Pulse events in Great Basin Desert shrublands: physiological responses of *Artemisia tridentata* and *Purshia tridentata* seedlings to increased summer precipitation

Ian G. Gillespie[a], Michael E. Loik[b],*

[a] *Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, USA*
[b] *Department of Environmental Studies, University of California, 1156 High Street, Santa Cruz, CA 95064, USA*

Abstract

Climate change models envision an increase in summer precipitation in eastern California and adjacent arid regions by 2050, due to anthropogenic activities. Changes in the frequency, intensity and spatial patterns of rainfall pulses are likely to influence seedling recruitment and establishment, and ultimately community composition and dynamics. The effects of altered water availability might be complicated by the effect of adult plants on resources and conditions, potentially altering seedling recruitment success and affecting community succession. We tested the hypotheses that: (1) an experimental pulse representing a 25% increase in summer precipitation would increase photosynthesis for *Artemisia tridentata* and *Purshia tridentata* seedlings, and (2) for *P. tridentata*, experimentally applied rainfall pulses lead to greater effects on photosynthesis for seedlings planted in open microsites compared to seedlings planted under the canopy of adult *A. tridentata* nurse plants. We tested these hypotheses based on measurements of plant water potential, CO_2 assimilation, and stress within Photosystem II (PSII). Water potential was higher (but not significantly) for seedlings 3 days following watering that simulated future summer monsoon rainfall pulses for both *A. tridentata* and *P. tridentata*. Water pulse treatment increased the quantum efficiency of PSII for *A. tridentata*, but not for *P. tridentata*. Water pulses increased transpiration nearly two-fold for seedlings of *A. tridentata*, but had no effect on gas exchange for *P. tridentata*. Transplanted *P. tridentata* seedlings growing in open microsites fixed twice as much CO_2 compared to transplanted seedlings growing under the canopy of adult *A. tridentata* shrubs, despite higher temperatures and photosynthetic photon flux density in the open. However,

---

*Corresponding author. Tel.: +1-831-459-5785; fax: +1-831-459-4015.

E-mail address: mloik@ucsc.edu (M.E. Loik).

neither location nor water pulse treatment affected chlorophyll *a* fluorescence from PSII. Our results suggest that for precipitation pulses in Great Basin Desert shrublands: (1) photosynthetic increases in response to additional summertime rainfall pulses will be greater for *A. tridentata* compared to *P. tridentata* seedlings and (2) open sites between adult shrubs are an important recruitment niche for *P. tridentata*.

1. Introduction

Resources in arid environments are often delivered as pulses rather than constant flows. Precipitation is particularly episodic, and spatially heterogeneous. Pulse events may affect growth of some species (Pugnaire et al., 1996), nutrient mineralization (Noy-Meir, 1973), nutrient acquisition by plants (Gebauer and Ehleringer, 2000), community interactions (Novoplansky and Goldberg, 2001) and niche partitioning (Schwinning and Ehleringer, 2001). While there have been some autecological and synecologcal studies of pulse effects on plant growth and interactions between species, few studies have examined the impact of future patterns of pulses on recruitment niches and seedling physiology.

General Circulation Models predict a 1–3°C increase in temperature for California (Field et al., 1999) and a 25–50% increase in precipitation by 2030–2050, and flood and drought events will likely become more extreme (Giorgi et al., 1994; Easterling et al., 2000). In the deserts of California, summer pulses of rainfall may increase in magnitude, frequency, and, or become more intense (Dessens, 1995; Field et al., 1999). The Hadley Centre for Climate Prediction's HadCM2 model predicts a 100% increase in precipitation for June, July, and August for a portion of the south-western United States, the CGCM1 model from the Canadian Centre for Climate Modelling and Analysis predicts an 80% increase in rainfall for the same period, and for one regional climate model, a 15% increase in summertime southerly monsoonal flow is predicted for the western Great Basin Desert, where the present study was conducted (Arritt et al., 2000). Due to the varied topography and climates of California, as well as uncertainty in climate models, generalizations regarding local changes in climate are more difficult to make compared to predictions for the entire state (Field et al., 1999). Changes in physical conditions and resource availability due to climate change are expected to force certain plant taxa to migrate north or to higher elevations, consequently causing large shifts in community distributions and composition (Davis and Zabinski, 1992; Peters and Lovejoy, 1992). For example, in the next century an expansion of savanna communities could potentially occur at the expense of shrublands in the foothills of California (Field et al., 1999), and desert shrublands of the south-west US may revert to grasslands (Neilson, 1995).

Altered resource availability in a future climate will cause changes in species interactions such as competition and facilitation (Bertness and Callaway, 1994; Holmgren et al., 1997; Field et al., 1999), however, these effects are not well understood (Shaver et al., 2000). Seedling recruitment dynamics may change in an altered climate, which may result in changes in species composition at the community level. Although plant communities may migrate in response to climate change, the ability to do so will be primarily dictated by seed dispersal and subsequent successful seedling establishment and survival. For arid and semi-arid ecosystems, this highlights the importance of understanding the effects on seedling physiology and species interactions of responses to pulse events.

In arid ecosystems, water is often a crucial, limited resource for plant recruitment, photosynthesis and growth, nutrient dynamics, and net ecosystem productivity (Smith et al., 1997; Reynolds et al., 1999). Natural plant establishment may be decreased by enhanced levels of stress in a future climate (Smith and Novak, 1990; Larcher, 1995). A change in water availability and other environmental variables is likely to affect seedling recruitment and establishment. However, adult shrubs can affect the physical microclimate experienced by seedlings, through the effects of shading on water availability and temperature stresses (Niering et al., 1963; De Jong and Klinkhamer, 1988; Franco and Nobel, 1989; Holmgren et al., 1997). Despite much research on the mechanisms underlying adult and seedling interactions, few studies have examined how climate change may affect nurse plant–seedling relationships. In order to understand how arid communities may respond to a future altered climate, it is important to understand the dynamics of plant–water relations and the community interactions that may be sensitive to pulse events.

In the present study, we experimentally addressed the effects of precipitation pulses during summer on seedling photosynthesis. The timing, length and intensity of rainfall events are naturally variable in arid regions; because there are a limited number of precipitation events per year, even an extra single event can have significant effects on plant survival and growth. We compared seedlings of *Artemisia tridentata* Nutt. (Asteraceae) (Big Sagebrush) and *Purshia tridentata* Pursh (Rosaceae) (Antelope Bitterbrush). Adults of *A. tridentata* have both deep and shallow roots to extract water at different depths at different times of the year, whereas *P. tridentata* adults have very deep roots (up to 5 m) and few shallow roots (Clements and Young, 2001). For seedlings however, roots of the two species likely overlap in distribution at shallow soil depths. Experiments were conducted in the western Great Basin Desert where summer precipitation is expected to increase in the future due to climate change (Field et al., 1999; Arritt et al., 2000). Although it seems intuitive that plants will conduct more photosynthesis when given extra water, not all species respond to additional water. In particular, the tendency to take up water is dependent upon root architecture, plant functional type, seasonality of precipitation, and plant phenology (Flanagan et al., 1992; Lin et al., 1996; Williams and Ehleringer, 1996; Schwinning and Ehleringer, 2001; Schwinning et al., 2002). Moreover, seedling recruitment in this system can be influenced by both facilitation by and competition with adult plants, and the relative importance of these factors can shift with time and resource availability (Bertness and Callaway, 1994; Callaway

et al., 1996). We tested the hypotheses that: (1) an experimental pulse representing a 25% increase in summer precipitation would increase water potential and photosynthesis for *A. tridentata* and *P. tridentata* seedlings, and (2) for *P. tridentata*, experimentally applied rainfall pulses lead to greater effects on photosynthesis for seedlings planted in open microsites compared to seedlings planted in the shade of adult *A. tridentata* nurse plants. We measured microclimatic conditions in open sites and under adult shrubs of *A. tridentata* including air temperature, soil temperature and photosynthetic photon flux density (PPFD; 400–700 nm). In order to measure the effects of experimental watering on the physiological performance of seedlings we measured plant water potential, diurnal patterns of photosynthetic gas exchange (CO_2 assimilation, stomatal conductance, transpiration, and water use efficiency), and chlorophyll *a* fluorescence from Photosystem II.

2. Materials and methods

2.1. Site description

This study was conducted at the Sierra Nevada Aquatic Research Laboratory (SNARL) of the Valentine Eastern Sierra UC Natural Reserve, in eastern California near the city of Mammoth Lakes ($37°37'$N, $118°50'$W, elevation 2100 m; Fig. 1A). The vegetation is characterized as sagebrush scrub (Barbour and Major, 1990), which is common throughout the Great Basin Desert. The dominant species are the shrubs *A. tridentata* and *P. tridentata*. Both shrub species and other vegetation occur in a matrix across the landscape with large interspaces between plants. Annual mean precipitation is less than 20 cm (Fig. 1B), which falls as winter snow, or as convective rainfall (from the Sierra Nevada snowpack) or as monsoonal summer rainfall (from the Gulf of California).

2.2. Experimental design

We conducted two field experiments both of which involved experimental water additions. In the first experiment we measured CO_2 assimilation, stomatal conductance and transpiration from seedlings of both *A. tridentata* and *P. tridentata* as a function of precipitation addition. For the second experiment, we transplanted seedlings of *P. tridentata* beneath the canopy of adult shrubs of *A. tridentata* and into the open spaces between shrubs to control for seedling age. Individual plants were compared to avoid effects of competition on responses to watering manipulations (experiments to test hypotheses regarding competition are ongoing). For watering manipulations, plastic lawn-edging was placed around individual plants in a circle with a radius 1.5 times the radius of the canopy. Water was added at 25% of the summer average of 26 mm for the mean from 1961 to 1990. Water volume was computed from the radius of the circle formed by the plastic edging multiplied by the fraction of annual precipitation. Water was added from a plastic
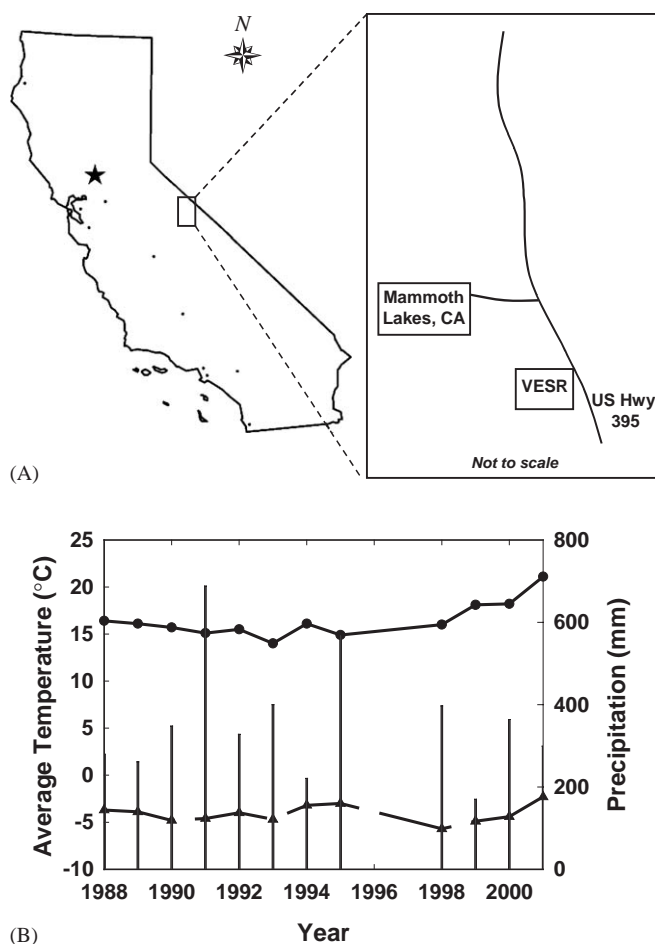
Fig. 1. Location (A) and climate (B) of Mammoth Lakes, California. Climate data are averages for the period 1987 to 2001, the only years for which continuous records are available. Data are from records collected at the Sierra Nevada Aquatic Research Laboratory of the UC Valentine Eastern Sierra Natural Reserve (VESR).

watering can at a height of approximately 1.0 m; canopy interception was allowed, and water was added slowly to prevent run-off and to allow percolation into the soil.

In May 2000, we randomly selected 10 seedlings of *P. tridentata* and 10 seedlings of *A. tridentata* growing naturally at SNARL. We randomly chose five individuals of each species that received water on the morning of 29 May; five of each species were left unwatered as controls. On 31 May we made diurnal gas exchange and chlorophyll fluorescence measurements at 2 h intervals starting at 0600 h and ending at 2000 h. The following morning we removed all seedlings with a razor blade and quickly placed them into a Scholander-type pressure chamber (P.M.S. Scientific, Santa Barbara, CA, USA) and measured predawn water potential.

On 14 June 2000 we transplanted 10 greenhouse grown seedlings of *P. tridentata* under the canopy on the north side of adult *A. tridentata* plants and 10 in the open spaces between shrubs. All *A. tridentata* adults had similar size canopies ranging in diameter from approximately 0.75 to 1.25 m. We chose to study *P. tridentata* seedlings because observations indicate that they recruit in both types of microsites, and we chose *A. tridentata* as the nurse plant because it is the dominant shrub at the field site. Seedlings were grown from seeds collected on site the previous year and were approximately 1.5 months old at time of planting. Seedlings were grown in a greenhouse in general purpose potting soil (Pro Mix HP, Premier Horticulture, Red Hill, PA) in 4×20.5 cm seedling tubes. Each seedling was immediately watered with approximately 0.25 l of water following the transplant to reduce transplant shock. We placed wire cages over all seedlings to reduce damage and mortality from herbivory; the cages reduced PPFD by about 20%. On 24 June 2000, we randomly selected five nurse seedlings and five open seedlings which received a water treatment equivalent to 6.54 cm of rainfall, similar to the estimated increase the region is predicted to receive from climate change (Field et al., 1999). The seedlings did not receive any ambient rainfall between transplanting and experiments. The following morning we made photosynthetic gas exchange and chlorophyll *a* florescence measurements on all transplanted seedlings.

CO$_2$ assimilation, stomatal conductance to water vapor, and transpiration were measured using an open-mode portable photosynthesis system (Model LI-6400, Li-Cor, Inc., Lincoln, NE, USA). Measurements were taken on the top portion of the plant because it fit entirely in the cuvette of the portable photosynthesis system. The CO$_2$ concentration within the leaf measurement chamber was maintained at $360 \, \mu mol \, mol^{-1}$. Leaf area used for gas exchange measurements was determined by tracing the leaf onto paper and subsequent comparison of the image to a known area and mass of paper.

Measurements of chlorophyll fluorescence were obtained with a pulse-modulated fluorometer (Model FMS1, Hansatech, Kings Lynne, England). Measurements were made on the first full size leaf down from the apical meristem. For leaves exposed to ambient PPFD, the intrinsic efficiency of excitation transfer (Barker and Adams, 1997) was calculated as $F'_v/F'_m = (F'_m - F'_o)/F'_m$. F_o was determined using a far-red pulse of light to excite PSI preferentially and to oxidize PSII. To assess the recovery of excitation energy transfer, leaves that were measured in ambient light were dark adapted (maximum 1 h due to sampling time), and the efficiency of excitation transfer was measured as $F_v/F_m = (F_m - F_o)/F_m$. The quantum efficiency of Photosystem II (PSII) was calculated as $(F'_m - F_s)/F'_m$.

Microclimate sensors were placed in the open and under the canopy of adult individuals of *A. tridentata*. The sensors recorded air and soil temperatures and photosynthetic photon flux density (PPFD; 400–700 nm). Air temperature was recorded approximately 2 cm above the soil surface underneath a white metal radiation shield. Soil temperature was made by placing thermistors approximately 1 cm under the soil surface. The microclimate sensors were connected to Li-Cor LI-1000 dataloggers that recorded the microenvironment at 15 min intervals.

2.3. Soil and vegetation sampling

To quantify vegetation characteristics at the study site, three 50 m transects were randomly laid out across the field site (USDI National Park Service, 2003). Cover of each species under the transect line was recorded to the nearest cm. This allowed us to calculate the relative percent cover of each species and the cover of bare ground between shrubs. We included all non-vegetative components as bare ground, including small twigs and other litter, and gravel less than 2 cm in diameter; no soil biotic crusts were observed. Relative percent cover for each species found along the transect lines was calculated as cover of a species/percent of non-bare ground. The frequency of seedlings of *A. tridentata* and *P. tridentata* was determined using detailed searches within ten 3×30 m belt transects placed adjacent to each line transect. For seedlings located under the canopy of adult shrubs, the identity of the adult species was recorded.

Five random soil samples were collected from underneath the canopy of adult *A. tridentata* plants and five from the open spaces between adult shrubs and had nutrient analyses performed at the Division of Agriculture and Natural Resources Laboratory at University of California, Davis. Soil samples were collected from 10 cm depth and air dried (at $80°C$ in a forced-draft oven) for 1 week. Soils were analysed for percent carbon (C), organic matter, total extractable nitrogen (N) and for Olsen-phosphorous (P), extractable potassium (K), calcium (Ca), and pH.

2.4. Statistical analyses

To measure the effects of watering on diurnal gas exchange and cholorophyll fluorescence of the naturally occurring seedlings we used a repeated measures analysis of variance (ANOVA). Additionally, to analyse the effects of the watering treatment on the naturally occurring seedlings during peak stress periods (midday), we used a one-way ANOVA. We used a two-way ANOVA to analyse the effect of the watering treatment and planting location (nurse plant vs. open microsites) on the dependent variables measured for transplanted *P. tridentata* seedlings. Soil analyses were done using a one-way ANOVA with location as the independent variable. All analyses were done with StatView 5.0 (SAS Institute Inc, Cary, NC, USA). Means and $\pm$ one standard error are reported throughout and $p < 0.05$ is considered significant.

3. Results

3.1. Vegetation and soil

A. tridentata had the greatest relative percent cover (34 ± 7) out of the 14 taxa cataloged from three transects. *P. tridentata* had the second highest relative percent cover of the taxa (21 ± 10). The next most dominant species was the exotic grass, *Bromus tectorum*, which comprised $13 \pm 8\%$ of the non-bare ground cover. Bare

ground—lacking dead organic matter, twigs, stems, or visible cryptobiotic crusts—occupied $44 \pm 8\%$ of the measured area. Cryptobiotic crusts are very rare in the grazed habitat of our site (the only crusts that have been found were in an area protected from grazing since the 1930s.) Most (82%) of *A. tridentata* seedlings were found in the canopy of *A. tridentata* adults, and the balance were in open microsites. For *Purshia tridentata*, 63% of the 35 seedlings located on the ten belt transects were in open microsites.

In the open microsites, mean percent soil C was 2.72 ± 0.92, organic matter was 2.812 ± 0.49 and N was 0.12 ± 0.42. Phosphorus (Olsen) was 31.04 ± 4.25 ppm and K was 215 ± 59 ppm. Ca was 4.7 ± 0.63 meq/100 mg and pH was 5.84 ± 0.18. For soils from underneath the canopy, mean percent C was 1.69 ± 0.27, organic matter was 1.91 ± 0.34 and N was 0.08 ± 0.02. Phosphorus (Olsen) was 29 ± 2.7 ppm and K was 149 ± 33 ppm. Ca was 3.6 ± 0.88 meq/100 mg and pH 5.86 ± 0.16. None of the differences in nutrient content between nurse plant canopy and open microsites were significant.

3.2. Naturally recruited seedlings in situ

The first field campaign between 25 May and 1 June 2000 focused on comparisons of photosynthetic responses for seedlings of *A. tridentata* and *P. tridentata* subject to precipitation additions. On 27 May, a typical day during which this portion of the study took place, mean PPFD was $538 \pm 78 \, \mu\text{mol m}^{-2} \text{s}^{-1}$. The mean temperature of the soil (T^{soil}) was $21.5°\text{C} \pm 1.0$ and mean air temperature (T^{air}) was $20.3°\text{C} \pm 1.4$. Diurnal fluctuations of T^{air} on 27 May ranged from approximately $4°\text{C}$ to $38°\text{C}$. The watering treatment did not significantly affect predawn water potential for either species. Water potential was -1.96 ± 0.12 MPa for watered seedlings, and -2.27 ± 0.20 MPa for non-watered controls of *A. tridentata*. For *P. tridentata* water potential was -2.03 ± 0.19 MPa for watered seedlings and -1.87 ± 0.17 MPa for controls.

Diurnal patterns of net CO_2 assimilation (A) were similar for seedlings of both *A. tridentata* and *P. tridentata* (Figs. 2A and B). Maximal assimilation rates were achieved at 1600 h, but both species had peaks of uptake at 0800 and 1000 h. Precipitation additions increased assimilation in both species but the differences were not significant. The repeated measures ANOVA (RMANOVA) for photosynthesis over the day indicated that the measured parameters significantly varied through time (for *A. tridentata*, $F = 15.34$, $p < 0.001$, and for *P. tridentata*, $F = 12.35$, $p < 0.001$), but there was no overall treatment or treatment $\times$ time interaction effects. Stomatal conductance to water vapor (g_s) was different for the two species throughout the diurnal period (Figs. 2C and D). *P. tridentata* seedlings had a peak of physiological activity at 1000 h at which g_s was greatest (RMANOVA: $F = 3.53$, $p = 0.006$), whereas for *A. tridentata* g_s was maximal at 0800 h (RMANOVA: $F = 10.05$, $p < 0.001$). The precipitation additions had no significant effect on g_s for *P. tridentata*. In contrast, the precipitation additions significantly increased g_s for *A. tridentata* at 0800 h ($F = 10.057$, $p = 0.0132$) and 1200 h ($F = 5.815$, $p = 0.0424$).
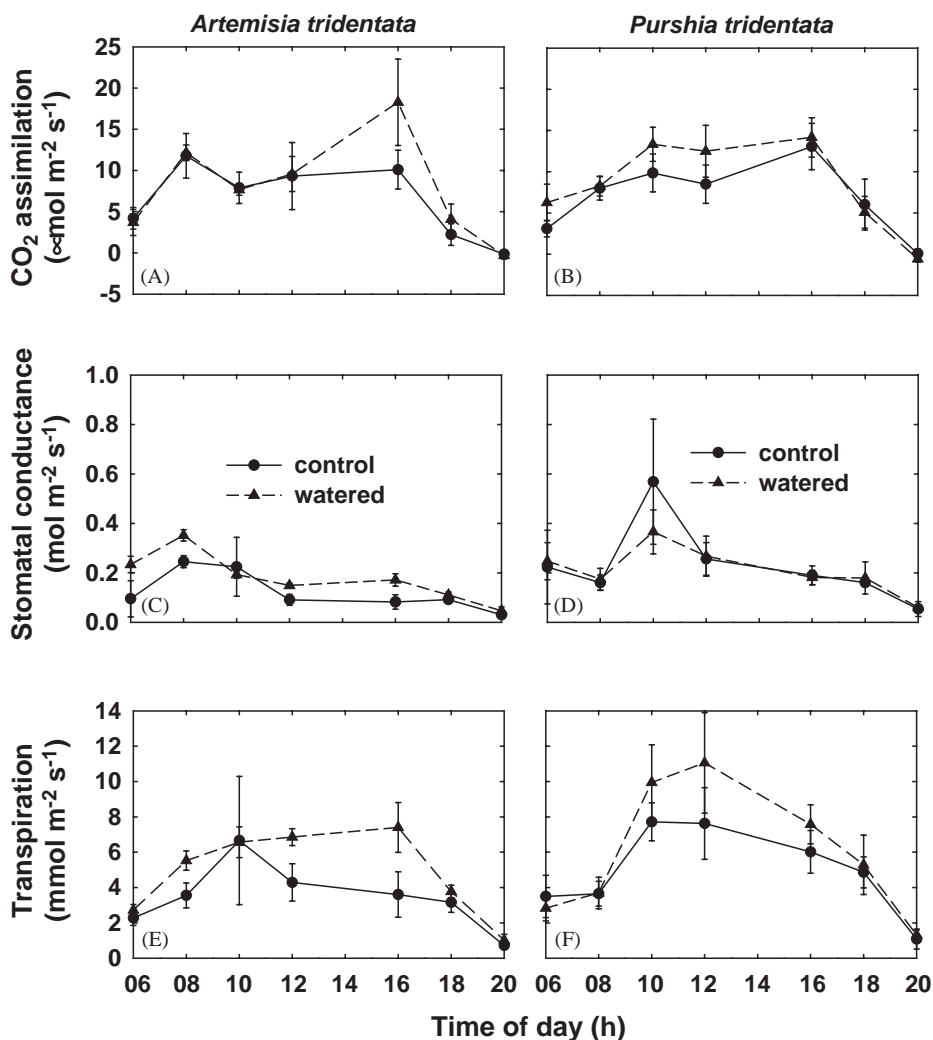
Fig. 2. Diurnal patters of CO_2 assimilation, A (A, B) and stomatal conductance to water vapor g_s (C, D) for control (circles) and watered (triangles) seedlings of $A. tridentata$ (A, C) and $P. tridentata$ (B, D). Data are means $\pm$ S.E. ($n = 5$).

Diurnal transpiration (E) was similar for both species. However, for $P. tridentata$, transpiration increased later in the morning (after 0800 h) in comparison to $A. tridentata$. For $P. tridentata$ water loss was maximal at 1200 h and decreased until measurements ended at 2000 h (RMANOVA: $F = 11.22$, $p < 0.001$). Water additions increased transpiration for $P. tridentata$: at 1200 h, E was $11.056 \pm 2.848 \, \text{mmol m}^{-2} \text{s}^{-1}$ for watered seedlings and $7.628 \pm 2.030 \, \text{mmol m}^{-2} \text{s}^{-1}$ for control seedlings, but these differences were not statistically different ($F = 0.961$,
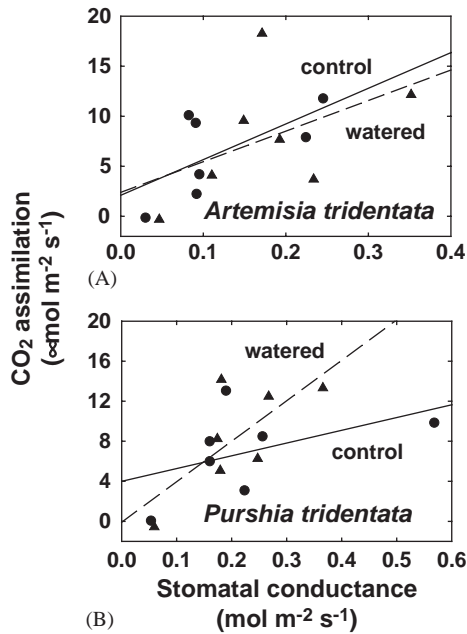
Fig. 3. Relationship between CO_2 assimilation and stomatal conductance to water vapor for *A. tridentata* (A) and *P. tridentata* (B) for control (circles) and watered (triangles) seedlings.

$p = 0.3556$). Watering did increase transpiration in *A. tridentata* at 0800 and 1200 h; however, this effect was only marginally significant ($F = 4.917$, $p = 0.0574$ and $F = 4.903$, $p = 0.0577$ for 0800 and 1200 h, respectively).

The two species exhibited different responses to watering for the relationship between CO_2 assimilation and stomatal conductance to water vapor (Fig. 3). For *A. tridentata*, the relationship was unchanged for seedlings treated with supplemental water. In contrast, the slope of the relationship between A and g_s increased three-fold for seedlings of *P. tridentata* two days after watering.

The quantum efficiency of PSII (F_v'/F_m') was similar for the two species (Figs. 4A and B). For both species, F_V'/F_M' was minimal at 1000 h, and their maximum values were reached in darkness at 2000 h. The watering treatment had different effects on quantum efficiency of PSII for *A. tridentata* and *P. tridentata*. Specifically, for *P. tridentata* precipitation additions increased quantum efficiency at 0800 h, however, this difference was only marginally significant ($F = 5.083$, $p = 0.0542$). There were no other significant effects of the watering treatment for either *P. tridentata* or *A. tridentata*.

3.3. Watering effects on the recruitment niche

The second field campaign between 14 and 29 June 2000 focused on comparisons of photosynthetic responses for seedlings of *P. tridentata* under nurse plants and in
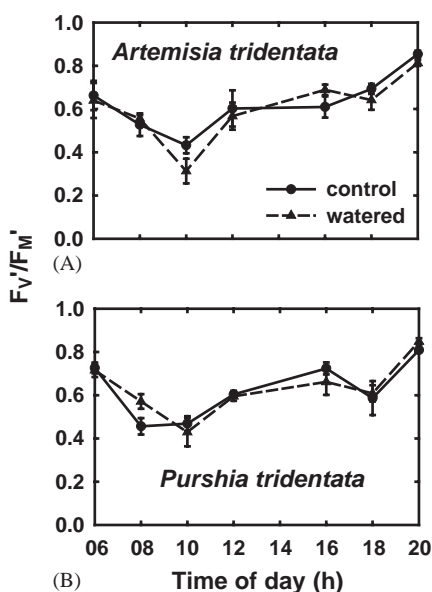
Fig. 4. Diurnal patters of quantum efficiency of Photosystem II (F_v'/F_m') for control (circles) and watered (triangles) seedlings of (A) *A. tridentata* and (B) *P. tridentata*. Data are means $\pm$ S.E. ($n = 5$).

open microsites, and in response to watering. Mean daily photosynthetic photon flux density in the open sites was $581 \pm 46\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ and under the canopy PPFD was $135 \pm 14\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ (Fig. 5) The mean temperature of the soil (T^{soil}) in the open was $25.5^{\circ}\text{C} \pm 0.2$ and under the canopy T^{soil} was $20.0^{\circ}\text{C} \pm 0.5$. The maximum air temperatures between open- and under-canopy sites were similar: $21.2^{\circ}\text{C} \pm 0.7$ for the open sites and $19.8^{\circ}\text{C} \pm 0.6$ under the adult plant canopies. Diurnal fluctuations of temperature from 26 to 29 June, a typical period during which these physiological measurements were taken, ranged from approximately 5°C to 41°C (Fig. 5).

The watering treatment did not significantly affect photosynthetic physiology (Table 1). However, the location of the seedlings (nurse vs. open microsites) did affect the physiology of the transplanted seedlings. Specifically, seedlings in open microsites had significantly greater net CO_2 uptake than the seedlings under the adult plant canopy ($F = 14.046$, $p = 0.0018$). Stomatal conductance was lower under nurse plants, but there were large errors about the mean. Seedlings under adult plant canopies were exposed to greater leaf vapor pressure deficits compared to seedlings in the open ($F = 36.481$, $p < 0.001$).

4. Discussion

Precipitation additions had varying physiological effects on both naturally occurring seedlings of *A. tridentata* and *P. tridentata*, as well as for seedlings of *P. tridentata* planted in nurse plant canopies or open microsites. At 1200 h, during the
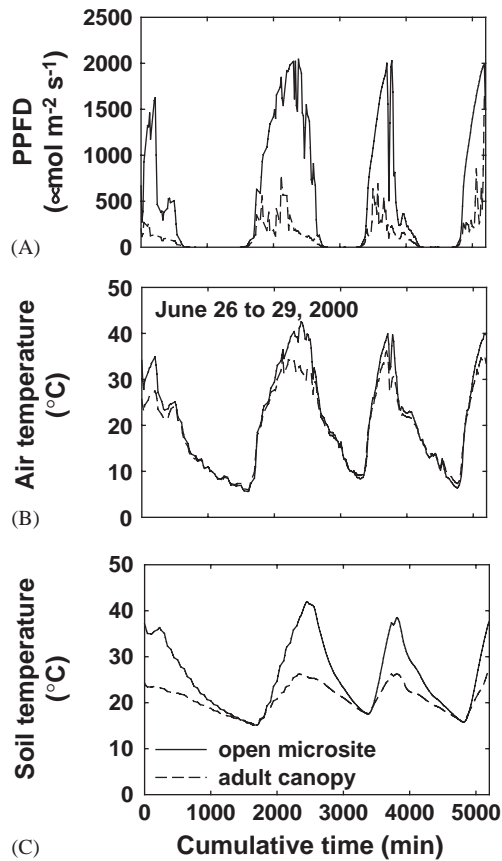
Fig. 5. Microclimatic conditions from 26 to 29 June 2000 between open microsites (solid lines) and in the shade of adult canopies (dashed lines). (A) Photosynthetic photon flux density, (B) air temperature and (C) soil temperature.

Table 1
Physiological parameters (CO_2 assimilation, stomatal conductance and quantum efficiency [dimensionless]) of seedlings of *P. tridentata* transplanted with and without water additions in open sites and canopy shade. Different letters denotes significant difference[a]

Location	Water addition	A ($\mu mol\,m^{-2}\,s^{-1}$)	g_s ($mmol\,m^{-2}\,s^{-1}$)	F'_v/F'_m	F_v/F_m
Open	Watered	$8.904 \pm 1.073a$	0.069 ± 0.012	0.696 ± 0.094	0.706 ± 0.044
Shade	Watered	$4.582 \pm 0.670b$	0.068 ± 0.023	0.755 ± 0.029	0.734 ± 0.064
Open	Control	$12.688 \pm 2.660a$	0.113 ± 0.035	0.656 ± 0.046	0.675 ± 0.059
Shade	Control	$5.404 \pm 0.687b$	0.050 ± 0.015	0.681 ± 0.083	0.815 ± 0.008

[a] Values are means $\pm$ S.E. for $n = 5$ plants.

most light-intensive part of the day, precipitation additions resulted in increased stomatal conductance and transpiration for *A. tridentata,* resulting in decreased water use efficiency. However, the precipitation additions did not impact g_s or E for

P. tridentata at 1200 h. Integrated over the entire day, the relationship between stomatal opening and photosynthetic CO_2 uptake was unchanged for watered compared to control *A. tridentata* seedlings; for *P. tridentata*, photosynthesis increased per unit stomatal opening, suggesting an upregulation of photosynthetic enzymes, and/or a change in stomatal behavior following watering. These results indicate that responses of the sensitive seedling life-history stage to future summertime precipitation patterns will differ for these two dominant species of the western Great Basin Desert. Precipitation additions did increase CO_2 assimilation rates of seedlings for both *P. tridentata* and *A. tridentata*, however, these results were not significant, likely due to small sample sizes used. It is also possible that with further water additions or different timing of additions, increased precipitation as predicted by climate change models might cause a more pronounced forcing of these shrub's CO_2 assimilation rates. The timing, length and intensity of rainfall events are naturally variable in arid regions, and future precipitation patterns are difficult to predict. Nonetheless, because there are a limited number of precipitation events per year, single events can have significant effects on plant survival and growth. Increased precipitation is not the only environmental variable associated with global climate change; increased temperature and elevated CO_2 concentrations will also impact photosynthesis (Drennan and Nobel, 2000; Loik et al., 2000; Lewis et al., 2001). In a future altered climate, recruitment success for species that can respond to additional water may benefit via reduced heat-induced photoinhibition. The ability of *A. tridentata* to use supplemental summer water for transpiration may allow it to have increased evaporative cooling and ultimately maintain leaf temperatures more conducive for optimal photosynthesis. Our results suggest that seedlings of *A. tridentata* may be better than seedlings of *P. tridentata* at coping with climate change because of their ability to utilize increased precipitation. Ultimately, seedlings of *A. tridentata* may be able to maintain higher photosynthetic rates than seedlings of *P. tridentata* in a future climate in which precipitation and temperature increase, and thereby allocate greater amounts of photosynthates to root production for water and nutrient acquisition.

Canopy gaps can be important for recruitment and maintenance of diversity in habitats with short growing seasons (Miller et al., 1999). Previous research has found that water additions increase the photosynthetic rates of adult *A. tridentata* plants (unpublished data of M.E. Loik) and this may result in an increase of canopy cover and a decrease of bare ground cover. Although bare ground comprises over 40% of the surface at our study site, greater biomass accumulation due to climate change by *A. tridentata* and perhaps other species, such as the invasive grass *Bromus tectorum*, may result in reduced availability of open space recruitment niches for *P. tridentata*. Interestingly, we found that transplanted seedlings of *P. tridentata* in the open sites had greater CO_2 assimilation rates (12.7 μmol CO_2 m^{-2} s^{-1}) than seedlings transplanted under nurse plants (5.4 μmol CO_2 m^{-2} s^{-1}) and the watering treatment had no effect. Although fitness is based upon survival and both above- and below-ground biomass accumulation, our results for photosynthetic rates suggest that the open sites between shrubs may be an important recruitment niche for *P. tridentata*. In this regard, we found that the majority of naturally occurring *P.*

tridentata seedlings were in open microsites between adult shrubs, suggesting that open spaces are where seedlings of *P. tridentata* naturally recruit at our study site. Nutrient differences between open and nurse plant canopy microsites were not significantly different, therefore we conclude that they probably are not a very important factor influencing the spatial pattern at our study site. Our gas exchange results suggest that open sites may be especially important for seedlings of *P. tridentata* because photosynthetic rates are unlikely to be limited by PPFD when growing there. On the contrary, seedlings of *A. tridentata* were more likely to be found under the canopy of adult shrubs. Given that (1) adults of *A. tridentata* may increase in size and reduce the open spaces between shrubs in a future altered climate and (2) seedlings of *P. tridentata* generally recruit in the open spaces between shrubs, there may be shift in community composition where *A. tridentata* rises to greater dominance at the expense of *P. tridentata*.

Characteristics of microsite locations (i.e. open vs. under the canopy of a nurse plant) can have direct and indirect effects on plants. For example, adult shrubs may be important for facilitating succession in arid environments because of their ability to trap airborne mycorrhizal spores (Allen and Allen, 1988), which may result in increased drought tolerance for seedlings of *A. tridentata* (Stahl et al., 1998). Adult shrubs may also provide seedlings refugia from trampling and damage from native herbivores, cattle, or other livestock (McAuliffe, 1984). Our results suggest that the ability of *P. tridentata* seedlings to maximize CO_2 assimilation will probably be more dependent on seedling location rather than an increase in summer precipitation, consistent with the observation that open spaces are important recruitment niches.

Water is a limiting resource for seedling establishment and recruitment in arid environments (Jones, 1991; Lauenroth et al., 1994; Scherff et al., 1994; Chambers, 1997) and our results suggest that seedling responses to increased precipitation in a future altered climate will be species-specific. Overall, *A. tridentata* responded more to the precipitation additions (increased stomatal conductance and transpiration) than did *P. tridentata*. Interestingly, Owens and Norton (1989) found that nurse plants increased survival of *A. tridentata* seedlings. However, our results suggest that in a future wetter climate the benefit of nurse plants may be lost because seedlings of *A. tridentata* may be able to tolerate the drier interspaces with additional water. The ability of *A. tridentata* seedlings to use additional precipitation may ultimately allow this species to colonize more stressful sites in comparison to *P. tridentata*. This difference may result in changes of species composition in portions of the Great Basin Desert where these species co-occur.

It is likely that in a future altered climate, g_s and E and perhaps CO_2 assimilation for seedlings of *P. tridentata* may not be affected by additional pulses of summer precipitation. The ability of *A. tridentata* and perhaps other species to respond to pulses of water will likely depend on previous precipitation patterns. That is, plants may respond differently to several small pulses versus one large pulse. The fact that during May and June of 2000, the time during which our study took place, there was no substantial rainfall certainly influenced our results. If there had been any precipitation events during our field campaigns we likely would have found different responses in *A. tridentata* and *P. tridentata*, as there may be a priming effect of

previous precipitation on root behavior, water uptake, and gas exchange. In this regard, Carpenter and West (1987) failed to find a biomass response of water additions to *A. tridentata* during an unusually wet season.

There is great uncertainty in climate change models regarding the frequency and intensity of precipitation events (Field et al., 1999; Arritt et al., 2000; Easterling et al., 2000). Until such uncertainties can be resolved, more experiments should be conducted to address the effects of different precipitation patterns (i.e. many small vs. a few large pulses) on plant communities and ecosystem function. Moreover, further studies combining multiple factors, such as increased CO_2 concentration, temperature and precipitation, would further our understanding of the relative importance of how different climatic components may affect plant physiology in a future altered climate. Such experiments will certainly help elucidate how plants may respond to the complexities of precipitation events that will change due to a future, altered climate.

Acknowledgements

References

Allen, E.B., Allen, M.F., 1988. Facilitation of succession by the nonmycrotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. American Journal of Botany 75, 257–266.

Arritt, R.W., Goering, D.C., Anderson, C.J., 2000. The North American monsoon system in the Hadley Centre coupled ocean-temperature GCM. Geophysical Research Letters 27, 565–568.

Barbour, M.G., Major, J., 1990. Terrestrial Vegetation of California. California Native Plant Society, Sacramento, CA, 1002pp.

Barker, D.H., Adams, W.W., 1997. The xanthophyll cycle and energy dissipation in differently oriented faces of the cactus *Opuntia macrorhiza*. Oecologia 109, 353–361.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends in Ecology and Evolution 9, 191–193.

Callaway, R.M., DeLucia, E.H., Moore, D., Nowak, R., Schlesinger, W.H., 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology 77, 2130–2141.

Carpenter, A.T., West, N.E., 1987. Indifference of mountain big sagebrush growth to supplemental water and nitrogen. Journal of Range Management 40, 448–451.

Chambers, J.C., 1997. Restoring alpine ecosystems in the western United States: environmental constraints, disturbance characteristics, and restoration success. In: Urbanska, K.M., Webb, N.R., Edwards, P.J. (Eds.), Restoration Ecology and Sustainable Development. Cambridge University Press, New York, pp. 167–187.

Clements, C.D., Young, J.A., 2001. Antelope bitterbrush seed production and stand age. Journal of Range Management 54, 269–273.

Davis, M.B., Zabinski, C., 1992. Changes in geographical ranges resulting from greenhouse warming: effects on biodiversity in forests. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven, CT, pp. 297–308.

De Jong, T.J., Klinkhamer, P.G.L., 1988. Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand dune area: the importance of water for differential survival and growth. Journal of Ecology 76, 393–402.

Dessens, J., 1995. Severe convective weather in the context of a nighttime global warming. Geophysical Research Letters 22, 1241–1244.

Drennan, P.M., Nobel, P.S., 2000. Repsonses of CAM species to increasing atmospheric CO_2 concentrations. Plant Cell and Environment 23, 767–781.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Means, L.O., 2000. Climate extremes: observations, modeling, and impacts. Science 289, 2068–2074.

Field, C.B., Daily, G.C., Davis, F.W., Gaines, S., Matson, P.A., Melack, J., Miller, N.L., 1999. Confronting Climate Change in California: Ecological Impacts on the Golden State. Ecological Society of America, Cambridge, MA, 62pp.

Flanagan, L.B., Ehleringer, J.R., Marshall, J.D., 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. Plant and Cell Environment 15, 831–836.

Franco, A.C., Nobel, P.S., 1989. Effects of nurse plants on the microhabitat and growth of cacti. Journal of Ecology 77, 870–889.

Gebauer, R.L.E., Ehleringer, J.R., 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81, 1415–1424.

Giorgi, F., Shields Brodeur, C., Bates, G.T., 1994. Regional climate change scenarios over the United States produced with a nested regional climate model: spatial and seasonal characteristics. Journal of Climate 7, 375–399.

Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. Ecology 78, 1966–1975.

Jones, G.P., 1991. Seedling survival and adult plant water relations of black sagebrush and big sagebrush in the Laramie Basin. Ph.D. Dissertation, University of Wyoming, Laramie.

Larcher, W., 1995. Physiological Plant Ecology. Springer, New York.

Lauenroth, W.K., Sala, O.E., Coffin, D.P., Kirchner, T.B., 1994. The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. Ecological Applications 4, 741–749.

Lewis, J.D., Lucash, M., Olszyk, D., Tingey, D.T., 2001. Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO2 and temperature. Plant Cell and Environment 24, 539–548.

Lin, G., Phillips, S.L., Ehleringer, J.R., 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. Oecologia 106, 8–17.

Loik, M.E., Redar, S.P., Harte, J., 2000. Photosynthetic responses to a climate-warming manipulation for contrasting meadow species in the Rocky Mountains, Colorado, USA. Functional Ecology 14, 166–175.

McAuliffe, J.R., 1984. Prey refugia and the distributions of two Sonoran Desert cacti. Oecologia 65, 319–321.

Miller, G.R., Geddes, C., Mardon, D.K., 1999. Response of the alpine gentian *Gentiana nivalis* L. to protection from grazing by sheep. Biological Conservation 87, 311–318.

Neilson, R.P., 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications 5, 362–385.

Niering, W.A., Whittaker, R.A., Lowe, C.H., 1963. The saguaro: a population in relation to environment. Science 142, 15–23.

Novoplansky, A., Goldberg, D.E., 2001. Effects of water pulsing on individual performance and competitive hierarchies in plants. Journal of Vegetation Science 12, 199–208.

Noy-Meir, I., 1973. Desert ecosystems, environment and producers. Annual Review of Ecology and Systematics 4, 25–41.

Owens, M.K., Norton, B.E., 1989. The impact of "available area" on *Artemisia tridentata* seedling dynamics. Vegetatio 82, 155–162.

Peters, R.L., Lovejoy, T.E., 1992. Global Warming and Biological Diversity. Yale University Press, New Haven, CT, 386pp.

Pugnaire, F.I., Hasse, P., Incoll, L.D., Clark, S.C., 1996. Response of the tussock grass *Stipa tenacissima* to watering in a semi-arid environment. Functional Ecology 10, 265–274.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., De Soyza, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecological Monographs 69, 69–106.

Scherff, E.J., Galen, C., Stanton, M.L., 1994. Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneus*. Oikos 69, 405–413.

Schwinning, S., Ehleringer, J.R., 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. Journal of Ecology 89, 464–480.

Schwinning, S., Davis, K., Richardson, L., Ehleringer, J.R., 2002. Denterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130, 345–355.

Shaver, G.R., Canadell, J., Chapin III, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., et al., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. BioScience 50, 871.

Smith, S.D., Novak, R.S., 1990. Ecophysiology of plants in the Intermountain lowlands. In: Osmond, C.B., Pitelka, L.F., Hidy, G.F. (Eds.), Plant Biology of the Basin and Range. Springer, New York, pp. 375.

Smith, S.D., Monson, R.K., Anderson, J.E., 1997. Physiological Ecology of North American Desert Plants. Springer, New York, 286pp.

Stahl, P.D., Schuman, G.E., Frost, S.M., Williams, S.E., 1998. Arbuscular mycorrhizae and water stress tolerance of Wyoming big sagebrush seedlings. Soil Science Society of America Journal 62, 1309–1313.

USDI National Park Service, 2003. Fire Monitoring Handbook. Boise (ID): Fire Management Program Center, National Interagency Fire Center, Boise, Idaho. 274pp.

Williams, D.G., Ehleringer, 1996. Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. Oecologia 106, 455–460.