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# A spring rainfall pulse causes greater *in situ* photosynthetic upregulation for *Bromus tectorum* compared to co-occurring native herbaceous species

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## ABSTRACT

The invasive grass *Bromus tectorum* fuels fires, displaces native species, and reduces wildlife habitat on sagebrush steppe throughout the western United States. Recently, it has spread from the Great Basin Desert into higher elevations of the eastern Sierra Nevada, where it coexists with natives but has not yet altered fire regimes. We evaluated effects of a springtime water pulse (+10 mm) in a drought year on photosynthesis for *B. tectorum* and co-occurring shallow-rooted native perennials *Achnatherum hymenoides*, *Elymus elymoides*, and *Lupinus argenteus* near the range limit of *B. tectorum* at ~2175 m in California. Watered *B. tectorum* had the largest increase in stomatal conductance (27%) of the four species. Watering increased $CO_2$ assimilation for *B. tectorum* by 78% over controls, compared to 17% for *A. hymenoides*, 2% for *E. elymoides*, and 29% for *L. argenteus*. Electron transport rate within Photosystem II increased for watered *B. tectorum* and *A. hymenoides*, but not for *E. elymoides* and *L. argenteus*. Instantaneous electron transport rate and carbon assimilation were more responsive for *B. tectorum* than natives following a spring water pulse during drought. Rapid upregulation of carbon uptake in spring in response to soil re-wetting during drought could facilitate *B. tectorum* spread at high elevation.

## 1. Introduction

Soil water content drives many ecosystem processes, particularly in arid and semi-arid ecosystems (Noy-Meir, 1973). Water availability for plants is a function of meteorological patterns that supply precipitation, combined with water demand driven by evapotranspiration (Loik et al., 2004). Soil moisture is not in constant supply, but becomes available following precipitation events (Austin et al., 2004; Peek and Forseth, 2009). Plants can rapidly exploit ephemeral increases in water and nutrient availability (Bilbrough and Caldwell, 1997; Bowman and Bilbrough, 2001; Loik, 2007). Changes in precipitation patterns in the future (Cayan et al., 2008; Maurer et al., 2007) will likely affect plant establishment, growth, and reproduction for certain plant species (Dalgleish et al., 2011; Lopez et al., 2008).

Arid and semi-arid ecosystems are highly sensitive to changes in both evaporative demand and soil moisture (Schwinning and Sala, 2004). The amount, type, and timing of precipitation exert strong influences on the structure and function of communities and ecosystems (Abatzoglou and Kolden, 2011; Brooks and Chambers, 2011; Loik et al., 2015). In the Great Basin Desert of the western United States, deeply rooted shrubs such as *Artemisia tridentata* Nutt.) and *Purshia tridentata* (Pursh) DC.) can obtain water from progressively deeper soils as water content decreases (Ehleringer and Dawson, 1992). Less is known about

resource acquisition in response to soil water pulses for smaller herbaceous plants that comprise a key portion of the α-diversity of these sites (Loik et al., 2013). Understanding how native grasses and small-statured forbs respond to pulses of soil water availability will be important for managing high desert biodiversity in a changing climate.

Invasive species have altered ecosystems worldwide, but less so at high elevations where climatic conditions, propagule pressure, and lack of disturbance have limited their expansion (Leger et al., 2009; Pauchard et al., 2009). Recently, the invasive annual grass *Bromus tectorum* L. (Poaceae, 'cheatgrass') has been increasing in abundance at high elevations in the western United States (Bromberg et al., 2011; Brown and Rowe, 2004; Concilio et al., 2013; Weltz et al., 2011). As the most ubiquitous invasive plant in the Intermountain West (Weltz et al., 2011), *B. tectorum* poses the greatest threat to sagebrush steppe. *Bromus tectorum* forms a positive feedback loop with fire; it densely colonizes bare ground, matures before native species, and becomes extremely flammable upon senescence, ultimately increasing fire frequencies in invaded ecosystems, and diminishing wildlife habitat quality (Billings, 1990; Brooks et al., 2004; Knapp, 1996; Miller et al., 2017; Whisenant, 1990). The continued rapid spread of *B. tectorum* threatens to displace > 40% of the current area of sagebrush steppe in the next 30 years (Chambers et al., 2007 and references therein). Climate change is likely to facilitate *B. tectorum* expansion into higher elevations by

increasing habitat suitability or altering competitive constraints, thereby favoring *B. tectorum* over native species (Compagnoni and Adler, 2014; Dukes and Mooney, 1999; Prevey and Seastedt, 2015). Management of *B. tectorum* requires better knowledge of its response to ephemeral soil water content during the growing season.

At the ecotone of the Great Basin Desert and the Sierra Nevada, populations of *B. tectorum* are sensitive to spatial and inter-annual variation in snow depth, soil water, and nitrogen (Concilio and Loik, 2013; Concilio et al., 2013; Griffith and Loik, 2010). However, we know little about the *in situ* patterns of photosynthesis for *B. tectorum* and the native herbaceous species at this site. Despite some greenhouse experiments (Dakheel et al., 1994; Link et al., 1995; Rice et al., 1992; Smith et al., 1987), we are not aware of any reports of the *in situ* patterns of photosynthesis for *B. tectorum*. Likewise, much of the research on *B. tectorum* has focused on invasions at lower elevations (Booth et al., 2003; Humphrey and Schupp, 2004; Mazzola et al., 2011; Rau et al., 2011), where impacts are extensive. At its upper extent in the Sierra Nevada, infestations are patchy and have not yet altered fire cycles (Brooks and Chambers, 2011), and populations are constrained by low temperatures and persistent snowpack (Concilio et al., 2013; Griffith and Loik, 2010). Typically, *B. tectorum* germinates in the fall but recruitment continues through the winter if snow cover is absent (Mack and Pyke, 1983). Yet, in the Sierra Nevada, deep winter snow typically prevents germination until spring (Griffith and Loik, 2010). Thus, the growing season for *B. tectorum* at high elevations is constrained to the time between snowmelt and summer drought, and spring precipitation could facilitate spread of this problematic species.

Our objective was to determine the ability of *B. tectorum* and neighboring native species to upregulate *in situ* photosynthetic carbon acquisition in response to a pulse of soil water during spring. We added water *in situ*, monitored photosynthetic responses for approximately two weeks, and estimated growth in May 2013. We hypothesized that ($H_1$) water additions would result in increased photosynthetic rates *in situ* relative to unwatered controls, demonstrating the capacity for springtime upregulation; and ($H_2$) because of traits that favor rapid springtime growth, *B. tectorum* responses to water additions would be greater than those of three neighboring native perennial species. We quantified the effects of a simulated spring rainfall event on *in situ* leaf-level gas exchange (stomatal conductance to water vapor, $g_s$, and leaf-level net $CO_2$ assimilation, *A*), and electron transport rate within Photosystem II (PSII) in chloroplasts of light-adapted leaves. We chose to monitor photosynthetic gas exchange and PSII activity because spring rainfall might shift the carbon balance toward greater rates of photosynthesis (*i.e.*, relative to respiration or photorespiration), and result in increased growth. The natives included bunchgrasses *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Poaceae) and *Elymus elymoides* (Raf.) Swezey (Poaceae), and the nitrogen-fixing *Lupinus argenteus* Pursh (Fabaceae).

## 2. Materials and methods

### 2.1. Study system

We conducted this study in a sagebrush steppe ecosystem adjacent to the Sierra Nevada Aquatic Research Laboratory of the University of California Valentine Eastern Sierra Natural Reserve. This site is located in the Inyo National Forest on the eastern slope of the Sierra Nevada near Mammoth Lakes, Mono County, California, USA (37°36′51″N/118°49′47″W, ~2175 m elevation). Co-dominant shrub species are *Artemisia tridentata* and *P. tridentata*; other woody or semi-woody shrubs, such as *Chrysothamnus nauseosus* Pall. ex Pursh (Asteraceae, 'rubber rabbitbrush') and *Rosa woodsii* Lindl. (Rosaceae, 'Woods' rose'), are present but less abundant (Orr and Howald, 2000). Several native bunchgrasses and forbs populate the site, including *Achnatherum hymenoides*, *E. elymoides*, and *L. argenteus*. *Bromus tectorum* coexists with native vegetation here but has been increasing in density over the last
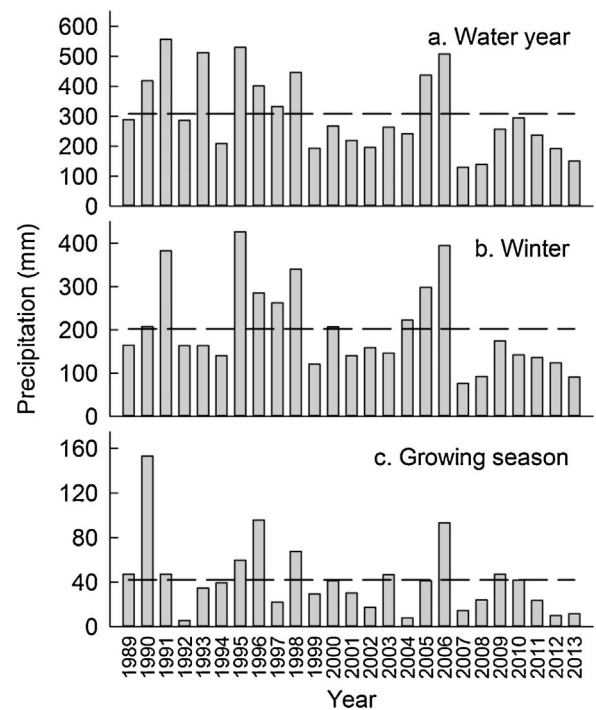


**Fig. 1.** Precipitation patterns at the study site from 1989 to 2013 (dashed lines represent 25-year averages) for the (a) water year (October 1–September 30), (b) winter period (November 1–March 31), and (c) growing season (April 1–June 30). The years on the abscissa correspond to the calendar year in which the period ends. All data were collected at the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra Reserve, < 2 km from the study site.

decade, while native herbaceous species richness has simultaneously declined (Concilio and Loik, 2013). Soils are sandy at the surface with gravel and larger rocks beneath and are derived from Holocene deposits of glacial alluvium and stream gravels (Orr and Howald, 2000). Soil bulk density at the study site is 1.4 ± 0.09 g cm$^{-3}$.

### 2.2. Climate of study site

An on-site weather station (< 2 km from the study site) has continuously monitored precipitation, air temperature, and relative humidity since 1987. Total water-year precipitation is highly variable (Fig. 1a), ranging from 557 mm in 1991 to 130 mm in 2007 (mean ± 1 SD = 308 ± 122 mm). The climate is Mediterranean and ~70% of precipitation falls as snow (Loik, 2007). January and July are usually the coldest and warmest months of the year, respectively. From 1988 to 2013, mean minimum and maximum air temperatures were −19 °C in January and 30 °C in July, respectively. Frost-free days average 121 per year (derived from Orr and Howald, 2000).

### 2.3. Study species

The three native perennial species that we selected to compare with *B. tectorum* make up a considerable portion of the herbaceous aboveground cover at this site (Concilio, 2013; Concilio and Loik, 2013; Loik et al., 2013) and are shallow-rooted and simultaneously spring-active with *B. tectorum*. *Achnatherum hymenoides* is a widespread and highly drought-tolerant bunchgrass in sagebrush steppe ecosystems (Ogle et al., 2013); *E. elymoides* has phenological similarities and reported competitive abilities with *B. tectorum* (Booth et al., 2003); and *L. argenteus* is one of the most common $N_2$-fixing legumes in high-elevation sagebrush steppe. Comparison of these four species demonstrates the potential diversity of functional responses of this ecotone plant community to rapid restoration of soil water availability, and how some of

the most common native herbaceous plant species of the Great Basin Desert compare to *B. tectorum* in terms of photosynthetic upregulation capacity. Moreover, we were able to quantify how the photosynthetic responses of these multiple, shallow-rooted herbaceous species responded to soil re-wetting during a historic drought.

### 2.4. Experimental design

To test the effects of a water pulse following extended drought conditions on study species, we watered plants (+10 mm $H_2O$) on 14-May-2013. This pulse size is larger than the most common rainfall event size class across arid and semiarid regions of the western United States—here 47% of all precipitation events are ≤5 mm (Loik et al., 2004)—but it is within the natural range of variation in May rainfall at this location (Loik, 2007). The combination of experimental watering and natural precipitation resulted in watered plants receiving 21 mm of total growing season (April–June) precipitation in 2013, half of the 25-year average (Fig. 1c) of 42 mm.

We haphazardly selected 10 individuals each of *B. tectorum*, *E. elymoides*, *A. hymenoides*, and *L. argenteus* within a grazing exclosure (fenced since 1999; D. Dawson, pers. comm.). Plants were generally not in contact with neighboring vegetation, and we did not remove any vegetation around the study plants. The heights of individual *A. hymenoides* ranged from 22 to 39 cm, *B. tectorum* ranged from 10 to 28 cm, *E. elymoides* ranged from 15 to 32 cm, and *L. argenteus* ranged from 19 to 50 cm tall. Plants were randomly assigned to either the "control" (no water added for five plants of each species) or " +$H_2O$" (five of each species) treatment. Water was applied to individual plants within a 0.5 × 0.5-m quadrat centered around each plant using a watering can held 1 m above the plant canopy. Water was added slowly to allow maximal infiltration and minimal surface runoff of plots.

#### 2.4.1. Soil moisture

We collected soil samples to ~8 cm depth using a shovel within the 0.5 × 0.5-m plot around study plants and recorded wet and oven-dry (105 °C for ~48 h) weights to calculate soil gravimetric water content (GWC) on a dry-weight basis (water weight divided by oven-dry weight). We collected soil samples ~one hour before and after watering on the day of the applied water pulse, and again eight days later.

#### 2.4.2. Photosynthesis

We measured the capacity for photosynthetic upregulation in terms of temporal responses to an experimental water addition of stomatal conductance to water vapor ($g_s$), instantaneous rates of $CO_2$ assimilation ($A$), and electron transport rate (ETR) using an open-mode portable photosynthesis system (LI-6400, Li-Cor Biosciences, Lincoln, NE, USA). We conducted measurements on a total of seven sampling dates after soil watering over a period of approximately two weeks to quantify temporal sensitivity of photosynthesis to an ephemeral soil water pulse, similar to that previously used for *Artemisia tridentata* and *Purshia tridentata* at this site (Loik, 2007). We measured gas exchange and fluorescence on light-adapted leaves simultaneously to quantify how stomatal conductance, electron transport rate within PSII, and $CO_2$ assimilation respond to brief periods of soil water availability. For all photosynthetic measurements with the LI-6400, vapor pressure deficit within the chamber was maintained at pre-measurement ambient levels. The $CO_2$ concentration within the leaf chamber was maintained at a constant level (400 µmol mol$^{-1}$) by scrubbing the incoming airstream with soda lime, and the subsequent addition of a precise amount of $CO_2$ *via* injection from a 25 g cartridge. Photosynthetically Active Radiation (PAR; 400–700 nm) within the chamber was maintained at 1500 µmol m$^{-2}$ s$^{-1}$ using the Li-Cor red-blue LEDs (90% red, 10% blue). Mature leaves were inserted into the cuvette (for grass species, leaves were aligned adjacent to one another without overlapping to fill the chamber; for *L. argenteus*, leaves were inserted to fill the chamber at their natural branch orientation), and photosynthetic measurements

were recorded when all stability criteria were met and the coefficient of variation for $A$ and $g_s$ combined was below 0.5%. We took all gas exchange measurements between 08:00 AM and 12:00 PM, recording three measurements per leaf and subsequently averaging the values (*i.e.*, one value per plant).

We estimated growth response to the added water pulse for all four species based on changes in height over 14 days in order to minimize destructive harvesting of the natives. We estimated growth as a modified relative growth rate based on original height and change in height over 14 days:

Estimated RGR = [1/original height] [height after 14 d − height at 0 d/14 d]

### 2.5. Statistical analyses

We used repeated-measures analyses of variance (RMANOVAs) to analyze plant physiological responses to treatments (df = 1), as well as repeated-measures effects (*i.e.*, within-subjects effects) of time and the interaction between time and treatment. To analyze relationships between continuous dependent variables (i.e., $g_s$ and $A$), we tested for homogeneity of slopes. We tested that data were normally distributed to meet assumptions for ANOVA. For all analyses, we considered differences at $P ≤ 0.05$ to be significant. We analyzed all results using JMP Pro (v. 11.0.0; SAS Institute, Cary, NC, USA).

## 3. Results

### 3.1. Meteorology

Water-year, winter, and growing season precipitation was below average throughout the study period (Fig. 1). In fact, the study year (2013) had the third-lowest water-year precipitation of the prior 25-year record, behind 2007 and 2008. Moreover, winter 2012–2013 had the second-lowest winter precipitation in the 25-year record (behind winter 2006–2007) and was the beginning of California's historic drought of 2012–2015. Spring 2013 had the fourth-lowest spring precipitation (behind 1992, 2004, and 2012). Hence, extreme drought conditions persisted throughout the study period. Monthly precipitation during the study period ranged from 58 mm in December 2012 to < 1 mm in March 2013 (Fig. 2a). The mean maximum air temperature
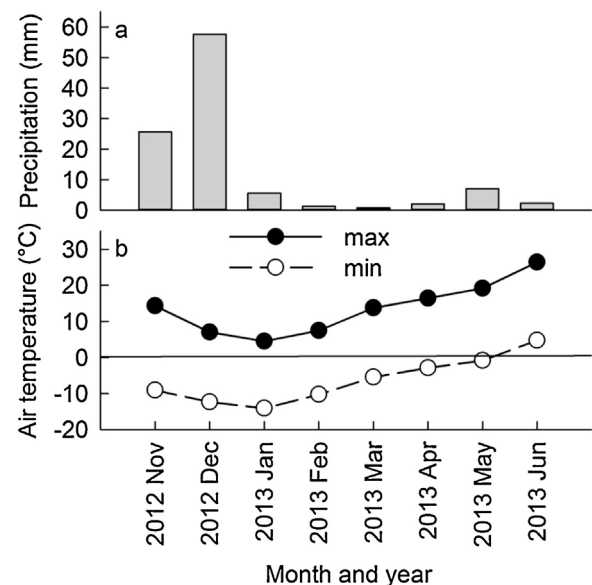
**Fig. 2.** Precipitation and temperature patterns during the study period (November 2012–June 2013). (a) Total monthly precipitation and (b) mean monthly maximum and minimum air temperatures at the study site.

was 26.4°C in July and the mean minimum temperature was -14.1°C in January (Fig. 2b). There were 47 frost-free days during the study period (November 2012–June 2013). Before we added water to plants on 14-May-2013, growing season precipitation totaled only 9 mm. A precipitation event of < 1 mm occurred on 15-May-2013, the day after water additions.

### 3.2. Soil moisture

The 10-mm water additions significantly increased soil moisture levels for all plots, which dried rapidly in subsequent days. In 2013, mean soil GWC for control and $+H_2O$ plots on the water addition day were < 1% and 10.1%, respectively ($F_{1,8} = 114.53$, $P < 0.0001$). Eight days later, mean soil GWC had decreased to < 1% for both control and $+H_2O$ plots.

### 3.3. In situ photosynthetic responses to watering

*In situ* instantaneous rates of $g_s$ considerably varied across species. *Bromus tectorum* controls had the lowest $g_s$ values (0.117 ± 0.00858 mol $H_2O$ m$^{-2}$ s$^{-1}$ [mean ± 1 SE]) and *L. argenteus* controls had the highest $g_s$ (0.226 ± 0.0284 mol $H_2O$ m$^{-2}$ s$^{-1}$); *A. hymenoides* and *E. elymoides* had intermediate values. Patterns for $g_s$ in response to watering differed across species (Fig. 3). *Bromus tectorum* (Fig. 3a) and *E. elymoides* (Fig. 3c) had significant responses of $g_s$ to added water, whereas *A. hymenoides* (Fig. 3b) and *L. argenteus* (Fig. 3d) did not (Table 1). Watering increased overall $g_s$ (i.e., averaged over the study period) for *B. tectorum* by 27%, *E. elymoides* by 22%, *L. argenteus* by 19%, and *A. hymenoides* by 17%.

The *in situ* photosynthetic assimilation of $CO_2$ likewise varied widely between species. *Lupinus argenteus* had the overall highest *average* rate of *A* (14.2 ± 1.69 μmol $CO_2$ m$^{-2}$ s$^{-1}$ [mean ± 1 SE]) and *B. tectorum* had the lowest *A* (4.99 ± 0.0770 μmol $CO_2$ m$^{-2}$ s$^{-1}$). Watering resulted in significantly higher rates of *A* compared to control plants (Fig. 4) for *B. tectorum* (Fig. 4a) and *L. argenteus* (Fig. 4d), but not for *A. hymenoides* (Fig. 4b) nor *E. elymoides* (Fig. 4c; Table 1). Watering increased overall *A* (compared to controls averaged over the study period) for *B. tectorum* by 78%, *L. argenteus* by 29%, *A. hymenoides* by 17%, and *E. elymoides* by 2%.

Carbon dioxide assimilation had a strong positive relationship with $g_s$ for all species (Fig. 5). The slopes of the regression lines did not

significantly differ between the control and $+H_2O$ treatment within any species. Comparing between species (Fig. 5), the slope for *B. tectorum* (*m* = 78.3) was significantly higher than that for the native species ($F_{3272} = 6.63$, $P = 0.0002$; *A. hymenoides*: *m* = 47.2, *E. elymoides*: *m* = 49.4, *L. argenteus*: *m* = 43.5). Based on photosynthesis and stomatal conductance, Water Use Efficiency (WUE) was significantly affected by experimental water additions (Table 1) for *B. tectorum* and *E. elymoides*, but not the other two species. All four species exhibited significant time and treatment × time effects on WUE in response to experimental water addition in spring.

The experimental addition of water in spring caused a marked increase in electron transport rate within PSII (ETR) for *B. tectorum* compared to control plants (Fig. 6). Watering significantly affected ETR (Table 1), with *B. tectorum* and *A. hymenoides* having significant responses to added water, whereas ETR for *E. elymoides* and *L. argenteus* was not affected by the watering treatment. There were significant effects of time on ETR for *B. tectorum* and *A. hymenoides*.

The ratio of electron transport rate in PSII to $CO_2$ assimilation (ETR/*A*) was only significantly affected by watering treatment for *L. argenteus* (Table 1). The results for *B. tectorum* and *A. hymenoides* might be considered marginally significant ($P = 0.07$–0.09). On the other hand, there were significant time and treatment × time effects on ETR/*A* for all four species.

Based on plant height before and after 14 days (Fig. 7), there was no effect of watering on estimated relative growth rate, yet *B. tectorum* grew more than the other species ($P = 0.0144$). There were also no significant treatment × species interactions on relative growth rate.

## 4. Discussion

We found that *in situ* photosynthesis for native perennial species and the highly problematic Great Basin invasive annual grass *Bromus tectorum* generally responded positively to an experimental increase in soil water content in May. These results indicate a capacity for *in situ* photosynthetic upregulation by this species in response to an ephemeral pulse of soil water availability. In most cases, watered plants tended to have higher values of $g_s$, *A*, and ETR relative to control plants, but they were not uniform for all photosynthetic characteristics across all four species. This is consistent with recent findings that some but not all aspects of photosynthesis may be affected by physical components of global change (Blackman et al., 2016). The responses of photosynthesis
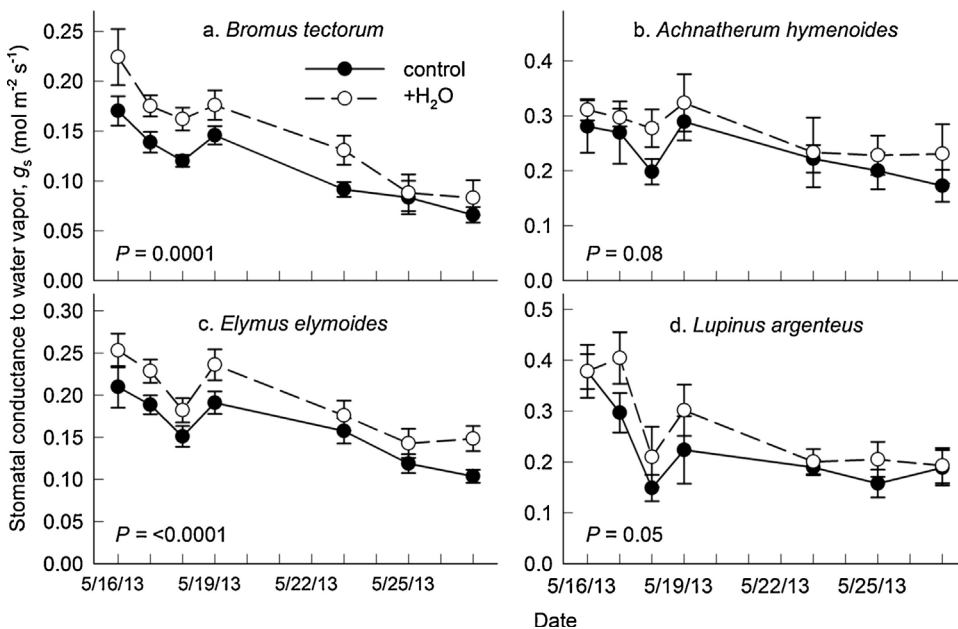


**Fig. 3.** Stomatal conductance to water vapor ($g_s$) for control and watered *B. tectorum* (a), *A. hymenoides* (b), *E. elymoides* (c), and *L. argenteus* (d). Note that the scales of the ordinate differ by species. Water additions occurred on 14-May-2013. Data are means ± 1 SE for n = 5 plants per treatment for each species.

**Table 1**

Repeated-measures ANOVA tests of the effects of the water addition treatment (trt), time (16-May-2013–27-May-2013), and the trt × time interactions on stomatal conductance to water vapor ($g_s$, mol m$^{-2}$ s$^{-1}$), leaf-level $CO_2$ assimilation ($A$, μmol m$^{-2}$ s$^{-1}$), electron transport rate (ETR, μmol e$^-$ m$^{-2}$ s$^{-1}$), Water Use Efficiency (WUE, unitless) and the ratio of electron transport rate to net $CO_2$ assimilation (ETR/$A$, unitless). Values in bold are significant at $P \leq 0.05$.

| Effect | $g_s$ | $A$ | ETR | WUE | ETR/$A$ |
|---|---|---|---|---|---|
| *Bromus tectorum* | | | | | |
| Trt | $F = 17.0$ | $F = 39.4$ | $F = 33.9$ | $F = 28.7$ | $F = 3.16$ |
| | $P = 0.0001$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ | $P = 0.09$ |
| Time | $F = 18.5$ | $F = 21.8$ | $F = 5.16$ | $F = 20.4$ | $F = 32.5$ |
| | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = 0.0003}$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ |
| Trt × time | $F = 0.64$ | $F = 0.51$ | $F = 0.99$ | $F = 15.3$ | $F = 10.4$ |
| | $P = 0.70$ | $P = 0.80$ | $P = 0.44$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ |
| *Achnatherum hymenoides* | | | | | |
| Trt | $F = 3.23$ | $F = 3.34$ | $F = 6.76$ | $F = 0.123$ | $F = 3.48$ |
| | $P = 0.08$ | $P = 0.07$ | $\boldsymbol{P = 0.01}$ | $P = 0.72$ | $P = 0.07$ |
| Time | $F = 2.20$ | $F = 2.87$ | $F = 2.55$ | $F = 20.1$ | $F = 30.7$ |
| | $P = 0.06$ | $\boldsymbol{P = 0.02}$ | $\boldsymbol{P = 0.03}$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ |
| Trt × time | $F = 0.16$ | $F = 0.35$ | $F = 1.23$ | $F = 66$ | $F = 10.6$ |
| | $P = 0.99$ | $P = 0.91$ | $P = 0.29$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ |
| *Elymus elymoides* | | | | | |
| Trt | $F = 17.7$ | $F = 0.121$ | $F = 0.0009$ | $F = 24.6$ | $F = 0.014$ |
| | $\boldsymbol{P = < 0.0001}$ | $P = 0.73$ | $P = 0.98$ | $\boldsymbol{P = < 0.0001}$ | $P = 0.90$ |
| Time | $F = 13.9$ | $F = 7.49$ | $F = 1.10$ | $F = 22.5$ | $F = 32.8$ |
| | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ | $P = 0.38$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ |
| Trt × time | $F = 0.24$ | $F = 0.84$ | $F = 0.43$ | $F = 10.3$ | $F = 3.12$ |
| | $P = 0.96$ | $P = 0.54$ | $P = 0.86$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = 0.02}$ |
| *Lupinus argenteus* | | | | | |
| Trt | $F = 3.95$ | $F = 8.39$ | $F = 1.72$ | $F = 0.155$ | $F = 9.87$ |
| | $P = 0.05$ | $\boldsymbol{P = 0.005}$ | $P = 0.20$ | $P = 0.70$ | $\boldsymbol{P = 0.004}$ |
| Time | $F = 8.25$ | $F = 3.98$ | $F = 1.60$ | $F = 12.6$ | $F = 8.98$ |
| | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = 0.002}$ | $P = 0.16$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = < 0.0001}$ |
| Trt × time | $F = 0.49$ | $F = 0.91$ | $F = 0.25$ | $F = 8.84$ | $F = 6.17$ |
| | $P = 0.82$ | $P = 0.49$ | $P = 0.96$ | $\boldsymbol{P = < 0.0001}$ | $\boldsymbol{P = 0.0004}$ |

were generally rapid after watering, but the four species did not respond to the same degree nor in terms of temporal patterns. Our results also reveal that *B. tectorum* had more pronounced responses (on a per cent basis, relative to controls) to added springtime water relative to native species, consistent with H$_2$. Over the course of the pulse-chase response, watering nearly doubled $A$ for *B. tectorum*, indicating considerable upregulation of photosynthesis by comparison to the native herbaceous species. Watering also increased $A$ for the native species *A. hymenoides* and *L. argenteus* (though to a smaller degree), but had negligible impacts on $A$ for *E. elymoides*. Despite greater relative increases for *B. tectorum*, the actual photosynthetic and stomatal conductance values were lowest of the four species. Because the
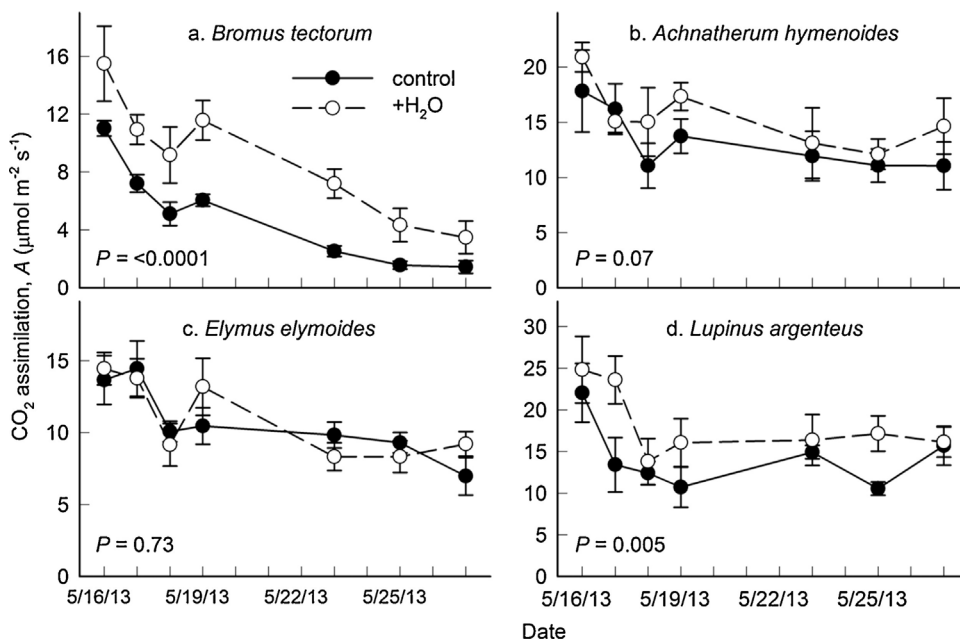


**Fig. 4.** Leaf-level $CO_2$ assimilation ($A$) for control and watered *B. tectorum* (a), *A. hymenoides* (b), *E. elymoides* (c), and *L. argenteus* (d). Note that the scales of the ordinate differ by species. Water additions occurred on 14-May-2013. Data are means ± 1 SE for n = 5 plants per treatment for each species.
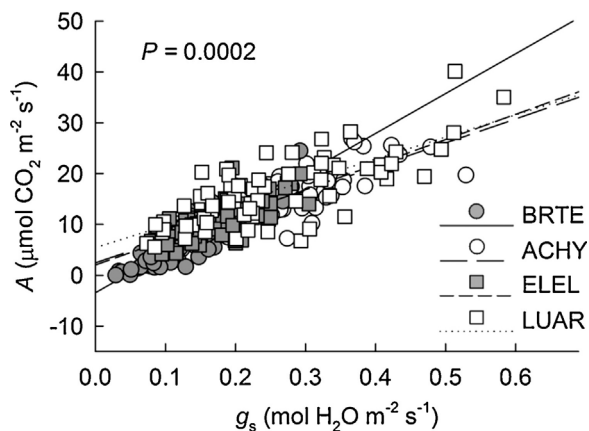
**Fig. 5.** Correlations between leaf-level $CO_2$ assimilation ($A$) and stomatal conductance to water vapor ($g_s$) for *B. tectorum* (BRTE), *A. hymenoides* (ACHY), *E. elymoides* (ELEL), and *L. argenteus* (LUAR). Water additions occurred on 14-May-2013.

photosynthetic physiology of Great Basin herbaceous species of this site have not been studied much, we do not know how our photosynthetic or stomatal conductance values of *B. tectorum* and the three natives compare. Global studies have shown higher rates of resource acquisition for invasive *vs.* native species, but these relationships are not always robust (Funk et al., 2017). Here we found a slight but non-significant impact of the rainfall pulse and *in situ* photosynthetic upregulation on *B. tectorum* growth two weeks later, suggesting that carbon may have been allocated to root or maintenance instead of growth respiration (Anadon-Rosell et al., 2017). This could potentially confer a selective advantage by initiating root growth followed by enhanced water and nutrient uptake that might not be indicated by aboveground growth. While increased summer precipitation may confer an advantage for native perennial species by increasing soil water availability for carbon uptake and allocation to growth and fitness (i.e., after *B. tectorum* has senesced), increased spring precipitation could facilitate *B. tectorum* expansion by increasing belowground resource acquisition during its short springtime growing season (Concilio et al., 2013). Effects of altered precipitation regimes on carbon acquisition could contribute to changes in fitness and future species distributions, depending on the amount, type, and timing of precipitation.

Across its invaded range, *B. tectorum* exhibits distinct "boom and

bust" cycles in response to inter-annual variation in precipitation, with drought years negatively impacting *B. tectorum* biomass (Balch et al., 2013; Bradley and Mustard, 2005; Concilio and Loik, 2013; Griffith and Loik, 2010). In addition, soil or leaf nitrogen may have affected photosynthetic responses to the simulated water pulse (Goedhart et al., 2010). Limiting resources can shift inter-annually; previous research at the study site found that *B. tectorum* was limited by water alone in a year with lower snow cover and spring precipitation, but was co-limited by water and nitrogen in a year with higher snow cover and spring precipitation (Concilio et al., 2013). Other work has shown that *B. tectorum* can acquire nitrogen more rapidly than native species at temperatures > 15 °C (Leffler et al., 2011). *Lupinus argenteus* sustained the highest *A* of the three study species, possibly due to its ability to fix nitrogen (Goergen et al., 2009). In this regard, the N-fixing shrub at this site, *Purshia tridentata*, usually has photosynthetic rates higher than neighboring shrubs of *Artemisia tridentata* (Loik, 2007; Loik et al., 2015). These results highlight the importance of interactions between species traits and inter-annual meteorological variation for driving responses of plants to altered patterns of springtime rainfall.

The watering treatment significantly affected WUE for both *B. tectorum* and *E. elymoides* (Table 1). Relative to native species, *B. tectorum* had higher WUE, demonstrating less constraint of photosynthesis by water. Watered plants generally had higher photosynthetic rates relative to controls. Watered plants were able to achieve higher maximum *A* and $g_s$ values than control plants, except for *E. elymoides*, which had significantly lower WUE (Table 1) suggesting conspicuous use of ephemeral soil water while it is available. Relative to grass species, *L. argenteus* had a greater range of values for ETR (Fig. 6), revealing greater photochemical efficiency and capacity to support Calvin Cycle substrate regeneration during springtime. Drought stress within plant cells may impair electron flow within PSII, due in part to production of reactive oxygen species that affects the repair processes of PSII (Lima Neto et al., 2017; Murata et al., 2007). Non-photochemical thermal, proton-gradient, or metabolic dissipation processes are upregulated by stressors such as high temperatures, high irradiance, and drought (Demmig-Adams and Adams, 2006; Jiang et al., 2006). Relative to *L. argenteus*, a lower range of values of ETR for the grasses suggests that they may have dissipated more energy through non-photochemical processes. The ratio ETR/A can infer the relative amount of electrons allocated to photorespiration compared to photochemistry; watering should reduce the ratio if photorespiration decreases relative to
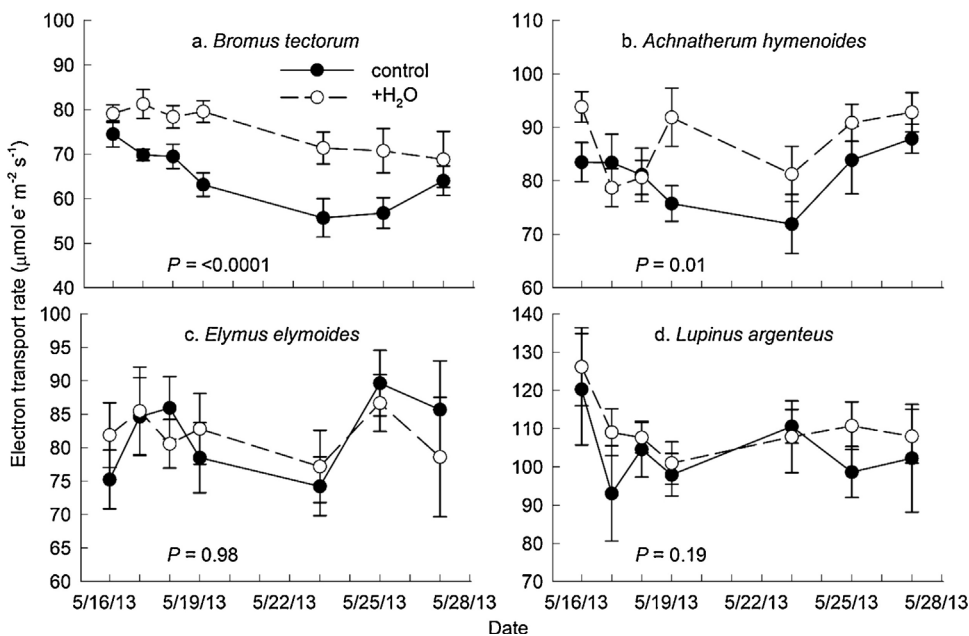


**Fig. 6.** Electron transport rate within Photosystem II (ETR) for control and watered (a) *B. tectorum*, (b) *A. hymenoides*, (c) *E. elymoides*, and (d) *L. argenteus*. Water additions occurred on 14-May-2013. Data are means ± 1 SE for n = 5 plants per treatment for each species.
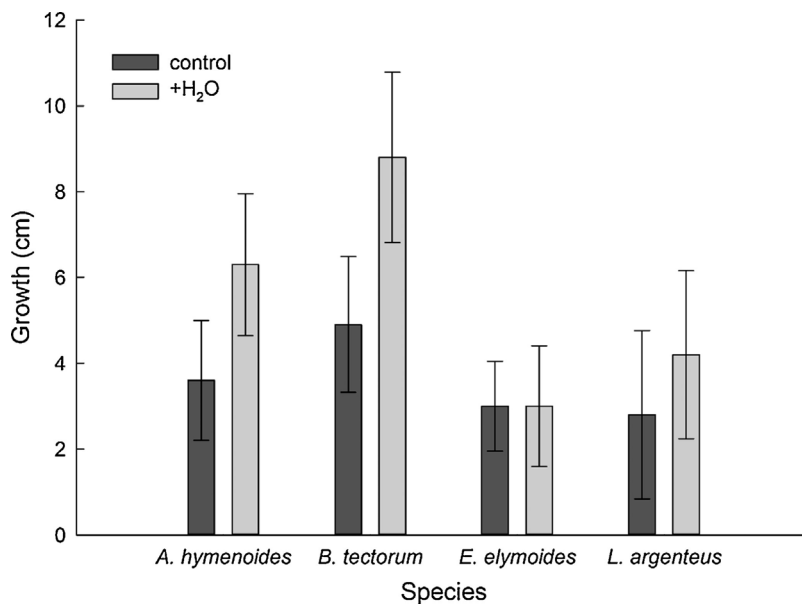
photochemistry (Feller, 2016). However, reductions in ETR/A were small and non-significant (except for *L. argenteus*), possibly due to the small sample sizes and decreasing values of $g_s$ and $A$ over time as soil water was depleted. Notably, photosynthesis of the nitrogen-fixing *L. argenteus* was more tolerant to drought stress than the native grass species, as evidenced by its comparatively higher range of values for ETR. These results indicate a diversity of *in situ* photosynthetic responses to ephemeral soil water availability during spring among co-occurring native herbaceous species and the invasive grass *Bromus tectorum* that heretofore have not been demonstrated.

Our results showed that *in situ* photosynthesis for *B. tectorum* was more responsive to supplemental springtime water than native species at this site, revealing highly opportunistic exploitation of ephemeral availability of soil moisture. Native species varied in their responsiveness to added water, with *A. hymenoides* and *L. argenteus* responding similarly to water additions, while *E. elymoides* was the least responsive. Notorious for its fire impacts, ecosystem transformations, rapid spread, and management challenges, *B. tectorum* invasion poses enormous threats to ecosystem integrity, which may intensify as climate continues to change. This is especially important at high elevations where *B. tectorum* impacts so far have been minimal (i.e., invasion is occurring but has not yet reached density thresholds sufficient to alter fire cycles). Moreover, increased temperatures will cause precipitation phase shifts from snow to rain and earlier snowmelt timing (Pavelsky et al., 2012). While we did not directly test a snow-to-rain shift, the combination of low snowfall and added springtime water in this study may be similar to the effects that will occur as a result of a greater proportion of precipitation falling as rain than as snow in the future at this location. The timing of *B. tectorum* seedling emergence differs between low and high elevations under current climatic conditions; emergence primarily occurs in the fall in low-elevation populations (Mack and Pyke, 1983), but usually not until spring in high-elevation populations (Griffith and Loik, 2010) such as our study site, where prolonged snow cover and cold temperatures restrict recruitment (Chambers et al., 2007). However, *B. tectorum* has the ability to opportunistically germinate when conditions are favorable, so if spring rainfall increases survivorship of recruits at high elevations, population growth rates may increase (Griffith and Loik, 2010).

Our results demonstrate that, at this high-elevation site, *B. tectorum* is able to upregulate *in situ* photosynthesis in response to an increase in springtime soil water to a greater extent than native species. As our study coincided with an extreme drought year, it would be interesting

to determine whether the diversity of photosynthetic patterns increases in other years with average or above-average winter and/or spring precipitation. Changes to the combined patterns of winter and spring precipitation and inter-annual variability are likely to impose significant complexity on carbon uptake by sagebrush steppe vegetation. Regardless of specific precipitation patterns, *B. tectorum* has rapid and highly plastic photosynthetic carbon acquisition responses to increases in soil water availability, which may enable this ecologically detrimental invasive species to increase the extent of its invasion at high elevations. Uncertainty about future precipitation patterns and the small window of opportunity to manage invasions necessitate close monitoring of high-elevation areas at risk of *B. tectorum* encroachment.

### Human and animal rights

This article does not contain any studies with human participants or animals performed by any of the authors.

### Declaration of interest

The authors declare that they have no conflict of interest.

### Submission declaration and verification

This work has not been published previously, is not under consideration for publication elsewhere, and, if accepted, will not be published elsewhere. Its publication is approved by all authors and by the responsible authorities where the work was carried out.

### Contributions

CW and ML conceived and designed the study. CW performed measurements and conducted statistical analyses. CW and ML wrote the paper.

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## References

Abatzoglou, J.T., Kolden, C.A., 2011. Climate change in western U.S. deserts: potential for increased wildfire and invasive annual grasses. Rangel. Ecol. Manage. 64, 471–478.

Anadon-Rosell, A., Hasibeder, R., Palacio, S., Mayr, S., Ingrisch, J., Ninot, J.M., Nogués, S., Bahn, M., 2017. Short-term carbon allocation dynamics in subalpine dwarf shrubs and their responses to experimental summer drought. Environ. Exp. Bot. 141, 92–102. http://dx.doi.org/10.1016/j.envexpbot.2017.07.006.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235.

Balch, J.K., Bradley, B.A., D'Antonio, C.M., Gómez-Dans, J., 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob. Change Biol. 19, 173–183.

Bilbrough, C.J., Caldwell, M.M., 1997. Exploitation of springtime ephemeral N pulses by six Great Basin plant species. Ecology 78, 231–243.

Billings, W.D., 1990. Bromus tectorum, a biotic cause of impoverishment in the Great Basin. In: Woodell, G.M. (Ed.), The Earth in Transition: Patterns and Processes of Biotic Impoverishment. Cambridge University Press Cambridge, UK, pp. 301–322.

Blackman, C.J., Aspinwall, M.J., de Dios, V.R., Smith, R.A., Tissue, D.T., 2016. Leaf photosynthetic, economics and hydraulic traits are decoupled among genotypes of a widespread species of eucalypt grown under ambient and elevated CO2. Funct. Ecol. 30, 1491–1500.

Booth, M.S., Caldwell, M.M., Stark, J.M., 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. J. Ecol. 91, 36–48.

Bowman, W.D., Bilbrough, C.J., 2001. Influence of a pulsed nitrogen supply on growth and nitrogen uptake in alpine graminoids. Plant Soil 233, 283–290.

Bradley, B.A., Mustard, J.F., 2005. Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. Remote Sens. Environ. 94, 204–213.

Bromberg, J.E., Kumar, S., Brown, C.S., Stohlgren, T.J., 2011. Distributional changes and range predictions of downy brome (Bromus tectorum) in Rocky Mountain National Park. Invasive Plant Sci. Manage. 4, 173–182.

Brooks, M.L., Chambers, J.C., 2011. Resistance to invasion and resilience to fire in desert shrublands of North America. Rangel. Ecol. Manage. 64, 431–438.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. Bioscience 54, 677–688.

Brown, C.S., Rowe, H.I., 2004. The unwelcome arrival of Bromus tectorum to high elevations. Proceedings of High Altitude Revegetation Workshop. Fort Collins, CO, pp. 1–12.

Cayan, D.R., Maurer, E.P., Dettinger, M.D., Tyree, M., Hayhoe, K., 2008. Climate change scenarios for the California region. Clim. Change 87, 21–42.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by Bromus tectorum? Ecol. Monogr. 77, 117–145.

Compagnoni, A., Adler, P.B., 2014. Warming, competition, and Bromus tectorum population growth across an elevation gradient. Ecosphere 5.

Concilio, A.L., Loik, M.E., 2013. Elevated nitrogen effects on Bromus tectorum dominance and native plant diversity in an arid montane ecosystem. Appl. Veg. Sci. 16, 598–609.

Concilio, A.L., Loik, M.E., Belnap, J., 2013. Global change effects on Bromus tectorum L. (Poaceae) at its high-elevation range margin. Glob. Change Biol. 19, 161–172.

Concilio, A.L., 2013. The spread of cheatgrass into the Eastern Sierra. Fremontia 41, 10–13.

Dakheel, A.J., Radosevich, S.R., Barbour, M.G., 1994. Effects of temperature and moisture on growth: interference and photosynthesis of Bromus tectorum and Taeniatherum asperum. Weed Res. 34, 11–22.

Dalgleish, H.J., Koons, D.N., Hooten, M.B., Moffet, C.A., Adler, P.B., 2011. Climate influences the demography of three dominant sagebrush steppe plants. Ecology 92, 75–85.

Demmig-Adams, B., Adams, W.W., 2006. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytol. 172, 11–21.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends Ecol. Evol. 14, 135–139.

Ehleringer, J.R., Dawson, T.E., 1992. Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ. 15, 1073–1082.

Feller, U., 2016. Drought stress and carbon assimilation in a warming climate: reversible and irreversible impacts. J. Plant Physiol. 203, 69–79.

Funk, J.L., Nguyen, M.A., Standish, R.J., Stock, W.D., Valladares, F., 2017. Global resource acquisition patterns of invasive and native plant species do not hold at the regional scale in Mediterranean type ecosystems. Biol. Invasions 19, 1143–1151.

Goedhart, C.M., Pataki, D.E., Billings, S.A., 2010. Seasonal variations in plant nitrogen relations and photosynthesis along a grassland to shrubland gradient in Owens Valley California. Plant Soil 327, 213–223.

Goergen, E., Chambers, J.C., Blank, R., 2009. Effects of water and nitrogen availability on nitrogen contribution by the legume, Lupinus argenteus Pursh. Appl. Soil Ecol. 42, 200–208.

Griffith, A.B., Loik, M.E., 2010. Effects of climate and snow depth on Bromus tectorum population dynamics at high elevation. Oecologia 164, 821–832.

Humphrey, L.D., Schupp, E.W., 2004. Competition as a barrier to establishment of a native perennial grass (Elymus elymoides) in alien annual grass (Bromus tectorum) communities. J. Arid. Environ. 58, 405–422.

Jiang, C.D., Gao, H.Y., Zou, Q., Jiang, G.M., Li, L.H., 2006. Leaf orientation, photorespiration and xanthophyll cycle protect young soybean leaves against high irradiance in field. Environ. Exp. Bot. 55, 87–96.

Knapp, P.A., 1996. Cheatgrass (Bromus tectorum L) dominance in the Great Basin Desert: history persistence, and influences to human activities. Glob. Environ. Change-Human Policy Dimens 6, 37–52.

Leffler, A.J., Monaco, T.A., James, J.J., 2011. Nitrogen acquisition by annual and perennial grass seedlings: testing the roles of performance and plasticity to explain plant invasion. Plant Ecol. 212, 1601–1611.

Leger, E.A., Espeland, E.K., Merrill, K.R., Meyer, S.E., 2009. Genetic variation and local adaptation at a cheatgrass (Bromus tectorum) invasion edge in western Nevada. Mol. Ecol. 18, 4366–4379.

Lima Neto, M.C., Cerqueira, J.V.A., Cunha, J.R.d., Ribeiro, R.V., Silveira, J.A.G., 2017. Cyclic electron flow, NPQ and photorespiration are crucial for the establishment of young plants of Ricinus communis and Jatropha curcas exposed to drought. Plant Biol. 19 (4), 650–659. http://dx.doi.org/10.1111/plb.12573.

Link, S.O., Bolton, H., Thiede, M.E., Rickard, W.H., 1995. Responses of downy brome to nitrogen and water. J. Range Manage. 48, 290–297.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., Belnap, J., 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141, 269–281.

Loik, M.E., Griffith, A.B., Alpert, H., 2013. Impacts of long-term snow climate change on a high-elevation cold desert shrubland, California, USA. Plant Ecol. 214, 255–266.

Loik, M.E., Griffith, A.B., Alpert, H., Concilio, A.L., Wade, C.E., Martinson, S.J., 2015. Impact of intra- versus inter-annual snow depth variation on water relations and photosynthesis for two Great Basin Desert shrubs. Oecologia 178, 403–414.

Loik, M.E., 2007. Sensitivity of water relations and photosynthesis to summer precipitation pulses for Artemisia tridentata and Purshia tridentata. Plant Ecol. 191, 95–108.

Lopez, B.C., Holmgren, M., Sabate, S., Gracia, C.A., 2008. Estimating annual rainfall threshold for establishment of tree species in water-limited ecosystems using tree-ring data. J. Arid. Environ. 72, 602–611.

Mack, R.N., Pyke, D.A., 1983. The demography of Bromus tectorum: variation in time and space. J. Ecol. 71, 69–93.

Maurer, E.P., Brekke, L., Pruitt, T., Duffy, P.B., 2007. Fine-resolution climate projections enhance regional climate change impact studies. EOS Trans. Am. Geophys. Union 88, 504.

Mazzola, M.B., Chambers, J.C., Blank, R.R., Pyke, D.A., Schupp, E.W., Allcock, K.G., Doescher, P.S., Nowak, R.S., 2011. Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by Bromus tectorum. Biol. Invasions 13, 513–526.

Miller, R.F., Naugle, D.E., Maestas, J.D., Hagen, C.A., Hall, G., 2017. Special issue: targeted woodland removal to recover at-risk grouse and their sagebrush-steppe and prairie ecosystems. Rangel. Ecol. Manage. 70, 1–8.

Murata, N., Takahashi, S., Nishiyama, Y., Allakhverdiev, S.I., 2007. Photoinhibition of photosystem II under environmental stress. Biochim. Biophys. Acta (BBA)-Bioenergetics 1767, 414–421.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4, 25–51.

Ogle, D., St. John, L., Jones, T., 2013. Plant Guide for Indian Ricegrass (Achnatherum Hymenoides). USDA-Natural Resources Conservation Service, Plant Materials Center, Aberdeen, ID.

Orr, B.K., Howald, A.M., 2000. A Flora of Valentine Eastern Sierra Reserve, Part II: Sierra Nevada Aquatic Research Laboratory. University of California, Santa Barbara, CA.

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., Arevalo, J.R., Cavieres, L.A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C.I., Naylor, B.J., Parks, C.G., Rew, L.J., Seipel, T., 2009. Ain't no mountain high enough: plant invasions reaching new elevations. Front. Ecol. Environ. 7, 479–486.

Pavelsky, T.M., Sobolowski, S., Kapnick, S.B., Barnes, J.B., 2012. Changes in orographic precipitation patterns caused by a shift from snow to rain. Geophys. Res. Lett. 39.

Peek, M.S., Forseth, I.N., 2009. Positive effects of soil nitrogen pulses on individuals can have negative consequences for population growth during drought in a herbaceous desert perennial. J. Ecol. 97, 440–449.

Prevey, J.S., Seastedt, T.R., 2015. Effects of precipitation change and neighboring plants on population dynamics of Bromus tectorum. Oecologia 179, 765–775.

Rau, B.M., Johnson, D.W., Blank, R.R., Lucchesi, A., Caldwell, T.G., Schupp, E.W., 2011. Transition from sagebrush steppe to annual grass (Bromus tectorum): influence on belowground carbon and nitrogen. Rangel. Ecol. Manage. 64, 139–147.

Rice, K.J., Black, R.A., Radamaker, G., Evans, R.D., 1992. Photosynthesis, growth, and biomass allocation in habitat ecotypes of cheatgrass (Bromus-tectorum). Funct. Ecol. 6, 32–40.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in and semiarid ecosystems. Oecologia 141, 211–220.

Smith, S.D., Strain, B.R., Sharkey, T.D., 1987. Effects of CO2 enrichment on four Great Basin grasses. Funct. Ecol. 1, 139–143.

Weltz, M.A., Coates-Markle, L., Narayanan, R., 2011. Wildfire and invasive plants in American deserts: a special features. Rangel. Ecol. Manage. 64, 429–430.

Whisenant, S.G., 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. In: McArthur, E.D., Romney, E.M., Smith, S.D., Tueller, P.T. (Eds.), General Technical Report INT-276. USDA Forest Service, Intermountain Research Station, Ogden, UT, pp. 4–10.