

UC Santa Cruz

UC Santa Cruz Previously Published Works

Title

Impact of intra- versus inter-annual snow depth variation on water relations and photosynthesis for two Great Basin Desert shrubs

Permalink

<https://escholarship.org/uc/item/8q02r7z6>

Journal

Oecologia, 178(2)

ISSN

0029-8549

Authors

Loik, Michael E
Griffith, Alden B
Alpert, Holly
et al.

Publication Date

2015-06-01

DOI

10.1007/s00442-015-3224-7

Peer reviewed

Impact of intra- versus inter-annual snow depth variation on water relations and photosynthesis for two Great Basin Desert shrubs

Michael E. Loik, Alden B. Griffith, Holly Alpert, Amy L. Concilio, Catherine E. Wade & Sharon J. Martinson

Oecologia

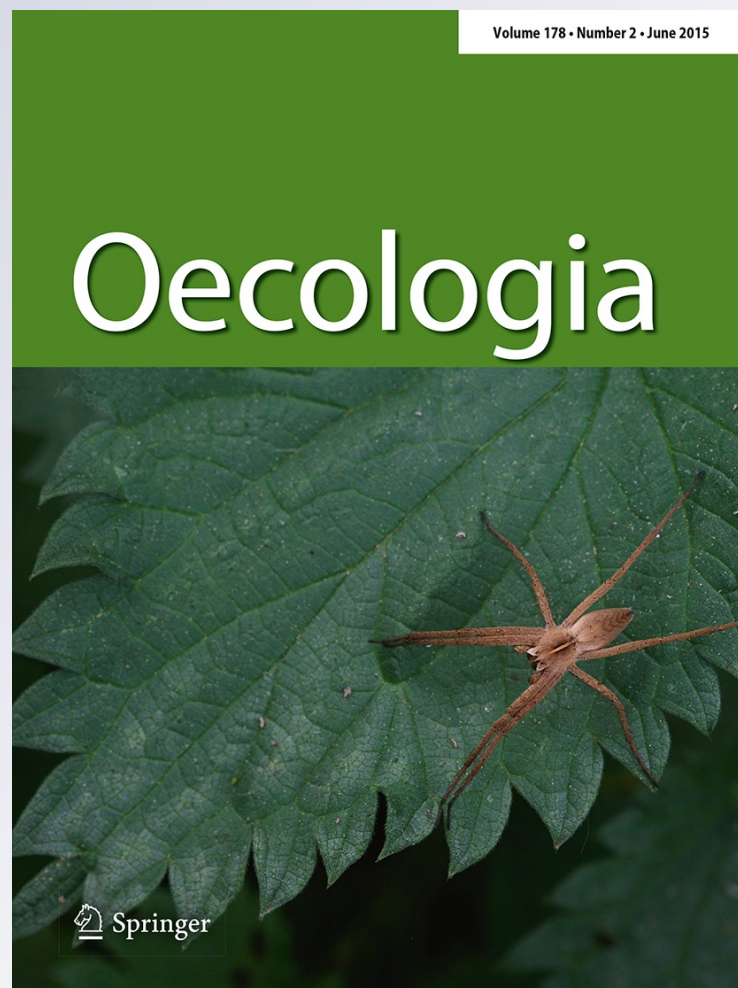
ISSN 0029-8549

Volume 178

Number 2

Oecologia (2015) 178:403-414

DOI 10.1007/s00442-015-3224-7



 Springer

Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Impact of intra- versus inter-annual snow depth variation on water relations and photosynthesis for two Great Basin Desert shrubs

Michael E. Loik · Alden B. Griffith · Holly Alpert ·
Amy L. Concilio · Catherine E. Wade ·
Sharon J. Martinson

Received: 16 July 2014 / Accepted: 12 January 2015 / Published online: 28 January 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract Snowfall provides the majority of soil water in certain ecosystems of North America. We tested the hypothesis that snow depth variation affects soil water content, which in turn drives water potential (Ψ) and photosynthesis, over 10 years for two widespread shrubs of the western USA. Stem Ψ (Ψ_{stem}) and photosynthetic gas exchange [stomatal conductance to water vapor (g_s), and CO_2 assimilation (A)] were measured in mid-June each year from 2004 to 2013 for *Artemisia tridentata* var. *vaseyana* (Asteraceae) and *Purshia tridentata* (Rosaceae). Snow fences were used to create increased or decreased snow depth plots. Snow depth on +snow plots was about twice that of ambient

plots in most years, and 20 % lower on –snow plots, consistent with several down-scaled climate model projections. Maximal soil water content at 40- and 100-cm depths was correlated with February snow depth. For both species, multivariate ANOVA (MANOVA) showed that Ψ_{stem} , g_s , and A were significantly affected by intra-annual variation in snow depth. Within years, MANOVA showed that only A was significantly affected by spatial snow depth treatments for *A. tridentata*, and Ψ_{stem} was significantly affected by snow depth for *P. tridentata*. Results show that stem water relations and photosynthetic gas exchange for these two cold desert shrub species in mid-June were more affected by inter-annual variation in snow depth by comparison to within-year spatial variation in snow depth. The results highlight the potential importance of changes in inter-annual variation in snowfall for future shrub photosynthesis in the western Great Basin Desert.

Communicated by David A. Pyke.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3224-7) contains supplementary material, which is available to authorized users.

M. E. Loik (✉) · A. B. Griffith · H. Alpert · A. L. Concilio ·
C. E. Wade · S. J. Martinson
Department of Environmental Studies, University of California,
1156 High Street, Santa Cruz, CA 95064, USA
e-mail: mloik@ucsc.edu

Present Address:

A. B. Griffith
Environmental Studies Department, Wellesley College, Wellesley,
MA 02481, USA

Present Address:

H. Alpert
Inyo-Mono Integrated Regional Water Management Program,
Mammoth Lakes, CA 93546, USA

Present Address:

A. L. Concilio
Institute of Arctic and Alpine Research, University of Colorado,
Boulder, CO 80309, USA

Keywords Antelope bitterbrush · Climate change · Sagebrush · Soil water · Water potential

Introduction

Precipitation patterns have changed for many regions of the USA since the early 1900s (Groisman et al. 2004; Vorosmarty and Sahagian 2000), and many general circulation models (GCMs) envision that terrestrial ecosystems will continue to experience altered precipitation patterns as a result of climate change (Hayhoe et al. 2004; Mearns et al. 1995). The relationships between the coupled atmosphere–ocean system and weather fronts that deliver snow to terrestrial ecosystems are not well understood (Saito et al. 2004); however, it is likely that wintertime snow climate and ecology will be particularly impacted by a warmer

atmosphere resulting from the accumulation of anthropogenic greenhouse gases (Lapp et al. 2005; Woo and Marsh 2005; Zierl and Bugmann 2005).

Climate changes that alter the amount of snowfall, snow depth, and the timing of snow melt will affect the composition and productivity of terrestrial vegetation (Jackson et al. 2001; Weltzin et al. 2003). Although there is an increasing understanding of how precipitation patterns drive plant and ecosystem processes (Breshears et al. 1997; Schwinning and Sala 2004), responses to snow climate are more complex compared to rain. For example, pulses of snowfall do not directly translate into soil moisture the same way that rainfall pulses do, largely because of the time lag between snowfall, snowmelt, and soil water infiltration (Loik et al. 2004a, b). Also, the snowpack undergoes multiple forms of mass and energy transitions over time, resulting in the loss of snow pack water to evaporation, ephemeral melt events, and sublimation (Cayan et al. 2001; Essery et al. 2003; Marks and Dozier 1992; Murray and Buttle 2005). As a result, plant responses to climate changes that affect snow depth and soil moisture cannot simply be assumed to be the same as plant responses to changing rainfall magnitude.

The ability to test ecological hypotheses of responses to altered precipitation is limited by the resolution and uncertainty within climate models (MacCracken et al. 2003; Miller et al. 2003). Although many climate model simulations suggest that the amount and seasonality of precipitation will change across the western USA within the next 50–100 years (MacCracken et al. 2003), the magnitude, timing, and even the sign (positive or negative) of the change, vary widely across models. For example, the Canadian Climate Model and the Hadley Climate Model GCM version 2 (HadCM2) predict that the location of our research site in eastern California, USA may receive 80–100 % more winter (December, January, February; DJF) precipitation by 2090–2099 in comparison to 1961–1990 (VEMAP Members 1995). Climate scenarios generated using the PCM, GFDL2.1, and HadCM3 models suggest reductions in Sierra Nevada snow pack by 30–90 % for the late twenty-first century (Hayhoe et al. 2004). More recently, downscaled climate model products have been generated utilizing ensemble approaches, such as in the Coupled Modeling Intercomparison Project (i.e., CMIP3 and CMIP5), which show changes from 8 % lower to over 50 % higher DJF precipitation (Table 1) in 2099 compared to the 1961–1990 baseline (Meehl et al. 2005, 2007; Taylor et al. 2012). It is unknown how changes in snowfall magnitude and timing will translate into altered snow pack depth, metamorphosis, and soil water availability (Loik et al. 2004a). Thus, it can be difficult to design effective experiments to better understand how changes in snow climate will affect plant processes when there are so many climate scenarios to consider.

Table 1 Range of percent change in annual or winter (December, January, February) precipitation for Mammoth Lakes, California determined by 16 general circulation models (GCM) using the Special Report on Emissions Scenarios A2 (high emission) for 1950–2099 in comparison to 1961–1990

GCM	Annual (%)	Winter (%)
BCCR-BCM2_0.1	0 to –8	0 to –4
CGCM3.1(T47)	–4 to +4	–4 to +4
CNRM-CM3	0 to –8	+8 to +12
CSIRO	0 to +4	0 to +8
ECHAM5 MPI-OM	0 to +8	+4 to +12
ECHO-G	–4 to –12	0 to –8
GFDL-CM2.0	–4 to –12	0 to +4
GFDL-CM2.1	–4 to –12	0 to –4
GISS-ER	0 to –8	–4 to +4
INM-CM3.0	+8 to +16	+8 to +16
IPSL-CM4.1	+17 to +25	>+50
MIROC3.2	–4 to –8	0 to –12
MRI CGCM2 3.2	+8 to +16	+8 to +16
NCAR CCSM3	–4 to –12	–4 to +4
NCAR PCM	–4 to +4	0 to –4
UKMO-HadCM3	–4 to –8	–4 to 0

Data were downscaled from the World Climate Research Programme's Coupled Model Intercomparison Project (CMIP) multi-model ensemble (Meehl et al. 2007) using a bias-correction spatial method to a 0.5° grid (Maurer et al. 2007), based on 1950–1999 data (Adam and Lettenmaier 2003)

Only a few experimental studies have tested the long-term effects of different magnitude or signs of precipitation change on physiological C and water fluxes, especially in response to changes in wintertime snow depth in high-elevation or high-latitude ecosystems (Walker et al. 1999; Loik et al. 2013). Microscale variation in snow depth and snow bank persistence helps to determine plant population patterns and photosynthetic productivity in these regions (Galen and Stanton 1993, 1995; Harte and Shaw 1995; Loik et al. 2004b; Price and Waser 1998; Walker et al. 1993, 1995; Yamagishi et al. 2005). For example, the earlier onset of melting driven by experimental infrared warming in the Rocky Mountains, Colorado causes certain species to be vulnerable to a longer drought in the subsequent summer, which can affect fitness (Lambrech et al. 2007; Saavedra et al. 2003; Shaw et al. 2000). In this study, we compared how stem water potential (Ψ_{stem}) and leaf-level photosynthetic processes [i.e., stomatal conductance to water vapor (g_s) and CO_2 assimilation (A)] for two widespread Great Basin Desert shrub species were affected by snow depth manipulations that both increased and decreased snow depth at amounts consistent with CMIP3 and CMIP5 outputs (Maurer et al. 2002, 2007; Meehl et al. 2007; Taylor et al. 2012). The objective of this study was

to assess how Ψ_{stem} and photosynthesis would respond to spatial experimental manipulations of snow depth within years in comparison to inter-annual variation in snow depth over 10 years. We conducted measurements at various time scales across multiple years because responses in single years may be very different than what can be resolved over inter-annual time scales. We employed snow fences established in the 1950s to simulate increased and decreased snow depth regimes similar to those for winter (DJF) envisioned by 16 downscaled climate model products (Table 1). Our study was based upon the assumption that differences in snow depth across time (10 years of inter-annual snowfall variation) or space (due to snow fences) would alter soil moisture availability following snow melt, plant uptake of water, leaf-level g_s , and photosynthetic CO_2 uptake. Our study site is typical of range and forest lands of the western US from the shrubland/forest ecotones of the eastern slopes of the Cascades and Sierra Nevada, across the Intermountain semideserts/deserts, the Nevada/Utah ranges, the Colorado Plateau, and the western slope of the Rocky Mountains. The co-dominant shrub species at our site—*Artemisia tridentata* and *Purshia tridentata*—have geographically widespread distributions covering about 1.37×10^8 ha across the region. Therefore, understanding the impacts of snow climate change on photosynthetic processes can improve models of C dynamics for cold, snow-dominated high-elevation arid and semi-arid shrub lands.

We tested the hypotheses that:

1. Soil moisture content in spring would be higher on research plots with greater antecedent winter snow depth—and lower on plots with reduced snow depth—compared to ambient-depth plots (referred to as “within-year spatial differences in snow depth”).
2. Differences in soil water availability would result in higher plant Ψ_{stem} and photosynthesis (g_s and A) for increased-depth plots, with opposite patterns for decreased-depth plots.
3. Seasonal patterns of Ψ_{stem} and photosynthetic gas exchange would become minimal on all plots during late summer following soil drying.
4. The effects of snow depth on soil water content, plant Ψ , and photosynthesis, would track inter-annual variation in ambient snowfall.

Materials and methods

Study site

Experiments were conducted at the ecotone between the Great Basin Desert shrub steppe and Sierra Nevada conifer forest near Mammoth Lakes, Mono County, California

(37°38'54"N, 118°58'19"W, 2,400 m a.s.l.). Besides the co-dominant shrubs *Artemisia tridentata* var. *vaseyana* and *P. tridentata*, other vegetation includes *Achnatherum thurberianum* (Poaceae) (Roemer and Schulties) Barkworth, *Elymus elemoides* (Poaceae) (Raf.) Swezey, *Eriogonum spergulinum* (Polygonaceae) Gray, *Carex* spp. (Cyperaceae), *Leptodactylon pungens* (Polemoniaceae) (Torrey) Rydb., *Gayophytum diffusum* (Polygonaceae) Torrey and A. Gray, and *Lupinus lepidus* (Fabaceae) [= *L. brewerii* A. Gray]. The conifers *Pinus contorta* (Pinaceae) Loudon and *Pinus jeffreyi* (Pinaceae) Grev. and Balf. occur sparingly throughout the sites.

The soils are derived from glacial and alluvial deposits, but primarily from volcanic material; soils are characterized as belonging to the Cozetica, Vitrandic Xerorthent, Cryopsammet, Haypress, and Torriothentic Haploxeroll families (Seney and Gallegos 1995). The soils at both 40 and 100 cm are loamy coarse sands; root mass between 0- and 40-cm depth is about 1.1 g (dry weight) m^{-2} and about 20 % of that at 100 cm. There are no restrictive petrocalcic layers in the soil above 100- to 150-cm depth at each of the snow fence sites (Seney and Gallegos 1995). The soils at all study sites have high rates of infiltration [15–50 cm h^{-1} (Loik 2007)], and gas and water permeability, and very little surface flow has been observed.

Experimental design

We statistically compared the variation in response variables (i.e., Ψ_{stem} , g_s , and A) as a function of three snow depth treatments: increased snow depth (+snow), decreased snow depth (–snow), and unmanipulated (ambient) snow depth. We monitored responses in the second and third week of June each year between 2004 and 2013, which is about 4–6 weeks following snowmelt depending on the ambient amount of snow each year. We also measured Ψ_{stem} , g_s , and A seasonally from May to September 2005.

Snow depth was manipulated by disrupting the prevailing wintertime laminar wind flow using snow fences that create an equilibrium snow drift (Tabler 1974). Snow fences create distinct spatial footprints of increased and decreased snow depth on the lee side of the fence, independent of the amount of ambient snow fall in a particular year (i.e., the location of increased and decreased snow depth is consistent from year to year).

Research plots were established in February 2003 on either side of eight snow fences situated adjacent to US Highway 395 in the Inyo National Forest, Mono County, California. The snow fences were installed by the California Department of Transportation (Caltrans) in the 1950s as part of road snow control efforts on US Highway 395. The snow fences occur over a 50-km transect along the west side of US Highway 395 from southeast of Mammoth

Lakes to east of June Lake, California. The fences are oriented approximately north–northwest to east–southeast, generally parallel to the direction of US Highway 395 at each site and generally perpendicular to the prevailing wind direction in winter. The fences range from 100 to 200 m away from the ditch of the highway. The snow fences are of the “Wyoming” type, 4 m in height, and 50 % in porosity (Tabler 1974). The fences vary from 100 to over 200 m in length; we selected our 100-m-long research plots (see below) so that they were located on relatively flat terrain, and at locations where adjacent fences do not overlap one another. There has been no mowing or brush control along the fences, and the fences are maintained annually by Caltrans. Maintenance is conducted via access roads located at the immediate base of the fence on the upwind base of each fence, where least damage to research plots could occur.

Based on snow depth patterns measured in January 2003 (and subsequently confirmed annually), we established for each snow fence a +snow, -snow, and ambient depth plot. Snow depth was measured on haphazardly assigned transects perpendicular to the snow fence. The transect ran from 50 m west (upwind) of the snow fence to -70 m east (downwind) of the fence. Snow depth was measured at 1-m intervals along the transect using snow poles in the first week of February each year (Loik et al. 2013). Each plot is 5 m wide \times 100 m long; the long axis of each plot is parallel to the snow fence. The ambient depth plots are centered 50 m upwind of the snow fences, the +snow plots are centered at the maximum measured snow depth 13 m downwind of the fences, and the -snow plots are located 70 m downwind of the fences where snow depth is ca. 80 % of the upwind ambient depth.

For each snow depth treatment plot, a line transect was established in the middle of the 5-m direction, for the length of the 100-m plot. Sites for repeated sampling were marked with rebar at 0, 25, 50, 75, and 100 m along the line transect. During each measurement campaign, Ψ_{stem} , g_s , and A were measured as described below for randomly selected individuals of the co-dominant shrubs *A. tridentata* and *P. tridentata* nearest to the rebar markers, resulting in a sub-sampling procedure for each transect and fence. These plants were permanently marked to facilitate repeated sampling from month to month and year to year. This approach resulted in a categorical comparison of response variables within a month, and repeated measurements across months and years (for further details, see “Data analysis”, below)

Meteorological data

Historic snow depths on 1 April for each year from 1928 to 2013 for this study site (Online Resource Fig. 1) were obtained from the California Data Exchange Center (<http://cdcc.water.ca.gov/index.html>). Daily precipitation (i.e.,

rain and melted snow water equivalents), snow fall, and snow depth for Mammoth Lakes were obtained from the National Climatic Data Center (www.ncdc.noaa.gov/oa/ncdc) for the period from June 2004 to July 2013. Downscaled CMIP3 and CMIP5 climate projections (Table 1) were obtained from http://gdo-dcp.ucllnl.org/downscales_cmip_projections/.

Soil moisture

Soil moisture for 2004 was measured gravimetrically in April for one sample for each treatment at each fence. In September 2004, one 20-cm-long Decagon ECH₂O dielectric aquameter probe (Decagon Devices, Pullman, WA) was buried vertically between 30- and 50-cm depths and another between 90- and 110-cm depths in each transect for all fences. ECH₂O probes were connected to RM5 data loggers set to record the voltage through the soil moisture probes at 12-h intervals from September 2004 up to and including May 2013.

Plant Ψ

Plant Ψ was measured during each measurement campaign in June for 2004–2013, and monthly from May to September 2005, for vegetative stems and leaves of *A. tridentata* and *P. tridentata*. Distal stem segments with spring leaves attached averaging 10 ± 3 cm in length were removed with small scissors from individuals at each repeated-measures sampling site (equaling five sub-samples from each plot), and placed in a plastic bag with a high internal relative humidity for transport from the plant to the pressure chamber. The time from sample removal to measurement was less than 15 min. Ψ was measured with a Scholander-type pressure chamber (3000 series; Soilmoisture Equipment, Santa Barbara, CA). Measurements of Ψ_{stem} were made between 0730 hours and noon local time. The order of plant sampling was randomly alternated among ambient, +snow, and -snow plots to avoid time-of-day bias; a preliminary analysis showed no time bias across this interval for either species. In June 2007, Ψ_{stem} was measured both pre-dawn and midday for both species across the three snow depth treatments for six of the snow fences.

Photosynthetic gas exchange

Photosynthetic gas exchange was compared for distal spring leaves (representing 2–3 cm of stem length) of *A. tridentata* and *P. tridentata* on ambient, +snow, and -snow plots for each of eight snow fences. Measurements were sub-sampled for five individuals of each species on ambient, +snow and -snow plots as described above. Leaves were spread out to minimize overlap, but measurements

represent projected area. Measurements occurred at the same time of day, season, and year as for Ψ measurements, but on different branches to minimize potential effects of stem removal on g_s and photosynthesis. Stems were marked with laboratory tape so that they could be photographed for computation of leaf area to correct gas exchange measurements (described below).

A and g_s were measured using a LI-6400 open-mode portable photosynthesis system (LI-COR, Lincoln, NE). Vapor pressure deficit within the chamber was maintained at pre-measurement ambient levels. The CO_2 concentration within the leaf measurement chamber was maintained at a constant level ($380 \mu\text{mol mol}^{-1}$) by scrubbing the incoming airstream with soda lime, and the subsequent addition of a precise amount of CO_2 via injection from an external cartridge. Photosynthetically active radiation (400–700 nm) within the chamber was maintained at $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ using LI-COR red-blue light-emitting diodes in the 2×3 -cm rectangular chamber. Leaf temperatures were recorded with a copper-constantan thermocouple pressed to the abaxial surface of the leaf within the cuvette. Distal, fully mature leaves were inserted into the cuvette at their natural branch orientation, and photosynthetic measurements were recorded when all stability criteria were met and the coefficient of variation (CV) for A and g_s combined was below 0.5 %. Usually, five to ten leaves were used at a time for both species because of their small size and arrangement on the branch.

The area of the leaves used for gas exchange measurements was determined by a digital photographic method. Branch ends used for gas exchange measurements were digitally photographed against a magenta background with a reference scale. Images were processed using Photoshop 7.0 (Adobe Systems, San Jose, CA) to highlight green photosynthetic tissue and to contrast it with non-photosynthetic stem portions of the image. Projected leaf area (cm^2) was then determined using Image J analysis software (Scion, Frederick, MD).

Data analysis

Shrub Ψ and photosynthetic gas exchange data were analyzed over the 10 years using a multivariate ANOVA (MANOVA). Repeated-measures effects (i.e., within-subjects effects) of time and the interaction between time and the snow depth treatment were examined using both MANOVA (Pillai's trace statistic was used for the interaction effect) and univariate ANOVA with the Greenhouse-Geisser adjustment. We rejected the null hypothesis when either the adjusted univariate or the multivariate test indicated a significant result (Looney and Stanley 1989; Quinn and Keough 2002). Data from the 0-, 25-, 50-, 75-, and 100-m sub-sampling sites of each transect were averaged

prior to all analyses. The Ψ data were log transformed to meet assumptions of normal distribution and heteroscedasticity. MANOVAs and univariate ANOVAs were conducted using JMP Pro (version 11.0.0; SAS Institute, Cary, NC).

Linear regression was used to determine the sensitivity of A and g_s measured in June of each year to maximal volumetric soil water content. Treatment averages (i.e., averaged across fences) for each species were plotted against values for the 10 years of the study. Regressions were fitted using SigmaPlot version 10 (Systat Software, Chicago, IL).

Results

Meteorology

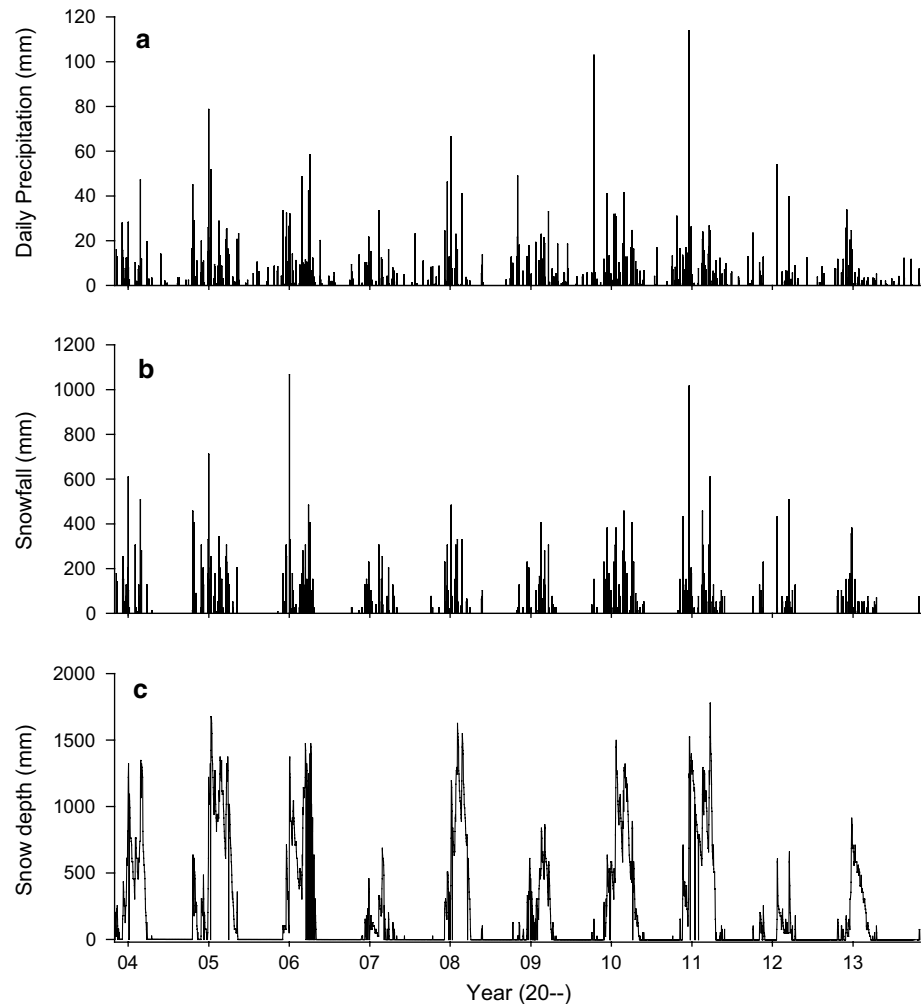
The high inter-annual variability of precipitation in this region is evident upon examination of detailed rain and snowfall patterns for the hydrologic years 2003/2004 to 2012/2013 (Fig. 1; a hydrologic year begins on 1 October for this region). First of October to 1 June cumulative precipitation varied from just over 300–850 mm across the 10 years of the study (Fig. 1a). The winter of 2006–2007 was the driest of the 10-year study period. By contrast, 2010–2011 was the highest snow fall winter of the 10-year study. In 6 of the 10 years, snow depth ranged from 100 to 150 cm; in other years it was around 50 cm, resulting in considerable inter-annual variation in snow depth (Fig. 1c). For the 1928–2013 period, 1 April snow depth measured in Mammoth Pass (elevation = 3,000 m a.s.l., about 25 km from the snow fence sites) averaged 136 cm with a CV of 48 % (Online Resource Fig. 1.)

Snow depth manipulation and soil moisture

The cumulative values for rain +snow precipitation in the interval from 1 October to 30 September varied from ca. 300 to 850 mm year^{-1} . The snow fence treatment was successful in altering snow depth, and the location of maximal and minimal snow depth zones was consistent for all winters between 2004 and 2013. Snow depth was always highest on +snow plots in all years (Fig. 2a), but in 2009 and 2012, there were no significant differences in snow depth when all three treatments were analyzed for all fences. Snow depth was higher on +snow compared to ambient and –snow plots for 5 of the 10 years (2005, 2007, 2008, 2011, and 2013.)

Maximal volumetric soil water content in May (i.e., following snow melt) generally reflected the inter-annual patterns of snow depth (Fig. 2b, c). Maximal water content at 40-cm depth (ca. 25 %) was greater than for 100-cm depth (maximal ca. 15 %). In 2006, 2008 and 2011, soil water content at 40-cm depth was higher on +snow plots

Fig. 1 Precipitation for the hydrologic years 2004–2013. **a** Total precipitation per event (vertical bars). **b** Snowfall per precipitation event. **c** Snow depth. Data were obtained from the Mammoth US Forest Service Ranger Station (via the National Climatic Data Center)



and lowest on –snow plots. For the 100-cm depth, there were no differences in soil water content across snow depth treatments for all years except 2011.

Plant Ψ_{stem}

Pre-dawn Ψ_{stem} measured in June 2007 was about -0.80 MPa for both species (Fig. 3a, d). During midday in June 2007, there were significant differences when the two species were compared (*P. tridentata* was lower; $F = 6.86$, $P = 0.04$) and there were marginally significant differences across the snow depth treatments (–snow lower; $F = 2.84$, $P = 0.10$). Midday Ψ_{stem} averaged -1.60 and -1.75 MPa across seasons for *A. tridentata* and *P. tridentata*, respectively, in June 2007. Between snow melt in May and the beginning of September 2005 (Fig. 3b, e), mean midday Ψ_{stem} decreased by about 1.0 MPa for *A. tridentata* on –snow plots, and by only 0.5 MPa for plants from ambient and +snow plots; similar patterns were observed for *P. tridentata*. Across the months of 2005, there were no significant differences in Ψ_{stem} due to snow treatment

until September, when values for plants on –snow plots were lower than for those on +snow and ambient plots ($F = 8.19$, $P < 0.01$).

Over the 10-year study period, Ψ_{stem} was lowest in 2004, and was rather constant between 2005 and 2013 (Fig. 3c, f). In general, shrubs on +snow plots tended to have the highest Ψ_{stem} and –snow plots tended to have the lowest Ψ_{stem} . The effect of time was significant for *A. tridentata* (MANOVA, $F = 115.6$, $P < 0.0001$; univariate, $P = 27.8$, $P < 0.0001$), but there were no significant within-year effects of the snow depth treatments on Ψ_{stem} (Table 2; Fig. 3c). However, for *P. tridentata* there were significant effects of both snow depth treatment and time on Ψ_{stem} (Table 2; Fig. 3f).

Photosynthetic gas exchange

The patterns of g_s and A from 2004 to 2013 reflected the inter-annual patterns of snow depth for both *A. tridentata* and *P. tridentata* (Fig. 4). g_s ranged from about 0.10–1.00 mol m⁻² s⁻¹ for both species between 2004 and 2013

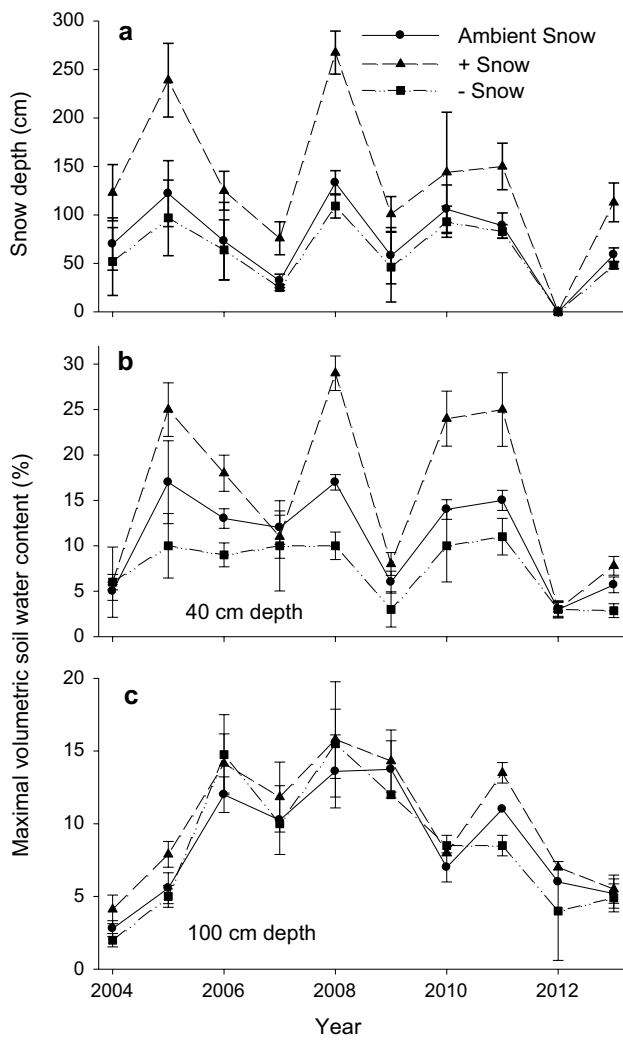


Fig. 2 **a** Snow depth on ambient (circles), increased (+Snow; triangle), and decreased snow depth (–Snow; squares) research plots. **b** Mean volumetric soil moisture content at 40-cm depth in May, from 2004 up to and including 2013. **c** Mean volumetric soil moisture content at 100-cm depth in May, from 2004 up to and including 2013. Data are mean \pm 1 SD for $n = 6$ snow fences per transect

(Fig. 4a, c). For the 10-year period, g_s for *A. tridentata* averaged $0.30 \text{ mol m}^{-2} \text{ s}^{-1}$ with a CV of 69 %. Mean g_s for *P. tridentata* was $0.38 \text{ mol m}^{-2} \text{ s}^{-1}$ (CV = 63 %). There were significant differences in g_s over the 10-year time period for both species (*A. tridentata* MANOVA $F = 59.0$, $P = 0.017$, univariate $F = 59.0$, $P < 0.0001$; *P. tridentata* MANOVA $F = 42.3$, $P = 0.023$, univariate $F = 33.5$, $P < 0.0001$) but no differences due to within-year snow depth treatments (nor any interactions; Table 2).

A varied about tenfold for *A. tridentata* and by 3.5 times for *P. tridentata* between dry and wet years (Fig. 4b, d). A averaged $10.72 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *A. tridentata* with a CV of 74 % from 2004 to 2013, and about $18.2 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *P. tridentata* (CV = 55 %). There

were significant differences in A for *A. tridentata* for both within-year snow depth treatment ($F = 4.20$, $P = 0.05$) and time (MANOVA, $F = 735$, $P = 0.001$; univariate, $F = 54$, $P < 0.0001$), but the interaction terms were not significant (Table 2). For *P. tridentata*, there were significant differences in A related to time (MANOVA, $F = 79.9$, $P = 0.012$; univariate, $F = 110$, $P < 0.0001$) but no within-year effects of snow depth treatments.

Both species exhibited pronounced seasonal increases in g_s and A in all treatments between May and September 2005 following the relatively wet winter of 2004–2005 (Online Resource Fig. 2). g_s increased steadily for both species and for all treatments from May to July 2005, and then decreased somewhat by September (Online Resource Fig. 2A, C). There were no significant differences in g_s due to snow depth treatment over this seasonal comparison. For *A. tridentata*, the net increase in A over the 4 months was about fourfold for plants on ambient-depth plots, and about 2.5-fold for plants on +snow and –snow plots (Online Resource Fig. 2B). Assimilation increased by a factor of about five for all treatments over the same period for *P. tridentata* (Online Resource Fig. 2D).

Discussion

Our results showed that inter-annual differences in snow depth resulted in significant effects on Ψ_{stem} , g_s , and A for both of these widespread, deeply rooted shrubs species of the Great Basin Desert. By contrast, there were minimal within-year effects of the spatial snow depth treatments caused by the snow fences, except for A for *A. tridentata* and Ψ_{stem} for *P. tridentata*. Soil moisture content in spring generally reflected within-year spatial differences in snow depth across treatments (ambient, +snow and –snow depths) in winter, consistent with hypothesis 1 (Figs. 1, 2). Soil water content mirrored inter-annual patterns of snow depth for the 10-year study period 2004–2013 (Fig. 2a, b) although differences between within-year spatial snow depth treatments (especially ambient and –snow) were not always distinct. However, the 20 % reduction in snow depth on –snow plots is quite consistent with outlooks derived from 16 downscaled climate models for altered DJF precipitation for this region (Table 1). Differences in soil water content were more pronounced at 40-cm compared to 100-cm depth in the soil for both snow depth treatments and years (Fig. 2b, c), and there were marginally significant differences in midday Ψ_{stem} across treatments (Fig. 3a, d), thus support for hypothesis 2 is equivocal. We hypothesized that g_s and A would decrease by the end of the summer (hypothesis 3) but in fact they were still quite substantial in September 2005; Ψ_{stem} , g_s , and A were not significantly different across snow depth treatments between May and

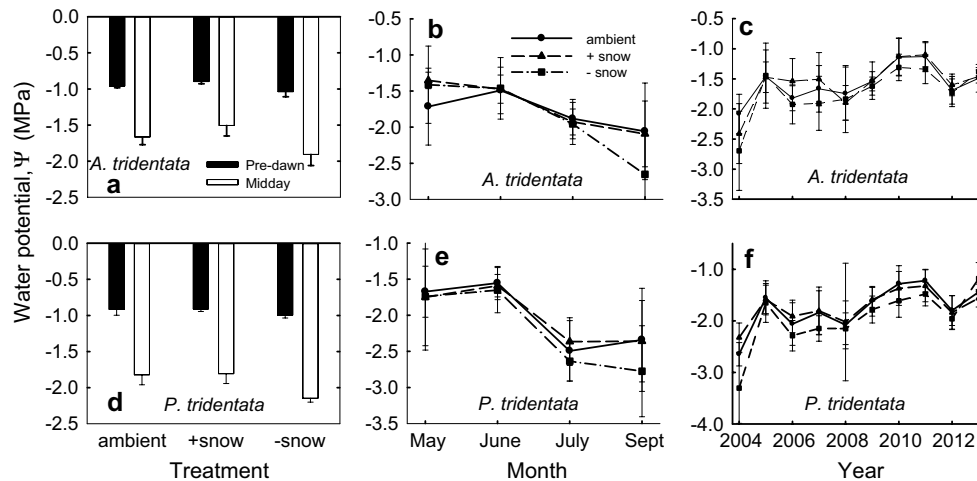


Fig. 3 Stem water potential (Ψ_{stem}) for *Artemisia tridentata* and *Purshia tridentata*. **a–d** Pre-dawn (open bars) and midday (filled bars) Ψ_{stem} . **b–e** Seasonal Ψ_{stem} from May up to and including September 2005 for plants sampled on ambient (circles), +snow (triangles),

and –snow (squares) plots. **c–f** Inter-annual Ψ_{stem} , measured in June 2004–2013. **a–f** Data are means \pm 1 SD, $n = 6$ snow fences. For abbreviations, see Fig. 2

September 2005 (Online Resource Fig. 2). Overall, results suggest that early summer Ψ and photosynthesis for both species respond more to inter-annual rather than intra-annual (spatial) variation in snow depth and soil moisture.

This region exhibits large variation in inter-annual snowfall (CV = 48 %) as evidenced by decadal records collected near our study site (Online Resource Fig. 1). Variation in shrub Ψ_{stem} across time scales was relatively minor, compared to the variation in snow fall, snow depth, and soil moisture. Although pre-dawn Ψ values were only about -1.00 MPa, and higher than for midday measurements, there were only marginal effects of snow depth on Ψ_{stem} . Ψ decreased slightly over the spring and to the end of the summer of 2005 for both species, but with no significant differences across treatments. These results suggest that the roots of both *A. tridentata* and *P. tridentata* had access to soil moisture for several months following snow melt, resulting in minimal stomatal limitations to photosynthesis. It is possible that relatively small amounts of snow are able to fully saturate the highly porous soil column at this site; soil moisture was maximal (ca. 25 %) at 40-cm and ca. 15 % at 100-cm depth in the wettest years, but the relationship between snow depth and soil moisture was not consistent between treatments and across years. It has been well demonstrated that *A. tridentata* is capable of appreciable movement of soil moisture from deep to shallow soil layers (Leffler et al. 2005; Naumburg et al. 2005; Ryel et al. 2004). Moreover, this species has a pattern of root growth and activity that progresses into deeper soils as the surface layers dry (Peek et al. 2005; Ryel et al. 2004). Our values of Ψ_{stem} for *A. tridentata* were somewhat higher than reported by others in different locations (Evans and Black

1993; Kolb and Sperry 1999; Shaw et al. 2000; Ryel et al. 2003), possibly due to microclimatic and soil texture differences across the large geographic distribution of this species. And, our study site generally receives more summer rainfall (but after the mid-June gas exchange measurement times in this study) than the eastern Great Basin Desert. Less is known about the water relations of *P. tridentata* (Young and Clements 2002), but this species rapidly responds to summer rainfall treatments, indicating summertime root activity near the surface when soil water is available (Loik 2007). In the present study *P. tridentata* had Ψ and seasonal assimilation patterns that suggest it may also access deep water. There was surprisingly little inter-annual variation in Ψ_{stem} across years for either species, despite the large variation in ambient snow fall and snow depth over the 10-year period. In fact, the CV for Ψ_{stem} was 19.5 % by contrast to a fivefold difference in snow depth and soil moisture variation over the 10-year period.

Based on established relationships between precipitation and plant production (Huxman et al. 2004; Knapp and Smith 2001), increasing or reducing snow depth and soil water availability should have caused a significant change in water relations and photosynthesis. Yet, our results showed that leaf-level photosynthesis did not exhibit significant within-year responses to the spatial differences in snow depth caused by the snow fences (except for *A* for *A. tridentata* and Ψ_{stem} for *P. tridentata*). One potential reason for the minimal within-year response is that there may be a confounding effect of soil water availability with the start of the growing season. Any advantages afforded by higher soil moisture availability on +snow plots may be offset by a later melt date (Harte and Shaw 1995). Likewise, leaf N

Table 2 Repeated-measures multivariate ANOVA (MANOVA) and univariate tests of the effects of snow depth (*Treatment*), time (2004–2013), and the treatment × time interactions on stem water potential (Ψ_{stem} ; MPa), stomatal conductance to water vapor (g_s ; $\text{mmol m}^{-2} \text{s}^{-1}$) and leaf-level CO_2 assimilation (A ; $\mu\text{mol m}^{-2} \text{s}^{-1}$)

Response	Effect	Test ^a	<i>F</i>	Num. <i>df</i>	Den. <i>df</i>	<i>P</i>
<i>Artemisia tridentata</i>						
Ψ_{stem}	Treatment	M	1.8005	2	15	0.1991
	Time	M	115.5863	9	7	<0.0001
	Time	UGG	27.84	3.9783	59.675	<0.0001
	Time × treatment	MPT	1.0876	18	16	0.4362
	Time × treatment	UGG	1.1145	7.9566	59.675	0.3667
g_s	Treatment	M	0.565	2	10	0.5855
	Time	M	58.9504	9	2	0.0168
	Time	UGG	59.0411	3.0739	30.739	<0.0001
	Time × treatment	MPT	0.9139	18	6	0.5969
	Time × treatment	UGG	0.9331	6.1478	30.739	0.4871
<i>A</i>	Treatment	M	4.1976	2	10	0.0475
	Time	M	735.3927	9	2	0.0014
	Time	UGG	53.9365	3.7246	37.246	<0.0001
	Time × treatment	MPT	1.3178	18	6	0.3888
	Time × treatment	UGG	1.9231	7.4492	37.246	0.0896
<i>Purshia tridentata</i>						
Ψ_{stem}	Treatment	M	13.0742	2	15	0.0005
	Time	M	150.6391	9	7	<0.0001
	Time	UGG	0.4382	3.9441	59.162	<0.0001
	Time × treatment	MPT	1.315424	18	16	0.1438
	Time × treatment	UGG	0.438239	7.8883	59.162	0.5917
g_s	Treatment	M	0.9655	2	10	0.4136
	Time	M	42.2671	9	2	0.0233
	Time	UGG	33.4677	1.6387	16.387	<0.0001
	Time × treatment	MPT	1.3238	18	6	0.3864
	Time × treatment	UGG	1.1702	3.2774	16.387	0.3542
<i>A</i>	Treatment	M	0.292	2	10	0.7529
	Time	M	79.8837	9	2	0.0124
	Time	UGG	110.1919	4.2932	42.932	<0.0001
	Time × treatment	MPT	0.7572	18	6	0.7016
	Time × treatment	UGG	2.3181	8.5865	42.932	0.0335

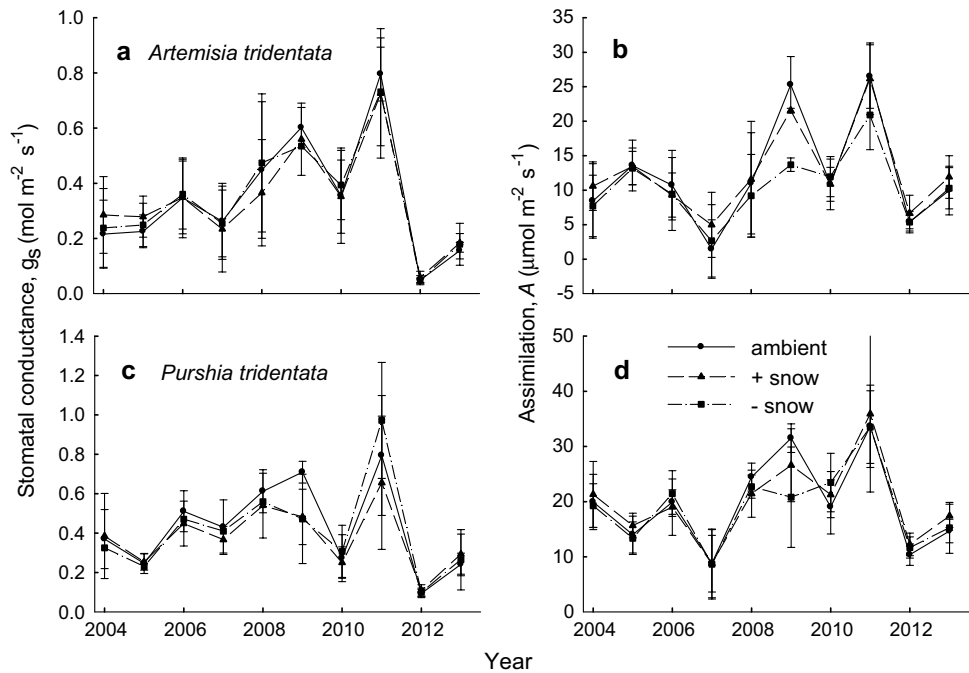
Values in italics are significant at $p < 0.05$ or less
 Num. *df* is the *df* in the numerator of the *F*-ratio, *den. df* is the *df* in the denominator of the *F*-ratio
^a Refers to MANOVA (*M*), univariate Greenhouse–Geisser adjusted (*UGG*), or MANOVA Pillai's trace (*MPT*)

content, and instantaneous conditions of air temperature and vapor pressure deficit may have confounded leaf-level photosynthetic responses to snow depth and soil moisture or otherwise shifted photosynthesis from stomatal to biochemical limitations (Leffler and Caldwell 2005; Leffler et al. 2004). It is possible that plants on the different plots are at different phenological stages based on melt timing, but we have not measured the potential differences in photosynthesis, leaf or flower production in relation to melt date over time. Also, some aspects of these shrubs (e.g., root depth) may have acclimatized over the ca. 50-year history of the snow fences to the effect of snow depth treatments on soil moisture availability (Atkin et al. 2000; Limousin et al. 2013; Luo et al. 2001). These shrubs are deeply rooted and can utilize soil water to 2- to 3-m depth (Caldwell et al. 1998; Peek et al. 2005; Ryel et al. 2004)

though our measurements of soil moisture only extended to 100-cm depth. Inter-annual variability in snow depth at our study site ($\text{CV} = 48\%$ for 1928–2013) is higher than for inter-annual precipitation variability for other arid sites of the western US (Knapp and Smith 2001; Loik et al. 2004a), so there may be some carry-over of deep soil moisture between high- and low-snowfall years.

Our results showed minimal effects of within-year spatial variation in snow depth on water relations and photosynthetic gas exchange, but snow fences can still be used to yield informative experiments. Our prior work (Loik et al. 2013) showed that above-ground cover for *P. tridentata* decreased while cover and biomass increased for several species of grasses and sedges. We also showed significant effects of both snow depth increases and decreases on annual tree ring increments for *Pinus jeffreyi*,

Fig. 4 **a, c** Stomatal conductance to water vapor and **b, d** photosynthetic CO₂ assimilation in mid-June 2004–2013 for plants sampled on ambient (circles), +snow (triangles), and –snow (squares) plots. Data are means \pm 1 SD, $n = 6$ snow fences for *A. tridentata* (**a, b**) and *P. tridentata* (**c, d**). For abbreviations, see Fig. 2



accumulation of dead woody debris, and total soil C (Loik et al. 2013). We have observed no significant differences in leaf area, leaf area index, leaf mass or shrub size for either of the shrub species across treatments or years (unpublished data, M. E. Loik). Therefore, the patterns we show here for Ψ and photosynthesis within and between years do not help to explain the previous community-level responses (Loik et al. 2013.) However, we have found considerable differences in seedling recruitment for both species (unpublished data, M. E. Loik), which may help explain aforementioned patterns of cover and biomass (Loik et al. 2013).

Numerous other studies have utilized snow fences to assess impacts of snow depth and melt timing on ecological patterns and processes (Sturges 1989; Walker et al. 1999). For some of these studies, increased snow depth caused earlier snow accumulation in autumn, longer snowpack duration (later melting), and warmer soil surface temperatures in winter, compared to sites with decreased snow (Walker et al. 1999). The snow accumulation and melt effects are similar at our site. Changes in species composition and canopy roughness have been documented for snow accumulation zones downwind from snow fences in a New Zealand alpine ecosystem (Smith et al. 1995). Likewise, snow fences along Interstate 80 in Wyoming have been shown to cause reduced plant diversity, growth, and cover (Perryman et al. 2000). Snow fences at Toolik Lake, Alaska and Niwot Ridge, Colorado resulted in increased plant growth, soil CO₂ flux, and system C loss in response to increased snow depth and soil warming (Walker et al. 1999). We have

also found changes in plant cover, invasive species, tree establishment and growth, and soil C associated with snow fences at this high-elevation, cold, semi-arid location in eastern California (Alpert and Loik 2013; Concilio and Loik 2013; Concilio et al. 2013; Griffith et al. 2010; Griffith and Loik 2010; Loik et al. 2013). Overall, these results from multiple locations and ecosystems highlight a variety of individual, community, and ecosystem consequences of altered snow depth in snow-dominated habitats.

Our results suggest that leaf-level photosynthesis for both of these widespread shrub species of the Great Basin Desert will be affected by climate changes that alter inter-annual variation in winter snow depth in the future. Based on 10-year sliding means and CVs, there have been no changes in 1 April snow depth variability between 1928 and 2013 (Online Resource Fig. 1). However, increases in inter-annual snow depth variability, earlier snow melt timing, or multi-year droughts may significantly affect leaf-level photosynthesis and C cycling in the future. Moreover, we focused on the physiological responses of established adults, whereas the responses of seedling recruitment and adult mortality (cf. Loik et al. 2013) may be more important for changes in C cycling patterns and processes in response to altered snow climate for this ecosystem in the future.

Author contribution statement ML designed the study; ML, AG, HA, AC, CW and SM performed measurements. ML and AG conducted statistical analyses. ML, AG, HA, AC, CW and SM wrote the paper.

Acknowledgments We thank the Student Challenge Awards Program (SCAP) of Earthwatch, and the M. Theo Kearney Foundation for Soil Science for financial support. This research was also supported by the US Department of Energy's Office of Science (Biological and Environmental Research) through the Western Regional Center of the National Institute for Climatic Change Research at Northern Arizona University (Merriam-Powell Center 35UZ-01). We thank the staff of the Valentine Eastern Sierra University of California Natural Reserve for housing and other logistics. The enthusiastic assistance of David T. Tissue, Lisa Patrick Bentley, Rosa Schneider, Lucy Lynn, Jack Rusk, Charles Weiss, and numerous Earthwatch SCAP volunteers helped make this research possible. We acknowledge the modeling groups, the Program for Climate Model Diagnosis and Intercomparison and the World Climate Research Programme (WCRP) Working Group on Coupled Modelling for their roles in making available the WCRP CMIP3 and CMIP5 multi-model data set. Support for these data sets is provided by the Office of Science, US Department of Energy. For CMIP the US Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals.

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

References

- Adam JC, Lettenmaier DP (2003) Adjustment of global gridded precipitation for systematic bias. *J Geophys Res Atmos* 108:1984–2012:108
- Alpert H, Loik ME (2013) *Pinus jeffreyi* establishment along a forest–shrub ecotone in eastern California, USA. *J Arid Environ* 90:12–21. doi:10.1016/j.jaridenv.2012.09.017
- Atkin OK, Holly C, Ball MC (2000) Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant Cell Environ* 23:15–26
- Breshears DD, Rich PM, Barnes FJ, Campbell K (1997) Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecol Appl* 7:1201–1215
- Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161
- Cayan DR, Kammerdiener SA, Dettlinger MD, Caprio JM, Peterson DH (2001) Changes in the onset of spring in the western United States. *Bull Am Meteorol Soc* 82:399–415
- Concilio AL, Loik ME (2013) Elevated nitrogen effects on *Bromus tectorum* dominance and native plant diversity in an arid montane ecosystem. *Appl Veg Sci* 16:598–609. doi:10.1111/avsc.12029
- Concilio AL, Loik ME, Belnap J (2013) Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. *Glob Change Biol* 19:161–172
- Essery R, Pomeroy J, Parviainen J, Storck P (2003) Sublimation of snow from coniferous forests in a climate model. *J Clim* 16:1855–1864
- Galen C, Stanton ML (1993) Short-term responses of alpine butterflies to experimental manipulations of growing-season length. *Ecology* 74:1052–1058
- Galen C, Stanton ML (1995) Responses of snowbed plant-species to changes in growing-season length. *Ecology* 76:1546–1557
- Griffith AB, Loik ME (2010) Effects of climate and snow depth on *Bromus tectorum* population dynamics at high elevation. *Oecologia* 164:821–832
- Griffith AB, Alpert H, Loik ME (2010) Predicting shrub ecophysiology in the Great Basin Desert using spectral indices. *J Arid Environ* 74:315–326
- Groisman PY, Knight RW, Karl TR, Easterling DR, Sun BM, Lawrimore JH (2004) Contemporary changes of the hydrological cycle over the contiguous United States: trends derived from in situ observations. *J Hydrometeorol* 5:64–85
- Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community—results of a climate-warming experiment. *Science* 267:876–880
- Hayhoe K et al (2004) Emissions pathways, climate change, and impacts on California. *Proc Natl Acad Sci USA* 101:12422–12427
- Huxman TE et al (2004) Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654
- Jackson RB et al (2001) Water in a changing world. *Ecol Appl* 11:1027–1045
- Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484
- Lambrech SC, Shattuck AK, Loik ME (2007) Combined drought and episodic freezing effects on seedlings of low- and high-elevation subspecies of sagebrush (*Artemisia tridentata*). *Physiol Plant* 130:207–217
- Lapp S, Byrne J, Townshend I, Kienzle S (2005) Climate warming impacts on snowpack accumulation in an alpine watershed. *Int J Climatol* 25:521–536
- Leffler AJ, Caldwell MM (2005) Shifts in depth of water extraction and photosynthetic capacity inferred from stable isotope proxies across an ecotone of *Juniperus osteosperma* (Utah juniper) and *Artemisia tridentata* (big sagebrush). *J Ecol* 93:783–793
- Leffler AJ, Ivans CY, Ryel RJ, Caldwell MM (2004) Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow- vs. deep-soil water in a glasshouse experiment. *Environ Exp Bot* 51:9–19
- Leffler AJ, Peek MS, Ryel RJ, Ivans CY, Caldwell MM (2005) Hydraulic redistribution through the root systems of senesced plants. *Ecology* 86:633–642
- Limousin JM et al (2013) Regulation and acclimation of leaf gas exchange in a pinon–juniper woodland exposed to three different precipitation regimes. *Plant Cell Environ* 36:1812–1825. doi:10.1111/pce.12089
- Loik ME (2007) Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecol* 191:95–108
- Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004a) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141:269–281
- Loik ME, Still CJ, Huxman TE, Harte J (2004b) In situ photosynthetic freezing tolerance for plants exposed to a global warming manipulation in the Rocky Mountains, Colorado, USA. *New Phytol* 162:331–341
- Loik ME, Griffith AB, Alpert H (2013) Impacts of long-term snow climate change on a high-elevation cold desert shrubland, California, USA. *Plant Ecol* 214:255–266
- Looney SW, Stanley WB (1989) Exploratory repeated measures analysis for two or more groups: review and update. *Am Stat* 43:220–225
- Luo YQ, Wan SQ, Hui DF, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413:622–625

- MacCracken MC, Barron EJ, Easterling DR, Felzer BS, Karl TR (2003) Climate change scenarios for the US National Assessment. *Bull Am Meteorol Soc* 84:1711–1723
- Marks D, Dozier J (1992) Climate and energy exchange at the snow surface in the alpine region of the Sierra-Nevada. 2. Snow cover energy-balance. *Water Resour Res* 28:3043–3054
- Maurer E, Wood A, Adam J, Lettenmaier D, Nijssen B (2002) A long-term hydrologically based dataset of land surface fluxes and states for the Conterminous United States*. *J Clim* 15:3237–3251
- Maurer EP, Brekke L, Pruitt T, Duffy PB (2007) Fine-resolution climate projections enhance regional climate change impact studies. *Eos Trans Am Geophys Union* 88:504
- Mearns LO, Giorgi F, McDaniel L, Shields C (1995) Analysis of daily variability of precipitation in a nested regional climate model—comparison with observations and doubled CO₂ results. *Glob Planet Change* 10:55–78
- Meehl G, Covey C, McAvaney B, Latif M, Stouffer R (2005) Overview of the coupled model intercomparison project (CMIP). *Bull Am Meteorol Soc* 86:89–93
- Meehl GA et al (2007) The WCRP CMIP3 multimodel dataset: a new era in climate change research. *Bull Am Meteorol Soc* 88:1383–1394
- Miller AJ et al (2003) Potential feedbacks between Pacific Ocean ecosystems and interdecadal climate variations. *Bull Am Meteorol Soc* 84:617–633
- Murray CD, Buttle JM (2005) Infiltration and soil water mixing on forested and harvested slopes during spring snowmelt, Turkey Lakes Watershed, central Ontario. *J Hydrol* 306:1–20
- Naumburg E, Mata-Gonzalez R, Hunter RG, McLendon T, Martin DW (2005) Phreatophytic vegetation and groundwater fluctuations: a review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environ Manage* 35:726–740
- Perryman BL, Laycock WA, Koch DW (2000) Investigation of herbaceous species adapted to snowfence areas. *J Range Manag* 53:371–375
- Peek MS, Leffler AJ, Ivans CY, Ryel RJ, Caldwell MM (2005) Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. *New Phytol* 165:171–180
- Price MV, Waser NM (1998) Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79:1261–1271
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Ryel RJ, Leffler AJ, Peek MS, Ivans CY, Caldwell MM (2004) Water conservation in *Artemisia tridentata* through redistribution of precipitation. *Oecologia* 141:335–345
- Saavedra F, Inouye DW, Price MV, Harte J (2003) Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. *Glob Change Biol* 9:885–894
- Saito K, Yasunari T, Cohen J (2004) Changes in the sub-decadal covariability between northern hemisphere snow cover and the general circulation of the atmosphere. *Int J Climatol* 24:33–44
- Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211–220
- Seney JP, Gallegos JA (1995) Soil survey of Inyo National Forest, West Area. United States Forest Service, Pacific Southwest Region, California
- Shaw MR, Loik ME, Harte J (2000) Gas exchange and water relations of two Rocky Mountain shrub species exposed to a climate change manipulation. *Plant Ecol* 146:197–206
- Smith B, Mark AF, Wilson JB (1995) A functional analysis of New Zealand alpine vegetation: variation in canopy roughness and functional diversity in response to an experimental wind barrier. *Funct Ecol* 9:904–912
- Sturges DL (1989) Response of mountain big sagebrush to induced snow accumulation. *J Appl Ecol* 26:1035–1041
- Tabler RD (1974) Design guidelines for the control of blowing and drifting snow. Strategic Highway Research Program, National Research Council, Washington
- Taylor KE, Stouffer RJ, Meehl GA (2012) An overview of CMIP5 and the experiment design. *Bull Am Meteorol Soc* 93:485–498
- Vorosmarty CJ, Sahagian D (2000) Anthropogenic disturbance of the terrestrial water cycle. *Bioscience* 50:753–765
- Walker DA, Halfpenny JC, Walker MD, Wessman CA (1993) Long-term studies of snow–vegetation interactions. *Bioscience* 43:287–301
- Walker MD, Ingersoll RC, Webber PJ (1995) Effects of interannual climate variation on phenology and growth of 2 alpine forbs. *Ecology* 76:1067–1083
- Walker MD et al (1999) Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrol Process* 13:2315–2330
- Weltzin JF et al (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53:941–952
- Woo MK, Marsh P (2005) Snow, frozen soils and permafrost hydrology in Canada, 1999–2002. *Hydrol Process* 19:215–229
- Yamagishi H, Allison TD, Ohara M (2005) Effect of snowmelt timing on the genetic structure of an *Erythronium grandiflorum* population in an alpine environment. *Ecol Res* 20:199–204
- Zierl B, Bugmann H (2005) Global change impacts on hydrological processes in Alpine catchments. *Water Res Res* 41:W0208. doi:10.1029/2004WR003447