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Drought-Net rainfall shelters did not cause nondrought effects on photosynthesis for California central coast plants

Michael E. Loik[1] (iD) | Josephine C. Lesage[1] | Timothy M. Brown[2] | Daniel O. Hastings[1]

[1] Department of Environmental Studies, University of California, Santa Cruz, California, USA

[2] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California, USA

Correspondence
Michael E. Loik, Department of Environmental Studies, University of California, 1156 High Street, Santa Cruz, CA 95064 USA.
Email: mloik@ucsc.edu

Abstract

Rainfall interception shelters are frequently used to study the ecological consequences of drought. One common shelter design employs V-shaped plastic troughs spaced on a supporting frame to intercept rainfall. Shading, reflection, and infrared radiation may alter the radiative environment under shelters in ways independent of their intended effect on soil moisture. We measured microclimate and several photosynthetic variables for watered, potted plants under rain-out shelters and in open-air, unsheltered plots. We tested whether the shelter infrastructure altered aboveground micrometeorology and photosynthesis for watered, potted plants of native Californian species: *Elymus glaucus*, *Eriogonum latifolium*, *Mimulus aurantiacus*, and *Morella californica*. We quantified the effects on photosynthesis in terms of light harvesting by photosystem II (PSII) and leaf-level gas exchange on open-air and shelter plots, the quantum yield of PSII for darkened leaves, dark respiration, and nocturnal stomatal conductance. The rain-out shelter reduced daily integrated photosynthetically active radiation by 20%. Air temperature, leaf temperature, and leaf-to-air vapour pressure difference were not different under shelters compared with controls during the day. Likewise, there were no effects of shelters on net CO_2 assimilation, stomatal conductance to water vapour (g_s), internal leaf (CO_2), or electron transport rate through PSII during the daytime. At night, T^{air} was 0.6°C higher under shelters, but there were no effects on dark respiration or stomatal conductance. Despite some differences in micrometeorology under rain-out shelters compared with open-air plots, there were little or no aboveground nondrought effects of the shelters on leaf-level photosynthesis for watered, potted plants of these California native plant species.

KEYWORDS

Elymus, *Eriogonum*, *Mimulus*, *Morella*, rain-out, stomatal conductance

1 | INTRODUCTION

Understanding and predicting drought effects resulting from climate change are important because of their widespread impacts on ecological, agricultural, and societal well-being (Dai, 2011; Marshall et al., 2008; Penuelas et al., 2013; Trnka et al., 2018). Particularly in arid and semiarid systems, drought is the climate change driver that is likely to have the biggest impact on terrestrial ecosystem structure and functions, including enhanced mortality for certain plant populations (Martinez-Vilalta & Lloret, 2016). Drought can also lead to modified responses to disturbances (Loehman et al., 2018), altered species distributions (Aubin et al., 2016), long-term changes in community structure (Hoover, Knapp, & Smith, 2014; LaForgia, Spasojevic, Case, Latimer, & Harrison, 2018; Ochoa-Hueso et al., 2018; Phillips et al.,

2018), widespread changes in ecosystem function (Tredennick, Kleinhesselink, Taylor, & Adler, 2018), and shifts in ecotone boundaries (Greenville et al., 2018).

It is difficult to fully understand the ecological consequences of drought without manipulative experiments because observations are complicated by temporal correlates with weather, topography, and soils. Whereas numerous studies have provided extensive information about site-specific responses of plants and ecosystems to changes in precipitation patterns, synthesis of experimental results can be confounded by differences in methodological approaches. For example, manipulative experiments often differ in magnitude, sign, and even direction of precipitation change (Weltzin et al., 2003). Nevertheless, syntheses of results from multiple experiments have resulted in important insights about ecological responses to precipitation (Huxman et al., 2004; Ogle et al., 2012; Ogle et al., 2015). Coordinated distributed experiments can help address the issue of idiosyncratic designs across experiments by promoting the use of uniform manipulations, measurements, and analytical approaches (Knapp et al., 2017).

The Drought-Net coordinated distributed experiment (https://drought-net.colostate.edu/) established the International Drought Experiment (IDE), a network-level distributed experiment that was designed and coordinated *a priori*, with common research protocols, measurements, and methodologies (Knapp et al., 2017). The main goal of the network is to assess potential mechanisms underlying ecosystem sensitivity to drought by comparing responses across many global locations and ecosystem types. A secondary goal is to encourage diverse participation by institutions and countries worldwide. The IDE protocol aims to keep initial infrastructure costs low to promote such accessibility and participation.

In order to assess the key features of precipitation for design of the network protocol, Drought-Net analysed precipitation from over 1,600 locations for 100 years and showed that wet years usually have multiple large precipitation events by comparison with average or drought years, whereas arid regions typically have more days between precipitation events (Knapp et al., 2015). The IDE protocol uses rainfall interception shelters (Yahdjian & Sala, 2002) to impose a reduction in precipitation to a level consistent with a 1-in-100 year extreme drought. This design utilizes the natural frequency of precipitation events but retains site-specific precipitation magnitude and seasonal timing; this is critical because precipitation amount varies widely across global biomes (Knapp et al., 2017). The IDE uses clear plastic V-shaped troughs to intercept rain and to divert the water off plots. Although proper control plots would include full infrastructure (by which rain would drop onto plots from inverted V-shaped troughs), funding constraints often preclude such controls. This means that control plots are often left open to the bulk air and lack the possible infrastructure effects, such as shortwave radiation reflection, shading of leaves, and longwave (infrared) radiation emission that may produce nondrought effects on photosynthesis and productivity in treatment plots.

This study was conducted to test for aboveground nondrought effects of the Drought-Net IDE protocol rain-out shelters on the microclimate, photosynthesis, and respiration of well-watered, potted plants by comparison with plants in nonsheltered plots open to the sky. We conducted this study during the summer in a California coastal prairie grassland in which much of the extant vegetation had undergone seasonal drying and senescence. Leaf-level photosynthetic physiology was compared for California native plant species (a grass, forb, subshrub, and shrub) after 6 days and 3 weeks exposure to conditions on open-air plots or under rain-out shelters built according to the Drought-Net protocol for the IDE. We tested the following hypotheses regarding unintended rain-out shelter effects: (a) photosynthetically active radiation (PAR; 400–700 nm) would be lower during the daytime under rain-out shelters by comparison with conditions on open plots, due to shading or reflection of shortwave radiation by the rain-out shelter infrastructure; (b) air temperatures would be warmer under the shelters at night, due to longwave emission from the rain-out shelter infrastructure; (c) there would be lower daytime photosystem II (PSII) electron transport, stomatal conductance to water vapour, and photosynthetic CO_2 assimilation for well-watered, potted plants under rain-out shelters compared with those on open plots; (d) there would be higher night-time respiration and nocturnal stomatal conductance and lower efficiency of PSII at night for plants under rain-out shelters compared with open plots; and (e) after 3-week exposure to conditions under rain-out shelters or in open plots, well-watered, potted plants would exhibit functional differences in PSII.

2 | MATERIALS AND METHODS

2.1 | Plant material

Experimental plants (*Elymus glaucus*, *E. triticoides* [Poaceae] Buckley; *Eriogonum latifolium* [Polygonaceae] Sm.; *Mimulus aurantiacus* [Phrymaceae] Curtis [Jeps.]; and *Morella californica* [Myricaceae] Wilbur) were grown outdoors under partial shade at the Plant Growth Facility on the UC Santa Cruz campus (36° 59′ 53.5596″ N, 122° 3′ 42.804″ W). Plants were started from locally collected seed inside a glasshouse with a mean daily temperature of 17°C (highs were approximately 10° above ambient and lows were near ambient temperature). After 8 weeks, the seedlings were moved outdoors and were grown in 15 cm-dia (3.79 l) pots in Premier Pro Mix HP inoculated with mycorrhizae. Individuals of *M. californica* were 2 years old at the time of experiments and were kept under the same conditions as the seedlings once they were moved outdoors. The other species were grown for another 8 weeks before being placed under rain-out shelters or in open-air "control" plots. Plants were watered daily to the flow-through point to prevent soil drying.

2.2 | Drought shelters

Drought (or rain-out) shelters were built in summer 2015 at Younger Lagoon Reserve at the UCSC Coastal Science Campus near Santa Cruz, California, USA (36° 57′ 6.8724″ N, 122° 3′ 47.592″ W, elev = 15 masl). Each shelter covers 4 × 4 m; research plots occupy the

central 2 × 2 m with a 1-m buffer along each edge under the shelter. The spacing between adjacent shelters is a minimum of 3 m.

The drought treatment is created by diverting 60% of ambient precipitation from plots using overhead rainfall interception shelters (Yahdjian & Sala, 2002). Precipitation is intercepted by polycarbonate plastic panels bent into a V-shaped trough, held over research plots on a support frame. The support frame is made of 1.9 cm outside diameter electrical tubing conduit. There are three parallel, horizontal bars at 60, 100, and 150 cm height above the ground, one each on the east and west edges of the plot, and one in the middle. Each horizontal bar was supported by three vertical posts. This design produces a "wedge-shaped" shelter (Figure S1) with an upper and lower edge above the plant canopy. Based on a wind rose for this site, shelters were oriented to WNW (275°) so that the downward slope of the troughs faced into the prevailing coastal winds, which can be quite strong at times. Although this orientation deviates from the Drought-Net protocol, it was necessary because of strong winds. And the tallest sides of our shelters point east and south to maximize PAR interception. Troughs were spaced on the frames to create 60% rainfall interception, corresponding to the first percentile extreme drought for this region. The troughs sit above the plant canopy and slope downward and empty into gutters on the lower end. The gutters empty into flexible drain pipes that channel water away from the plots. The surrounding edges of the 4 × 4 m plots were trenched and lined with a 6-mil plastic to a depth of 50 cm prior to the construction of the overhead shelter infrastructure.

2.3 | Micrometeorological conditions

Air temperature ($T_{50}{}^A$), relative humidity (RH), and PAR (400–700 nm) were monitored at 50 cm height above the ground on one rain-out shelter and one open-air plot every minute, and average values were recorded every 10 min on Campbell Scientific Model 200× data loggers. Air temperature and relative humidity were measured using Vaisala Humitter HMP50 sensors in static radiation shelters at 50 cm above the soil surface, which was about 25 cm below the polycarbonate troughs of the shelter. We used a Li-Cor Model 190S quantum sensor to detect PAR at 50 cm above the soil surface. Additional air and leaf temperatures were obtained from the photosynthesis measurements described below.

2.4 | Photosynthesis measurements

We placed well-watered and fertilized plants in 20 cm diameter black pots directly on the soil surface under n = 5 shelters and n = 5 open plots in August 2016. Plants were watered every 2 to 3 days thereafter. There was no shading from neighbouring plants because the vegetation under the shelters had undergone seasonal senescence. Plants were momentarily moved from under shelters for watering, so that drained water did not enter shelter plot soils. Five days after placing the potted plants under the shelters or on open plots, we measured air temperature adjacent to the leaf (T^{air}), leaf temperature (T^{leaf}),

leaf-level stomatal conductance to water vapour (g_s), and net CO_2 assimilation (A) using two cross-calibrated Li-Cor LI-6400-XT portable photosynthesis systems. The following night, we measured leaf temperature, dark respiration, and tested for any nocturnal stomatal conductance. We also used a chlorophyll fluorometer with the LI-6400 to measure the apparent quantum efficiency of PSII in the dark-adapted state for leaves of the five species on open and shelter plots. Last, we tested for changes in chloroplast-level photosynthetic processes after 3-week deployment under rain-out shelters or on open-air plots based on the photosynthetic light dose-response model ("A-Q curves"). These comparisons tested the potential for slower structural and functional responses within PSII under the rain-out shelters and on open-air plots.

Photosynthetic gas exchange responses to the micrometeorological conditions under the rain-out shelters were compared with those for open-air "control" plots. We chose to monitor these processes because decreased photosynthesis due to the nondrought effects of the shelter infrastructure might shift the carbon balance from net gain (via photosynthesis) towards net loss (via respiration) and result in reduced growth and survival. We compared photosynthesis for plants under rain-out shelters and open-air plots using instantaneous or "spot" measurements. We measured photosynthetic gas exchange of leaves with two cross-calibrated, open-mode portable photosynthesis systems (LI-6400XT, Li-Cor Inc., Lincoln, NE, USA) and assessed light harvesting by PSII with integrated leaf chamber fluorometers (LCF, Model LI-6400-40).

For all photosynthetic measurements, individual leaves were enclosed in the leaf cuvette using the 2-cm^2 area of the LCF. The flow rate was set to 500 μmol s^{-1}, the block temperature was maintained at 25°C, PAR (400–700 nm) was kept at a light-saturating 1,500 μmol m^{-2} s^{-1} (generated by red and blue LEDs in the LCF), and the leaf-to-air vapour pressure difference (VPD^L) was maintained between 1.2 and 1.8 kPa using the desiccant adjustment. Leaf temperatures were recorded with a copper-constantan thermocouple pressed to the abaxial surface of the leaf within the cuvette. Photosynthetic measurements were recorded when all stability criteria were met when the coefficient of variation for A and g_s combined was <0.5%, which generally required no longer than 4 min. Leaves were exposed to ambient irradiation for at least 2 hr before measurements of electron transport rate (ETR) in PSII. Steady-state conditions were confirmed in preliminary experiments.

Photosynthetic (A) responses to light (Q) were measured at an ambient CO_2 concentration of 400 μmol mol^{-1} for 12 light levels between 1,500 and 0 μmol m^{-2} s^{-1}. Photosynthesis (A, g_s, C_i, and ETR) and microclimate adjacent to leaves (T^{air}, T^{leaf}, and VPD^L) were measured at PAR of 1,500, 1,000, 750, 500, 350, 200, 100, 50, 20, 10, and 0 μmol m^{-2} s^{-1}. Plants were allowed to acclimate to light intensity changes for 4 to 5 min before measurements were recorded. For measurements of chlorophyll a fluorescence from PSII (i.e., daytime ETR and night-time F_V/F_M), we used an integrated LI-6200-40 fluorometer. Leaves were exposed to ambient PAR (e.g., for ETR) or dark-adapted between 01:00 and 04:00 hr for full reduction of PSII before F_V/F_M measurements (Logan, Adams, & Demmig-Adams,

2007; Maxwell & Johnson, 2000). We used a rectangular saturating flash of 0.8-s duration, an intensity of 8, a modulation of 20 kHz, and the filter was set at 50. The measurement was conducted with the intensity at 5, the filter at 1, the gain was 10, and the modulation was 20 kHz.

Daytime photosynthetic measurements were made between 08:00 and 14:00 hr local time, and night-time measurements were made between 01:00 and 05:00 hr.

2.5 | Data analysis

Initial statistical analyses of the micrometeorological and physiological data revealed unequal variances, so we used nonparametric comparisons of variables measured under rain-out shelters and on open-air plots. We used unpaired, two-sample Mann–Whitney U tests to examine the likelihood that values of each micrometeorological or physiological parameter from different treatments were drawn from the same distribution. Analyses were conducted in R Statistical Environment version 3.5.1 (R Core Team (2018). We initially compared five species, but in most cases, we show data for four of the five species because (a) two of the species are grasses from the same genus (*Elymus*) with very similar responses to one another, and (b) A-Q curves did not fully iterate to a solution for two of the species due to low photosynthetic rates.

The photosynthetic dose-response to light (the A-Q light response curve) was modelled as a nonrectangular hyperbola per Marshall and Biscoe (1980):

$$A_n = \frac{\Phi PAR + A_{max} - \sqrt{(\Phi PAR + A_{max})^2 - 4\theta \Phi PARA_{max}}}{2\theta} - R_d, \quad (1)$$

where A_n is net assimilation rate (μmol CO_2 m^{-2} s^{-1}), Φ is the initial quantum yield (mol CO_2 mol photons^{-1}), PAR is the photosynthetic photon flux density (μmol photons m^{-2} s^{-1}), A_{max} is the maximum photosynthetic rate (μmol CO_2 m^{-2} s^{-1}), θ is a dimensionless curvature parameter, and R_d is daytime respiration (μmol CO_2 m^{-2} s^{-1}). The parameters were estimated using non-linear least squares regression in R 3.5.1 (R Core Team, 2018) with code from (Heberling, Brouwer, & Kalisz, 2017).

3 | RESULTS

3.1 | Microclimate under rain-out shelters

Microclimatic conditions under the rain-out shelters were generally similar to those on open-air plots with some exceptions (Figure 1). Instantaneous levels of PAR (400–700 nm) were up to 70% higher on open-air compared with rain-out shelter plots, though this only occurred for a few minutes during the day when the infrastructure caused temporary shading on the PAR sensor at 50 cm above the ground. Integrated over the daytime, shelter shade reduced PAR by 20%. Air temperature ($T_{50}{}^A$) and water vapour pressure deficit
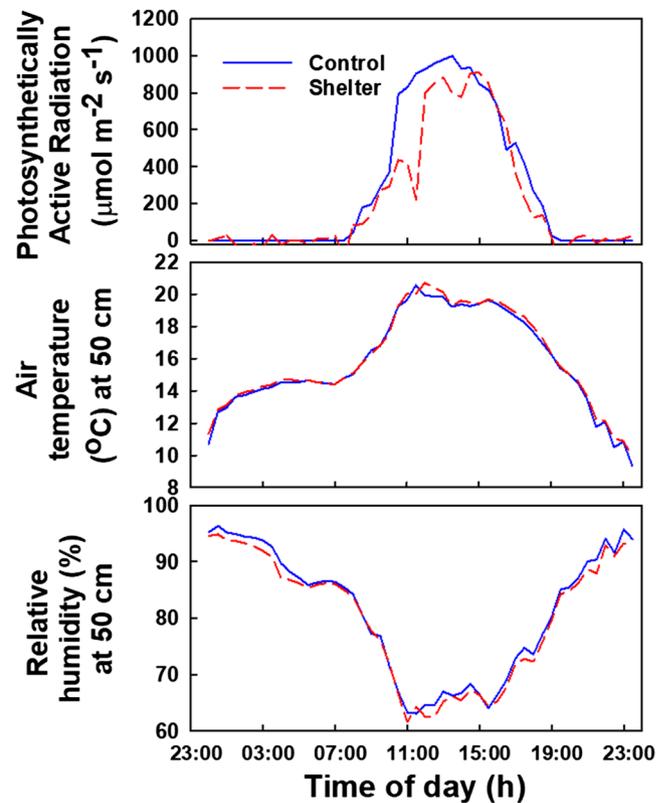

FIGURE 1 Diel micrometeorological conditions in open-air "control" plots and under rain-out shelters. (a) Photosynthetically active radiation (400–700 nm). (b) Air temperature at 50 cm height above the ground, adjacent to study leaves. (c) Relative humidity at 50 cm height above the ground, adjacent to study leaves. Data are shown for conditions in an open-air control plot (blue) and under a rain-out shelter (red) in August 2016

($VPD_{50}{}^L$) at 50 cm were not significantly different over the course of 24 h, though $T_{50}{}^A$ under the rain-out shelter was higher for ~1 hr than $T_{50}{}^A$ on open-air plots during the middle of the day (Figure 1). A similar pattern was observed for $VPD_{50}{}^L$, which was lower under shelters than in the open for about 2 hr. Air temperature at 50 cm height was ~0.6° higher under shelters versus in the open plots at night (Table 1).

3.2 | Daytime photosynthesis

Compared across species, net leaf-level CO_2 assimilation (A) on open plots varied from 7.33 (0.74; mean [*SE*], n = 5) μmol m^{-2} s^{-1} for the woody shrub species *M. californica* to 21.5 (1.74) μmol m^{-2} s^{-1} for the perennial bunchgrass *Elymus glaucus* (Figure 2). Stomatal conductance to water vapour (g_s) similarly increased from the woody shrub to grass species. Leaf internal CO_2 concentration (C_i) was lower for *M. californica* compared with the other species and was the only daytime physiological response variable to be significantly different for plants under rain-out shelters compared with those on open-air plots. Likewise, the rate of electron transport through PSII (*ETR*) for *M. californica* was about one third that for the herbaceous perennial *E. latifolium*.

TABLE 1 Daytime micrometeorological conditions adjacent to leaves in open-air, control plots ("open"), and under rain-out shelters ("shelter")

Species	Treatment	VPD_{50}^L (kPa)	T_{50}^A (°C)	T_{50}^L (°C)
Elymus glaucus	Open	1.07 (0.14)	22.7 (1.2)	23.3 (1.4)
	Shelter	0.99 (0.12)	22.0 (1.1)	22.4 (1.4)
Eriogonum latifolium	Open	0.94 (0.10)	22.6 (1.0)	22.9 (1.2)
	Shelter	1.06 (0.12)	23.0 (1.2)	23.4 (1.4)
Mimulus aurantiacus	Open	1.04 (0.12)	22.5 (1.1)	23.1 (1.3)
	Shelter	1.16 (0.17)	23.2 (1.3)	23.7 (1.6)
Morella californica	Open	1.10 (0.13)	22.5 (0.6)	23.6 (1.0)
	Shelter	1.20 (0.11)	22.6 (1.0)	23.7 (1.2)

Note. Data are leaf-to-air vapour pressure deficit (VPD_{50}^L, kPa), air temperature (T_{50}^A, °C), leaf temperature (T_{50}^L, °C) at a height of 50 cm above the ground under rain-out shelters, and open-air "control" plots. Data are means and standard errors for $n = 5$ plants (except $n = 4$ for *E. glaucus* on shelter plots).
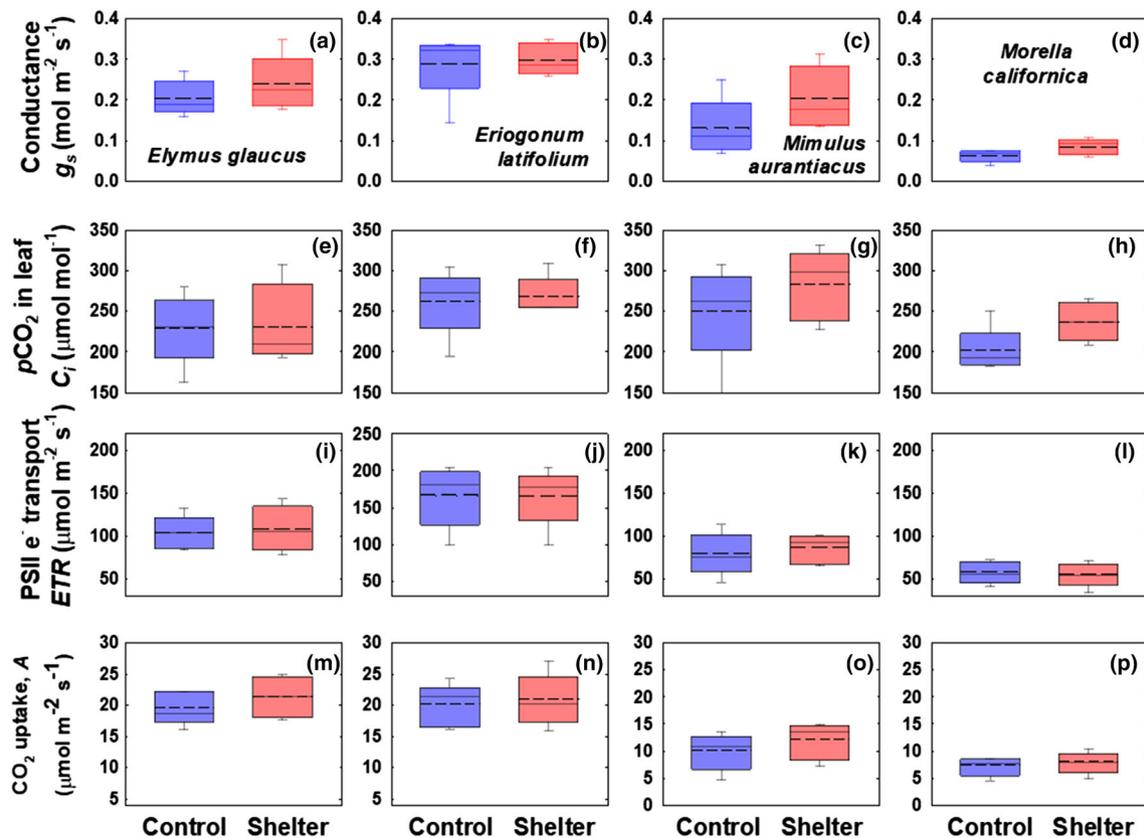

FIGURE 2 Leaf-level steady-state photosynthesis for *Elymus glaucus* (a, e, i, m), *Eriogonum latifolium* (b, f, j, n), *Mimulus aurantiacus* (c, g, k, o), and *Morella californica* (d, h, l, p) in open-air "control" plots (blue) and under rain-out shelters (red). Leaf-level photosynthetic processes were quantified as stomatal conductance to water vapour (g_s, panels a–d), leaf internal CO_2 concentration (C_i, panels e–h), electron transport through photosystem II (*ETR*, panels i–l), and instantaneous CO_2 assimilation (*A*; panels m–p). Data are mean (dashed line), median (solid line), standard error (box), and standard deviation (whiskers) for $n = 5$ measurements per species and treatment

There were no differences in air temperature near the canopy (T^{air}) or leaf temperature (T^{leaf}) nor leaf-to-air vapour pressure deficit (VPD^L) during the daytime on open compared with rain-out shelter plots (Table 1). There were few significant differences between plants under rain-out shelters compared with those on open plots in terms of net photosynthesis, stomatal conductance, internal CO_2 concentration, or electron transport rate in PSII (Table 1; Figure 2).

3.3 | Night-time physiology

Air temperature during the night near the leaves (T_n^{air}) of *M. californica* was significantly higher under rain-out shelters (Table 2). Leaf temperatures at night were somewhat higher under rain-out shelters compared with open plots for all species, but not significantly so.

TABLE 2 Night-time micrometeorological conditions adjacent to leaves and instantaneous steady-state leaf-level photosynthetic physiology in open-air, control plots ("open"), and under rain-out shelters ("shelter")

Species	Treatment	T^{air} (°C)	T^{leaf} (°C)	R_d (µmol m^{-2} s^{-1})	C_i (µmol mol^{-1})	g_s^n (µmol m^{-2} s^{-1})	F_V/F_M (unitless)
Elymus glaucus	Open	15.1 (0.1)	14.2 (0.1)	−2.92 (0.50)	417 (6)	0.249 (0.049)	0.780 (0.004)
	Shelter	16.2 (0.1)	15.4 (0.1)	−1.43 (0.10)	419 (11)	0.129 (0.044)	0.797 (0.006)
Eriogonum latifolium	Open	15.1 (0.2)	13.4 (0.4)	−1.16 (0.27)	400 (1)	0.661 (0.230)	0.798 (0.003)
	Shelter	15.9 (0.0)	14.9 (0.0)	−1.87 (0.15)	430 (6)	0.091 (0.022)	0.826 (0.002)
M. aurantiacus	Open	15.1 (0.1)	13.7 (0.1)	−0.81 (0.24)	400 (3)	0.411 (0.129)	0.763 (0.015)
	Shelter	15.3 (0.4)	13.9 (0.6)	−1.55 (0.46)	405 (3)	1.868 (1.313)	0.778 (0.010)
Morella californica	Open	**15.2 (0.3)**	14.3 (0.4)	−2.09 (0.97)	426 (14)	0.195 (0.131)	0.653 (0.011)
	Shelter	**16.7 (0.6)**	15.8 (0.6)	−0.73 (0.18)	424 (16)	0.084 (0.050)	0.565 (0.071)

Note. Data include air temperature (T^{air}), leaf temperature adjacent to leaves (T^{leaf}), net respiratory CO_2 flux (R_d), nocturnal stomatal conductance to water vapour (g_s^n), and apparent quantum efficiency of photosystem II for dark-adapted leaves (F_V/F_M). Data are means and standard errors for $n = 5$ plants (except $n = 4$ for E. glaucus on shelter plots). Bold indicates significant differences between values at the $P < .05$ level as determined by Mann–Whitney U tests.

The apparent quantum yield of PSII for dark-adapted leaves (F_V/F_M) measured between 01:00 and 05:00 hr was above 0.700 for all species except M. californica (Table 2). Dark respiration (R_d) varied from −0.73 (0.18) µmol m^{-2} s^{-1} for M. californica under shelters to −2.92 (0.50) µmol m^{-2} s^{-1} for E. glaucus on open plots. There were no clear trends between nocturnal (g_s^n) and diurnal stomatal conductance (g_s) when comparing species or between rain-out shelter and open-air plots. There were no significant differences for any of the photosynthetic traits for plants under rain-out shelters compared with open-air plots.

3.4 | A-Q after 3 weeks

Three weeks after the start of experiments, we tested the potential for slower structure–function responses of PSII to the micrometeorological conditions under the drought shelter by using the A-Q dose-response model. On the basis of plant survival and A-Q curve convergence, we focused on E. triticoides, M. aurantiacus, and M. californica. Mean values for light-saturated photosynthesis (A_{max}), dark respiration (R_d), and quantum yield (Φ) for E. triticoides and M. aurantiacus underneath the rain-out shelters were not significantly different than for plants on open-air plots, based on Student's t tests (Figure S2). Sample sizes precluded t test comparisons for M. californica.

4 | DISCUSSION

We found minimal differences between microclimatic conditions on open-air plots and under shelters, particularly for air temperature adjacent to leaves (T_{50}^A) and relative humidity. Using the original design upon which our rain-out shelters are based, Yahdjian and Sala (2002) found similar reductions in instantaneous PAR of 10% to 20%, depending on the amount of incoming PAR. Their maximal daytime air temperatures were between 5° cooler to 2° warmer than ambient, and daily minimal temperatures were within 2° of ambient. This is a greater diel variation between rain-out shelter and ambient than what

we observed under our rain-out shelters compared with open-air plots. Many other studies have tested for aboveground effects of rain-out shelters. For example, continuous rain-out roofs in Arizona, USA, resulted in minimal effects on wind speed, air temperature, or relative humidity at plant height (English, Weltzin, Fravolini, Thomas, & Williams, 2005). For a grassland drought study in Germany, shelters reduced PAR by 10% and had little effect on air temperature under shelters compared with open-air controls (Signarbieux & Feller, 2012). Large interception troughs in New Mexico, USA, affected near-surface air temperatures by up to 4°, and an air temperature effect was found in relation to distance from the troughs (Pangle et al., 2012). In some cases, effects of rain-out shelters on air temperature were smaller than our night-time increase of ~0.6 K (Kundel et al., 2018; Vogel et al., 2013), whereas other studies found a larger effect on temperature (Power et al., 2016). Overhead rain-out shelters almost always reduce instantaneous PAR (Power et al., 2016). Our shelters caused a reduction in mean integrated daily PAR by about 20%, lower than the reduction of PAR in southeast Australia (Power et al., 2016), but similar in proportion to reductions in midday short-wave or net radiation in Germany (Kreyling et al., 2017). We found no differences in PSII function revealed by the A-Q analysis after plants were under shelters or on open-air plots for 3 weeks. Notably, the 20% reduction in daily integrated PAR under shelters results in almost no effect on net leaf-level CO_2 assimilation. Other studies have shown important feedbacks on microclimatic conditions under rain-out shelters driven by seasonal weather patterns and vegetation type (Carlyle, Fraser, & Turkington, 2011; Kreyling et al., 2017). We note that our measurements were conducted under relatively calm, clear conditions in coastal California, USA, and results may be different in other locations. Moreover, we do not know about the effects of the rain-out shelters on wind speed or summertime coastal fog deposition in our plots. Our rain-out shelters allow quite a bit of light into plots from the sides, especially from the southern edge which is the side with the tallest vertical supports. We did not test the effect of the polycarbonate on UV or other light quality parameters, but this could be important depending on the availability of plastic. Polycarbonate absorbs UV effectively (Loik et al., 2017), which could influence plant

growth (Tevini & Teramura, 1989). We also did not detect much of a penumbral effect of light transmission through the polycarbonate edge on variation in PAR as the sun's angle changes. These potential effects warrant further examination. Nevertheless, we conclude that there are minimal differences in air temperature and relative humidity on open-air plots compared with under shelters in our system.

Almost none of the leaf-level photosynthetic traits were significantly affected by rain-out shelter conditions after 6 days (daytime A, g_s, ETR, and night-time g_s^n or F_V/F_M) or 3 weeks (as photosynthesis-light response curve variables Φ, R_d, or A_{max}) of treatment for the four species. In fact, the only physiological measurement that was marginally significantly different ($P = .056$) on open-air plots versus under rain-out shelters was leaf internal pCO_2 (C_i) for M. californica. Because the plants were well-watered and fertilized in pots, their physiology should have been de-coupled from the drought shelter effects on soil water content, and any differences should be due to aboveground micrometeorological conditions associated with the shelters. Responses to drought shelters may be related to functional group type, as forbs and legumes exposed to drought did not have significant changes in stomatal conductance and net CO_2 uptake, whereas grasses had reduced gas exchange under drought shelters at certain elevations in Germany (Bollig & Feller, 2014; Signarbieux & Feller, 2012). Leaf- and canopy-level responses of photosynthesis to soil moisture under drought shelters may not be symmetrical to increased precipitation effects, resulting in different resource use efficiencies (Zhang et al., 2017). And ambient weather patterns can affect the physiological responses of plants to conditions under drought shelters. In this regard, leaf water potential, stomatal conductance, and quantum efficiency can differ under shelters on warm compared with cool days, yet there were no aboveground effects of drought shelters on photosynthetic physiology for a phytometer experiment in Germany (Kreyling et al., 2017).

We utilized species from different families that are common in central coastal California and represent different life forms and combinations of traits: a grass species Elymus glaucus, a long-lived perennial herbaceous forb E. latifolium, a semiwoody subshrub M. aurantiacus, and the woody shrub M. californica. Little is known of the photosynthetic physiology of these species, although there appear to be trade-offs between resource acquisition and drought for E. glaucus (Balachowski & Volaire, 2018). Some life history trade-offs might appear minor but cause important interactions with drought (Shriver, 2017). Moreover, we used potted, watered, fertilized plants, so they were presumably not affected by competition for light, water, or nutrients as would be plants rooted in the soil of plots. For plants with roots in the ground, competition may complicate responses to the different physical effects (shading, reflection, and infrared radiation emission) of the rain-out shelter infrastructure (Concilio, Nippert, Ehrenfeucht, Cherwin, & Seastedt, 2016). For example, some studies have found interactions of disturbance or trophic relationships (Gill et al., 2018) or soil invertebrates (Johnson, Staley, McLeod, & Hartley, 2011) with drought. Additionally, soil microbial communities may be affected by changes in soil temperature in addition to moisture under rain-out shelters (Cable et al., 2011; Ochoa-Hueso et al., 2018), but we used sterilized soil so this may not be an issue for our potted plants.

When it comes to in situ drought experiments, it may be possible in some habitats or locations to use rain-out shelters to reduce precipitation with minimal unintended, nondrought micrometeorological effects on photosynthesis. However, full control infrastructure (i.e., inverted experimental controls and open-air infrastructure controls) should be used where possible because some other factors that we have not considered (e.g., raindrop size) might be importantly affected by control structures. We recommend that investigators test for nondrought effects on micrometeorology and photosynthetic physiology as part of in situ precipitation manipulation experiments, especially if open-air plots are used as controls. We conclude that the lack of major differences found for air temperature and relative humidity on open-air plots and under shelters means the shelter design (Yahdjian & Sala, 2002) employed by the coordinated distributed experiment network Drought-Net can be used to manipulate rainfall with minimal unintended effects on aboveground conditions.

AUTHOR CONTRIBUTIONS

M. L. and J. L. conceived the ideas and designed the methodology. T. B. and M. L. constructed the rain-out shelters. M. L. and J. L. collected the data. M. L., J. L., and D. H. analysed the data. M. L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the University of California's Dash Data Repository.

ORCID

Michael E. Loik https://orcid.org/0000-0003-0847-6778

REFERENCES

Aubin, I., Munson, A. D., Cardou, F., Burton, P. J., Isabel, N., Pedlar, J. H., ... McKenney, D. (2016). Traits to stay, traits to move: A review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environmental Reviews*, 24, 164–186. https://doi.org/10.1139/er-2015-0072

Balachowski, J. A., & Volaire, F. A. (2018). Implications of plant functional traits and drought survival strategies for ecological restoration. *Journal of Applied Ecology*, 55, 631–640. https://doi.org/10.1111/1365-2664.12979

Bollig, C., & Feller, U. (2014). Impacts of drought stress on water relations and carbon assimilation in grassland species at different altitudes.

Agriculture Ecosystems & Environment, 188, 212–220. https://doi.org/10.1016/j.agee.2014.02.034

Cable, J. M., Ogle, K., Lucas, R. W., Huxman, T. E., Loik, M. E., Smith, S. D., … Welker, J. M. (2011). The temperature responses of soil respiration in deserts: A seven desert synthesis. *Biogeochemistry, 103*, 71–90. https://doi.org/10.1007/s10533-010-9448-z

Carlyle, C. N., Fraser, L. H., & Turkington, R. (2011). Tracking soil temperature and moisture in a multi-factor climate experiment in temperate grassland: Do climate manipulation methods produce their intended effects? *Ecosystems, 14*, 489–502. https://doi.org/10.1007/s10021-011-9425-y

Concilio, A. L., Nippert, J. B., Ehrenfeucht, S., Cherwin, K., & Seastedt, T. R. (2016). Imposing antecedent global change conditions rapidly alters plant community composition in a mixed-grass prairie. *Oecologia, 182*, 899–911. https://doi.org/10.1007/s00442-016-3684-4

Dai, A. G. (2011). Drought under global warming: A review. *Wiley Interdisciplinary Reviews-Climate Change, 2*, 45–65. https://doi.org/10.1002/wcc.81

English, N. B., Weltzin, J. F., Fravolini, A., Thomas, L., & Williams, D. G. (2005). The influence of soil texture and vegetation on soil moisture under rain-out shelters in a semi-desert grassland. *Journal of Arid Environments, 63*, 324–343. https://doi.org/10.1016/j.jaridenv.2005.03.013

Gill, R. A., O'Connor, R. C., Rhodes, A., Bishop, T. B. B., Laughlin, D. C., & St Clair, S. B. (2018). Niche opportunities for invasive annual plants in dryland ecosystems are controlled by disturbance, trophic interactions, and rainfall. *Oecologia, 187*, 755–765. https://doi.org/10.1007/s00442-018-4137-z

Greenville, A. C., Burns, E., Dickman, C. R., Keith, D. A., Lindenmayer, D. B., Morgan, J. W., … Einoder, L. (2018). Biodiversity responds to increasing climatic extremes in a biome-specific manner. *Science of the Total Environment, 634*, 382–393. https://doi.org/10.1016/j.scitotenv.2018.03.285

Heberling, J. M., Brouwer, N. L., & Kalisz, S. (2017). Special issue: Interactions between white-tailed deer and invasive plants in North American forests effects of deer on the photosynthetic performance of invasive and native forest herbs. *Aob Plants, 9*. https://doi.org/10.1093/aobpla/plx011

Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology, 95*, 2646–2656. https://doi.org/10.1890/13-2186.1

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., … Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature, 429*, 651–654. https://doi.org/10.1038/nature02561

Johnson, S. N., Staley, J. T., McLeod, F. A. L., & Hartley, S. E. (2011). Plant-mediated effects of soil invertebrates and summer drought on aboveground multitrophic interactions. *Journal of Ecology, 99*, 57–65. https://doi.org/10.1111/j.1365-2745.2010.01748.x

Knapp, A. K., Avolio, M. L., Beier, C., Carroll, C. J., Collins, S. L., Dukes, J. S., … Jentsch, A. (2017). Pushing precipitation to the extremes in distributed experiments: Recommendations for simulating wet and dry years. *Global Change Biology, 23*, 1774–1782. https://doi.org/10.1111/gcb.13504

Knapp, A. K., Hoover, D. L., Wilcox, K. R., Avolio, M. L., Koerner, S. E., La Pierre, K. J., … Smith, M. D. (2015). Characterizing differences in precipitation regimes of extreme wet and dry years: Implications for climate change experiments. *Global Change Biology, 21*, 2624–2633. https://doi.org/10.1111/gcb.12888

Kreyling, J., Khan, M., Sultana, F., Babel, W., Beierkuhnlein, C., Foken, T., … Jentsch, A. (2017). Drought effects in climate change manipulation experiments: Quantifying the influence of ambient weather conditions and rain-out shelter artifacts. *Ecosystems, 20*, 301–315. https://doi.org/10.1007/s10021-016-0025-8

Kundel, D., Meyer, S., Birkhofer, H., Fliessbach, A., Mader, P., Scheu, S., … Birkhofer, K. (2018). Design and manual to construct rainout-shelters for climate change experiments in agroecosystems. *Frontiers in Environmental Science, 6*. https://doi.org/10.3389/fenvs.2018.00014

LaForgia, M. L., Spasojevic, M. J., Case, E. J., Latimer, A. M., & Harrison, S. P. (2018). Seed banks of native forbs, but not exotic grasses, increase during extreme drought. *Ecology, 99*, 896–903. https://doi.org/10.1002/ecy.2160

Loehman, R. A., Bentz, B. J., DeNitto, G. A., Keane, R. E., Manning, M. E., Duncan, J. P., … Lockman, I. B. (2018). Effects of climate change on ecological disturbance in the Northern Rockies. In *Climate Change and Rocky Mountain Ecosystems* (pp. 115–141). United States: Springer.

Logan, B. A., Adams, W. W., & Demmig-Adams, B. (2007). Avoiding common pitfalls of chlorophyll fluorescence analysis under field conditions. *Functional Plant Biology, 34*, 853–859. https://doi.org/10.1071/FP07113

Loik, M. E., Carter, S. A., Alers, G., Wade, C. E., Shugar, D., Corrado, C., … Kitayama, C. (2017). Wavelength-selective solar photovoltaic systems: Powering greenhouses for plant growth at the food-energy-water nexus. *Earth's Future, 5*, 1044–1053. https://doi.org/10.1002/2016EF000531

Marshall, B., & Biscoe, P. V. (1980). A model for C3 leaves describing the dependence of netphotosynthesis on irradiance. *Journal of Experimental Botany, 31*(1), 29–39.

Marshall, J. D., Blair, J. M., Peters, D. P. C., Okin, G., Rango, A., & Williams, M. (2008). Predicting and understanding ecosystem responses to climate change at continental scales. *Frontiers in Ecology and the Environment, 6*, 273–280. https://doi.org/10.1890/070165

Martinez-Vilalta, J., & Lloret, F. (2016). Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Global and Planetary Change, 144*, 94–108. https://doi.org/10.1016/j.gloplacha.2016.07.009

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence—A practical guide. *Journal of Experimental Botany, 51*, 659–668. https://doi.org/10.1093/jexbot/51.345.659

Ochoa-Hueso, R., Collins, S. L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W. T., Sinsabaugh, R. L., … Power, S. A. (2018). Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Global Change Biology, 24*, 2818–2827. https://doi.org/10.1111/gcb.14113

Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., … Tissue, D. T. (2015). Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters, 18*, 221–235. https://doi.org/10.1111/ele.12399

Ogle, K., Lucas, R. W., Bentley, L. P., Cable, J. M., Barron-Gafford, G. A., Griffith, A., … Tissue, D. T. (2012). Differential daytime and nighttime stomatal behavior in plants from North American deserts. *New Phytologist, 194*, 464–476. https://doi.org/10.1111/j.1469-8137.2012.04068.x

Pangle, R. E., Hill, J. P., Plaut, J. A., Yepez, E. A., Elliot, J. R., Gehres, N., … Pockman, W. T. (2012). Methodology and performance of a rainfall manipulation experiment in a pinon-juniper woodland. *Ecosphere, 3*, 1–20 art28. https://doi.org/10.1890/ES11-00369.1

Penuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., … Jump, A. S. (2013). Evidence of current impact climate change on life: A walk from genes to the biosphere. *Global Change Biology, 19*, 2303–2338. https://doi.org/10.1111/gcb.12143

Phillips, B. B., Shaw, R. F., Holland, M. J., Fry, E. L., Bardgett, R. D., Bullock, J. M., & Osborne, J. L. (2018). Drought reduces floral resources for

pollinators. *Global Change Biology*, 24, 3226–3235. https://doi.org/10.1111/gcb.14130

Power, S. A., Barnett, K. L., Ochoa-Hueso, R., Facey, S. L., Gibson-Forty, E. V. J., Hartley, S. E., … Johnson, S. N. (2016). DRI-Grass: A new experimental platform for addressing grassland ecosystem responses to future precipitation scenarios in south-east Australia. *Frontiers in Plant Science*, 7, 1373. https://doi.org/10.3389/fpls.2016.01373

R Core Team (2018) R: A language and environment for statistical computing.

Shriver, R. K. (2017). Rainfall variability and fine-scale life history tradeoffs help drive niche partitioning in a desert annual plant community. *Ecology Letters*, 20, 1231–1241. https://doi.org/10.1111/ele.12818

Signarbieux, C., & Feller, U. (2012). Effects of an extended drought period on physiological properties of grassland species in the field. *Journal of Plant Research*, 125, 251–261. https://doi.org/10.1007/s10265-011-0427-9

Tevini, M., & Teramura, A. H. (1989). UV-B effects on terrestrial plants. *Photochemistry and Photobiology*, 50, 479–487. https://doi.org/10.1111/j.1751-1097.1989.tb05552.x

Tredennick, A. T., Kleinhesselink, A. R., Taylor, J. B., & Adler, P. B. (2018). Ecosystem functional response across precipitation extremes in a sagebrush steppe. *PeerJ*, 6, e4485. https://doi.org/10.7717/peerj.4485

Trnka, M., Hayes, M., ek Jurečka, F., Anderson, M., Brázdil, R., Brown, J., … Eitzinger, J. (2018). Priority questions in multidisciplinary drought research. *Climate Research*, 75, 241–260. https://doi.org/10.3354/cr01509

Vogel, A., Fester, T., Eisenhauer, N., Scherer-Lorenzen, M., Schmid, B., Weisser, W. W., & Weigelt, A. (2013). Separating drought effects from roof artifacts on ecosystem processes in a grassland drought experiment. *Plos One*, 8, e70997. https://doi.org/10.1371/journal.pone.0070997

Weltzin, J. F., Loik, M. E., Schwinning, S., Williams, D. G., Fay, P. A., Haddad, B. M., … Zak, J. C. (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, 53, 941–952. https://doi.org/10.1641/0006-3568(2003)053[0941:ATROTE]2.0.CO;2

Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, 133, 95–101. https://doi.org/10.1007/s00442-002-1024-3

Zhang, B. W., Tan, X. R., Wang, S. S., Chen, M. L., Chen, S. P., Ren, T. T., … Han, X. G. (2017). Asymmetric sensitivity of ecosystem carbon and water processes in response to precipitation change in a semi-arid steppe. *Functional Ecology*, 31, 1301–1311. https://doi.org/10.1111/1365-2435.12836

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