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Coastal fog enhances physiological function of seaside daisies (*Erigeron glaucus*)

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Abstract.—Seaside daisy (*Erigeron glaucus*) is a plant native to fog-influenced coastal dune habitat in California. Seaside daisy is an important nectar plant to a variety of pollinators, especially butterflies, and is commonly used in coastal dune habitat restoration projects. In San Francisco, pollinator habitat restoration is critical for preserving species that would have otherwise been lost to urbanization. Advancing our basic understanding of how microclimate conditions (coastal fog in particular) impact the physiological function of the seaside daisy is an important first step to developing climate change–resilient habitat restoration plans. In semiarid Mediterranean ecosystems, coastal fog can augment plant water status in otherwise drought-stressed plants through fog drip to the soil, reduction of atmospheric stress, and/or leaf wetting that can result in foliar uptake of fog water. While there is a high degree of uncertainty as to how coastal fog frequency may be impacted by climate change, historical observations show a 33% decline in coastal fog along the Pacific Coast. As the climate continues to change, the potential reduction of this crucial water resource may negatively impact the plants within foggy environments. However, the importance of coastal fog in supporting the physiological function of seaside daisies has not yet been studied. We conducted a manipulative fog experiment to understand the relative importance of coastal fog and irrigation to the physiological function of seaside daisy plants. In a controlled chamber, plants were exposed to the following treatment groups: (1) fog and irrigation, (2) fog only, (3) irrigation only, and (4) neither fog nor irrigation. We measured leaf-level photosynthesis rates and stomatal conductance using a portable photosynthesis system (Model Li-6800, LICOR Biosciences). We monitored microclimate conditions in each chamber as well as shallow soil moisture (5 cm) in a subset of the study plants. We found that photosynthesis rates increased when plants experienced simulated fog events, regardless of irrigation; irrigated plants increased by 26%, whereas nonirrigated plants increased by 31%. We also found that soil moisture was a weak predictor of photosynthesis rates, suggesting that heightened photosynthesis rates during fog events were not driven by fog drip to the soil in our study. Our results strongly suggest that fog matters to the function of this important nectar plant species and that the mechanism is likely foliar uptake of fog water. Our study informs how coastal fog events can increase the likelihood of survival for seaside daisies and therefore improve overall pollinator habitat quality.

Resumen.—La margarita costera (*Erigeron glaucus*) es una planta autóctona del hábitat de dunas costeras influenciada por la niebla en California. Es una especie de planta nectarífera importante para diversos polinizadores, especialmente mariposas, además, es utilizada habitualmente en proyectos de restauración de hábitats de dunas costeras. En San Francisco, la restauración del hábitat de polinizadores es fundamental para preservar especies que, de otro modo, se habrían perdido a causa de la urbanización. Avanzar en la comprensión básica sobre cómo las condiciones microclimáticas, en particular la niebla costera, afectan la función fisiológica de la margarita costera, es el primer paso importante para desarrollar planes de restauración de hábitats resistentes al cambio climático. En los ecosistemas mediterráneos semiáridos, la niebla costera puede aumentar el estado hídrico de las plantas, mediante el goteo de la niebla en el suelo, que de otro modo estarían sometidas a la sequía, reduciendo el estrés atmosférico, y/o la humectación de las hojas que puede dar lugar a la absorción foliar del agua de la niebla. Aunque existe una gran incertidumbre sobre cómo el cambio climático podría afectar la frecuencia de la niebla costera, las observaciones históricas muestran un descenso del 33% en la niebla costera a lo largo de la costa del Pacífico. A medida que el clima continúa cambiando, la posible reducción de este recurso hídrico crucial, podría afectar negativamente a las plantas dentro de los entornos con niebla. Sin embargo, aún no se ha estudiado la importancia de la niebla costera en el soporte de la función fisiológica de las margaritas costeras. Nosotros, realizamos un experimento de manipulación de la niebla para comprender la importancia relativa de la niebla costera y del riego en la función fisiológica de la margarita costera. En una cámara controlada, las plantas fueron expuestas a los siguientes grupos de tratamiento: (1) niebla y riego, (2) sólo niebla, (3) sólo riego, y (4) sin niebla y sin riego. Con un sistema de fotosíntesis portátil (Modelo Li-6800, LICOR Biosciences), medimós las tasas de fotosíntesis a nivel de hoja y la conductancia estomática. Monitoreamos las condiciones del microclima en cada cámara, y la humedad superficial del suelo (5 cm) en un subconjunto de las plantas de estudio. Encontramos que las tasas de fotosíntesis aumentaron cuando las plantas experimentaban eventos de niebla simulada, independientemente del riego: las

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plantas regadas aumentaron un 26%, mientras que las no regadas aumentaron un 31%. Además, la humedad del suelo fue un predictor débil de las tasas de fotosíntesis, lo que sugiere que el aumento de las tasas de fotosíntesis durante los eventos de niebla no fueron impulsados por el goteo de la niebla en el suelo en nuestro estudio. Nuestros resultados sugieren enfáticamente que la niebla es importante para la función de esta significativa especie de planta nectarífera, y que el mecanismo es probablemente la absorción foliar del agua de la niebla. Nuestro estudio informa cómo los eventos de niebla costera pueden aumentar la probabilidad de supervivencia de las margaritas costeras y, por lo tanto, mejorar la calidad general del hábitat de los polinizadores.

The seaside daisy (*Erigeron glaucus*) is a perennial flowering shrub, native to the coastal bluffs and sand dunes of California and Oregon. It is commonly planted in pollinator gardens and restored habitats because it produces an abundance of bright purple and yellow composite flowers throughout most of the year (winter, spring, and summer), which support a wide variety of pollinators. The color and composition of its flowers tend to attract butterflies, in particular. In San Francisco, seaside daisy plants are a reliable nectar resource for many pollinators, including the threatened Coastal Green Hairstreak (*Callophrys viridis*) butterfly (Nature in the City 2016). A local nonprofit organization, Nature in the City, established the Green Hairstreak Corridor, which is a network of 11 stepping-stone habitats to improve connectivity within the city. The Green Hairstreak Corridor relies on the flowering of seaside daisies to support the Green Hairstreak butterfly during flight season. While these plants receive very little irrigation from site stewards after the initial outplanting, seaside daisies continue to thrive and provide floral resources for the Green Hairstreaks and countless other pollinators. Since many of the Green Hairstreak Corridor restored habitats are frequently inundated by dense coastal fog, it is reasonable to hypothesize that coastal fog events offset water stress to these plants and help maintain photosynthesis during the summertime. Yet, the relative importance of fog and irrigation in supporting the physiological function of seaside daisy plants remains unclear.

From tropical montane forests to arid deserts, fog plays a crucial role in the functioning of ecosystems around the world (Weathers et al. 2020). Fog supports plants in myriad ways, such as augmenting plant water availability (Dawson 1998, Vasey et al. 2012, Baguskas et al. 2016a, 2016b, Fischer et al. 2016), buffering heat stress (Oliphant et al. 2021), and transporting nutrients (Weathers et al. 2020). Studies have shown that fog becomes even more of a vital resource in areas where water is limited, such as in arid and semiarid ecosystems (Fischer et al. 2009, Weathers et al. 2020). There are 3 primary mechanisms by which fog can alleviate water stress: (1) lower temperatures and higher relative humidity reduce evapotranspiration rates (Burgess and Dawson 2004, Fischer et al. 2009, Chung et al. 2017, Baguskas et al. 2021); (2) deposition of fog droplets on surfaces results in fog drip to the soil (Ewing et al. 2009, Fischer et al. 2016, Baguskas et al. 2016b); and (3) the leaves take up fog water directly (Burgess and Dawson 2004, Limm et al. 2009, Eller et al. 2013, Gotsch et al. 2014, Baguskas et al. 2016a). Fog drip is largely influenced by canopy structure (Ewing et al. 2009, Vasey et al. 2012, Weathers et al. 2020). For example, Ewing et al. (2009) found that the water stress of California redwood trees was lower at the fog-inundated forest edge compared to the interior forest. Many plants in foggy areas also have the capacity to absorb water directly through their leaves; this ability is known as foliar uptake (Burgess and Dawson 2004, Limm et al. 2009). Limm et al. (2009) found that 80% of the plant species they studied in the redwood forest (i.e., canopy trees, shrubs, understory ferns, etc.) relied on foliar uptake to hydrate leaves. Vasey et al. (2012) studied dry-season water potential (Ψ_{min}) along a coast-to-interior fog gradient in chaparral shrubs of Central California. Compared to interior chaparral regions, maritime chaparral regions had less negative Ψ_{min} (i.e., higher water status) and greater beta diversity of plants, which was attributed to greater water availability from the summertime marine layer (Vasey et al. 2012). The relatively low canopy height of such regions likely increases fog drip to the soil, while providing sufficient leaf wetting to support foliar uptake (Vasey et al. 2012).

Fog frequently inundates the California coastline during the summertime months

(June–August), alleviating plant water stress and heat stress during an otherwise warm and dry period. Although there is a high degree of uncertainty as to how coastal fog frequency may be impacted by climate change, historical observations show a 33% decline in coastal fog along the Pacific Coast (Johnstone and Dawson 2010), and this pattern could possibly continue in the future (Torregrosa et al. 2014). The reduction of coastal fog could possibly threaten the survival of plants in coastal ecosystems (such as the seaside daisies in sand dunes of San Francisco) by reducing a water resource during the driest months of the year. Such changes would have negative impacts on habitat quality. Studies have shown that a decrease in plant water status from drought results in fewer floral resources, thus limiting floral attractiveness to pollinators and plant reproduction overall (Carroll et al. 2001, Burkle and Runyon 2016). Investigating how coastal fog potentially alleviates the water stress of seaside daisies (and therefore supports plant function) is an important first step to maintaining resilient pollinator habitats in a warmer, drier future.

Summertime coastal fog inundates the sand dune habitat where seaside daisies are found, and it is likely that the plants within this habitat rely heavily on coastal fog to support plant function. Plants in restored sand dune habitat are also irrigated episodically. In this study, we addressed this research question: How do coastal fog events and irrigation impact the physiological function of seaside daisy plants, an important nectar source to many pollinators? We hypothesized that coastal fog would enhance the leaf-level physiological function, namely photosynthesis rates, of seaside daisy plants, especially for those that do not experience regular irrigation. To test our hypothesis, we conducted a manipulative chamber experiment where we exposed seaside daisy plants to varied levels of fog and irrigation, and then we measured the physiological responses of the daisies.

METHODS

Plant Care

We purchased 20 cultivated 1-gallon seaside daisy plants, of the Sebastian variety, from Literacy for Environmental Justice's (LEJ) native plant nursery approximately one year prior to the start of our experiment. LEJ's native plants are commonly used in local habitat restoration projects and are the same source of seaside daisy plants used for Nature in the City's habitat restoration in the Green Hairstreak Corridor. We grew the seaside daisy plants inside the San Francisco State University greenhouses, where they were watered regularly and occasionally fed with Milorganite All Purpose Non-Burning fertilizer (NPK ratio = 6-4-0). Approximately one year after purchase, we transplanted the seaside daisies into 2-gallon pots using GreenAll Natural and Organic Potting Soil. Plants were then moved outdoors and given one feeding of fertilizer to help them re-establish. They were grown outside at the same location as our fog experiment for approximately 3 months before the start of our experiment and were given even and consistent watering. Before the start of the experiment, all plants experienced a week-long dry-down period where they received no watering at all.

Chamber Structure

Seaside daisy plants were placed inside of 2 plastic chambers, a fog chamber and a control chamber (Fig. 1). Both chambers were outdoors, elevated above the ground, and placed on a platform made of wooden planks and cinder blocks. Spacing between the wooden planks (about 2 inches) allowed for moderate airflow in and out of the chambers. Chambers were constructed with a PVC pipe frame (86 cm × 86 cm × 86 cm) and fitted plastic sheets covering all sides except for the bottom. Two holes were cut into the opposing side walls to allow air to flow through the chamber. A semirigid aluminum duct attached an ultrasonic humidifier (Model MBH12, Mainland Mart Corp.) to the fog chamber through one of the chamber's side holes. The ultrasonic humidifier we used produces fog droplets approximately 10 microns in diameter (Baguskas et al. 2016a). We installed a fan inside each chamber to ensure that wind speed was similar in both chambers. Onto the left inside wall of each chamber, 360° desk fans with 4 speeds were clipped pointing diagonally to promote mixing. The control chamber fan was set to the maximum speed (i.e., speed 4). The fog chamber fan was set to a lower speed (i.e., speed 2) to offset the added wind speed from the fog machine.

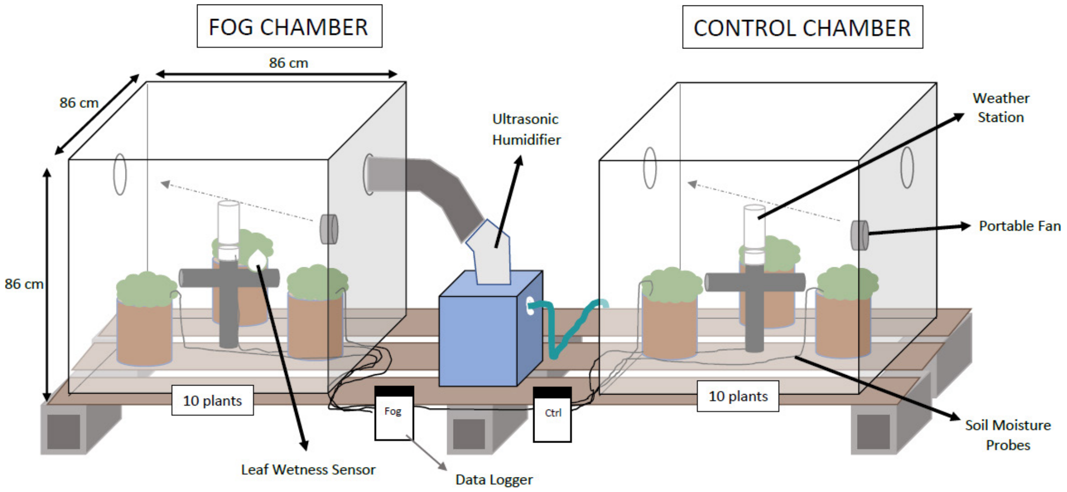

Fig. 1. Diagram of chamber structure and instruments used in a controlled fog experiment.

Environmental Conditions

We installed an all-in-one micrometeorological sensor (ATMOS 41, Meter Group, Inc.) in the middle of each chamber to monitor microclimate conditions during simulated fog events (Fig. 1). We monitored solar radiation ($W \cdot m^{-2}$), precipitation (mm), wind speed ($m \cdot s^{-1}$), air temperature (°C), vapor pressure (kPa), and vapor pressure deficit (VPD, kPa). In addition, one leaf wetness sensor (PHYTOS 31, Meter Group, Inc.) was installed in the fog chamber to monitor leaf wetness during fog events (Fig. 1).

Volumetric soil moisture probes (ECH20 EC-5, Meter Group, Inc.) were inserted vertically from the soil surface (about 5 cm depth) into 2 plants per treatment group to measure soil water content ($m^3 \cdot m^{-3}$) (Fig. 1). This placement allowed us to detect any small changes in shallow soil moisture that might occur from fog drip. Microclimate and soil moisture observations were recorded every 15 min.

Experimental Design

We exposed plants to varied levels of fog and irrigation, and then we measured leaf-level physiological responses. Seaside daisy plants ($N = 20$) were randomly separated into the following 4 treatment groups ($n = 5$ plants per treatment group): fog and irrigation (Fog + Irr), fog only (Fog), irrigation only (Irr), and control (Ctrl), which received neither fog nor irrigation (Table 1). This experiment was conducted entirely outdoors. Seaside daisy plants were grown under ambient conditions and were only placed within plastic chambers during morning treatment events.

Simulated fog treatments were administered for 3 consecutive days per week for 6 weeks between mid-February and March 2021. Simulated fog events began in the morning, just before sunrise, from 07:00 to 09:00. We chose 2 h in the morning because that time is typically when fog is prevalent. We limited our simulation to a 2-h duration because fog generated by the ultrasonic humidifier sufficiently immersed plant canopies within that time.

Plastic covers were placed over the PVC frames 15 min prior to the official start time (06:45). This allowed fog to fully saturate the fog chamber by the start of the 2-h treatment events. Plastic covers were taken off immediately after each event (09:00) so that leaves had time to dry off before we measured leaf gas-exchange rates. Both chambers followed the same procedure, the only difference being that the control chamber did not experience fog.

All plants received some water to ensure plant survival for the duration of the experiment. However, irrigated plants received more consistent water than the nonirrigated plants. Irrigated plants (Fog + Irr and Irr) each received 1 L of water on the night before the start of each treatment week. During heat

TABLE 1. Fog and irrigation treatment groups used in a controlled fog experiment (n = 5 plants per treatment group, N = 20 plants total).

Treatment groups	Fog	No fog
Irrigation	Fog + Irrigation (Fog + Irr)	Irrigation only (Irr)
No irrigation	Fog only (Fog)	Control (Ctrl)

waves, when soil dried rapidly, irrigated plants also received an additional 1 L of water at the end of the week to keep the soil moist. Nonirrigated plants (Fog and Ctrl) only received water when plants reached their wilting point. Even so, nonirrigated plants were only watered at the end of each treatment week (i.e., soil moisture was at its lowest point during the experiment before plants were hydrated).

Physiological Measurements

Following simulated fog events, plants were placed in the sun for approximately 1 h to allow leaves to fully dry off before we measured leaf physiology. To measure leaf gas-exchange rates, we used a portable photosynthesis system (Model Li-6800, LI-COR Biosciences). Two leaves per plant were sampled from all plants in the fog and control chambers between midmorning and early afternoon (10:00–13:00), following the simulated fog events. Plant survey measurements were collected on sunny, warm days. We sampled plants on a total of 5 days during the study period.

All leaf gas-exchange measurements were taken with 2-cm^2 aperture in the leaf chamber. Each leaf sampled filled the entire aperture area. Constant settings included pump flow (500 µmol · s^{-1}), chamber pressure (ΔP_{cham} = 0.1 kPa), carbon dioxide concentration within the sample analyzer (CO2_s = 400 µmol · m^{-1}), fan speed (10,000 rpm), geometry (broad leaf), and oxygen (21%).

Due to fluctuating cloud patterns during measurement hours, we chose to control light levels in the leaf chamber. Prior to the experiment, we constructed a series of light response curves from 4 different seaside daisy plants to find the light saturation point where maximum photosynthesis occurred (Supplementary Material 1). While each plant varied slightly, maximum photosynthesis generally occurred around 1800 µmol · m^{-2}s^{-1} (Supplementary Material 1). Therefore, we adjusted fluorometer settings for light levels within the leaf chamber (Q_{in}) to maintain 1800 µmol · m^{-2} s^{-1} for plant survey measurements.

Leaf temperature (T_{leaf}) and relative humidity of the air within the leaf chamber (RH_{air}) were allowed to vary based on ambient conditions; T_{leaf} ranged from 18 to 21 °C and RH_{air} ranged from 50% to 70%.

Statistical Analysis

We calculated the average physiological response (photosynthesis rates and stomatal conductance) of both leaves per plant. We then calculated the average physiological response of all plants per treatment group (n = 5 per treatment group). We tested for a normal distribution in the data using the Shapiro–Wilk test and found that the data were normally distributed. An analysis of variance (ANOVA) was performed to test for differences in physiological responses between treatment groups. If the ANOVA was significant ($P < 0.05$), we performed a post hoc Tukey HSD (honest statistical difference) test to identify the treatment groups that differed significantly from one another. We tested for an interaction between fog and irrigation treatments with respect to photosynthesis. Statistical analyses were performed using '*aov*' and '*Tukey HSD*' statistical packages in RStudio version 1.0.143.

Micrometeorological observations were recorded every 15 min from each sensor and then aggregated by averaging over the 2 h of each chamber experiment. We then calculated the average conditions in the fog and control chambers, pooling all 6 sampling days. We calculated the average volumetric soil moisture (5 cm) of both plants per treatment group. An ANOVA and a post hoc Tukey HSD test were performed to identify significant differences between treatment groups for both micrometeorological and soil moisture observations.

We also performed a least-squares regression analysis to test for the correlation between leaf-level photosynthesis and environmental factors (ambient temperature, VPD, and soil

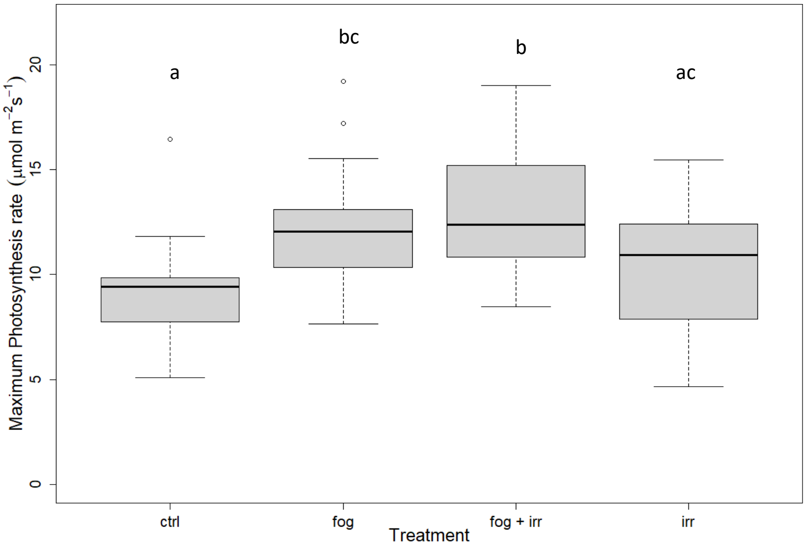

Fig. 2. Box plots of maximum photosynthesis rate (µmol · m^{-2}s^{-1}) by treatment group (Control [Ctrl], fog only [Fog], irrigation only [Irr], and fog and irrigation [Fog + Irr]) following 2-h simulated morning fog events. Heavy black lines within boxes represent averages; box edges represent 25th and 75th percentiles; whiskers represent minimums and maximums; and circles represent outliers. Letters above the box plots represent significant differences between treatment groups ($\alpha = 0.05$); results from the Tukey HSD test are shown in Table 3.

TABLE 2. Average photosynthesis, stomatal conductance, soil moisture, vapor pressure deficit, and ambient temperature by treatment group. Means are given with standard deviations.

Treatment groups	Photosynthesis (µmol · m^{-2}s^{-1})	Stomatal conductance (mol · m^{-2}s^{-1})	Soil moisture (m^3 · m^{-3})	Vapor pressure deficit (kPa)	Ambient temperature (°C)
Fog + Irrigation	13.08 ± 3.01	0.15 ± 0.15	0.25 ± 0.04	0.15 ± 0.14	8.64 ± 1.85
Fog only	12.11 ± 2.63	0.13 ± 0.13	0.07 ± 0.02	0.15 ± 0.14	8.64 ± 1.85
Irrigation only	10.39 ± 3.01	0.11 ± 0.11	0.25 ± 0.02	0.26 ± 0.19	7.45 ± 0.72
Control	9.24 ± 2.21	0.09 ± 0.09	0.05 ± 0.02	0.26 ± 0.19	7.45 ± 0.72

moisture) within each treatment group. Explanatory factors were not autocorrelated. This statistical analysis was performed using the *'lm'* statistical package in RStudio version 1.0.143.

RESULTS

In both the irrigated and nonirrigated groups, plants that received fog had higher average maximum photosynthetic rates (A_{max}) than plants that did not receive fog (irrigated: $A_{max(Fog+Irr)} = 13.08 \pm 3.01$ µmol · m^{-2}s^{-1}, $A_{max(Irr)} = 10.39 \pm 3.01$ µmol · m^{-2}s^{-1}; nonirrigated: $A_{max(Fog)} = 12.11 \pm 2.63$ µmol·m^{-2}s^{-1}, $A_{max(Ctrl)} = 9.24 \pm 2.21$ µmol·m^{-2}s^{-1}) (Table 2, Fig. 2). For plants that received fog, this increase in A_{max} was greater in nonirrigated plants than in irrigated plants, where nonirrigated plants increased by 31% ($\Delta A_{max(Fog)\,-\,(Ctrl)} = 2.87$ µmol · m^{-2}s^{-1}), and irrigated plants increased by 26% ($\Delta A_{max\,(Fog\,+\,Irr)\,-\,(Irr)} = 2.69$ µmol · m^{-2}s^{-1}). In other words, fog became more important when soil moisture was low. Differences in A_{max} between treatment groups were significant ($P < 0.05$), with the exception of Fog + Irr versus Fog ($P = 0.523$), Irr versus Ctrl (P = 0.454), and Fog versus Irr ($P = 0.100$) (Table 3). This lack of difference suggests that plants within the same chamber functioned similarly, despite differences in soil moisture. There were no significant interactions between fog and irrigation treatments that influenced plant function (Fig. 3).

Similarly, plants that received fog had higher average stomatal conductance (g_s),

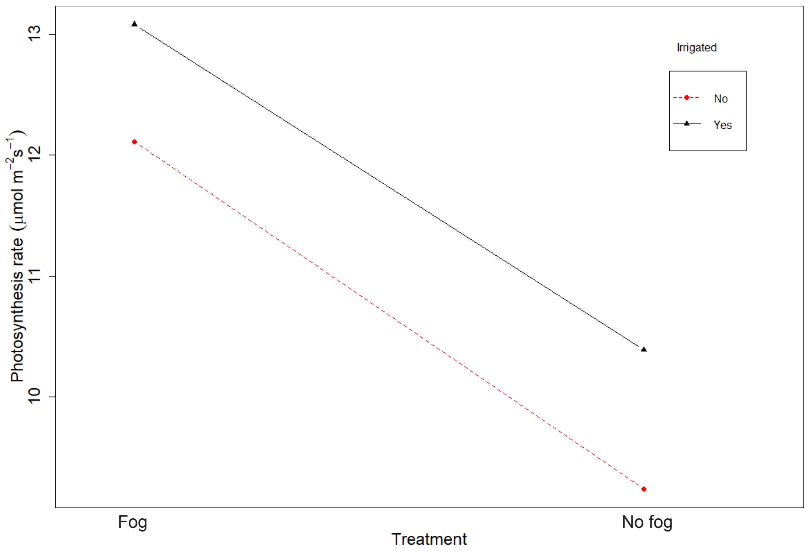

Fig. 3. Norm of reaction plot between fog and irrigation treatments with respect to photosynthesis ($\mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$).

TABLE 3. ANOVA and Tukey HSD test results comparing the actual difference (Δ) and significance value (*P*) of photosynthesis, stomatal conductance, soil moisture, and ambient temperature between treatment groups.

	Photosynthesis ($\mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$)		Stomatal conductance ($\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$)		Soil moisture ($\text{m}^3 \cdot \text{m}^{-3}$)		Ambient temperature (°C)	
Treatment groups	Δ	*P*	Δ	*P*	Δ	*P*	Δ	*P*
Fog vs. Ctrl	2.87	0.000***	0.05	0.006**	0.01	0.202	1.19	0.018**
Fog+Irr vs. Ctrl	3.84	0.000***	0.06	0.000***	0.20	0.000***	1.19	0.018**
Irr vs. Ctrl	1.15	0.454	0.02	0.529	0.20	0.000***	−2.66	1.000
Fog+Irr vs. Fog	0.97	0.523	0.02	0.523	0.18	0.000***	0.00	1.000
Irr vs. Fog	−1.72	0.100	−0.03	0.225	0.18	0.000***	−1.19	0.018**
Irr vs. Fog+Irr	−2.69	0.003**	−0.04	0.009**	0.00	0.999	−1.19	0.018**

*$P < 0.05$
** $P < 0.01$
*** $P < 0.001$

regardless of irrigation (irrigated: $g_{s\ \text{Fog + Irr}} = 0.15 \pm 0.15\ \text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, $g_{s\ \text{Irr}} = 0.11 \pm 0.11\ \text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$; nonirrigated: $g_{s\ \text{Fog}} = 0.13 \pm 0.13\ \text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, $g_{s\ \text{Crtl}} = 0.9 \pm 0.09\ \text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$) (Table 2, Fig. 4). Differences in g_s were significant, with the exception of Fog + Irr versus Fog ($P = 0.523$), Irr versus Ctrl ($P = 0.529$), and Fog versus Irr ($P = 0.225$) (Table 3).

Average soil moisture (SM) was similarly high between the irrigated plants ($\text{SM}_{\text{Fog + Irr}} = 0.25 \pm 0.04\ \text{m}^3 \cdot \text{m}^{-3}$; $\text{SM}_{\text{Irr}} = 0.25 \pm 0.02\ \text{m}^3 \cdot \text{m}^{-3}$) and similarly low between nonirrigated plants ($\text{SM}_{\text{Fog}} = 0.07 \pm 0.02\ \text{m}^3 \cdot \text{m}^{-3}$; $\text{SM}_{\text{Ctrl}} = 0.05 \pm 0.02\ \text{m}^3 \cdot \text{m}^{-3}$) (Table 2, Fig. 5). Soil moisture differed significantly between plant groups, with the exception of Fog + Irr versus Irr ($P = 0.99$) and Fog versus Ctrl groups ($P = 0.202$) (Table 3).

Mean ambient temperature was 1.2 °C warmer in the fog chamber (8.6 °C) than in the control chamber (7.5 °C), and this difference was statistically significant (Table 2, Fig. 6). This increase was unlike natural conditions, where fog would typically result in cooler ambient temperatures. Therefore, this temperature increase may have resulted from other factors such as heating from the fog machine or a latent heat flux from condensation. Mean VPD in the fog chamber (0.15 kPa) was 53% lower than in the control chamber (0.26 kPa), indicating that the air was drier in the control chamber (Table 2), and this difference was significant ($P = 0.004$). Treatment,

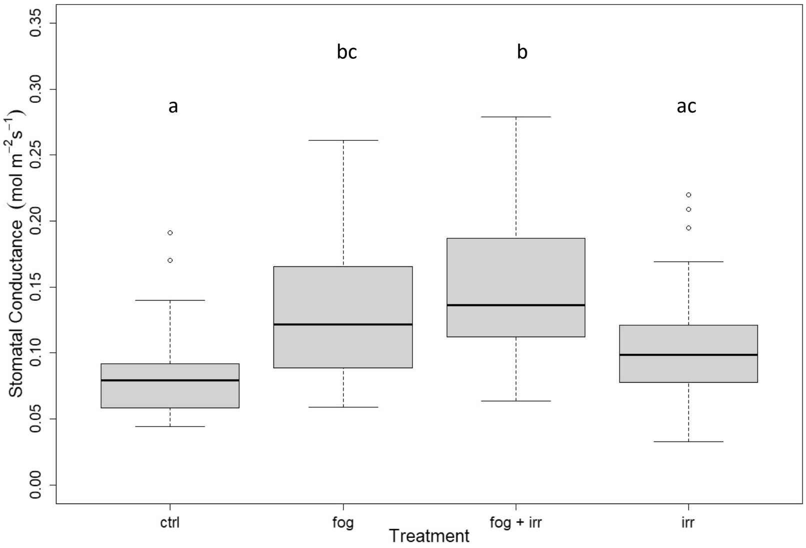

Fig. 4. Box plots of stomatal conductance (mol · m^{-2}s^{-1}) by treatment group (Control [Ctrl], fog only [Fog], irrigation only [Irr], and fog and irrigation [Fog + Irr]) following 2-h simulated morning fog events. Heavy black lines within boxes represent averages; box edges represent 25th and 75th percentiles; whiskers represent minimums and maximums; and circles represent outliers. Letters above box plots represent significant differences between treatment groups (α = 0.05); results from the Tukey HSD test are shown in Table 3.

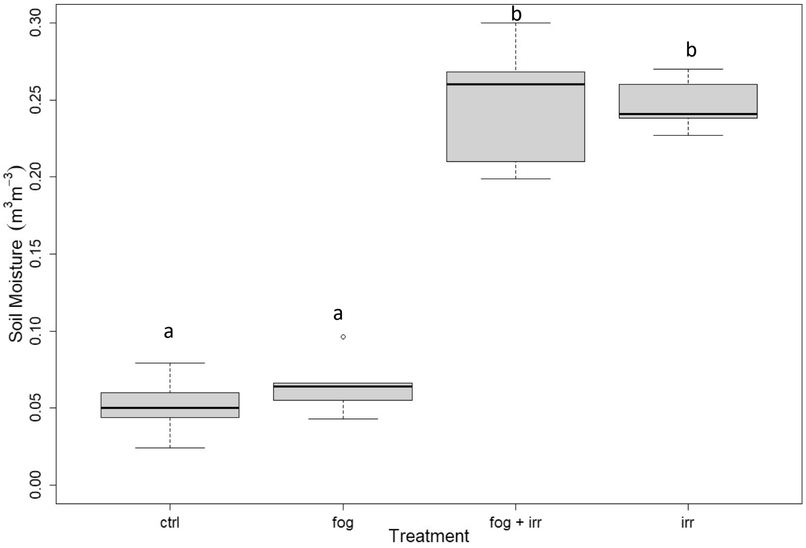

Fig. 5. Box plots of soil moisture (m^3 · m^{-3}) by treatment group (Control [Ctrl], fog only [Fog], irrigation only [Irr], and fog and irrigation [Fog + Irr]), measured as combined averages during 2-h simulated fog events. Heavy black lines within boxes represent averages; box edges represent 25th and 75th percentiles; whiskers represent minimums and maximums; and circles represent outliers. Letters above box plots represent significant differences between treatment groups (α = 0.05); results from the Tukey HSD test are shown in Table 3.

temperature, and soil moisture were highly significant explanatory factors and explained 30% of the variation in photosynthesis (R^2 = 0.303). VPD was moderately significant but likely also influenced photosynthesis and stomatal conductance.

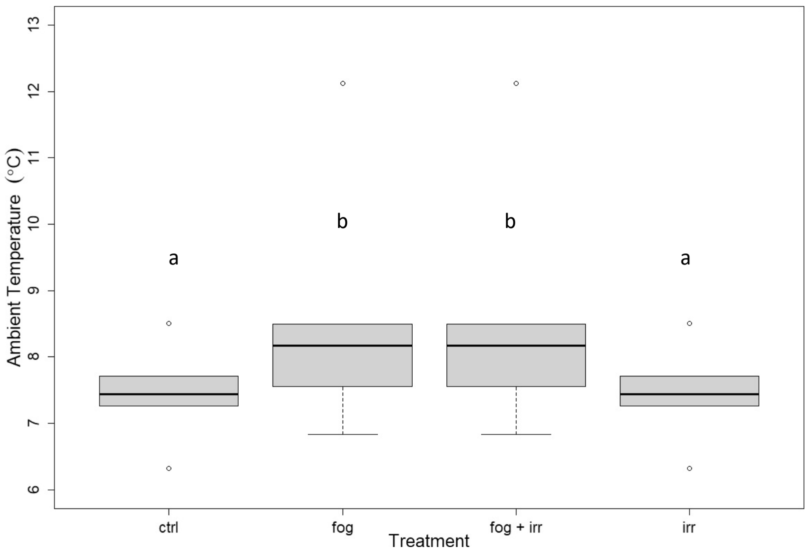

Fig. 6. Box plots of ambient temperature (°C) by treatment group (Control [Ctrl], fog only [Fog], irrigation only [Irr], and fog and irrigation [Fog + Irr]), measured as combined averages during 2-h simulated fog events. Heavy black lines within boxes represent averages; box edges represent 25th and 75th percentiles; whiskers represent minimums and maximums; and circles represent outliers. Letters above box plots represent significant differences between treatment groups ($\alpha = 0.05$); results from the Tukey HSD test are shown in Table 3.

Leaf wetness in the fog chamber ranged from 439 to 467 mV with a dry baseline of 435 mV, indicating that the simulated fog events successfully wet the leaves of seaside daisy plants (Supplementary Material 2). This information is supplemented by visual observations noting that the leaves of plants within the fog chamber appeared wet after fog events. In contrast, the leaves of plants within the control chamber appeared dry (Supplementary Material 2).

Discussion

Our results show that simulated fog events had a positive effect on leaf-level physiological function (A_{max} and g_s) (Figs. 2, 4). Photosynthetic rates of plants in the fog treatment groups were consistently higher than those for plants that did not receive fog, regardless of soil water content (Table 2, Fig. 2). This increase was greater in nonirrigated plants, which supports our hypothesis that fog would enhance physiological function, especially when plants did not receive irrigation. These results suggest that fog is a crucial water resource during periods of low soil moisture, such as during the prolonged summertime drought conditions in California. Our interpretation of these results is consistent with other studies that found that plant function is ameliorated during fog events during otherwise dry conditions (Burgess and Dawson 2004, Fischer et al. 2009, Vasey et al. 2012, Eller et al. 2013, Baguskas et al. 2016a, 2016b). Fischer et al. (2009) conducted a several-year analysis of Bishop pine trees and found that fog drip and cloud shading reduced annual drought stress by 56%. Our study strongly suggests that seaside daisies are efficient at utilizing coastal fog water to support photosynthesis, and this result likely also translates to the importance of coastal fog to the long-term survival of this species.

We found that the positive effect of fog treatments on plant physiology were partially driven by differences in microclimate conditions between the fog and control chambers, such as warmer temperatures and lower VPD in the fog chamber (Table 2, Fig. 6). These results are consistent with Berry et al. (2016), in which VPD explained the majority of variation in daytime plant water use in a tropical montane cloud forest. Soil moisture also contributed to explaining variation in photosynthesis (Fig. 5). Similar to Baguskas et al. (2016a), we found slightly warmer ambient temperatures in the fog chamber compared to the control chamber. Even so, the difference in ambient temperature between chambers was small (1.2 °C) and likely did not contribute largely to variation in plant physiology. Rather, the dominant effects of fog were likely more strongly driven by plant water availability, which has a longer-lasting impact on photosynthesis, as we also see in Baguskas et al. (2016a).

We were surprised to find that fog-only plants had higher photosynthetic rates than irrigation-only plants (Table 2, Fig. 2), despite low soil moisture in the fog-only group (Table 2, Fig. 5). We hypothesize that the mechanism underlying this pattern is foliar uptake of fog water, which improves the water status of leaves and thereby improved photosynthetic rates. Gotsch et al. (2014) found that foliar wetting occurred 34% of the time in a tropical montane cloud forest and led to a 9% recovery of water transpired during the dry season. Simonin et al. (2009) found that leaf wetting supported photosynthesis of California coast redwood trees, which significantly decoupled the soil-plant continuum. Similarly, Baguskas et al. (2016a) found that, although plants which received both fog drip and fog immersion had the highest photosynthesis rates, leaf wetting alone was sufficient in supporting photosynthesis of Bishop pine saplings. In addition, we found that fog-treated plants had slightly higher soil moisture than no-fog plants (Table 2, Fig. 5), which we hypothesize could be the result of fog drip increasing shallow soil moisture. There were no significant differences in soil moisture between irrigated plants (fog and irrigation versus irrigation only, $P = 0.999$), nor between nonirrigated plants (fog only versus control, $P = 0.202$), suggesting that fog drip likely did not contribute to the variation in plant function that we observed in this study (Table 3, Fig. 5). Although we did observe slightly higher soil moisture in fog-treated plants, the actual differences in soil moisture were negligible ($\Delta SM_{(Fog\ +\ Irr)\ -\ (Irr)} = 0.0002\ m^3 \cdot m^{-3}$; $\Delta SM_{(Fog)\ -\ (Ctrl)} = 0.0134\ m^3 \cdot m^{-3}$) and within the instrument's accuracy limits ($\pm 0.03\ m^3 \cdot m^{-3}$). It is important to note that our study exposed plants to simulated fog for brief 2-h events; however, in their natural environment, plants would be exposed to much longer and more frequent fog events. While fog drip does not appear to be a strong driver of photosynthesis in our study, it is likely still an important water resource for naturally occurring seaside daisy plants.

Restored sand dune habitats in the Green Hairstreak Corridor each vary in levels of fog inundation and site stewardship, and most plants do not receive frequent irrigation. Based on the results from our study, maximizing fog exposure is a low-cost, natural solution to improve water availability, plant growth, and overall survival of seaside daisies. From a management perspective, focusing restoration efforts on western-facing, windward habitats in San Francisco, where fog inundation is greater than on inland or leeward sites, will likely improve the probability of seaside daisy survival. Installing fog collectors at restored sites may also help to alleviate water stress during drought periods. Fog harvesting for irrigation has been demonstrated to be a successful approach, such as in a reforestation effort where seedling survival was greater with fog water inputs (Estrela et al. 2009). Leveraging local topographic variation to harvest fog could be achieved by placing other efficient fog-harvesting plants such as coastal sagebrush at the top slopes of restored habitats. This would allow gravity-fed irrigation from fog drip to be directed downslope to other plants to support plant function. Increasing fog drip will likely improve survival of important plants, which will improve habitat quality and help support coastal Green Hairstreak butterflies, as well as other pollinator communities.

In their natural environment, seaside daisies likely benefit from both foliar uptake and fog drip as they are exposed to longer, more frequent fog events. However, the results from this experiment are significant because they highlight the role of leaf wetting alone in supporting plant function. The results from this study show that seaside daisies are well adapted to their foggy environments and rely on both foliar uptake and fog drip to support photosynthesis when soil moisture is limited. To the best of our knowledge, there have been no other studies that have explored leaf-level physiology of seaside daisy plants. Our findings provide a better understanding of the relationships between coastal fog and this important nectar resource, with greater implications for effective habitat restoration.

CONCLUSION

We demonstrate that coastal fog can enhance the physiological function of seaside daisy plants. We found that physiological function increased when plants were exposed to simulated fog events, and that this increase was greater in nonirrigated plants. As the climate changes and we see longer, more frequent drought periods, seaside daisies will likely rely more heavily on coastal fog to support photosynthesis. However, past studies have shown a historical decline in coastal fog along the Pacific coast, and this trend may be more extreme in urbanized areas where fog frequency is lower than in nonurbanized areas (Williams et al. 2015). Climate change and the reduction of fog will likely hinder the survival of naturally occurring seaside daisies, and such threats to plant survival could also have further implications for other species that depend on those plants. Studies have shown that limited water availability also results in fewer floral resources available to pollinators, influencing the plant–pollinator interactions on which entire ecosystems depend (Carroll et al. 2001, Burkle and Runyon 2016). In habitats that have already been destroyed or fragmented from urbanization, the reduction of fog poses an even greater threat to sensitive species that rely on seaside daisies, such as the Coastal Green Hairstreak butterfly. In order to protect these species, it is imperative that we understand how changes to environmental conditions may affect plant health. The results from our study strongly suggest that coastal fog be included in habitat restoration decisions within the Green Hairstreak Corridor and coastal, fog-influenced pollinator habitat more broadly. Designing habitats in a way that increases water availability (e.g., installing fog collectors and encouraging gravity-fed irrigation) will likely increase the chances of survival for seaside daisy plants and therefore improve overall habitat quality for the pollinators that rely on this valuable resource.

SUPPLEMENTARY MATERIAL

Two online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol82/iss3/9).

SUPPLEMENTARY MATERIAL 1. Light response curves from 4 different seaside daisy plants, used to find the light saturation point where maximum photosynthesis occurred.

SUPPLEMENTARY MATERIAL 2. Average leaf wetness (mV) during simulated fog events within the fog chamber. Threshold values ≥435 mV indicate a wet leaf. Reference photos illustrate the differences between wet and dry leaves.

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LITERATURE CITED

BAGUSKAS, S.A., J.Y. KING, D.T. FISCHER, C.M. D'ANTONIO, AND C.J. STILL. 2016a. Impact of fog drip versus fog immersion on the physiology of Bishop pine saplings. Functional Plant Biology 44:339–350.

BAGUSKAS, S.A., A.J. OLIPHANT, R.E. CLEMESHA, AND M.E. LOIK. 2021. Water and light use efficiency are enhanced under summer coastal fog in a California agricultural system. Journal of Geophysical Research: Biogeosciences 126:e2020JG006193.

BAGUSKAS, S.A., C.J. STILL, D.T. FISCHER, C.M. D'ANTONIO, AND J.Y. KING. 2016b. Coastal fog during summer drought improves the water status of sapling trees more than adult trees in a California pine forest. Oecologia 181:137–148.

BERRY, Z.C., S.G. GOTSCH, F. HOLWERDA, L.E. MUÑOZ-VILLERS, AND H. ASBJORNSEN. 2016. Slope position influences vegetation–atmosphere interactions in a tropical montane cloud forest. Agricultural and Forest Meteorology 221:207–218.

BURGESS, S.S.O., AND T.E. DAWSON. 2004. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. Plant, Cell and Environment 27: 1023–1034.

BURKLE, L.A., AND J.B. RUNYON. 2016. Drought and leaf herbivory influence floral volatiles and pollinator attraction. Global Change Biology 22:1644–1654.

CARROLL, A.B., S.G. PALLARDY, AND C. GALEN. 2001. Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). American Journal of Botany 88:438–446.

Chung, M., A. Dufour, R. Pluche, and S. Thompson. 2017. How much does dry-season fog matter? Quantifying fog contributions to water balance in a coastal California watershed. Hydrological Processes 31: 3948–3961.

Dawson, T.E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117: 476–485.

Eller, C.B., A.L. Lima, and R.S. Oliveira. 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis* (Winteraceae). New Phytologist 199:151–162.

Estrela, M.J., J.A. Valiente, D. Corell, D. Fuentes, and A. Valdecantos. 2009. Prospective use of collected fog water in the restoration of degraded burned areas under dry Mediterranean conditions. Agricultural and Forest Meteorology 149:1896–1906.

Ewing, H.A., K.C. Weathers, P.H. Templer, T.E. Dawson, M.K. Firestone, A.M. Elliott, and V.K. Boukili. 2009. Fog water and ecosystem function: heterogeneity in a California redwood forest. Ecosystems 12:417–433.

Fischer, D.T., C.J. Still, C.M. Ebert, S.A. Baguskas, and A. Park Williams. 2016. Fog drip maintains dry season ecological function in a California coastal pine forest. Ecosphere 7:e01364.

Fischer, D.T., C.J. Still, and A.P. Williams. 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. Journal of Biogeography 36: 783–799.

Gotsch, S., H. Asbjornsen, F. Holwerda, G. Goldsmith, A. Weintraub, and T. Dawson. 2014. Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. Plant, Cell and Environment 37:261–272.

Johnstone, J.A., and T.E. Dawson. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. Proceedings of the National Academy of Sciences of the United States of America 107:4533–4538.

Limm, E.B., K.A. Simonin, A.G. Bothman, and T.E. Dawson. 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161:449–459.

Nature in the City. 2016. Discover the Green Hairstreak Corridor. San Francisco, CA. http://natureinthecity.org/green-hairstreak

Oliphant, A.J., S.A. Baguskas, and D.M. Fernandez. 2021. Impacts of low cloud and fog on surface radiation fluxes for ecosystems in coastal California. Theoretical and Applied Climatology 144:239–252.

Simonin, K.A., L.S. Santiago, and T.E. Dawson. 2009. Fog interception by *Sequoia sempervirens* (D. Don) crowns decouples physiology from soil water deficit. Plant, Cell and Environment 32:882–892.

Torregrosa, A., T.A. O'Brien, and I.C. Faloona. 2014. Coastal fog, climate change, and the environment. Eos, Transactions of the American Geophysical Union 95:473–474.

Vasey, M.C., M.E. Loik, and V.T. Parker. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California. Oecologia 170:325–337.

Weathers, K.C., A.G. Ponette-González, and T.E. Dawson. 2020. Medium, vector, and connector: fog and the maintenance of ecosystems. Ecosystems 23: 217–229.

Williams, A.P., R.E. Schwartz, S. Iacobellis, R. Seager, B.I. Cook, C.J. Still, G. Husak, and J. Michaelsen. 2015. Urbanization causes increased cloud base height and decreased fog in coastal Southern California. Geophysical Research Letters 42:1527–1536.

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