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Water relations and photosynthesis along an elevation gradient for *Artemisia tridentata* during an historic drought

Charlotte C. Reed[1] · Michael E. Loik[1]

Abstract Quantifying the variation in plant–water relations and photosynthesis over environmental gradients and during unique events can provide a better understanding of vegetation patterns in a future climate. We evaluated the hypotheses that photosynthesis and plant water potential would correspond to gradients in precipitation and soil moisture during a lengthy drought, and that experimental water additions would increase photosynthesis for the widespread evergreen shrub *Artemisia tridentata* ssp. *vaseyana*. We quantified abiotic conditions and physiological characteristics for control and watered plants at 2135, 2315, and 2835 m near Mammoth Lakes, CA, USA, at the ecotone of the Sierra Nevada and Great Basin ecoregions. Snowfall, total precipitation, and soil moisture increased with elevation, but air temperature and soil N content did not. Plant water potential (Ψ), stomatal conductance (g_s), maximum photosynthetic rate (A_{max}), carboxylation rate (V_{cmax}), and electron transport rate (J_{max}) all significantly increased with elevations. Addition of water increased Ψ, g_s, J_{max}, and A_{max} only at the lowest elevation; g_s contributed about 30 % of the constraints on photosynthesis at the lowest elevation and 23 % at the other two elevations. The physiology of this foundational shrub species was quite resilient to this 1-in-1200 year drought. However, plant water potential and photosynthesis corresponded to differences in soil moisture across the gradient. Soil re-wetting in early summer increased water potential and photosynthesis at the lowest elevation. Effects on water relations and photosynthesis of this widespread, cold desert shrub species may be disproportionate at lower elevations as drought length increases in a future climate.

Abbreviations

A	Rate of photosynthetic CO_2 assimilation (μmol CO_2 m^{-2} s^{-1})
Ci	Intercellular CO_2 concentration (μmol mol^{-1})
Q	Photosynthetic photon flux (μmol photons m^{-2} s^{-1})
g_s	Conductance for H_2O diffusion through the stomata (mol H_2O m^{-2} s^{-1})
A_{max}	Light-saturated rate of CO_2 assimilation (μmol CO_2 m^{-2} s^{-1})
V_{cmax}	Maximum RuBP-saturated rate of carboxylation (μmol CO_2 m^{-2} s^{-1})
J_{max}	Maximum rate of electron transport (μmol e^{-} m^{-2} s^{-1})
R_{dark}	Dark respiration (μmol CO_2 m^{-2} s^{-1})
LCP	Light compensation point irradiance level at which CO_2 assimilation equals CO_2 respiration (μmol photons m^{-2} s^{-1})
Φ	Maximum quantum yield moles of CO_2 fixed per mole of quanta absorbed
Ψ_{stem}	Plant stem water potential (MPa)
iWUE	Integrated water use efficiency (μmol mol^{-1})

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Introduction

Drought is a global phenomenon, and arid regions are expected to get drier due to climate change (Dai 2011; McDowell et al. 2015; Sheffield et al. 2012). Drought is common and can be persistent in many parts of the United States where synoptic meteorological patterns, topography, local features, and microsite conditions affect precipitation patterns and soil water (Knapp et al. 2015b; Loik et al. 2004; Sun et al. 2015). Long-term drought has affected the central and southeast United States in recent years (Berdanier and Clark 2015; Knapp et al. 2015a), and California in 2015 is experiencing a 1-in-1200 year drought (Griffin and Anchukaitis 2014; Williams et al. 2015). State-wide 2013 precipitation averages for California were less than 34 % of historic averages (Swain et al. 2014), with trends continuing into 2014 and 2015. Anthropogenic warming has increased the ongoing risk of drought for California (Diffenbaugh et al. 2015; Mann and Gleick 2015). Drought is a major limiting factor for many ecological processes, particularly in arid and semi-arid regions (Zhou et al. 2013). If the California drought of 2012–2015 is part of a "new normal", or if it is similar to what happens at the onset of megadroughts (Cook et al. 2015), then it is important to know how the severe water limitation affects carbon acquisition for modeling vegetation productivity and distribution (Sun et al. 2015).

Many plant and ecosystem patterns and processes are affected by precipitation characteristics, which determine soil water availability and vegetation productivity (Knapp et al. 2015b; Loik et al. 2004; Sala et al. 2015). Combined with other stresses such as invasive species, pests, and wildfire, drought affects the distribution and function of key species, populations, and ecosystems (Abatzoglou and Kolden 2011; Anderegg et al. 2015). Severe drought and warming temperatures reduce hydraulic conductivity and photosynthetic ability (Osakabe et al. 2014), and lead to vegetation mortality (McDowell and Allen 2015). The outcome can result in changes of vegetation distribution, reduced habitat quality, increased wildfire risk, and altered water quality and quantity (Lohmann et al. 2012). Indeed, large portions of the global forest is in decline due in part to the effects of long-term drought (Allen et al. 2015).

The linkages between the physical environment, water relations, and leaf-level photosynthetic gas exchange can reveal the early-onset effects of drought. Reductions in soil water availability and plant water potential generally cause decreases in stomatal opening and carbon uptake for growth (DePuit and Caldwell 1973; Flexas et al. 2014; Osakabe et al. 2014). At the cellular level, drought can affect leaf biochemistry via regulation of the amount of activated RuBisCo that is available for carboxylation, and also by affecting the rate of electron transport through Photosystem II that helps regenerate the carboxylation substrate RuBP (Flexas et al. 2014; Zhou et al. 2013). The magnitude of the response to drought likely varies with resource gradients, such as for the variation in soil moisture, nutrients, and minimum and maximum air temperatures that occur at different elevations. Typically, soils have higher water content and temperatures are cooler at higher elevations due to orographic effects. Maximum photosynthetic rate (A_{max}) and stomatal conductance (g_s) have been found to increase with elevation (Friend et al. 1989), presumably as a result of greater soil water content or less stressful air temperatures. Photosynthetic biochemistry, limited by either carboxylation efficiency (V_{cmax}) or electron transport rate (J_{max}) (Long and Bernacchi 2003), has also been shown to vary for species that occur over elevation gradients, with both parameters generally increasing with elevation (Fan et al. 2011; Shi et al. 2006). However, these results have not been entirely consistent, and studies that describe the relationship between J_{max} and elevation are few, especially during severe drought when changes may be most apparent. Similarly, V_{cmax} and J_{max} have been shown to decrease with decreasing soil water availability for *Quercus douglasii* in the western Sierra Nevada (Xu and Baldocchi 2003; Zhou et al. 2013), indicating the sensitivity of photosynthetic biochemistry to drought. Many studies have also described a decrease in A_{max}, V_{cmax}, and J_{max} with decreasing nutrient availability, particularly nitrogen, although J_{max} is generally less sensitive to nutrient availability (Xu and Baldocchi 2003; Zhang and Dang 2006).

Steep environmental gradients can result in rapid or large differences in physiological processes, and provide an opportunity to improve modeling of species' responses to future climatic changes (Kooyers et al. 2014). Effects of a changing climate might show up along gradients where abiotic resources and conditions change abruptly over space and time, such as occurs for the eastern slope of the Sierra Nevada in California. It might be expected that plants at lower elevations with drier soils show greater drought effects compared to plants at higher elevations. The evergreen shrub mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle (Asteraceae) is widespread throughout the Great Basin Desert, occurring at elevations from 800 to 3100 m (NCRS 2004), a gradient over which conditions differ considerably (Loik et al. 2004). *Artemisia tridentata* possesses deep roots for accessing water in soil layers that are recharged with winter precipitation, which primarily occurs as snowfall (Richards and Caldwell 1987), and shallow roots which allow it to access smaller summer precipitation pulses (Loik 2007). Because seasonal precipitation patterns are likely to undergo changes at the regional scale for our study site in the future (Eng et al. 2015; Taylor et al. 2012; Warner et al. 2015), *A. tridentata* has the potential to experience distributional shifts, possibly as a

retraction of lower elevation distribution boundaries due to drier soils. On the other hand, episodic summer precipitation events may help sustain plant water potential at levels that allow for appreciable photosynthetic carbon acquisition. We tested hypotheses about these possibilities at different elevations of the Great Basin Desert—Sierra Nevada Conifer ecotone of eastern California during the lengthy drought of 2012–2014. Likewise, we tested for water limitation by re-watering soils along an elevation gradient to show the degree of recovery of water potential and photosynthesis during June and July, when rainfall is minimal at this location (Loik 2007).

The objective of this study was to evaluate the responses of water relations and photosynthesis to historic drought for *A. tridentata* ssp. *vaseyana* across an elevation gradient. Specifically, our goal was to quantify differences between relatively low and high elevation plants, and to evaluate the relative stomatal and biochemical limitations to photosynthesis during the drought, in order to test the following hypotheses. First, photosynthesis and water potential would increase from relatively lower to higher elevations, corresponding to differences in annual precipitation and soil moisture across elevations. We expected the lowest, driest site to have the lowest soil moisture content, plant stem water potential (Ψ_{stem}), stomatal conductance (g_s), and photosynthesis (A). The second hypothesis predicted that watering would increase photosynthetic characteristics for plants at all sites, based on the assumption that increased soil water content would cause an increase in Ψ_{stem}, g_s, and A_{max}. The last hypothesis predicted that there would be greater constraints to photosynthesis attributed to stomatal compared to biochemical limitations, based on the assumption that drought limits photosynthesis via plant water status and regulation of stomatal conductance.

Materials and methods

Study sites

Three research sites were selected along a 700-m elevation gradient at the Great Basin-eastern Sierra Nevada ecotone near Mammoth Lakes, Mono County, CA, USA, which is typical of *Artemisia tridentata* habitats in other parts of the Intermountain West (Sturges 1975). The low-elevation site is located at the Sierra Nevada Aquatic Research Laboratory of the University of California's Valentine Eastern Sierra Natural Reserve, south of Mammoth Lakes at 2135 m elevation (Loik 2007). Vegetation at this site is sagebrush steppe, and soil consists of well-drained sandy loam of the Watterson family (Seney and Gallegos 1995). Although the surrounding area receives seasonal grazing, the experimental sites have been protected by fencing for

over 10 years. The mid-elevation site at 2315 m elevation is near the junction of Deadman Road and US Highway 395 and is approximately 12 km north of Mammoth Lakes (Loik et al. 2013, 2015). Vegetation at the site is primarily sagebrush steppe with a sparse distribution of *Pinus jeffreyi* and *P. contorta*. Soil at the site is a well-drained loamy coarse sand of the Vitrandic Xerorthents family (Seney and Gallegos 1995). The high-elevation site is located adjacent to the Minaret Vista parking lot in the Inyo National Forest accessed by California State Route 203, at 2835 m elevation. Site vegetation consists predominately of high alpine dry meadow, and the soil at the site is characterized as primarily rock outcrop (Seney and Gallegos 1995). The two higher sites have not been grazed for over 50 years.

Past land use in the region has included livestock grazing, mining, and timber harvesting (Morris and Rowe 2014). Current land use is primarily for recreation, with both mid- and high-elevation sites under the management of the United States Forest Service (USFS), administered by the Inyo National Forest. The low-elevation site is utilized primarily for research and education under the management of the UC Natural Reserve System, and surrounded by the Inyo National Forest, Bureau of Land Management, and Los Angeles Department of Water and Power properties.

Meteorological data

Historical (24-year) precipitation and minimum/maximum air temperature were obtained from weather stations adjacent to each site. Climate data for the low- and mid-elevation sites were obtained from Remote Automated Weather Stations (RAWS) from the Western Regional Climate Center (www.wrcc.dri.edu). The weather station for the low-elevation site was at the Valentine Eastern Sierra Reserve, and for the mid-elevation site was at the Crestview USFS Fire Station. Data for the high-elevation site were obtained from the California Data Exchange Center (www.cdec.water.ca.gov), from the Mammoth Pass (MHP) weather station.

Experimental design

At each elevation, we randomly selected 12 plants with an average canopy diameter of 30 ± 4 cm that were located at a minimum distance of 5 m from one another. Initial measurements were made on all 12 plants within a 3-day period. Then, 6 of these plants were watered, and all 12 plants were re-measured 3 days after watering. The time interval between watering and post-watering measurements was selected based on a previous study of responses to watering for *A. tridentata* over time, in which responses were maximal at 2–3 days and declined thereafter (Loik 2007).

We used seasonal rather than annual amounts (i.e., MAP) of precipitation to determine the amount of water to add, as it is more realistic for summer precipitation patterns at this site. Water addition aimed to increase soil moisture to a point similar to that in years with average summer precipitation. In other words, we aimed to relieve summer drought. Each plant selected for watering received 5 cm of water, added with a watering can at an average distance of 1 m above the plant canopy. Water was added to a circular area (diam = 30 cm) corresponding to the drip line of the plant canopies. Water was added slowly to minimize surface runoff, and water volume added to each plant averaged 14 ± 4 L (depending on details of individual plant canopy size). The characteristics of long-term and 2013 precipitation, and how the 5 cm of water addition compares to 2013 totals at each elevation, are shown in Table S1. All measurements were made between mid-June and mid-July 2014 before the onset of the summer monsoon in this region.

Soil properties and nutrients

Five soil sampling locations were selected corresponding to study plants, and samples were collected within a 20-cm radius of the base of each plant. Depth of soil collection was approximately 20 cm based on the average depth of shallow roots (Loik 2007). Soil properties analyzed were total cation exchange capacity (meq 100 g^{-1}) and organic matter (%). Soil nutrients analyzed included estimated nitrogen release (kg ha^{-1}), phosphorus, potassium, calcium, magnesium, sodium, iron, manganese, zinc, and aluminum (mg kg^{-1}). Soil properties and nutrients were analyzed at Brookside Laboratories (New Bremen, OH, USA).

Soil moisture and plant water potential

Soil moisture was measured at a depth of 20 cm within 20 cm of the base of each study plant at each elevation. We collected samples between 0900 and 1100 hours local time on the same day that all other measurements were obtained for each specific plant. Soils were weighed and dried in an oven at 105 °C for 48 h. Post-drying soil weight was recorded, and initial soil moisture (%) calculated. Soil moisture was calculated both pre- and post-watering for all plants.

Plant stem water potential (Ψ_{stem}) was measured for all study plants at each elevation on the same day that all other measurements for that plant were obtained. Measurements were obtained between 0800 and 1000 hours. Vegetative stems averaging 10 cm were clipped from each plant using small scissors, and placed in a plastic bag for transport to the pressure chamber. Time between collection and measurement was no longer than 30 min. Water potential measurements were obtained using a Scholander-type pressure chamber (3000 Series; Soilmoisture Equipment, Santa Barbara, CA, USA).

Photosynthetic gas exchange

We measured photosynthetic gas exchange responses to CO_2 and light (A–C_i and A–Q curves; Sharkey et al. 2007) for each study plant using an open-mode portable photosynthesis system (model LI-6400; LI-COR, Lincoln, NE, USA). Leaf area was determined by estimation compared to area standards, and leaves were spread out to minimize overlap. All pre- and post-watering measurements were made on the same set of leaves for each plant. Photosynthetic (A) and stomatal conductance to water vapor (g_s) responses to leaf-internal CO_2 (C_i) were measured at a saturating irradiance of 1500 μmol photons m^{-2} s^{-1} for 12 concentrations of CO_2 between 0 and 1500 μmol mol^{-1}. Plants were exposed to ambient gas chamber CO_2 for approximately 5 min before beginning measurements to ensure that A was steady-state (Long and Bernacchi 2003), and for approximately 4–5 min between changes in CO_2 concentration. Photosynthetic (A) response to light (Q) was measured at an ambient CO_2 concentration of 400 μmol CO_2 mol^{-1} for 12 light levels between 2000 and 0 μmol CO_2 m^{-2} s^{-1}. Plants were allowed to acclimate to light intensity changes for approximately 2–3 min before measurements were recorded. Measurements were made in the morning when leaf temperature was generally between 15 and 30 °C. For all plants, leaf temperature and atmospheric pressure were also recorded.

From the A–C_i data, curve parameters were determined using Sharkey et al. (2007), and included maximum rate of carboxylation (V_{cmax}), and maximum rate of electron transport (J_{max}), both of which were evaluated at a standard temperature of 25 °C. From the A–Q data, curve parameters were determined using Marshall and Biscoe (1980), Thornley and Johnson (1990), and http://landflux.org, and included maximal photosynthetic rate (A_{max}), dark respiration (R_{dark}), quantum yield (Φ), and light compensation point (LCP).

Foliar carbon and nitrogen

Leaf samples were collected from 6 of the 12 study plants at each site. Two vegetative stems were clipped from plants using small scissors and dried at room temperature in paper bags for 2 months prior to being prepared for analysis. Leaves were removed from the stem and ground to a fine powder using a ball mill. Foliar %N, %C, C:N, and δ^{15}N and δ^{13}C were analyzed using a Carlo Erba Model NC2500 Elemental Analyzer (CE Elantech, Lakewood, NJ, USA) interfaced to a ThermoFinnegan Delta Plus XP isotope ratio mass spectrometer at the UC Santa Cruz Stable Isotopes Laboratory (Santa Cruz, CA, USA).

Data analysis

Soil moisture, nutrients, water potential, photosynthetic gas exchange, and leaf C and N data were analyzed using a one-way analysis of variance (ANOVA) to evaluate effects of elevation. At each site, t tests were used to evaluate effects of watering on measured parameters because the scale of the elevation gradient (700 m) overwhelmed the scale of watering experiments (0.5 m). The assumption of normal distribution was tested using a Shapiro–Wilk test on residuals. For comparisons where transformations did not result in normal distributions of the data, nonparametric tests [Wilcoxon rank sum (z test statistic), or Kruskal–Wallis (χ^2 test statistic)] were used. All analyses were conducted using JMP Pro (v.11.0.0; SAS Institute, Cary, NC, USA), and $p < 005$ has been considered significant throughout.

Results

Meteorology

Historic precipitation from 1990 to 2014 varied greatly among years, and was generally highest at 2835 m, and lowest at 2135 m (Fig. 1a). During the 9-month period leading up to and during the study, total precipitation which included both rain and snowfall was about 15 % of years before the drought, greatest at 2835 m, and much lower and often similar at 2315 and 2135 m for all months excluding July and August 2014 (Fig. 1b). During February, the month with the highest precipitation, the difference in precipitation between the highest and lowest sites was 193 mm. Additionally, mean maximum air temperature was generally lowest at 2835 m, and warmer at 2315 and 2135 m (Fig. 1c). One exception was that mean maximum air temperature at 2835 m was 0.7 K higher than that at 2135 m during May 2014. Mean minimum air temperature was generally lowest at 2135 and 2315 m, and highest at 2835 m, contrary to adiabatic lapse rate expectations (Fig. 1c). For example, during the 2 months with the greatest minimum air temperature differences between sites (December 2013 and January 2014), the highest elevation had a mean minimum temperature 6.2 and 6.4 K higher than the 2135 and 2315 m sites, respectively.

Soil moisture and plant water potential

Soil moisture at 20 cm was 1.2 % higher at 2315 m compared to 2135 m, and differed by 5 % between 2315 and 2835 m for unwatered plots (Fig. 2); differences were significant across elevations ($F = 20.2$, $P < 0.0001$; Table 2). Soil moisture increased with watering at all sites except 2835 m, where the effect was marginally significant
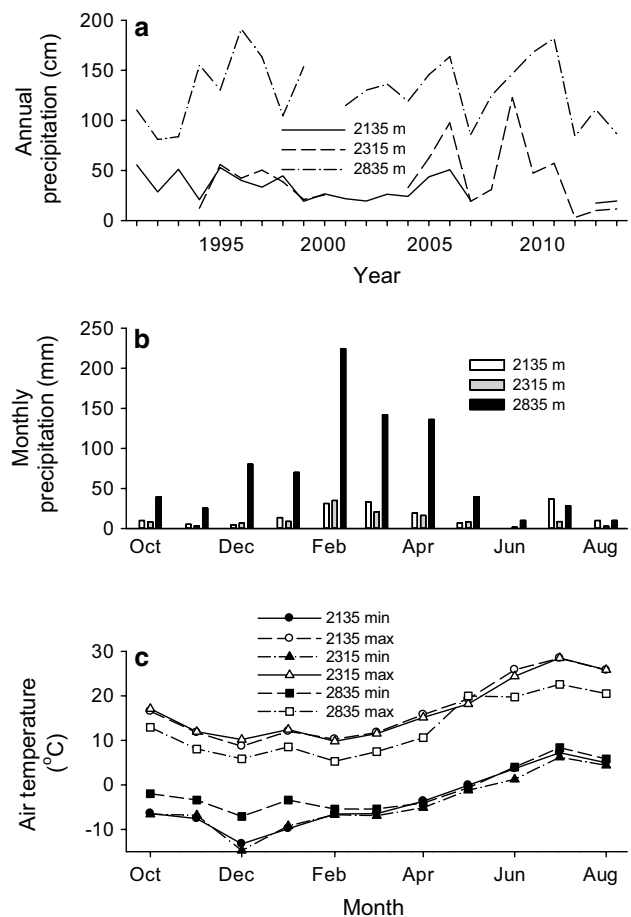

Fig. 1 **a** Annual precipitation (rainfall + snow) at each 2135, 2315, and 2835 m over a 24-year period. *Breaks in lines* indicate missing data. **b** Total monthly precipitation (rainfall + snow) at 2135, 2315, and 2835 m from 1 October 2013 to 1 September 2014. **c** Mean maximum (*top*) and minimum (*bottom*) monthly temperatures at 2135, 2315, and 2835 m from 1 October 2013 to 1 September 2014. *Open symbols* are maximum temperature and *filled symbols* are minimum temperature; *circles* (*solid lines*), *triangles* (*dash-dot lines*), and *squares* (*dashed lines*) represent temperatures at 2135, 2315 and 2835 m, respectively

($F = 2.0$, $P = 0.0740$; Table 3). Watering increased soil moisture by roughly 3 % after 3 days at each site. Results were consistent with observed precipitation differences at individual sites over the 9-month period leading up to the measurements. Plant stem water potential (Ψ_{stem}) also increased significantly with elevation ($\chi^2 = 29.8$, $P < 0.0001$; Fig. 2). Between the lowest and highest elevations, Ψ_{stem} for control plants increased roughly 2.8 MPa ($z = 4.2$, $P < 0.0001$), and differences were significant between all elevations (Table 2). However, the lowest elevation was the only site that showed a significant increase in Ψ_{stem} after the watering treatment ($F = 2.2$, $P = 0.0284$; Fig. 2; Table 3), after which it increased by 0.7 MPa.
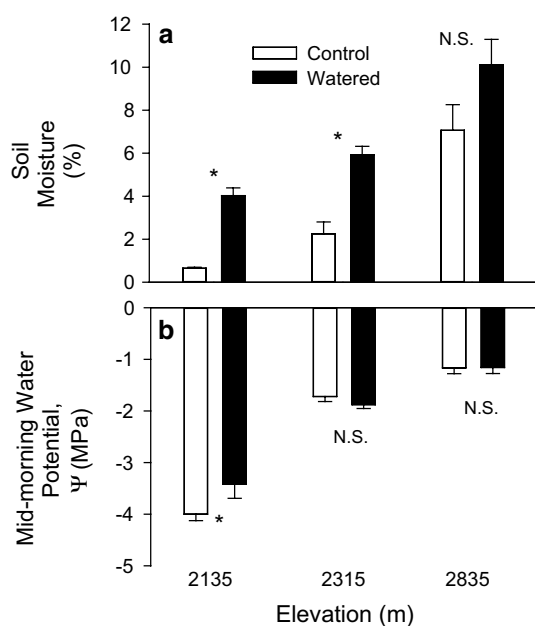
Fig. 2 a Soil moisture at 20 cm depth and **b** plant stem water potential (Ψ_{stem}) for *Artemisia tridentata* at 2135, 2315, and 2835 m, before (*open bars*) and after (*filled bars*) watering. Stem water potential was measured between 0800 and 1000 h. $N = 6$ plants per elevation (± 1 SE). *$p < 0.05$ between control and watered plants

Soil properties and nutrients

Many soil properties and nutrients differed significantly across elevations (Table 1). Total exchange capacity differed significantly ($\chi^2 = 10.50$, $P = 0.0052$), was greatest at 2835 m, and lowest at 2315 m (values at 2835 and 2315 m did not differ). Organic matter averaged 3.6 % at the highest elevation versus 1.5 % at the mid elevation ($F = 8.2$, $P = 0.0057$; Table 1). Across elevations, estimated nitrogen availability also differed significantly

($F = 11.9$, $P = 0.0014$); it was highest at 2835, lowest at 2315, and increased by 32.4 kg ha^{-1} between the two sites. Phosphorus differed significantly with elevation ($\chi^2 = 10.8$, $P = 0.0044$), and decreased by about 100 kg ha^{-1} from 2135 to 2835 m. Potassium followed the same trend as exchange capacity, organic matter, and N-availability, and was greatest at 2835 m, lowest at 2315 m, and significant across elevations ($F = 13.9$, $P = 0.0007$).

Photosynthetic gas exchange

In general, A–Q and A–Ci photosynthetic responses were greatest for plants at the highest elevation and the curves displayed qualitative differences (Fig. 3). The initial slope of the A–Q response differed between 2135 m and the two higher elevations (Fig. 3a). The fitted A–C_i response increased with elevation (Fig. 3c). Mean g_s for control plants ranged from 0.05 to 0.37 mol m^{-2} s^{-1} from the lowest to highest elevation, and significantly differed across elevations ($F = 21.9$, $P < 0.0001$), and between all sites (Fig. 4a; Table 2). Differences were also significant across elevations for A_{max} ($F = 18.0$, $P < 0.0001$); it was lowest at 2135 m and increased by roughly five-fold across elevations (Fig. 4b). In addition, maximum carboxylation rate (V_{cmax}) increased nearly four-fold with elevation (Fig. 4c) for control plants and differences across elevations were significant ($F = 13.0$, $P < 0.0001$; Table 2). Based on the demand function, the A–Ci curves indicated that stomatal limitation of photosynthesis (relative to biochemical limitation) was higher at the lower compared to the highest site (Table 2). Maximum rate of electron transport (J_{max}) approximately doubled between 2135 and 2835 m (Fig. 4d) for control plants, and differences were significant between the highest and two other elevations ($\chi^2 = 12.5$, $P = 0.0019$; Table 2). Quantum yield (Φ) was lower at 2135 m compared to the other two elevations (Fig. 4e).

Table 1 One-way ANOVA results across and between elevations (2135, 2315, 2835 m) for soil physical and chemical properties, and foliar C and N properties

Independent variable	F	df	P	Order
Total exchange capacity (meq 100 g^{-1})	10.50[a]	2	**0.0052**	$2315 < (2135 = 2835)$
Organic matter (%)	8.19	2	**0.0057**	$(2135 = 2315) < 2835$
N release (kg ha^{-1})	11.89	2	**0.0014**	$(2135 = 2315) < 2835$
P (mg kg^{-1})	10.84[a]	2	**0.0044**	$2135 > (2315 = 2835)$
S (mg kg^{-1})	3.15[a]	2	0.2066	$2135 = 2315 = 2835$
δ^{13}C (‰)	10.04	2	**0.0017**	$2135 > (2315 = 2835)$
% C	0.57	2	0.5761	$2135 = 2315 = 2835$
δ^{15}N (‰)	39.24	2	**<0.0001**	$2135 > 2835 > 2315$
% N	0.52	2	0.6073	$2135 = 2315 = 2835$
C:N ratio	1.25	2	0.3152	$2135 = 2315 = 2835$

Data are F values; $n = 5$ plants per elevation, $n = 6$ for δ^{13}C, %C, δ^{15}N, %N, C:N; *bold type* indicates statistical significance ($P < 0.05$)

Order indicates differences between sites

[a] Kruskal–Wallis test used due to non-normal data at one or more sites, test statistic $= \chi^2$
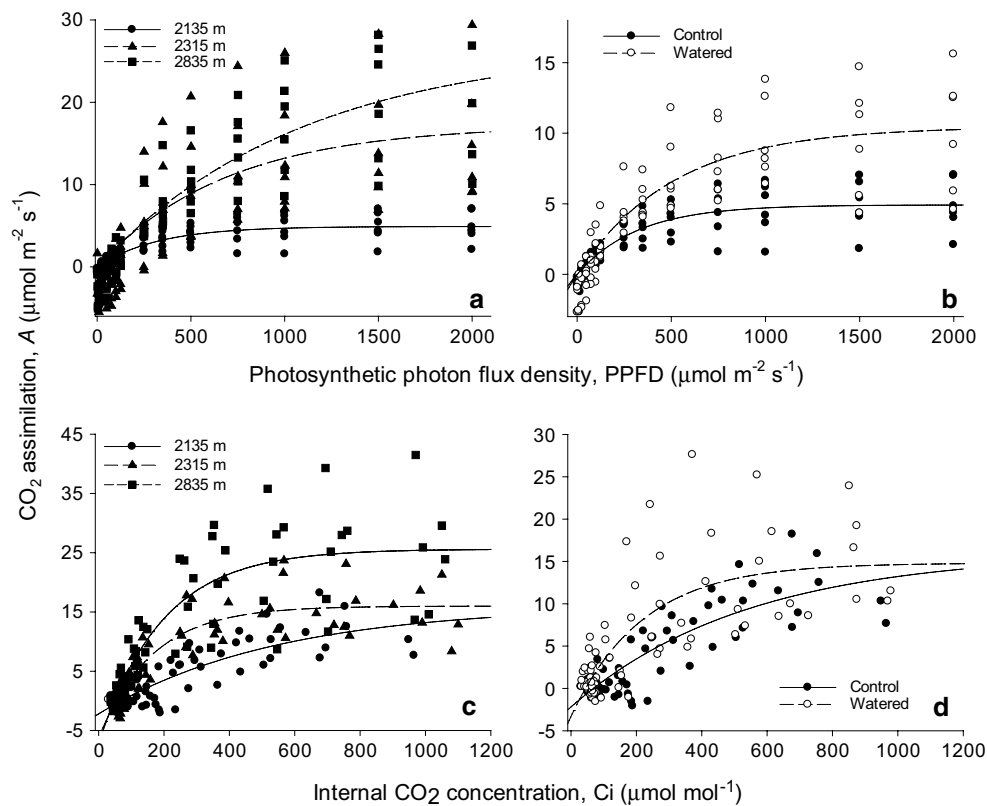
Fig. 3 Response of photosynthetic CO_2 assimilation (*A*) to absorbed PAR (*Q*; **a**, **b**), and intercellular CO_2 concentration (*Ci*; **c**, **d**) for *Artemisia tridentata* at 2135 (*circles*, *solid lines*), 2315 (*triangles*, *large dashed lines*), and 2835 m (*squares*, *short dashed lines*; **a**, **c**), and before (*circles*, *solid lines*) and after (*triangles*, *dashed lines*) watering for plants at 2135 m site (**b**, **d**). $n = 6$ plants per elevation or watering treatment

The addition of water resulted in an overall upregulation of photosynthetic rates only at the lowest elevation (Fig. 3). Watering approximately doubled photosynthetic rates of the *A–Q* response at 2135 m (Fig. 3b) but did not impact plants at the two higher elevations. Watering caused the fitted $A–C_i$ response of plants at 2135 m to exhibit rates similar to those at 2315 m (Fig. 3d). Based on the modeled *A–Q* and $A–C_i$ responses, both A_{max} and J_{max} were higher for watered plants ($t = 2.8$, $P = 0.0326$; $z = 2.5$, $P = 0.0131$ respectively; Fig. 4b, d). Stomatal conductance was significantly higher for watered plants, but only at the lowest elevation ($t = 3.8$, $P = 0.0035$; Table 3; Fig. 4a). After the application of the watering treatment, stomatal conductance increased from a mean of 0.05 ± 0.006 (mean $\pm$ 1 SE) to 0.09 ± 0.007 mol m^{-2} s^{-1} ($t = 3.8$; $P = 0.0035$). Mean A_{max} increased by approximately 7.3 µmol m^{-2} s^{-1}, and mean J_{max} increased by 70 % after watering. There were no significant effects of watering on V_{cmax}, R_{dark}, Φ, or LCP (Fig. 4c; Table 3; results not shown for R_{dark} or LCP).

Foliar carbon and nitrogen

Both $\delta^{15}N$ and $\delta^{13}C$ were greatest at 2135 m and lowest at 2315 m (Table 1), whereas there were no significant differences in %C, %N or C:N across elevations. $\delta^{13}C$ differed significantly across elevations ($F = 10.0$, $P = 0.0017$), and increased by 2.4 ‰ between 2315 and 2835 m, but was not significant between 2315 and 2835 m. Based on the established relationship between carbon isotope discrimination ($\delta^{13}C$) and integrated water use efficiency (iWUE) (Lambers et al. 1998), plants at the lowest elevation had the greatest iWUE compared to those at the two higher sites. $\delta^{15}N$ varied significantly across elevations ($F = 39.2$, $P < 0.0001$), and increased by approximately three-fold between 2315 and 2135 m, and by five-fold between 2135 and 2835 m.

Discussion

Sagebrush (*Artemisia tridentata* ssp. *vaseyana*) had positive rates of net carbon uptake at all elevations even though
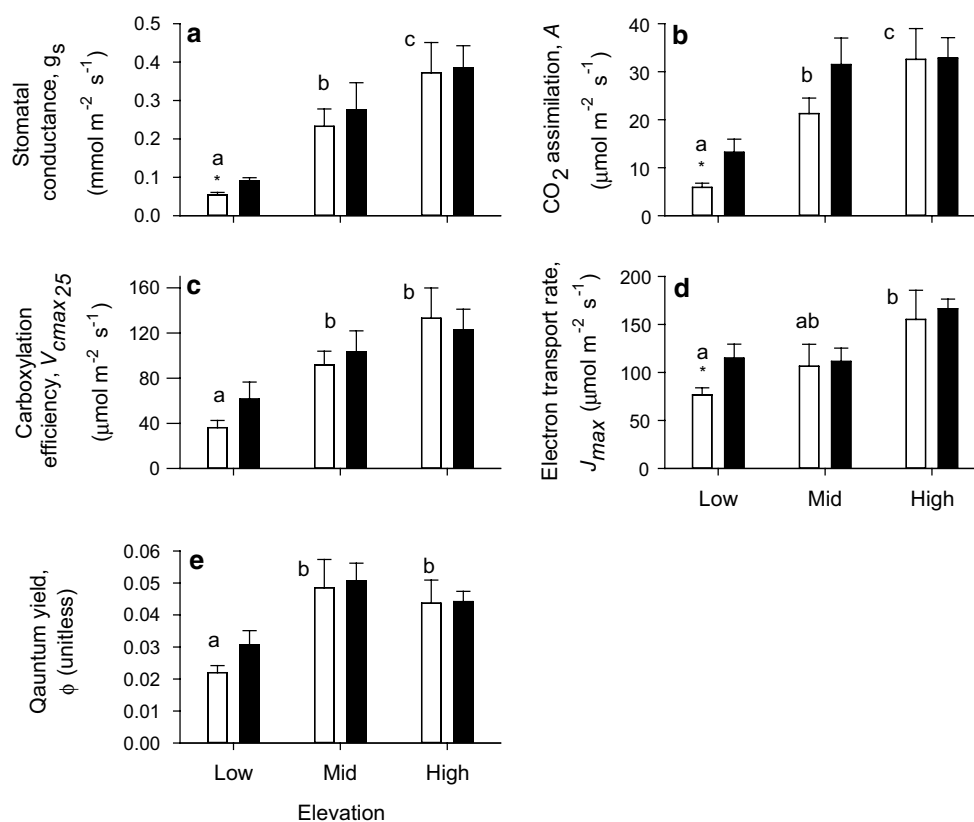
Fig. 4 Photosynthesis for *Artemisia tridentata* at 2135, 2315, and 2835 m, before (*open bars*) and after (*filled bars*) watering. **a** Stomatal conductance (g_s) **b** maximum CO_2 assimilation (A_{max}) **c** maximum rate of carboxylation (V_{cmax}), **d** maximum rate of electron transport (J_{max}), **e** quantum yield for Photosystem II (Φ). $n = 6$ plants per elevation (± 1 SE). *Letters* indicate significant differences between elevations; *$p < 0.05$ between control and watered plots

Table 2 One-way ANOVA for effect of elevation on soil moisture, plant stem water potential, and photosynthetic parameters

Independent variable	Elevation (m)	2135 versus 2315 m	2135 versus 2835 m	2315 versus 2835 m
Soil moisture (%)	**20.21****	**−2.52***	**−9.00****	**−6.63****
Plant water potential (MPa)	**30.84****[a]	**4.21****[b]	**4.21****[b]	**3.96****[b]
V_{cmax} (μmol m^{-2} s^{-1})	**13.05****	**−3.06***	**−4.97****	−1.91
J_{max} (μmol m^{-2} s^{-1})	**12.50****[a]	0.90[b]	**3.38****[b]	**2.43***[b]
Stomatal conductance (mol m^{-2} s^{-1})	**21.89****	**−3.77****	**−6.35****	**−2.58***
A_{max} (μmol m^{-2} s^{-1})	**10.84****	**−4.28****	**−6.02****	−1.60
Quantum yield, φ	**8.55****	**−4.32****	**−3.35****	1.05
R_{dark} (μmol m^{-2} s^{-1})	**17.98****	**3.91****[b]	**3.26****[b]	**2.18***[b]
LCP (μmol m^{-2} s^{-1})	**20.63****[a]	**−4.00****	−1.50	**2.54***
Stomatal limitation (%)	**3.39***	0.95	**2.58***	1.63

Data for the elevation effect are F values ($df = 2$), $n = 12$ plants per elevation. Values in *bold type* are significant, indicated as * $P < 0.05$ or ** $P < 0.01$

[a] Kruskal–Wallis rank sum used due to non-normal data at one or more sites, test statistic: Kruskal–Wallis = χ^2. V_{cmax} and J_{max} were modeled for plants at a PAR = 1500 μmol m^{-2} s^{-1} and $T = 25$ °C; A_{max}, R_{dark} and LCP were modeled from measurements made at $pCO_2 = 400$ ppm

[b] Statistical result from a Wilcoxon rank sum test

Table 3 Effect of watering on soil moisture, plant stem water potential, and photosynthetic parameters at each elevation ($df = 2$)

Independent variable	Watering effect		
	2135 m	2315 m	2835 m
Soil moisture (%)	**10.18****	**5.95****	2.00
Water potential (MPa)	**2.19***[a]	−0.96[a]	0.06
Stomatal conductance (mol m^{-2} s^{-1})	**3.82****	0.55	0.14
A_{max} (µmol m^{-2} s^{-1})	**2.77***	1.63	0.04
V_{cmax} (µmol m^{-2} s^{-1})	1.67	0.56	−0.34
J_{max} (µmol m^{-2} s^{-1})	**2.48***[a]	0.20	0.38
Quantum yield, φ	1.92	0.21	0.07
LCP (µmol m^{-2} s^{-1})	1.18	0.27	−1.29
R_{dark} (µmol m^{-2} s^{-1})	1.71	1.00[a]	−0.99

Data are t values, $n = 12$ plants per elevation, 6 per treatment; *bold type* indicates significance (* $P < 0.05$; ** $P < 0.01$)

[a] Wilcoxon rank sum used due to non-normal data at one or more sites, test statistic = z. V_{cmax} and J_{max} were modeled based on measurements for plants at a PAR = 1500 µmol m^{-2} s^{-1} and $T = 25$ °C; A_{max} was modeled from measurements made at $pCO_2 = 400$ ppm

this region was experiencing a severe multi-year drought. Plant stem water potential and photosynthesis increased with annual precipitation and soil moisture along the elevation gradient. Experimentally added water caused an increase in water potential and certain aspects of photosynthesis at the driest site (g_s, A_{max}, J_{max}). These results suggest differential sensitivity of photosynthesis to water addition along this gradient. *Artemisia tridentata* has a distribution covering about 1.37×10^8 ha and is arguably one of the most widespread shrub species in the United States. Subspecies *vaseyana* is generally associated with more mesic sites than other subspecies (Kolb and Sperry 1999), which suggests it may be sensitive to drying conditions in the future. Previous studies on *A. tridentata* var. *vaseyana* at this site showed variation of stomatal conductance (g_s) and photosynthetic CO_2 assimilation (A) in response to snow depth in the previous winter over 10 years (Loik et al. 2015), indicating sensitivity to snowmelt soil water availability. Elsewhere, warming affects soil moisture and the ability of *A. tridentata* to conduct photosynthesis at 2070 m in Colorado, USA (Shaw et al. 2000). Photosynthesis by *A. tridentata* is also dependent on antecedent soil water conditions (Ogle et al. 2015). Moreover, at times when soil surface layers have dried, *A. tridentata* can spatially shift the depth of water access to deeper roots to maintain photosynthetic capacity (Leffler and Caldwell 2005). Our results showed little response of Ψ_{stem} to watering at the two higher elevations, suggesting that plants at these sites may be using deeper roots to access water. The plasticity of certain water relations and photosynthetic characteristics might allow sagebrush to be resilient to climate change

at higher elevations; however, lower elevation populations might experience reduced carbon uptake, such as due to reduced snowfall in the future (Lute et al. 2015). On the other hand, *A. tridentata* var. *vaseyana* showed rapid upregulation of g_s and A in response to summer watering at the lowest elevation of the present study (Loik 2007). Perhaps plants at this elevation have a greater number of summer-active shallow roots to obtain water from summer rainfall. In any case, patterns of carbon acquisition for *A. tridentata* depend on various aspects of soil water availability that operate at different spatial and temporal scales, which will make it challenging to project productivity or distribution changes for this foundational species, or broader impacts for dryland vulnerability to climate change.

Gradients in soil water availability affected the relative amount of stomatal and biochemical limitations to photosynthesis. Not surprisingly, plants at the lowest elevation had the lowest stomatal conductance and highest iWUE based on $\delta^{13}C$ (Ehleringer et al. 1985). In comparison to biochemical limitations, stomatal limitation determined from the $A–C_i$ relationship varied between roughly 30 % at the lowest elevation to 23 % at the highest elevation, and was not affected by watering. These results reflect a moderate flexibility in the relative amount of stomatal versus biochemical control over photosynthetic capacity for *A. tridentata* between the lowest and highest elevations. Carboxylation efficiency and electron transport rate through Photosystem II (i.e., V_{cmax} and J_{max}), increased with elevation, suggesting that both RuBP carboxylation and regeneration are limited by reduced soil moisture at the lowest site. The increase of g_s, A_{max}, V_{cmax}, and J_{max} is generally consistent with previous studies that described photosynthetic variation along elevation gradients (Fan et al. 2011; Friend et al. 1989) and with variable soil water availability (Wei et al. 2008; Xu and Baldocchi 2003). Overall, these results suggest that the limitation of photosynthesis by stomata compared to biochemistry changes somewhat with elevation for *A. tridentata* ssp. *vaseyana*, but not with soil re-wetting. The importance of longer-term seasonal plasticity in stomatal versus biochemical limitations on carbon acquisition is yet to be fully determined in this region.

We predicted that re-watering in early summer would lead to an increase in plant stem water potential, stomatal conductance, and photosynthesis at all elevations. However, soil re-watering only stimulated photosynthesis of *A. tridentata* at the lowest site. Previous work showed that the recovery of photosynthesis for *A. tridentata* following water additions in summer is rapid (reaching a maximum in 2–3 days), and dependent on both the magnitude and timing of precipitation (Loik 2007). Re-watering increased electron transport through Photosystem II (J_{max}) at our lowest elevation, suggesting that the historic drought may be limiting regeneration of RuBP. However, not all photosynthetic

variables responded to watering, including the maximum rate of carboxylation, suggesting that the amount of activated RuBisCo may not be limiting photosynthesis. These results are in contrast with previous studies that describe decreases in V_{cmax} in relation to drought for grassland species in central Europe, and also as part of a larger meta-analysis of 22 tree and shrub species (Signarbieux and Feller 2011; Zhou et al. 2013). Antecedent water content helps determine photosynthetic responses to more recent precipitation events for many desert shrubs species of the western USA, including *A. tridentata* (Ogle et al. 2015). The hypothesis that certain photosynthetic limitations are determined by antecedent water awaits further testing, such as whether there is a hierarchy of processes that downregulate as antecedent soil water dries over time. Also, there is little understanding of how the rate of soil re-watering affects photosynthetic recovery, as the rate of soil moisture infiltration varies widely following slow spring snowmelt compared to rapid summer thunderstorm inundation.

Gradients in temperature or nitrogen may have contributed to the photosynthetic gas exchange patterns that we observed along the elevation gradient (Wullschleger 1993). However, foliar %N was constant across elevations and did not correspond to elevational differences in V_{cmax}, J_{max}, or A_{max}, so we conclude that variability in photosynthetic rate is not related to leaf or soil N content. Likewise, temperature differences across elevations were highly variable, and did not always vary as expected based on the adiabatic lapse rate, possibly due to katabatic drainage of cold air (Hidore et al. 2010) or microclimatic effects of topography and nearby forest cover. Thus, elevational differences in precipitation, soil moisture, and Ψ_{stem} across the gradient likely drive the carboxylation rate and electron transport limitations that we observed. Elsewhere, photosynthetic biochemistry varies for species that occur over elevation gradients, with both V_{cmax} and J_{max} generally increasing with elevation (Fan et al. 2011; Shi et al. 2006), including for *Quercus douglasii* nearby in the western Sierra Nevada (Xu and Baldocchi 2003).

Soil properties and other nutrient differences were highly variable across elevations, which could have influenced photosynthetic processes. For example, we found that $\delta^{15}N$ varied across the elevation gradient, and was most positive at the lowest elevation. Foliar $\delta^{15}N$ is known to vary across environmental gradients and in response to availability of resources, and affects photosynthesis and respiration (Craine et al. 2009). Percent of CO_2 lost to dark respiration was greatest at the mid-elevation (20 % of A_{max}), roughly equal at the low and high elevations (11 %), and neither increased nor decreased after watering at any site. For R_{dark}, results were inversely related to foliar $\delta^{15}N$ differences across sites, and quantum yield results were inversely related to water use efficiency. It is not clear

whether there is a causal relationship between any of these patterns. Other biotic or abiotic factors may have contributed to the observed elevational variation. For example, *A. tridentata* shrubs live in close proximity to individuals of the nitrogen-fixing species *Purshia tridentata* at the middle elevation site (Loik et al. 2013; Webster et al. 1967). At the higher elevation site, *A. tridentata* co-occurs with nitrogen-fixing *Lupinus* spp., which may account for the less positive $\delta^{15}N$ (Halvorson et al. 1992). It has also been shown that foliar $\delta^{15}N$ increases with decreasing precipitation (Austin and Sala 1999) and increasing annual temperature (Amundson et al. 2003). This suggests that some of the elevational variation in foliar $\delta^{15}N$ may be related to climatic variability whereas some part may be due to the nature of the plant community. Further controlled experiments will be necessary to accurately quantify these relationships. In any case, indirect impacts of drought on nutrient availability will likely complicate projections of vegetation productivity or distribution based on soil water content alone.

This study shows that water relations and photosynthesis varied across the ecotone over which *A. tridentata* ssp. *vaseyana* occurs in eastern California. Also, leaf-level photosynthesis was rapidly upregulated by re-watering in summer at the lowest elevation. Combined, these results suggest that for plants along elevation gradients we cannot assume they will respond in the same manner or timing to changes in soil water availability, which could complicate "space-for-time" models of climate change impacts. Although climate model outputs for the study region are highly variable, Sierra Nevada snowpack is expected to be substantially reduced and temperatures will increase by the end of the twenty-first century (Cayan et al. 2008; Hayhoe et al. 2004). Regional climate model projections for this location (CMIP5, RCP8.5) suggest a drying of about 1 mm per day in July for 2090–2099 (Abatzoglou and Brown 2012). The frequency and duration of drought events cannot be readily ascertained from such model scenarios. Nevertheless, a general consensus is that earlier snowmelt and warmer temperatures will enhance drought conditions for California (Lute et al. 2015; Mann and Gleick 2015). Climate change will likely have the most significant impacts at elevations in montane regions where winter precipitation shifts between rain and snow (Beniston 1997). The precipitation patterns of our study region are driven not just by orographic uplift but also by passage of synoptic fronts through physical features. For example, snow storms are funneled through Mammoth Pass and result in highly localized differences in precipitation. The lowest site of this study at 2135 m is most likely to experience the earliest effects of climatic change, as this is currently the approximate elevation of the Sierra Nevada snowline for this region (Jeton et al. 1996). Other regional climate changes include earlier snowmelt timing and greater

evapotranspiration associated with higher temperatures, which result in longer drought duration, lower soil moisture, and dry vegetation (Keshta et al. 2012; Null et al. 2010; Westerling et al. 2006). Thus, it is difficult to project with much certainty how episodic drought will impact this elevation gradient, but one possibility is disproportionate drying at the lower elevations. The flexibility and rapid upregulation of photosynthesis following re-wetting probably helped *A. tridentata* survive similar droughts in the past, and may be important for surviving future droughts. Although our results suggest greater sensitivity of photosynthesis of *A. tridentata* to drought at lower compared to higher elevations, a complete understanding of how this will affect dryland vulnerability to climate change will require (1) improvements in regional-scale modeling of episodic drought, and (2) continued improvement of our knowledge about how this widely distributed shrub species will physiologically respond to future drought conditions.

Author contribution statement CCR and MEL designed the experiments; CCR conducted the experiments and analyzed the results; CCR and MEL wrote the paper.

Compliance with ethical standards

Conflict of interest The experiments described herein comply with the current laws of the United States of America. The authors declare that they have no conflict of interest.

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