s11104-015-2489-2

Rodríguez-Rodríguez, J. A., Mancera Pineda, J. E., Melgarejo, L. M., & Medina Calderón, J. H. (2018). Functional traits of leaves and forest structure of neotropical mangroves under different salinity and nitrogen regimes. *Flora*, *239*, 52–61. https://doi.org/10.1016/j.flora.2017.11.004

Rundel, P. W. (1982). Water uptake by organs other than roots. In O. L. Lange, P. S. Nobel, C. B. Osmond, & H. Ziegler (Eds.), *Physiological plant ecology II: Water relations and carbon assimilation* (pp. 111–134). Berlin, Heidelberg: Springer Berlin Heidelberg.

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, *20*, 147–157. https://doi.org/10.1111/gcb.12341

Sandoval-Castro, E., Dodd, R. S., Riosmena-Rodríguez, R., Enríquez-Paredes, L. M., Tovilla-Hernández, C., López-Vivas, J. M., … Muñiz-Salazar, R. (2014). Post-glacial expansion and population genetic divergence of mangrove species *Avicennia germinans* (L.) Stearn and *Rhizophora mangle* L. along the Mexican Coast. *PLoS ONE*, *9*, e93358. https://doi.org/10.1371/journal.pone.0093358

Schreel, J. D. M., & Steppe, K. (2019). Foliar water uptake changes the world of tree hydraulics. *NPJ Climate and Atmospheric Science*, *2*, 1. https://doi.org/10.1038/s41612-018-0060-6

Schreel, J. D. M., & Steppe, K. (2020). Foliar water uptake in trees: Negligible or necessary? *Trends in Plant Science*. https://doi.org/10.1016/j.tplants.2020.01.003

Schreel, J. D. M., Van de Wal, B. A. E., Hervé-Fernandez, P., Boeckx, P., & Steppe, K. (2019). Hydraulic redistribution of foliar absorbed water causes turgor-driven growth in mangrove seedlings. *Plant, Cell & Environment*, *42*, 2437–2447. https://doi.org/10.1111/pce.13556

Sheaves, M. (2005). Nature and consequences of biological connectivity in mangrove systems. *Marine Ecology Progress Series*, *302*, 293–305. https://doi.org/10.3354/meps302293

Simard, M., Fatoyinbo, L., Smetanka, C., Rivera-Monroy, V. H., Castañeda-Moya, E., Thomas, N., & Van der Stocken, T. (2019). Mangrove canopy height globally related to precipitation, temperature and cyclone frequency. *Nature Geoscience*, *12*, 40–45. https://doi.org/10.1038/s41561-018-0279-1

Steppe, K., Vandegehuchte, M. W., Van de Wal, B. A. E., Hoste, P., Guyot, A., Lovelock, C. E., & Lockington, D. A. (2018). Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove *Avicennia marina*. *Tree Physiology*, *38*, 979–991. https://doi.org/10.1093/treephys/tpy024

Sternberg, L. D. S. L., & Swart, P. K. (1987). Utilization of freshwater and ocean water by coastal plants of Southern Florida. *Ecology*, *68*, 1898–1905. https://doi.org/10.2307/1939881

Stock, B. C., & Semmens, B. X. (2016). *MixSIAR GUI user manual*. Version 3.1. Retrieved from https://github.com/brianstock/MixSIAR/

Wuebbles, D. J., Easterling, D. R., Hayhoe, K., Knutson, T., Kopp, R. E., Kossin, J. P., … Wehner, M. F. (2017). Our globally changing climate. In D. J. Wuebbles, D. W. Fahey, K. A. Hibbard, D. J. Dokken, B. C. Stewart, & T. K. Maycock (Eds.), *Climate science special report: Fourth national climate assessment* (pp. 35–72). Washington, DC: U.S. Global Change Research Program.

Yan, X., Zhou, M., Dong, X., Zou, S., Xiao, H., & Ma, X.-F. (2015). Molecular mechanisms of foliar water uptake in a desert tree. *AoB Plants*, *7*, plv129. https://doi.org/10.1093/aobpla/plv129

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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