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REGULAR ARTICLE

Warming and increased precipitation frequency on the Colorado Plateau: implications for biological soil crusts and soil processes

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Abstract
Aims Changes in temperature and precipitation are expected to influence ecosystem processes worldwide. Despite their globally large extent, few studies to date have examined the effects of climate change in desert ecosystems, where biological soil crusts are key nutrient cycling components. The goal of this work was to assess how increased temperature and frequency of summertime precipitation affect the contributions of crust organisms to soil processes.
Methods With a combination of experimental 2°C warming and altered summer precipitation frequency applied over 2 years, we measured soil nutrient cycling and the structure and function of crust communities.
Results We saw no change in crust cover, composition, or other measures of crust function in response to 2°C warming and no effects on any measure of soil chemistry. In contrast, crust cover and function responded to increased frequency of summer precipitation, shifting from moss to cyanobacteria-dominated crusts; however, in the short timeframe we measured, there was no accompanying change in soil chemistry. Total bacterial and fungal biomass was also reduced in watered plots, while the activity of two enzymes increased, indicating a functional change in the microbial community.
Conclusions Taken together, our results highlight the limited effects of warming alone on biological soil crust communities and soil chemistry, but demonstrate the substantially larger effects of altered summertime precipitation.

Keywords Colorado Plateau · Biological soil crusts · Climate change · Soil chemistry

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Introduction

Globally, changes in temperature and precipitation are expected to influence ecosystem processes, such as nutrient cycling (Finzi et al. 2011; Luo et al. 2006), primary productivity (Rustad et al. 2001), and species

distribution patterns (Parmesan and Yohe 2003). Effects of climate change on soil processes, including soil nutrient cycling and carbon sequestration, have been demonstrated experimentally across a range of ecosystems (Luo et al. 2006; Melillo et al. 2002), including tundra, low tundra, grassland, and forest ecosystems. Across a range of ecosystems, soil respiration rates, net nitrogen (N) mineralization rates, and plant productivity all increase in response to warming (Rustad et al. 2001). In fact, short-term heterotrophic soil respiration is related positively to increasing temperature and studies showing increases in soil respiration are likely reflecting microbial depletion of labile carbon pools (Allison et al. 2010; Knorr et al. 2005). However, long-term responses show a level of acclimation in soil respiration (Bradford et al. 2008). Additionally, changes in precipitation and soil moisture availability moderate the ability of plants to respond to warming through negative effects on nutrient cycling (Austin and Vitousek 1998; Medlyn et al. 2000; Pepper et al. 2005). Overall, the capacity of ecosystems to respond can be dampened by N limitation (van Groenigen et al. 2006; Finzi et al. 2011). Together, this data suggests that soil responses to global change are complex and likely depend spatial and temporal scales of observation. Lacking in much of this research is a focus on how soil processes across arid ecosystems are responding to changes in climate (but see Smith et al. 2009; Maestre et al. 2010), despite their large extent. Indeed, much of what we know about the effects of warming on ecosystem function comes from research in temperate and alpine systems, with little comprehensive information about effects in drylands.

The Colorado Plateau, which is classified as semiarid, with total annual precipitation ranging from 130–250 mm year^{-1}, is located within a transition zone between the winter-dominated systems fed from the Gulf of Alaska and the summer-dominated convection storms from the Gulf of Mexico (Schwinning et al. 2008), resulting in monsoonal rainfall patterns during summer months and cold winters with significant snow inputs. The Intergovernmental Panel on Climate Change (Christensen et al. 2007) projects that temperatures at lower elevations within the Colorado Plateau are expected to rise by 4 to 6°C by 2100, a large increase for an already warm biome (Seager et al. 2007). There is more uncertainty associated with the global climate models in their predictions of future precipitation regimes for the desert southwest, including for the Colorado Plateau (Smith et al. 2005), with some models predicting increased winter and summer rainfall (Weltzin et al. 2003), along with increased frequency of El Niño events and extreme precipitation events (Easterling et al. 2000), and other models predicting a shift towards drier conditions and more frequent, smaller pulse events (Karl et al. 1995; Kunkel et al. 2003; Kim 2005; Smith et al. 2005; Schwinning et al. 2008). These predictions can have very different consequences for ecological processes in desert ecosystems. Regardless of the specific model, shifts in precipitation patterns, when coupled with increasing temperatures, will likely result in overall transition to a much drier climate (NAST 2000; Seager et al. 2007; Seager and Vecchi 2010).

In dryland ecosystems, biological soil crusts, composed primarily of fungi, algae, cyanobacteria, lichens, and mosses, are abundant and play integral roles in soil processes and ecosystem function. They can completely cover plant inter-space surfaces in undisturbed areas and thus constitute 70% or more of the living ground cover where they are common (Belnap 1994). They create microtopography that influences water retention, infiltration (Eldridge et al. 2010) and seed germination in vascular plants (Belnap 2006; Deines et al. 2007). Components of biological soil crusts also fix and supply atmospheric nitrogen (N) and carbon (C) to underlying soil food webs in these sparsely vegetated systems (Barger et al. 2006; Turetsky 2003) and contribute a large proportion of overall soil respiration in semiarid ecosystems (Castillo-Monroy et al. 2011). The type and abundance of crust species affects C and N fixation rates: well-developed crusts that contain dark-colored mosses, lichens, and cyanobacteria (hereafter referred to as "dark" crusts) can fix more C and N than light-colored, early successional crusts (hereafter referred to as "light" crusts), which are dominated by light cyanobacteria (Lange 2001; Housman et al. 2006; Grote et al. 2010). In addition, increasing temperatures increase both C and N fixation up to a certain point, after which inhibition occurs (Belnap 2002; Grote et al. 2010, Castillo-Monroy et al. 2011).

The physiological performance and contribution of these living crusts to ecosystem processes is linked directly to climate, specifically hydration and temperature (Austin et al. 2004; Belnap et al. 2004; Grote et al. 2010). The transition to warmer climate and a shift in precipitation patterns is likely to result in more

frequent and rapid dessication of soil crust organisms. Additionally, a decrease in overall event size (and thus the duration of time the crust organisms are wet) or an increase in the frequency of small precipitation events may decrease the amount of C these organisms can fix. Together, warming and changes in hydration period are expected to reduce the ability of these organisms to function within a positive carbon balance (Belnap et al. 2004; Barker et al. 2005, Mishler and Oliver 2009). This, in turn, can reduce the photosynthetic capacity, chlorophyll content, and the production of UV protective pigments in soil photosynthetic organisms (Bowker et al. 2002; Belnap et al. 2004, Bowker et al. 2008a). Lack of C can also inhibit nitrogen fixation as a direct result of higher temperatures, because crusts will dry faster (Belnap 2002), and because C stores are required for N fixation (Belnap 2002). As soils in this region are already low in C and N, decreased inputs from crusts are expected to limit soil food web activity (Belnap 2003). With a combination of experimental warming and altered summer precipitation frequency, we designed an experiment to assess how soil nutrient cycling and the structure and function of biological crust communities responds to predicted future changes in climate. We hypothesized that direct effects of climate on soils processes, coupled with indirect effects through changes in BSC community composition and physiological function, would influence soil nutrient dynamics.

Materials and methods

Study site description

The study site is located on the Upper Colorado Plateau, near Castle Valley, UT (38.67485 N, −109.4163 W, 1310 m.a.s.l). This area is characterized as a cool desert ecosystem, receiving approximately 65% of the annual precipitation in winter months. The soils at the study site are classified as sandy loam, calcerous, Rizno series (Grand County Soil Survey, Table 1). Soil bulk density at this site is 1.35 g/cm^3. This site is dominated by two perennial grasses, *Pleuraphis jamesii* (syn. *Hilaria jamesii*), *Achnatherum hymenoides* (syn. *Stipa hymenoides*), a shrub *Atriplex confertifolia*, and biological soil crust cover that fills the interspaces between plants. The biological soil crust cover is dominated by cyanolichens in the genus *Collema* (*C. tenax* and *C. coccophorum*), the cyanobacterium *Microcoleus vaginatus*, and the moss *Syntrichia caninervis*.

Experimental design

Four treatments (+2°C, +2°C + Water, Water, Control) were applied factorially from fall 2005 until fall 2008 to 20 2×2.5 m plots and replicated five times in a randomized block design. The warming treatments were delivered using one 800 W infrared radiant heater (Kalglo Model MRM-1208, Kalglo Electronics Company, Inc, Bethlehem, PA), with modified reflectors (see Harte et al. 1995) installed at 1.3 m above the surface of the plot. All lamps were oriented in a north–south direction in relation to the plots (Harte et al. 1995; Kimball 2005). The lamps emit a constant 60Wm^{-2}, equivalent to a target soil warming of +2°C at 2 cm soil depth. Control plots had dummy lamps of the same size and shape as the real lamps, but these did not contain a heating element. Several models predict a shift towards more frequent, but smaller summertime precipitation regime for the Colorado Plateau (Karl et al. 1995; Kunkel et al. 2003; Kim 2005; Smith et al. 2005; Schwinning et al. 2008). To simulate this shift, our watering regime was applied during the summers of 2006–2008, delivering smaller rain events more frequently. We aimed at ½ the average event size, delivered 2× more frequently than the 30-year historical average, which translated to 2 mm rain events delivered 2–3 times per week starting in mid-June and continuing until mid-September. This watering regime yielded 39 watering events in 2006, 36 in 2007, and 37 in 2008. Simulated rainfall was provided with hand pump sprayers.

To monitor changes in soil temperature and soil moisture in each plot, we installed a Campbell CS-616 soil moisture sensor and one four-tipped thermopile (24 ga. Type T-thermocouple wire) at each of 3 depths: 2, 5, and 15 cm. Thermopiles provide an average temperature across the tips, allowing sampling of greater spatial variability while only using one input location on a datalogger. The sensors were wired into multiplexers attached to Campbell CR10X dataloggers (Campbell Scientific, Logan, UT). We installed a meteorological station at our research site that measures air temperature and relative humidity, precipitation, net radiation, wind speed and direction.

Table 1 Repeated measures MANOVA source table, summarizing effects of warming and watering treatments over time on pigment concentrations (mg g soil^{-1}). Chlorophyll *b* results are omitted from *Collema* because they do not contain this pigment

Dependent Variable	Source	df	*Collema*	Cyanobacteria	*S. caninervis*
Chlorophyll *a*	Between	3	0.33	0.06	<0.0001
	Within (time)	3	<0.0001	<0.0001	<0.0001
	Time×treatment	9	0.05	0.03	<0.0001
Scytonemin	Between	3	0.93	0.37	0.48
	Within (time)	3	<0.0001	0.002	<0.0001
	Time × treatment	9	0.2	0.007	0.16
Xanthophyll subgroup	Between	3	0.38	0.03	<0.0001
	Within (time)	3	<0.0001	<0.0001	<0.0001
	Time × treatment	9	0.06	0.02	0.0002
Canthoxanthin	Between	3	0.75	0.12	0.76
	Within (time)	3	<0.0001	<0.0001	0.0006
	Time × treatment	9	0.2	0.64	0.83
Echinenone	Between	3	0.29	0.01	0.27
	Within (time)	3	<0.0001	0.006	0.0002
	Time × treatment	9	0.12	0.04	0.75
Chlorophyll *b*	Between	3	NA	0.08	<0.0001
	Within (time)	3	NA	0.0007	<0.0001
	Time × treatment	9	NA	0.57	<0.0001
β-Carotene	Between	3	0.004	0.0003	<0.0001
	Within (time)	3	<0.0001	<0.0001	<0.0001
	Time × treatment	9	0.004	0.0005	0.0007

Biological soil crust reponses

To measure changes in biological soil crust cover in response to treatments, we established 4 permanent locations within each plot and assessed soil crust cover in the spring and fall annually, using a 0.25 m^2 frame gridded quadrat placed on the soil at a point 1 m from the corner of each plot. At 20 interception points within the gridded quadrat, individual soil crust species and ground cover were recorded. Percent cover of each species was calculated as the number of hits of each species.

To examine physiological responses to warming and pulsing precipitation, we measured cyanobacteria, *Collema* lichens, and *S. caninervis* photosynthetic capacity (as F_v/Fm), C and N isotopes, and pigment concentrations. Light-adapted chlorophyll fluorescence, F_v/F_m, was measured in the field on randomly selected samples of cyanobacteria, *Collema* lichens, and *S. caninervis* (each sample consisting of a majority of each cover type) using a portable pulse amplitude fluorometer (PAM-2000, Walz Inc., Germany), using the saturation pulse method (Bilger et al. 1995) in January and May 2006 and September 2007, after two seasons of increasing the frequency of summertime precipitation. A measure of fluorescence yield gives an estimate of the function of PS II and a measure of the overall efficiency of the photosynthetic process. Live moss and *Collema* spp. samples were collected from the upper 0–0.5 cm of soil in January, May, and September 2006 and 2007. All samples were sifted with a 2 mm sieve and ground with a mortar and pestle; the 0–0.5 cm depth samples were ground and all samples sent to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University for C and N isotope analyses. Crust organisms synthesize pigments to protect against UV stress, quench free radicals (Garcia-Pichel and Castenholz 1991; Garcia-Pichel and Castenholz 1993), and cope with heat shock (Xu et al. 2009). Concentrations of pigments were determined on a per tissue mass basis (μg/g soil) using HPLC analysis on acetone-extracted samples (Karsten and Garcia-Pichel 1996) and identified using peak areas integrated from photodiode array data at 436 nm and commercial standards (DHI Water and Environment, Denmark), with the exception of scytonemin. The scytonemin standard was not available

commercially; therefore, we modified its extinction coefficient from 112.6 Lg^{-1} cm^{-1} at 384 nm to 60.8 Lg^{-1} cm^{-1} at 436 nm. Zeaxanthin, lutein, and myxoxanthophyll were grouped for analyses and referred to as xanthophylls based on their similarity in function, absorbance spectra, retention times, and difficulty in distinguishing among them.

Soil responses

Soil collection methods

Baseline soil chemistry and texture analyses were carried out on soils collected from 0 to 10 cm depths from all experimental plots (n=20) and 4 additional areas outside the plots. We collected and composited 20 subsamples of soils from each plot in each block at two depths (0–0.5 and 0–10 cm). Samples were split and analyzed for isotopes at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University and for soil nutrients, texture, soil organic matter, and soil chemistry at the Soil and Plant Analysis Laboratory, Brigham Young University. This same soil collection procedure was continued for isotopic analysis throughout the experiment. Splits from 0 to 10 cm depths were also analyzed for both total and active bacterial biomass and fungal biomass by direct microscopy at Soil Foodweb Oregon, LLC. After the initial characterization, resin-extractable nutrient concentrations were measured in situ seasonally using resin strips coated with cation and anion resins (2×2 cm, Ionics, Inc., Watertown, MA) glued to acrylic rods (2.5×0.5×15.25 cm) and soaked overnight in saturated NaCl, followed by rinsing with deionized water, and air-dried prior to use. One anion and one cation rod were inserted to a depth of 1 to 3 cm back-to-back. These rod pairs were replicated three times per plot per sample time. Resin rods were left in the soil for approximately 3 months before being replaced from 2006 to 2008. Ions were extracted from resin rods using 0.5 N HCl in 2006 and 2 M KCl in 2007 and 2008 and the extracts were shipped overnight for analyses at the Soil and Plant Analysis Laboratory, Brigham Young University. To ensure that the glue used did not contain nitrogen or alter our results, we carried out a separate experiment with known concentrations of N in solution and found no nitrogen contamination from the glue.

To examine how warming and altered frequency of summer precipitation affected N availability, field and lab soil incubations were performed. Soil samples were collected from 0 to 10 cm depths from each plot. Soils were passed through a 2 mm sieve and a subsample was extracted in the field to serve as the baseline concentrations of inorganic N in the soil. Ions from field soils were extracted with 50 mL 2 M KCl, stored for 24 h at room temperature, and filtered. A second subsample was incubated in a 150 mL screw cap urine cups in the dark at room temperature for 7 days and extracted following the same procedure and net NO_3^- and NH_4^+ are presented as the difference between field and lab incubations. Soil extracts were analyzed at the Colorado Plateau Analytical Laboratory, Northern Arizona University.

Enzyme assay

In order to assess how warming and altered frequency of summer precipitation affects the functional capacity of the microbial community, we assayed the activities of eight extracellular enzymes within 48 h of soil collection: β-1,4-glucosidase (βG), β-1,4-cellobiohydrolase (CBH), β-1,2-N-acetylglocosaminidase (NAG), Phenol oxidase (PhOx), Peroxidase (Perox), Phosphatase (PHOS), L-leucine aminopeptidase (LAP), and Urease. Four enzymes are involved in soil C and nutrient cycling: βG and CBH catalyze cellulose degradation, NAG breaks down chitin and fungal cell walls, PhOx and Perox degrade lignin, PHOS is involved with protein breakdown and is an indicator of organic phosphorus cycling, LAP catalyses the hydrolysis of N-terminus from proteins and peptides, and Urease targets urea (Saiya-Cork et al. 2002; Allison and Treseder 2008; Sinsabaugh et al. 2008; Sinsabaugh 2010). Soil samples were collected in May and August 2006 and May and September 2007 from two soil depths 0–0.5 cm and 0–10 cm for soil enzyme assays. Soils were put on ice and shipped overnight to University of Vermont, where the activity of the protocol of Saiya-Cork et al. (2002) was followed with the following modifications. 100 ml of 50 mM bicarbonate buffer (pH 8.2) was added to 1.0 g of soil. Eight replicate wells of 200 μL aliquots per sample were dispensed into 96-well microplates. A 50 μL portion of substrate solution containing fluorogenically labeled substrates (methylumbelloferone, MUB) were added to each well for β-1,4 cellobiohydrolase, β-1,3 glucosidase, β-1,4-

N-acetylglucosaminidase (NAGase), phosphatase, and L-leucine aminopeptidase. Microplates were incubated in the dark at 20°C for 3 h. Fluorescence was quantified using a microplate fluorometer (FLx800, Bio-Tek Instruments, Inc., Winooski, VT, USA) with 360 nm excitation and 460 nm emission filters. The oxidative enzymes Perox and PhOx, as well as urease, were quantified spectrophotometrically in clear polystryrene 96-well, 300 μL microplates, using the substrate 10 mM 1-3,4-dihydroxyphenylalanine (L-DOPA) and 0.3% hydrogen peroxide (for peroxidase) and incubating in clear plates for 1.5 h at 20°C and reading absorbance on a microplate spectrophotometer (Bio-Tek) with a 460 nm filter. Corrections were made for standards, plate, and buffer. All enzyme activities are expressed in units of nmol h^{-1} g^{-1}.

Analyses

All statistical analyses were performed using JMP 8.0 software (SAS Institute). To examine the effects of treatments on BSC cover, measures of soil chemistry and soil pigment concentrations through time, we used a repeated-measures MANOVA, with treatment as the main factor and block as a random effect. Tukey Kramer's post-hoc tests were used for comparisons among groups. Linear regression analysis was used to examine the correlation between the change in moss, lichen, and cyanobacteria cover. Because there were baseline differences in fluorescence yield among treatments before treatments were applied, we calculated the percent change between the measurements in the fall of 2007 and initial baseline measurements from January 2006 for analyses. Two-way ANOVA was used to determine the effects of warming and increased frequency summer precipitation on fluorescence quantum yield. Repeated-measures MANOVA was used to examine the effects of treatments over time on *Collema* lichens and *S. syntrichia* isotopes. To examine the responses of individual enzymes to warming and precipitation treatments within each season, we used a two-way ANOVA, with block as a random effect.

Results

The experimental site experienced above-average monthly temperatures for the majority of August 2005–October 2008, compared with the 30-year mean. Precipitation at this site exceeded the 30-year mean during September and October 2005, March and October of 2006, April, August, September, and December 2007, and February 2008 and was either similar to or below average for all other months (Fig. 1a).

The warming treatment delivered an average additional downward IR flux of 60 Wm^{-2}. Over a 24 h period, we achieved surface warming of >0°C <5°C for 70% of the daytime and 82% of the nighttime hours (Fig. 1b). At a depth of 5 cm, soil temperatures were within this range 81% of the daily 24 h period and 94% of nighttime hours. At 15 cm, soil temperatures were within this range 88% of the 24 h period and 92% of nighttime hours. Overall, average temperature differentials were +2.0°C at the soil surface, +1.9°C at 5 cm below the surface, and +1.6°C at 15 cm in the heated plots (Fig. 1b). However, we obtained little or no warming during the daytime in the summer months. As the sun passed overhead, daily temperature differentials (i.e., the difference between warmed and their respective control plots) fluctuated between 0°C and 5°C, but these are short-lived (<0.5 h) events typically due to shadows cast from the overhanging lamps, or vegetation when the sun angle is low. Other periods with temperature differentials outside of the desired range occurred occasionally, as has been discussed in other studies using these IR lamps (Harte et al. 1995; Kimball 2005).

Biological soil crust responses

Microcoleus-dominated cyanobacterial communities constituted 50% of crust cover at the start of the experiment, with *S. caninervis* 22% and *Collema* spp. 5–7%. Moss cover declined over time (Wilk's $\lambda=0.54$, $F_{(12,190)}=4.20$, $p<0.0001$; Fig. 2a), with a 90–100% reduction in cover in the watered plots within the first year of the experiment, regardless of warming treatment. We saw a concomitant increase in cyanobacteria cover over time (Wilk's $\lambda=0.34$, $F_{(12,190)}=7.91$, $p<0.0001$), increasing an average of 64% in watered plots over the course of the experiment (Fig. 2b). There was a significant negative linear relationship between change in moss cover and change in cyanobacteria cover ($R^2=0.7$, $p<0.0001$), as the dead moss was replaced by cyanobacteria. In contrast, there was no change in *Collema* lichen cover throughout the experiment, regardless of treatment (F test $F_{(3,190)}=0.02$, $p=0.7$) and no relationship between

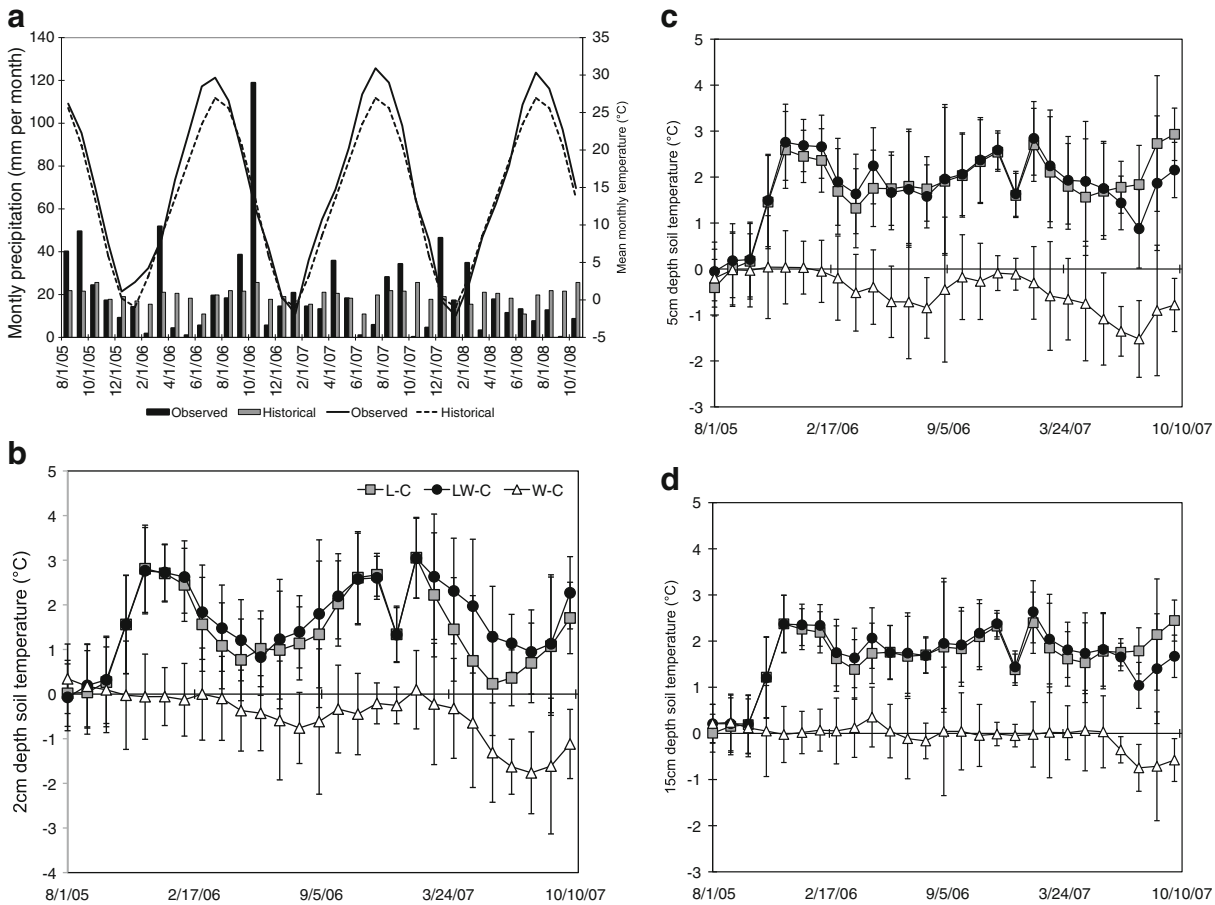

Fig. 1 **a** Observed mean monthly temperature (*solid lines*, right *y*-axis) and observed monthly precipitation (*solid bars*, left *y*-axis) recorded at the experimental site in Castle Valley, UT between September 2005 and October 2008. Historical mean monthly temperature (*dashed lines*, right *y*-axis) and historical total monthly precipitation (*open bars*, left *y*-axis) are presented from 1971 to 2000 monthly records from Castle Valley, UT (www.ncdc.noaa.gob). **b** Soil temperature differentials between warmed, warmed and watered, watered and control plots between September 2005–September 2008 at three soil depths: **b** 2 cm, **c** 5 cm, and **d** 15 cm

change in moss cover and change in *Collema* lichen cover (R^2=0.01, p=0.59).

Of the seven pigments investigated, all pigment concentrations varied seasonally. The effects of warming and watering treatments were pigment and species-specific (Table 1). We found significant decreases in chlorophyll *a* (Wilk's λ=0.33, $F_{(9,34)}$=2.16, p=0.05, Fig. 3a) and β-carotene concentrations (Wilk's λ=0.21, $F_{(9,34)}$=3.37, p=0.005, Fig. 3b), and a marginally significant reduction in xanthophyll concentrations (Wilk's λ=0.35, $F_{(9,34)}$=2.06, p=0.06) for *Collema* lichens in watered plots, but no effect of warming alone and no interaction between warming and watering. Similarly, we saw significant decreases in chlorophyll *a* (Wilk's λ=0.05, $F_{(9,34)}$=9.64, p<0.0001, Fig. 5b), chlorophyll *b* (Wilk's λ=0.07, $F_{(9,34)}$=7.45, p<0.0001), xanthophylls (Wilk's λ=0.13, $F_{(9,34)}$=5.02, p=0.0002), and β-carotene (Wilk's λ=0.15, $F_{(9,34)}$=4.41, p=0.0007) in response to watering, but not warming, for *S. caninervis*. The initial decreases in chlorophyll *a* and β-carotene pigment concentrations following the first season of more frequent summer precipitation were followed by temporary recovery in the spring of 2007. However, the concentrations of these pigments were further reduced by a second summer of watering (Fig. 3). Scytonemin (F test $F_{(3,14)}$=1.75, p=0.002) and xanthophyll (F test $F_{(3,14)}$=3.5, p<0.0001) concentrations in cyanobacteria changed over time, but inconsistently in response to watering or warming treatments, while chlorophyll *a* (Wilk's λ=0.31, $F_{(9,34)}$=

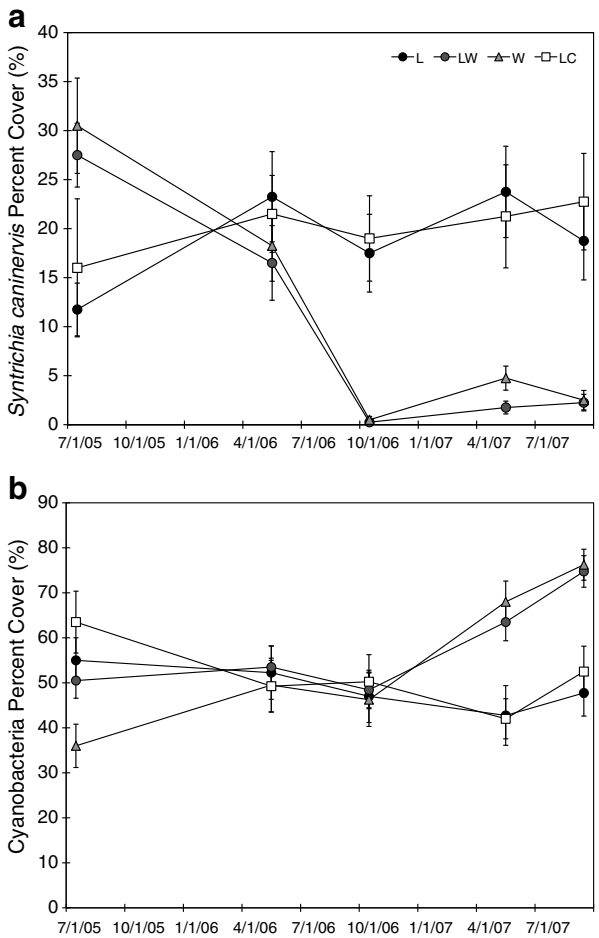

Fig. 2 Change in **a** *S. caninervis* and **b** cyanobacteria percent cover (mean of 5 replicate plots per treatment ± SE) over time in C (control), L (Lamp), LW (Lamp+Water) and W (Water) plots. Statistically significant differences are denoted with *. Photographs of **c**) healthy *S. caninervis* in a control plot and **d**) dead *S. caninervis* in a watered plot

2.36, p=0.03, Fig. 5c), echinenone (Wilk's λ=0.32, $F_{(9,34)}$=2.30, p=0.04), and β-carotene (Wilk's λ=0.14, $F_{(9,34)}$=4.60, p=0.0005) decreased in concentration in watered plots after the second field season.

Between the beginning of the experiment in January 2006 and September 2007, there were significant changes in quantum yield F_v/F_m across treatments for *Collema* lichens (ANOVA $F_{(3,19)}$= 3.6, p=0.04) and for *S. caninervis* (ANOVA $F_{(3,19)}$=4.14, p=0.02), with decreases in yield in watered plots relative to controls (Fig. 4). Post-hoc Tukey-Kramer comparisons confirmed that *Collema* lichens in warmed plots had greater quantum yield than the warmed and watered plots. In contrast, quantum yield of *S. caninervis* was greater in control plots than in watered plots. There was no effect of warming alone on quantum yield.

We found no significant effects of treatments over time on C isotope ratios of *Collema* spp. (Wilk's λ= 0.42, $F_{(12,30)}$=0.96, p=0.51; Fig. 5a). Nitrogen isotopes in *Collema* became marginally more positive over time in watered plots (Wilk's λ=0.21, $F_{(12,30)}$=1.94, p=0.07; Fig. 5a). For *S. caninervis*, there was no significant effect of treatments on C isotopes over time (Wilk's λ=0.62, $F_{(6,30)}$=1.36, p=0.26; Fig. 5b) and N isotope values became more positive in watered plots over time (Wilk's λ=0.35, $F_{(6,30)}$=3.45, p=0.01; Fig. 5b).

Soil responses

Soil chemistry

No initial differences across treatments were apparent in baseline soil chemistry or texture (Table 2). Neither

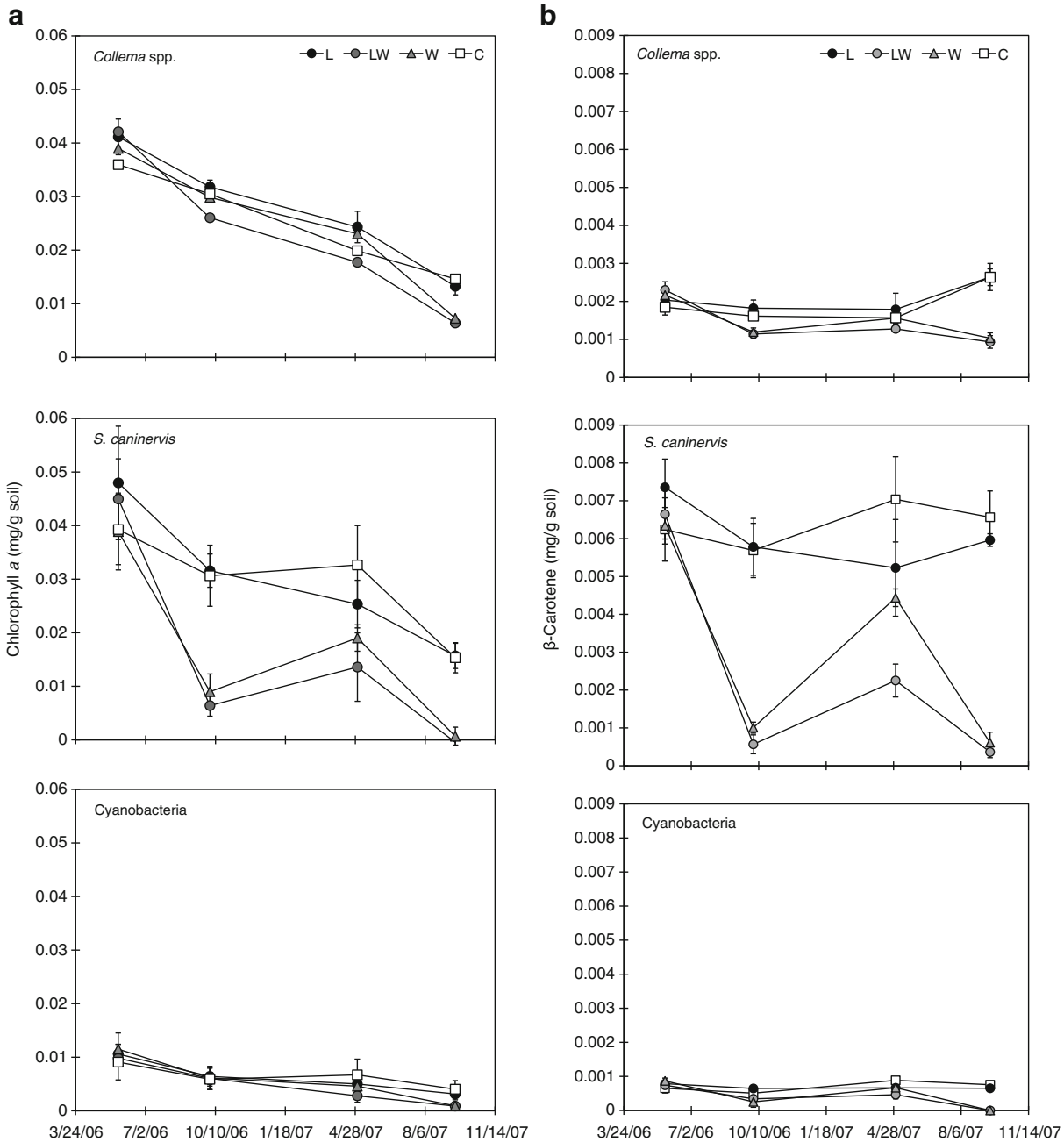

Fig. 3 Concentrations of **a** chlorophyll *a* and **b** β-Carotene pigments in *Collema* spp., *Syntrichia caninervis*, and cyanobacteria across time (mean of 5 replicate plots per treatment ± SE)

warming nor watering affected soil inorganic N at 0–10 cm soil depths (Table 3). Additionally, both percent organic matter and total N changed seasonally, but were not affected by warming or watering. We saw marginally significant differences among treatments in field resin-extractable NO_3^- (Wilk's λ=0.55, $F_{(12,88)}$= 1.83, p=0.06) but not NH_4^+ (p=0.13) and post-hoc Tukey's indicated that plots in the watering treatment were different from control plots, before watering treatment was initiated. There were no consistent

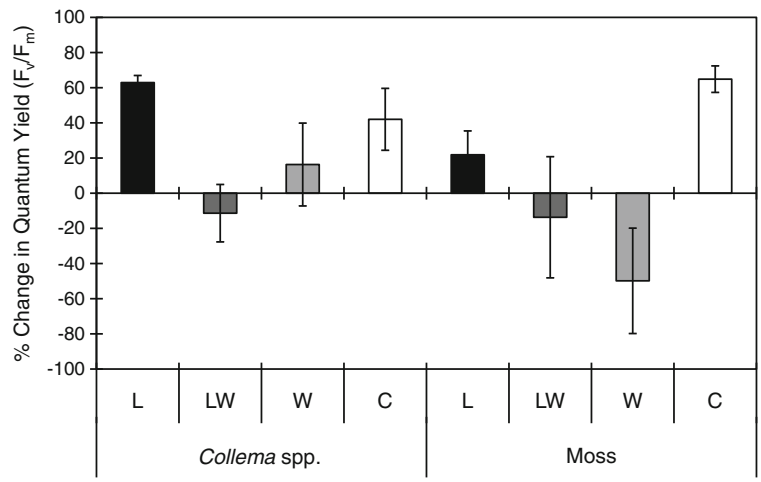

Fig. 4 Percent change in quantum yield F_v/F_m for *Collema* spp. and *Syntrichia caninervis* between January 2006, at the start of the experimental treatments, and September 2007, after two seasons of warming and more frequent pulsing precipitation (mean of 5 replicate plots per treatment ± SE). Different letters indicate statistically significant differences at α= 0.05. All other comparisons are not statistically significantly different

changes of resin-extractable non-N ions, including Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn, with respect to treatments through time. Biological soil crust organisms occur at the soil surface and the direct influence of crusts on soil chemistry was greater at the soil surface (0–0.5 cm depth) than at depths 0–10 cm. However, in 0–0.5 cm soils, treatments had no effect on percentage of organic matter in September 2006, and no effect on total N in September 2007, after a second year of warming and watering.

Total and active bacteria and fungi

Abundances of active and total bacterial and fungal biomass were similar among treatments in May 2006. After one season of watering, active bacterial biomass

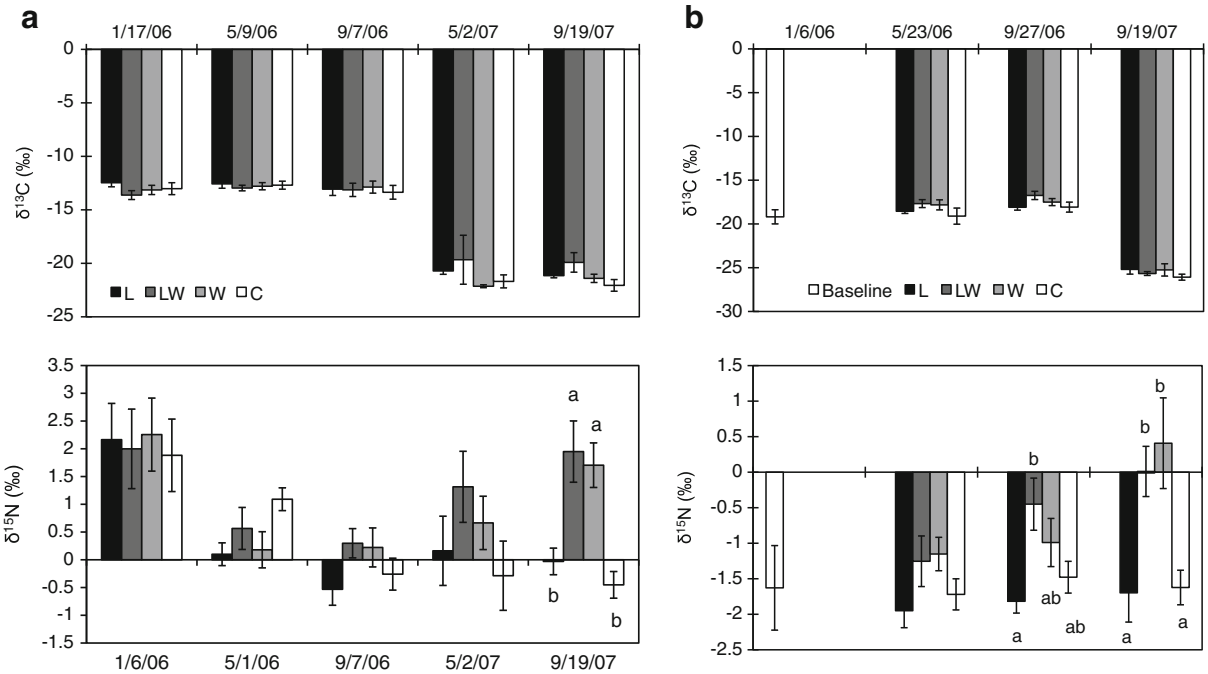

Fig. 5 Carbon and nitrogen isotopes from soils collected in 2006 for **b** *Collema* spp. and **b** *Syntrichia caninervis* (mean of 5 replicate plots per treatment ± SE). Different letters indicate statistically significant differences at α=0.05. All other comparisons are not statistically significantly different

Table 2 Baseline soil chemistry (Mean ± SE, n=25) and mean texture classes (rounded to the nearest 1%) from soils collected from 0 to 10 cm depths on 11/9/05

Soil Chemistry	
ppm P	10.40±2.51
ppm K	82±5.9
%OM (*)	0.82±0.2
pH	7.77±0.05
CEC meq\100 g	9.79±4.39
ppm Zn (*)	0.16±0.01
ppm Fe	3.56±0.23
ppm Mn (*)	1.52±0.11
ppm Cu	0.25±0.06
ppm Ca-EX (*)	3313±231
ppm Mg-EX (*)	124±11.7
ppm K-EX (*)	125±16.5
ppm Na-EX (*)	37±4
ppm total N (*)	290±22.67
%$CaCO_3$ (*)	6.97±0.29
Soil Texture	
Sand (%)	70
Clay (%)	13
Silt (%)	16
Very coarse (%)	1
Coarse (%)	2
Medium (%)	13
Fine (%)	38
Very fine (%)	11

Asterisks indicate significant differences among blocks. Sand separate classes are broken down as follows: very coarse >1< 2 mm, coarse >0.5<1 mm, medium >0.25<0.5 mm, fine >0.1< 0.25 mm, and very fine >0.05<0.1 mm

decreased in watered plots an average of 2.81 μg g^{-1} soil, while active bacterial biomass increased in all other plots (Table 4). Total bacterial biomass increased across plots, but the magnitude of increase was greater in control and warmed plots, relative to watered plots. Active fungal biomass was reduced in warmed plots, while it increased in control plots between May and September 2006 and total fungal biomass decreased across all plots, but we saw the largest decreases occurred in watered plots.

Enzyme responses

Soil enzyme activity varied between soil depths, with 0–10 cm soil cores reporting much lower enzyme activity than 0–0.5 cm cores. Within the shallow (0–0.5 cm) soil cores, watering treatment significantly increased CBH (ANOVA $F_{(3,19)}$=2.81, p=0.05) and βG (ANOVA $F_{(3,19)}$=2.29, p=0.09) enzyme activity in May 2007, one year after watering was initiated, and marginally increased the activity of Perox (ANOVA $F_{(3,19)}$=2.95, p=0.06) in September 2007, after the second season of watering. No other effects of either warming or watering on the activity of other enzymes occurred at the 0–0.5 cm soil depth. Within the deeper (0–10 cm) soils, the activity of CBH (ANOVA $F_{(3,19)}$=3.2, p=0.05) and βG (ANOVA $F_{(3,19)}$=3.1, p=0.05) increased in watered, but not warmed plots, in May 2006. Urease activity was significantly reduced in watered plots, relative to non-watered, in September 2007 (ANOVA $F_{(3,19)}$=7.5, p= 0.0024). After a second season of watering and warming, between May and September 2007, CBH activity decreased by 20–44% in both warmed and watered plots, relative to a 30% increase the control plots (ANOVA $F_{(3,19)}$=3.5, p=0.04), as well as a 30–45% reduction in βG (ANOVA $F_{(3,19)}$=3.61, p=0.04) in watered plots, relative to non-watered, and a 55–90% reduction in urease activity (ANOVA $F_{(3,19)}$=3.64, p= 0.04) in warmed and watered plots, relative to control plots.

Discussion

Effects of warming

The majority of studies that examine the effects of climate warming on nutrient availability and soil processes have been conducted at high elevation and high latitude sites, where soil moisture is not limiting (e.g. Chapin et al. 1995; Rustad et al. 2001; Klein et al. 2007). Few studies have been performed in desert ecosystems, where soil moisture is limiting for much of the growing season and where biological soil crusts play critical roles in the cycling of nutrients, serving as important sources of fixed C and N to belowground communities. Recently, Maestre and colleagues (2010) found an increase in soil respiration with warming in a semi-arid Mediterranean ecosystem and this effect was progressively larger in plots with substantial BSC cover. Based on previous observations (Belnap et al. 2006), we hypothesized that 2°C warming would lead to changes in biological soil crust cover and that those

changes would in turn affect soil nutrient dynamics and other associated measures of ecosystem function. We also hypothesized that nutrient transformations would be affected by warming and changes in precipitation, independently of changes associated with crust cover. However, similar to Darby et al. 2011, our results show very little effect of warming on any of our measures. Importantly, effects of warming alone were very limited on any individual constituents of the biological soil crust community. This may be attributed to the large plasticity of these organisms with regards to temperature tolerance or the potential of these organisms to recover from heat stress. Summer surface temperatures can range from 15 to 75°C over the course of a day; therefore, an increase of 2°C when crusts are dry may well be within their functional range (Stark et al. 2009). Moss and lichen species, especially those common in arid ecosystems, are highly desiccation-tolerant (Brown and Bates 1990; Mishler and Oliver 2009; Lüttge et al. 2011) and have a number of mechanisms in place to ensure survival through periods of drought. During extended periods of drought, crust function is virtually suspended and aside from UV stress, crust organisms are impervious to environmental stressors (Stark et al. 2009). Therefore, it may be largely irrelevant how warm the conditions are when crusts are dry. Additionally, moss, lichens, and cyanobacteria also synthesize pigments that screen against incoming UV radiation (Karsten 2008) and quench free radicals generated by UV light (Garcia-Pichel and Castenholz 1991; Kumar et al. 1996). The warming treatment in our experiment alone did not constitute additional UV radiation and therefore, did not necessitate the production of additional pigments, but it is possible that some pigments are produced to deal with osmotic stress associated with warmer conditions (Bowker et al. 2008b). In fact, echinenone, a part of a group of pigments that protect cells from oxygen radicals generated by UV (Karsten et al. 1998) that must be replaced after exposure to intracellular UV (Castenholz and Garcia-Pichel 2000), increased in concentration in cyanobacteria in response to warming. The increase of this pigment indicates that cyanobacteria were experiencing some level of photo-oxidative damage in warmed plots.

Globally, nighttime minimum temperatures over the past century have increased more than the daytime maximum temperatures (Karl et al. 1995; Easterling et al. 1997; Vose et al. 2005). Similarly, future projections for North America indicate the effects of warming will be more pronounced in winter months and more moderate during the already hot summer months. In support of these predictions, we saw a positive effect of warming on wintertime fluorescence of *Collema*, when exposure to warmer temperatures occurs while soil moisture is high. This translated to increased photosynthetic activity during months when these lichens may otherwise be covered under snow for at least a part of the winter. Studies have shown *Collema* respond positively to increases in temperature, with increased photosynthetic rates (Lange et al. 1998), increased fluorescence and increased N fixation (Belnap et al. 2004). What remains unknown is whether prolonged exposure to warmer temperatures during winter months would offset faster soil drying during drier months. Although we did not observe stimulation of photosynthetic function in *Collema* during the spring months, when water is less limiting, a 2°C warming may be insufficient to achieve a stimulatory response, when compared to the control. Other factors besides water may also co-limit *Collema* response to temperature in the field.

In addition to seeing no measurable effect of warming on BSC cover and function, there were no effects of warming alone on isotope ratios of C and N, and any soil element. This overall lack of response in most measures may be due to our inability to consistently heat the soils sufficiently during the summer months, when high solar radiation and heat swamped out the lamp effects during the daytime hours. Other studies have reported difficulty in achieving consistent desired warming during summer months (Harte et al. 1995; Kimball 2005; Kimball et al. 2008, but see Maestre et al. 2010). Therefore, we were unable to add stress to the organisms or affect soil processes at a time when the effects are potentially the greatest. Alternatively, the lack of measurable effects in warmed plots may be caused by a trade-off between stressing crust organisms during summer months and increasing water availability and function in the late fall, winter, and early spring months, when water is not limiting and most of the C and N fixation occurs. If this is indeed the cause, the effective season when BSCs are functional may be extended by warming more than reducing the time for function when these organisms experience warming-induced stress. It is also possible that BSC phenology is shifted to functioning earlier in

Table 3 Soil chemistry means ± SE from soils collected from 20 composited subsamples from each plot in each block at 0–10 cm depth (except organic matter, which was also collected from 0 to 2 cm depth)

Parameter	Winter 2006	Spring 2006	Fall 2006	Winter 2007	Spring 2007	Fall 2007
Soil NO_3^- (mg NO_3^-/L)						
+2°C	2.2±0.28	4.91±0.6[ab]	2.78±0.88			
+2°C + water	2.34±0.3	5.89±1.03[a]	1.71±0.51			
Watered	2.61±0.27	5.84±0.68[a]	2.14±0.46			
Control	2.17±0.43	3.92±0.41[b]	2.01±0.61			
Soil NH_4^+(mg NH_4^+/L)						
+2°C	0.03±0.02	0	0			
+2°C + water	0.001±0.001	0	0			
Watered	0.008±0.005	0	0.001±0.001			
Control	0.006±0.006	0	0.007±0.007			
Resin-extractable NO_3^- (mg NO_3^-/L)						
+2°C	32±10.1	2.3±0.62	19±2.9	0.56±0.12		
+2°C + water	27.3±4.6	4.3±1.8	28.6±4.6	0.58±0.11		
Watered	15.6±1.9	1.1±0.3	30±4.1	0.45±0.09		
Control	26±6.06	1.5±0.37	28±5.9	0.48±0.09		
Resin-extractable NH_4^+ (mg NO_3^-/L)						
+2°C	0.76±0.14	2.8±0.7	0.55±0.05	1.2±0.35		
+2°C + water	1.26±0.54	2.7±1.2	0.6±0.05	0.9±0.25		
Watered	1.6±0.8	0.35	0.53±0.06	0.9±0.22		
Control	0.65±0.2	0.66±0.06	0.9±0.18	0.5±0.14		
Total N (ppm)						
+2°C		461±45.4	65±13.7	197±20.2	136±9.7	115±27.2
+2°C + water		413±21.7	98±21.2	175±17.2	154±9.5	85±23.6
Watered		484±32.4	120±26.8	217±9.2	170±19.4	88±21.4
Control		465±47	113±25.3	230±27.6	131±14.8	95±26.7
% Organic matter (0–2 cm)						
+2°C			0.5±0.23			1.43±0.14
+2°C + water			0.81±0.19			1.14±0.24
Watered			0.72±0.09			1.4±0.2
Control			0.75±0.23			1.51±0.18
% Organic matter (0–10 cm)						
+2°C			0.38±0.08		0.41±0.06	1.1±0.03
+2°C + water			0.58±0.07		0.43±0.06	1.08±0.03
Watered			0.5±0.1		0.38±0.06	1.14±0.04
Control			0.5±0.19		0.35±0.06	1.13±0.02

Missing cells indicate no measurements were done at those time points. Small letters indicate significant differences among means

the growing season, without changing the overall length of the season. In this case, we would expect to find no effect of warming on BSC function and overall C uptake. Finally, there are additional pathways for the loss of C and N from soils that we did not measure, including soil respiration and NH_3 volatilization, which are both expected to increase with warming (Billings et al. 2002a; Grote et al. 2010).

Despite the lack of direct effects of warming on BSCs and soil chemistry, there were some effects on total bacterial and fungal biomass. Soil organisms control soil organic matter (SOM) decomposition and

Table 4 Total and active bacterial and fungal biomass (Mean ± SE μg g soil $^{-1}$) and change in total and active bacterial and fungal biomass (Mean ± SE μg g soil $^{-1}$) between May and September 2006, one season after warming and pulsing precipitation treatments were applied. Two replicate soils were collected per plot from across all experimental plots (n=20)

Date	Treatment	Active bacterial biomass	Total bacterial biomass	Active fungal biomass	Total fungal biomass
5/30/06	Control	14.14±1.54	425.6±53.76	2.41±0.68	164.6±12.97
	+2°C	15.06±1.18	502.1±113.78	5.29±1.09	230.3±27.6
	+2°C+water	13.38±0.68	444.5±110.2	4.32±0.71	210.1±21.93
	Watered	18.15±1.77	509.4±63.56	6.38±1.68	225.5±29.63
9/13/06	Control	16.24±1.79	550±81.43	4.85±2.31	99.48±10.04
	+2°C	16.08±0.99	675±12.07	5.08±2.28	132.08±16.37
	+2°C + water	14.52±1.11	634.8±76.04	3.19±0.8	114.48±15.82
	Watered	15.34±1.64	556.2±102.61	7.06±1.44	103.12±4.25
Change	Control	2.10±1.84	124.4±103.13	3.32±3.06	−65.12±17.44
	+2°C	1.02±1.27	172.9±126.08	−0.20±3.37	−98.22±38.54
	+2°C + water	1.14±1.76	190.3±186.18	−1.0±1.34	−95.62±31.16
	Watered	−2.81±1.88	46.8±124.38	0.79±2.18	−122.38±29.34

changes in soil microbial activities can be expected to affect overall nutrient availability and the terrestrial C budget (Allison et al. 2010). Additionally, extracellular enzymes excreted by soil microbes play important roles in the degradation and transformation of soil organic matter. After one season, warming reduced both active bacterial and fungal biomass, while total bacterial biomass increased. Allison and Treseder (2008) find similar results with respect to both active bacterial and fungal abundance, while Zhang et al. (2005) report an increase in the ratio of fungi to bacteria as a result of +2°C warming in their study, as well as a shift in microbial community structure and metabolic potential. These results indicate that microbial and fungal activity is suppressed with warming, even when overall abundance remains unchanged, suggesting a change in community structure and function. There is also evidence that enzyme activity can remain unchanged (Allison and Treseder 2008) or decline with warming (Allison et al. 2010), which contrasts our findings. In our study, the activity of cellulose-degrading enzymes CBH and βG increased in warmed plots after 1.5 years of warming. This suggests that there is some potential for microbial functional response to warming, with the response likely greater with warming above +2°C. The microbial response we saw was associated with little or no change in all measures of N. Other studies report suppression of decomposition rates and reduced nutrient availability as water becomes limiting (Allison and Treseder 2008), whereas studies in regions where water is not limiting show stimulation of N mineralization and N availability in response to warming (e.g., Zhang et al. 2005; Allison and Treseder 2008).

Effects of altered precipitation frequency

As we expected, increased frequency of precipitation had a large effect on biological soil crust community composition, though not on all community members. After one season of increased frequency of summer precipitation, live moss cover declined and the following year, we measured additional mortality of *S. caninervis* in watered plots, resulting in a drop from 22% cover at the beginning of the experiment (November 2005) to only 3% cover by 2007 (Reed et al. 2012, in review). Similar responses of *S. caninervis* to increased frequency in small summertime rain events were also reported in the Mojave Desert, where moss showed reduced physiological function and lower growth and reproduction rates (Barker et al. 2005; Stark et al. 2011). The loss in moss cover in our plots was followed by an increase in early-successional, light cyanobacteria cover, which became dominant across soils previously covered by moss. However, the shift from a moss-dominated biological soil crust community to one that is almost entirely dominated by cyanobacteria was not associated with changes in soil C and N after 2 years, despite the fact that moss and

cyanobacteria differ in their ability to fix C and N. This is likely a reflection of a mismatch between scales of observation. Mosses constitute only 22% of soil cover at our site and their effects on soil nutrients may be diluted when soils are collected at the plot scale.

In contrast to our expectations, the cover of the most common lichen, *Collema*, as well as other lichens, remained unchanged throughout the experiment, though there were some signs of physiological stress in watered plots. More frequent summer precipitation affected the concentrations of a range of pigments in *Collema*, including chlorophyll *a*, the xanthophyll group, echinenone, chlorophyll *b*, and β-carotene. Chlorophyll *a* steadily declined over time in *Collema*, and combined with changes in quantum yield and N isotope differences, there is some evidence that increasing frequency of summer precipitation was stressing lichens and their ability to photosynthesize and fix C and recover from UV stress. Overall changes in biological crust community composition were expected to affect soil nutrient cycling. Indeed, at the Mojave Global Change Facility, added summer rain stimulated N fixation by the crust community (Billings et al. 2003), but had no effect on net N mineralization (Billings et al. 2002a, b). Similarly, there were no effects of increased frequency of summer precipitation on N mineralization and no measurable changes in soil nutrient C and N, even after two years.

Both increasing soil temperatures and more frequent wetting and drying cycles can alter microbial community composition and accelerate the production and activity of enzymes (Henry et al. 2005; Chung et al. 2007; Allison and Martiny 2008). The reduction we saw in both active and total bacterial and fungal biomass in watered plots may be a direct response to watering, though it is likely an indirect response to the reduction of moss cover, as soil microfauna have been shown to be more abundant under moss-lichen soil crusts than under cyanobacterial crusts (Darby et al. 2007). In addition to stressing crusts, increasing the frequency of precipitation led to an increase in the production and activity of some soil enzymes. Both CBH and βG degrade cellulose, a process that is generally considered to be N-limited. Indeed, the increase in the ratio of Ln (BG)/Ln (NAG and LAP), which can be used as a proxy for C:N acquisition activity, suggests rates of decomposition were faster in watered plots. Urease cleaves ammonia groups from carbon to yield ammonia, which is a product of N fixation. A reduction in the overall activity and total biomass of bacteria and fungi with watering, this increased production was likely due to specific groups of bacteria and/or fungi, rather than the decomposer microbial community as a whole. However, despite the increase in soil enzyme activity and a likely associated increase in decomposition, there were no consistent changes in soil chemistry and nutrient availability that correlated directly with watering treatments or indirectly with changes in biological soil crust cover. This may be due to the short time between when we started the experiment and sampling time. Alternatively, the increase in enzyme production was insufficient to affect soil nutrient concentrations.

In combination, these results have important implications for future dryland ecosystem structure and function, which may be more responsive to changes in precipitation regime than changes in temperature. Warming 2°C above ambient did not lead to direct changes BSC cover and function or in soil nutrient cycling. However, the prediction of future warming in this region is 4–6°C. Although soil nutrient cycles in desert ecosystems may be well-buffered against a small increase in temperature, larger temperature increases may elicit stronger responses, especially when coupled with decreased soil moisture availability. Additionally, there may exist a time lag between temperature and precipitation changes and ecosystem responses, especially if changes in precipitation occur at decadal or longer time scales. Biological soil crusts are generally dessication tolerant in arid ecosystems and their already limited annual activity time may be incrementally decreasing as climate shifts to warmer and drier conditions, impacting their ability to fix C and N and gradually decreasing their contribution to soil nutrient cycling. We report some indication that in arid ecosystems, despite being well-adapted to warm and dry conditions, biological soil crusts are likely to respond to shifts in precipitation regimes within one to two years. The shift from moss and lichen-dominated to cyanobacterially-dominated biological crust communities may impact not only soil nutrient cycling, but also ecosystem energy balance due to the replacement of dark lichen and moss with light cyanobacteria (Finzi et al. 2011). Changes in land surface albedo can influence soil surface temperatures, snowmelt, soil evaporation rates, and can feedback to influence air temperature changes at regional scales (Juang et al.

2007; Lyons et al. 2008). When coupled with changes in precipitation patterns, the combined effects of warming and reduced water availability may push these systems into an alternative state, with consequences for nutrient cycling.

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