

Reductions in daily soil temperature variability increase soil microbial biomass C and decrease soil N availability in the Chihuahuan Desert: potential implications for ecosystem C and N fluxes

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Abstract

Maximum and minimum soil temperatures affect belowground processes. In the past 50 years in arid regions, measured reductions in the daily temperature range of air (DTR_{air}) most likely generated similar reductions in the unmeasured daily temperature range of soil (DTR_{soil}). However, the role of DTR_{soil} in regulating microbial and plant processes has not been well described. We experimentally reduced DTR_{soil} in the Chihuahuan Desert at Big Bend National Park over 3 years. We used shade cloth that effectively decreased DTR_{soil} by decreasing daily maximum temperature and increasing nighttime minimum temperature. A reduction in DTR_{soil} generated on average a twofold increase in soil microbial biomass carbon, a 42% increase in soil CO_2 efflux and a 16% reduction in soil NO_3^- -N availability; soil available NH_4^+ -N was reduced by 18% in the third year only. Reductions in DTR_{soil} increased soil moisture up to 15% a few days after a substantial rainfall. Increased soil moisture contributed to higher soil CO_2 efflux, but not microbial biomass carbon, which was significantly correlated with DTR_{soil} . Net photosynthetic rates at saturating light (A_{sat}) in *Larrea tridentata* were not affected by reductions in DTR_{soil} over the 3 year period. Arid ecosystems may become greater sources of C to the atmosphere with reduced DTR_{soil} , resulting in a positive feedback to rising global temperatures, if increased C loss is not eventually balanced by increased C uptake. Ultimately, ecosystem models of N and C fluxes will need to account for these temperature-driven processes.

Keywords: Chihuahuan Desert, *Larrea tridentata* (creosotebush), plant physiology, soil available N, soil microbial biomass, soil respiration, soil temperature fluctuations

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Introduction

Temperature is an important regulator of chemical, physical and biological processes that occur in soil and, therefore, affects key ecosystem functions such as decomposition and primary production (Hobbie, 1996; Pregitzer & King, 2005; Lin *et al.*, 2010). However, there is a gap in our understanding of how variation in temperature within the soil affects microbial and plant function. In particular, we know very little about the role of daily soil temperature range (DTR_{soil}) on these functions and subsequently on ecosystem functioning.

To determine how climate change may affect DTR_{soil} , we assessed current and predicted patterns of surface air temperature, which has been measured more extensively and systematically around the globe than soil temperature has since the late 1800s. During the last century, mean global air temperatures rose by 0.74 °C

and may increase up to 6.4 °C (relative to the period 1980–1990) by the end of this century (IPCC, 2007). Long-term temperature records show that these increases were due to minimum surface air temperatures (T_{min}) increasing at a faster pace than maximum temperatures (T_{max}) (Vose *et al.*, 2005; Zhou *et al.*, 2009). A greater increase in T_{min} relative to T_{max} has been attributed to increased greenhouse gases, including water vapor, which trap long-wave radiation at night (Karl *et al.*, 1993; Easterling *et al.*, 1997; Dai *et al.*, 1999; Zhou *et al.*, 2009). The result of this asymmetric warming is that global daily surface air temperature range ($DTR_{air} = T_{max} - T_{min}$) has decreased by -0.07 °C per decade (Vose *et al.*, 2005; Zhou *et al.*, 2009). However, there is spatial variability in DTR_{air} trends; the decline is 43% stronger in arid and semiarid regions compared with the global trend (Zhou *et al.*, 2009). Furthermore, DTR_{air} may continue to decline concomitant with rising mean global temperatures (Robeson, 2002) with the declining DTR_{air} trend anticipated to be stronger in arid and semiarid areas.

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In ecosystems with low vegetation cover, soil temperatures at shallow depth are dependent upon the prevailing air temperatures and the heat storage characteristics of the particular soil (Nobel & Geller, 1987; Kemp *et al.*, 1992), resulting in similar daily temperature patterns between air and soil temperatures but with different amplitudes. For arid landscapes, DTR_{soil} is greater than in mesic areas because arid regions have little cloud cover and low vegetation cover, thereby increasing the amount and duration of solar radiation reaching the soil surface and heating soil far above daily maximum air temperatures (Parton, 1984; Kemp *et al.*, 1992; Pregitzer & King, 2005; Zhou *et al.*, 2007). At night, during periods of low atmospheric water vapor, heat loss from desert soils is also high (Nobel, 1991). The combination of daytime and nighttime energy exchange characteristics generates large DTR_{soil} for much of the year. For example, Hadley (1970) found that during a summer day with minimal wind activity, the soil surface temperature in a sandy creosote-flat in the Sonoran Desert reached 80 °C and exhibited DTR_{soil} of 45 °C. Moreover, desert soils have high surface albedo and, therefore, low emissivity (Zhou *et al.*, 2007), resulting in reduced outward long-wave radiation. As a consequence of soil thermal storage capacity, soils may retain heat such that soil temperatures are higher after air temperatures have seasonally declined. It is likely that irrespective of changes in T_{min} or T_{max} , reductions in DTR_{soil} , which have probably decreased concomitant with reductions in DTR_{air} , will have consequences for the functioning of arid ecosystems.

Soil microbes play key roles in ecosystem function through decomposition of soil organic matter (SOM), N mineralization and nitrification, and consequently, influence plant nutrient uptake and production (Wardle *et al.*, 2004; Bardgett *et al.*, 2005). Soil warming experiments have generally shown increased soil CO₂ efflux rates and nutrient availability (McHale *et al.*, 1998; Rustad *et al.*, 2001; Melillo *et al.*, 2002) and decreased microbial biomass (Zogg *et al.*, 1997; Arnold *et al.*, 1999; Bradford *et al.*, 2008; Frey *et al.*, 2008). However, responses may vary in direction and magnitude, including exhibiting no effect (Sprent, 1987; Rustad *et al.*, 2001; Belay-Tedla *et al.*, 2009). In deserts, nitrogen (N) is the second limiting factor (after water) to plant productivity and microbial activity (Fisher *et al.*, 1988; Peterjohn & Schlesinger, 1990; Schlesinger *et al.*, 2006). Therefore, changes in N cycling or pools often have profound effects on ecosystem functioning.

Soil temperature can exert a direct influence on primary productivity because it affects nutrient uptake through changes in root form and function (Bassirirad, 2000; Pregitzer & King, 2005); for example, when plant

growth is not limited by other factors, root growth, ion uptake per unit root length and respiration may increase with increased soil temperature (Clarkson & Warner, 1979; Kaspar & Bland, 1992; Atkin *et al.*, 2000; Bassirirad, 2000). However, nutrient acquisition by the plant is ultimately dependent on soil nutrient availability, which is controlled by microbial activity. Soil N availability in deserts is an important regulator of leaf physiology and above-ground net primary productivity (Fisher *et al.*, 1988; Lajtha & Whitford, 1989; Patrick *et al.*, 2009; Robertson *et al.*, 2009).

We assessed the physiological response of *Larrea tridentata* ([DC] Cov.; creosotebush) to link below-ground changes in N cycling to plant performance. *Larrea tridentata* is a dominant and representative species of arid landscapes, widely distributed across warm deserts in North America (Chew & Chew, 1965). This evergreen shrub shows a high degree of photosynthetic acclimation to seasonal changes in air temperature (Strain & Chase, 1966; Mooney *et al.*, 1978), thus exhibiting similar net photosynthetic rates in winter and summer despite large differences in daily mean air temperature (Strain, 1969). It is extremely drought-tolerant and remains photosynthetically active year-round even at predawn water potentials <−6 MPa (Odening *et al.*, 1974; Reynolds *et al.*, 1999). *Larrea tridentata* is well-suited for this study because it has positively responded to increased soil N (Lajtha & Schlesinger, 1986; Fisher *et al.*, 1988), and the evergreen trait allows us to link C and N dynamics across seasons, which would not be possible with deciduous species or with annuals that only persist for a portion of the year.

Not only has the role of DTR_{soil} on ecosystem functioning not been well described, but also arid systems are underrepresented in experimental soil temperature manipulation experiments (Rustad *et al.*, 2001). Given that this is the first study to elucidate the role of DTR_{soil} in ecosystem function, we employed a nontraditional approach to soil temperature manipulations, to predict how a reduction in DTR_{soil} may affect microbial function. Our goal was to elucidate the role of DTR_{soil} on soil microbial biomass, soil N availability, soil CO₂ efflux rates and plant physiology in the Chihuahuan Desert. We reduced DTR_{soil} by shading the soils to simultaneously reduce the amount of solar radiation received by the soil surface during the daytime and increase nighttime minimum temperatures by reducing re-radiation of heat to the atmosphere. We hypothesized that a decrease in DTR_{soil} would (i) increase soil microbial biomass and, consequently, increase soil CO₂ efflux rates by reducing daily temperature extremes and associated physiological stress to the soil microbial community; (ii) soil microbes would utilize soil exchangeable N (in the forms of NH₄⁺-N and NO₃⁻-N)

before *L. tridentata* thereby reducing N available to plants; and (iii) photosynthesis in *L. tridentata* would be reduced in response to a reduction in soil available N.

Materials and methods

Study site

The study site was located in a creosote bajada in the Pine Canyon watershed (N29°13'43" latitude, W103°10'12" longitude; elevation 962 m) of Big Bend National Park in the Chihuahuan Desert in Texas. In addition to our study plant *Larrea tridentata* (creosotebush), other dominant plants at the site are *Agave lechuguilla* (Torr.) (Lechuguilla), *Leucophyllum frutescens* ((Berland.) I.M. Johnston.) (ceniza) and *Opuntia* sp. (cacti). Soils are classified as very gravelly fine sandy loam from the Chilicotal series, with a pavement of igneous gravel covering 80% of the soil surface (Cochran & Rives, 1985). Soil texture in the upper 15 cm of soil is 53% sand, 36% silt and 11% clay (Waters Agricultural Laboratories Inc., Owensboro, KY, USA).

Since the 1950s, this site experienced a DTR_{air} trend of -0.18 °C per decade [Fig. 1; National Climatic Data Center (NCDC); <http://www.ncdc.noaa.gov/oa/ncdc.html>; Panther Junction COOP ID 416792], a decrease that was nearly twice as strong as the trend in other arid regions (Zhou *et al.*, 2009). Mean annual precipitation (MAP) was 357 mm (range 146–571 mm) for the 30 year period 1979–2008 (NCDC). Precipitation primarily occurs during the summer monsoonal period between June and September (56%) while winters are fairly dry (Fig. 2a). The 30 year average of annual maximum air temperature is 26.2 °C (range 24.2–27.8 °C) and annual minimum temperature is 11.9 °C (range 10.3–14.7 °C) with hot summers and cool winters. From March through October soil temperatures at 15 cm depth are higher than air temperatures

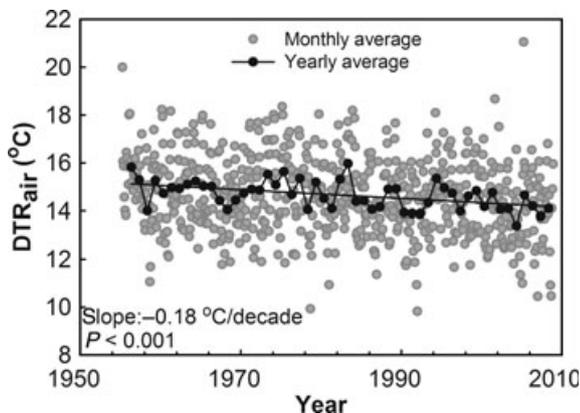


Fig. 1 Monthly and annual daily temperature range of surface air temperatures (DTR_{air}) recorded at Panther Junction, Big Bend NP, TX, ca. 10 km from our site. Data were obtained from the National Climatic Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>); Panther Junction COOP ID 416792) and spans the period from 1955 to 2008. The regression line is a measure of the annual decline in DTR_{air}.

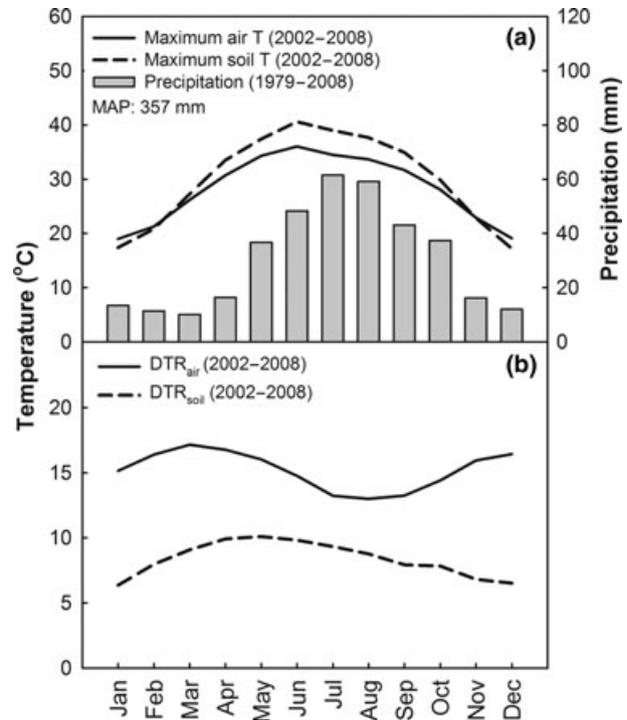


Fig. 2 (a) Average monthly maximum air and soil temperatures in experimental plots for the years 2002–2008 and average monthly precipitation for the years 1979–2008. (b) Daily temperature range for surface air temperature and soil temperature at 15 cm depth (DTR_{air} and DTR_{soil}, respectively) averaged for each month for the years 2002–2008.

(Fig. 2a). The 7 year monthly average (2002–2008) of DTR_{air} and DTR_{soil} showed that DTR_{air} is greatest in March (17.2 °C) and progressively decreases to a low of 13.0 °C in August; DTR_{soil} at 15 cm depth is highest in May (10.1 °C) after which it decreases to its lowest value of 6.4 °C in January (Fig. 2b).

Soil temperature manipulation

In June 2006, eight 4 × 3 m plots were established in the creosote bajada with each plot containing at least two *L. tridentata* plants. In four plots, soil temperature was experimentally manipulated to reduce DTR_{soil} while the remaining four plots were controls. In April 2008, a fifth plot was added to both the control and treatment plots. Soil temperature was manipulated by placing large-pore, interlocking wood-fiber erosion control blankets (Curlex®; American Excelsior Company, Arlington, TX, USA) on the soil surface; blankets were replaced each year in late winter/early spring. To avoid altering potential plant competition for resources by restricting plant growth, we cut incisions into the blankets to allow plant (woody and succulent perennials) penetration through the blankets. In addition, blanket properties allowed plants to grow through them following germination.

Beginning in June 2006, air temperature (at 1 m height) and soil temperature (at 15 cm depth) were measured continuously using HOBO® data loggers (H08-031-08; Onset Computer

Corporation, Bourne, MA, USA). Starting in April 2008, soil volumetric water content (VWC) was monitored at 15 cm depth every 4 h in two shaded and two exposed plots using EM-50 data loggers and EC-5 dielectric ECH₂O probes (Decagon Devices, Inc., Pullman, WA, USA).

Belowground measurements

We sampled in September 2006 (for initial data), April and September of 2007 and May, June, July and August of 2008. The sampling scheme in the years 2007 and 2008 was designed to sample toward the end of the dry season (spring) and during the historically rainy season (summer/early fall). Two soil samples per plot, ca. 300 g each, were collected from the upper 15 cm of soil. Soils were kept cold in the field and transferred to a 4 °C cold room upon return to the laboratory where they were kept until analyzed. Soil microbial biomass carbon (MBC) was determined using the chloroform fumigation-extraction method (Vance *et al.*, 1987). This procedure is widely used in many ecosystems and is recognized as a valid approach for estimating MBC (Martens, 1995; Joergensen & Brookes, 2005). Fumigation kills the live portion of the microbial community by lysing their cells, thereby releasing C and increasing extractable C levels in the soil sample compared with the nonfumigated replicate. In short, two replicates of each soil sample (5 g dry weight equivalent) were fumigated by chloroform or left un-fumigated for 48 h in vacuumed desiccators. Soils were then shaken in 50 mL 0.5 M K₂SO₄ to extract C compounds and filtered with ashless Whatman 43 filter paper (Whatman, Inc., Florham Park, NJ, USA). The resulting solution was analyzed spectrophotometrically (Genesys™ 5; Spectronic Instruments, Inc., Leeds, UK) at 280 nm to determine concentrations of organic C compounds. MBC was estimated using the difference in absorbance readings between the fumigated and un-fumigated samples (Nunan *et al.*, 1998). Soil extractable ammonium (NH₄⁺), nitrate (NO₃⁻) and SOM were analyzed by Waters Agricultural Laboratories Inc. Total soil C and N were analyzed using a CE Elantech elemental analyzer (NCS 2500; ThermoQuest, Milan, Italy). Gravimetric soil water content was determined by oven-drying soils at 60 °C for 24 h.

Starting in May 2008, soil CO₂ efflux was measured monthly in each plot over a 2 h period in the morning (8:30–10:30 hours) using a closed-loop, dynamic soil respiration system (LI-6400-09; LI-COR, Lincoln, NE, USA). Soil CO₂ efflux measurements were measured on bare soil using preinstalled PVC soil collars to minimize air leaks. The measurements were repeated three times per plot and the average of these constituted the CO₂ efflux rate for that plot.

Plant measurements

Beginning in April 2007, we collected plant physiological data and plant samples; plant data were collected synchronously with soil collections to link aboveground with belowground dynamics. Leaf-level light-saturated net CO₂ assimilation rates (A_{sat}), stomatal conductance (g_s) and transpiration rates (E) of *L. tridentata* were measured at saturating photosynthetic photon flux densities of either 1850 (in winter/early spring) or

2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (in summer/early fall) using a portable photosynthesis system equipped with a red/blue LED light source (LI-6400-02B; LI-COR Inc.). Measurements were taken within a 2 h interval (08:30–10:30 hours) during peak photosynthetic activity, determined prior via photosynthetic measurements at 2 h intervals over a 24 h period. A terminal shoot was randomly chosen from each plant (two plants per plot) and maintained in the cuvette at the prevailing ambient air temperature and leaf-to-air vapor pressure deficit (VPD_l) in the field. After gas exchange measurements, leaves were removed from the cuvette and leaf area was determined in the laboratory using a flatbed scanner and image editing software. Subsequently, A_{sat} measurements from the field were corrected for leaf area obtained in the laboratory by using the re-computation function of the Li-6400 OPEN software (Version 5.3). Specific leaf area (SLA) was determined by dividing the leaf area by the dry weight of the corresponding leaves.

Predawn xylem water potential (Ψ_{pre}) was measured on gas exchange plants a few hours prior to photosynthetic measurements using a Scholander-type pressure chamber (Model 600; PMS Instrument Company, Albany, OR, USA). Samples were collected at 04:00 hours and analyzed before sunrise. Twelve of 108 samples had lower Ψ_{pre} than we could measure (< -10 MPa). To fulfill the requirements of the multivariate analysis, we estimated missing Ψ_{pre} from the linear relationship between the natural logs (ln) of leaf water content and Ψ_{pre} ($r^2 = 0.85$).

Leaf samples were dried in an oven and then finely ground using a Pica blender mill (Model 2601; Cianflone Scientific Instruments, Corp., Pittsburgh, PA, USA) before chemical analyses. Leaf C and N were analyzed using a CE Elantech elemental analyzer (NCS 2500; ThermoQuest).

Statistical analyses

A mixed-effects analysis of variance (ANOVA) was performed using SYSTAT (Version 12; Systat Software Inc., Chicago, IL, USA) to examine the effects of reduced DTR_{soil} on soil microbial biomass and soil nutrient levels. Fixed effects in the analyses included date, treatment (shading or exposed) and their interaction. As plots were repeatedly sampled, plot ID was added as a random factor. This mixed-effects design accommodated the addition of a fifth plot for both the shaded and exposed soils in 2008. Natural log transformations were conducted as necessary to homogenize the variances.

A principal components analysis (PCA) was performed on above- and below-ground variables using plot-level data (MATLAB Version 6.5; The Mathworks, Inc., Natick, MA, USA). We used the PCA to visually detect relationships between plant and microbial function by reducing the multidimensional relationships among the variables to a two-dimensional window with the first two principal components as the axes. To normalize data distributions and treat variables equally, all variables were natural log-transformed prior to PCA analysis. Prior to transformation, negative values of Ψ_{pre} were converted to positive values. We also employed a discriminant function analysis to identify the variables most strongly associated with observed treatment and seasonal differences.

We quantified the linear dependence between two variables, including environmental variables (DTR_{soil} , soil T_{max} , soil T_{min} , and VWC), by calculating the Pearson's product-moment correlation (r) coefficient. The product of the correlation with itself (i.e. r^2) is the proportion of variance explained by the observed relationship. For the ANOVA and the Pearson's r , values were considered significant when $P \leq 0.05$.

Results

Environmental variables

Herein, our field measurement periods of 2006, 2007, and 2008 will be referred to as the first, second, and third year of our experiment, respectively. The first year of our study was the warmest and driest; average precipitation was 24% below MAP (271 mm) and annual maximum and minimum temperatures were 1.1 and 1.2 °C above the 30 year average. Both the second and third years had average precipitation (398 and 332 mm, respectively) and average maximum (T_{max}) and minimum (T_{min}) air temperatures (<0.6 °C deviation from the 30 year average; Fig. 3a). During the 3 year experimental period, DTR_{air} varied seasonally with an average fluctuation of 13.2 °C during the warmer summer months (JJA) and 16.4 °C during the cooler winter months (DJF; Fig. 3b).

Shading significantly reduced DTR_{soil} (mean DTR_{soil} of shaded plots was 7.5 °C compared to 9.5 °C in control plots). The reduction in DTR_{soil} by shading was accomplished by reducing daytime T_{max} by 1.4 °C and increasing nighttime T_{min} (Fig. 3c) by 0.6 °C on average during the 3 year study, thereby effectively decreasing the daily amplitude of temperature change, while minimally altering average daily temperature (−0.3 °C) compared with exposed soils. Application of the shade cloth to the soil temperature manipulation plots reduced DTR_{soil} throughout the experimental period, but this effect varied seasonally (Fig. 3d). The shade cloth effectively reduced DTR_{soil} to a greater degree in summer (2.8 °C) than in winter (1.3 °C), because average daytime reductions and nighttime increases in soil temperature were greater in summer (−2.1 and +0.7 °C, respectively) than in winter (−1.0 and +0.3 °C, respectively).

Reductions in DTR_{soil} increased retention of soil moisture such that average soil moisture could be up to 15% higher in shaded plots a few days after a substantial rainfall event (Fig. 4). Soil moisture remained higher in shaded plots until soils dried substantially to ca. 3% VWC, after which soil moisture was similar in both treatments. Soil moisture showed a significant date × treatment interaction (Table 1) whereby the

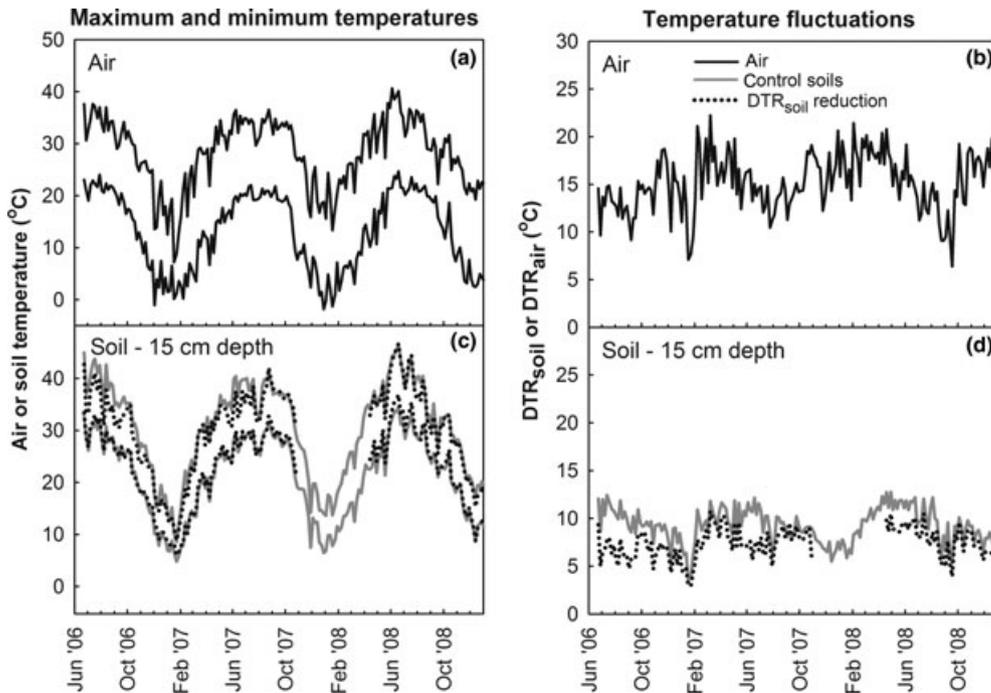


Fig. 3 Five-day averages of: maximum and minimum surface air temperatures (a), daily temperature range of surface air temperatures (DTR_{air}) (b), maximum and minimum soil temperatures recorded at 15 cm depth for control soils and soils with reduced DTR_{soil} (c), and daily temperature range of soil temperatures recorded at 15 cm depth for control soils and soils with reduced DTR_{soil} (d). Data span the study period from June 2006 until end of December 2008.

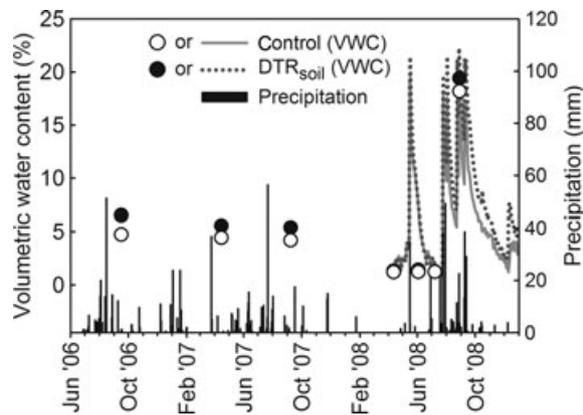


Fig. 4 Volumetric soil water content (VWC) of control soils or soils with reduced DTR_{soil} . Data were calculated from the gravimetric (via oven-drying) water content (plotted as symbols with means ± 1 SE) or measured continuously with soil moisture sensors that monitor the dielectric constant of the soil (installed in April 2008). Daily precipitation data for the study period from June 2006 until end of December 2008 were recorded at Panther Junction, Big Bend NP, and obtained from the Western Regional Climate Center (<http://www.wrcc.dri.edu/>).

effects of a reduction in DTR_{soil} on soil moisture levels were greater in the wetter summer than in the drier spring (Fig. 8b). The increase in VWC in shaded plots was strongly correlated with reductions in soil T_{max} ($r^2 = 0.50$; $P < 0.001$).

Microbial biomass, soil CO_2 efflux and soil nutrients

A reduction in DTR_{soil} doubled MBC in the third year, which was considerably higher than the MBC response in previous years; temporal patterns of MBC were similar between treatments across years (Fig. 5a, Table 1) and were much higher in soils with reduced DTR_{soil} regardless of season. Subsequently, the treatment effect was stronger than the seasonal effect (Fig. 8b). The only significant correlation between MBC and observed environmental variables (VWC, DTR_{soil} , soil T_{max} , and soil T_{min}) was between MBC and DTR_{soil} ($r^2 = 0.14$; $P = 0.01$); $r^2 \leq 0.01$ for all other correlations.

Soil CO_2 efflux was on average 42% higher in soils with reduced DTR_{soil} compared with controls (Fig. 5b, Table 1). Rates were generally low during dry, inter-pulse periods (0.28 and $0.37 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in exposed and shaded plots, respectively), but were an order of magnitude higher (up to $5.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$) in August of the third year following a precipitation pulse of 29 mm that increased soil moisture to $>15\%$. This large precipitation event generated 9.3 and 11.0 times greater soil CO_2 efflux rates in exposed and shaded soils, respectively, compared with previous measurements when VWC was $<2\%$. Soil CO_2 efflux was significantly positively correlated ($r^2 = 0.34$; $P < 0.001$) to soil temperature, but showed the strongest positive relationship with VWC ($r^2 = 0.77$; $P < 0.001$).

Table 1 Statistical results showing the mean and the standard error of the mean (SE), and F -values from a mixed-effects ANOVA model that tested for the main effects of date, treatment and their interaction on plant and soil variables from 2006 until 2008

Variable	Exposed soils (mean \pm SE)	Reduced DTR_{soil} soils (mean \pm SE)	Date	Treatment	Date \times treatment
<i>Soil</i>					
NH_4^+-N ($\mu\text{g g}^{-1}$)	2.78 \pm 0.33	2.46 \pm 0.24	38.8***	0.30	6.52***
$NO_3^- - N$ ($\mu\text{g g}^{-1}$)	6.55 \pm 0.39	5.43 \pm 0.32	74.1***	14.2***	2.66*
Microbial biomass C ($\mu\text{g g}^{-1}$)	46.3 \pm 4.3	98.8 \pm 10.0	3.68***	14.3***	1.80
Soil N (mg g^{-1})	0.59 \pm 0.01	0.62 \pm 0.01	6.79***	1.01	5.83***
Soil C (mg g^{-1})	5.54 \pm 0.14	6.39 \pm 0.16	7.85***	4.94*	3.53**
Volumetric water content (%)	5.24 \pm 0.73	6.01 \pm 0.77	1414***	18.6***	4.01***
Soil organic matter (%)	1.07 \pm 0.03	1.13 \pm 0.04	95.9***	3.13	4.21**
Soil CO_2 efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.87 \pm 0.27	1.31 \pm 0.40	64.9***	6.09*	0.43
<i>Plant</i>					
A_{sat} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	6.64 \pm 0.58	6.90 \pm 0.70	87.7***	0.47	1.47
g_s ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.08 \pm 0.01	0.09 \pm 0.02	64.0***	0.61	0.97
E ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$)	1.67 \pm 0.20	1.74 \pm 0.24	64.6***	0.24	0.51
VPD_L (kPa)	2.48 \pm 0.18	2.38 \pm 0.17	1108***	1.47	4.47***
Leaf [N] (mg g^{-1})	24.1 \pm 0.34	24.1 \pm 0.51	22.8***	0.00	2.1
Ψ_{pre} (MPa)	-4.82 \pm 0.53	-4.67 \pm 0.59	281***	0.12	1.66
SLA ($\text{cm}^2 \text{ g}^{-1}$)	63.7 \pm 2.58	64.4 \pm 2.72	165***	0.07	2.39*

The number of '*' indicates significance at $P < 0.001$ (***), $0.001 \leq P \leq 0.01$ (**), and $0.01 < P < 0.05$ (*). Plant variables of *Larrea tridentata* are: net photosynthetic rates at saturating light intensity (A_{sat}), stomatal conductance (g_s), transpiration rate (E), leaf-to-air vapor pressure deficit (VPD_L), leaf N content (leaf [N]), predawn xylem water potential (Ψ_{pre}), and specific leaf area (SLA).

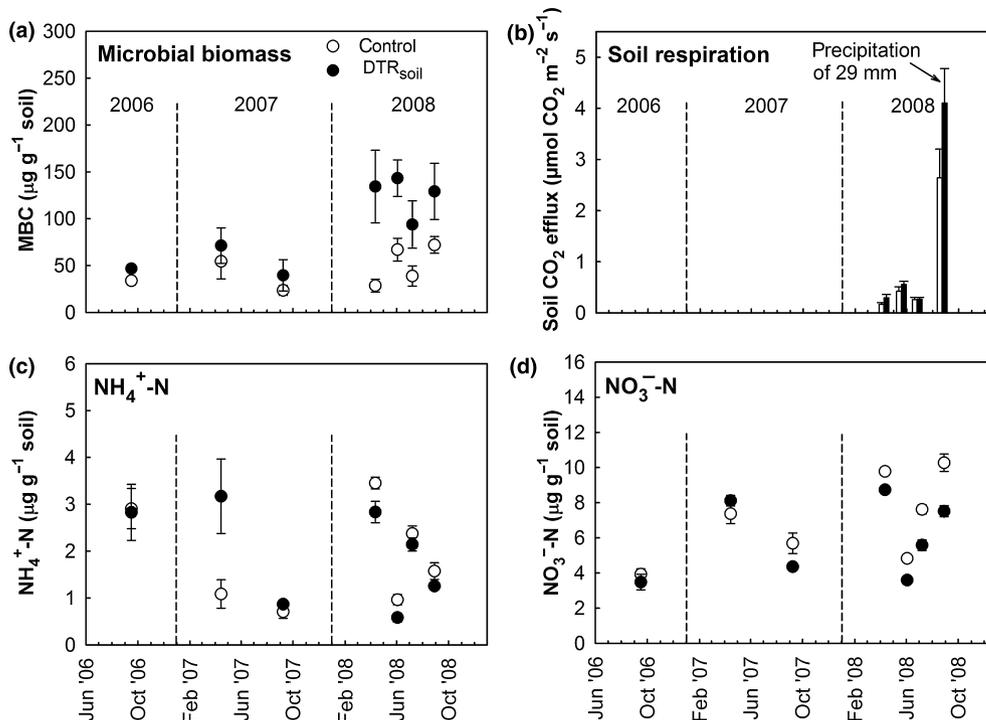


Fig. 5 (a) Microbial biomass carbon, (b) soil CO₂ efflux rates, (c) soil exchangeable NH₄⁺-N, and (d) soil exchangeable NO₃⁻-N in control soils and soils with reduced DTR_{soil} for the study period 2006–2008. Values are plotted as means ± 1 SE.

For soil exchangeable NH₄⁺-N, there was no observable pattern of shading on NH₄⁺-N in the first or second year. However, in the third year, when microbial biomass exhibited the greatest response to reduced DTR_{soil}, NH₄⁺-N was lower (by 18%) in shaded soils compared with exposed soils (Fig. 5c, Table 1). Patterns of soil NH₄⁺-N availability were similar in all treatments across years except in the spring of the second year, when soil NH₄⁺-N variability was extremely high in soils with reduced DTR_{soil}. To determine what caused temporal variability in soil exchangeable NH₄⁺-N levels, we calculated correlations between environmental variables (DTR_{soil}, soil *T*_{max}, and VWC) and NH₄⁺-N. No significant correlations were found, which suggested that soil NH₄⁺-N availability was more directly affected by other factors. To examine whether biological uptake was a factor in the decline of NH₄⁺-N levels, we examined the relationship between soil NH₄⁺-N and belowground biological activity (i.e. soil CO₂ efflux). We observed a steep nonlinear decline in soil available NH₄⁺-N with increased soil CO₂ efflux. At low soil CO₂ efflux (<1 µmol m⁻² s⁻¹), available NH₄⁺-N was 3.6 ± 0.2 µg g⁻¹ (mean ± 1 SE; maximum of 10.4 µg g⁻¹), whereas at higher CO₂ efflux (>1 µmol m⁻² s⁻¹) soil available NH₄⁺-N was 1.4 ± 0.1 µg g⁻¹ (mean ± 1 SE; maximum of 2.1 µg g⁻¹). We found no relationship between MBC and NH₄⁺-N irrespective of season (Fig. 8a).

Reduction in DTR_{soil} significantly reduced soil exchangeable NO₃⁻-N throughout the experiment (16% lower; Fig. 5d, Table 1); reductions in soil NO₃⁻-N due to shading were greater in the third year (22% lower) than in previous years, concomitant with the largest increase in MBC in these plots. Seasonal effects were stronger than treatment effects as soil NO₃⁻-N was generally higher in spring than in summer, while treatment effects contributed less to observed seasonal NO₃⁻-N patterns (Figs 5d and 8b). The stronger seasonal effect resulted in a negative correlation between soil *T*_{max} and soil NO₃⁻-N ($r^2 = 0.48$; $P < 0.001$) and an absence of a correlation with MBC as MBC was affected by reduction in DTR_{soil}, but not by season. We found a significant inverse relationship between SOM content (i.e. a source of N for microorganisms) and soil exchangeable NO₃⁻-N ($r^2 = 0.29$; $P < 0.001$). There was no correlation between DTR_{soil} and NO₃⁻-N ($r^2 = 0.02$), indicating that DTR_{soil} was not directly regulating seasonal NO₃⁻-N dynamics.

There was no main effect of reduced DTR_{soil} on total soil N. However, total soil N was higher on two occasions, once in the fall of the second year and once in the summer of the third year (not shown), resulting in a significant date × treatment interaction (Table 1). Soil C increased significantly with a reduction in DTR_{soil} (15%; Table 1). Reduced DTR_{soil} increased soil C starting in fall of the second year and it remained higher

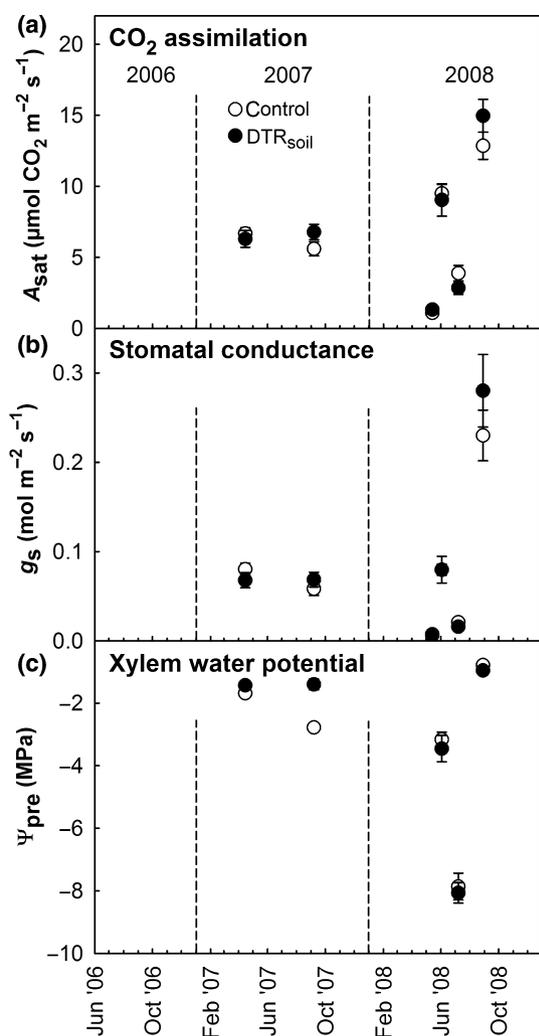


Fig. 6 (a) Net photosynthetic rates at saturating light intensity (A_{sat}), (b) stomatal conductance (g_s), and (c) predawn xylem water potential (Ψ_{pre}) of *Larrea tridentata* growing in control soils and in soils with reduced DTR_{soil} . May 2008 values of Ψ_{pre} could not be measured accurately due to embolisms. Values are plotted as means \pm 1 SE.

thereafter. There was no significant main effect of DTR_{soil} on SOM (Table 1). There was a significant interaction of date with treatment as the seasonal increase in SOM from spring to summer in DTR plots (from 0.80% to 1.30%) was greater than the seasonal increase in control soils (from 0.88% to 1.18%).

Plant physiology

Shading did not significantly alter A_{sat} , g_s , Ψ_{pre} , E , VPD_L , leaf [N] or SLA (Fig. 6 and/or Table 1) despite alterations to soil thermal regime and increased VWC. Seasonal effects were much stronger (Fig. 8b) as plant physiology was strongly influenced by more favorable

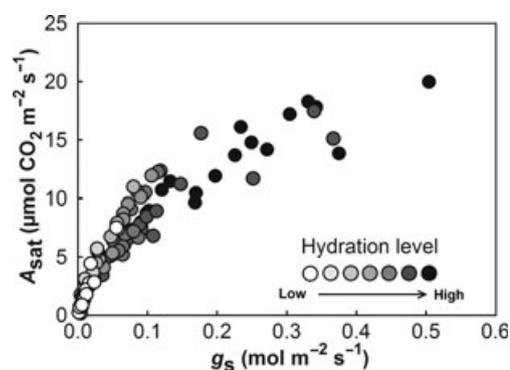


Fig. 7 Relationship between net photosynthetic rates at saturating light intensity (A_{sat}) and stomatal conductance (g_s) as a function of plant water potential.

plant water status in response to precipitation events, which occurred more frequently in summer, and not to changes in DTR_{soil} ; for example, higher Ψ_{pre} increased g_s ($r^2 = 0.81$; $P < 0.001$), resulting in greater A_{sat} (Fig. 7). Most of the variation in A_{sat} and E was explained by g_s ($r^2 = 0.94$ and 0.85 , respectively), suggesting strong stomatal regulation of carbon uptake and water loss. A weaker, but significant, negative correlation was found between g_s and VPD_L ($r^2 = 0.28$; $P < 0.001$), suggesting a limited influence of VPD_L on physiology. There was no relationship between mass-based leaf [N] and A_{sat} regardless of Ψ_{pre} .

Relationships between soil microbial and plant function

The strongest correlations between soil and plant variables were observed between soil VWC and numerous plant variables (Fig. 8a). Greater soil moisture (higher VWC) significantly reduced plant water stress (higher Ψ_{pre} ; $r^2 = 0.73$; $P < 0.001$) and indirectly affected other plant variables (A_{sat} , g_s , E , and SLA) via its effect on Ψ_{pre} .

There were no significant correlations between soil exchangeable NO_3^- -N and plant variables, although leaf [N] showed a seasonal response whereby leaf [N] was higher in spring, concomitant with higher soil NO_3^- -N (Fig. 8a and b). There were significant ($P < 0.001$) negative correlations between soil exchangeable NH_4^+ -N and E ($r^2 = 0.48$), A_{sat} ($r^2 = 0.32$), g_s ($r^2 = 0.35$), and Ψ_{pre} ($r^2 = 0.35$), suggesting greater uptake of available NH_4^+ -N in physiologically active plants. However, because all physiological variables were inter-correlated, we determined partial correlations between NH_4^+ -N and these variables. The only significant partial correlation was between NH_4^+ -N and Ψ_{pre} ($r^2 = 0.25$; $P < 0.001$), which indicated that all other correlations between NH_4^+ -N and plant physiological variables were due to their correlations with Ψ_{pre} .

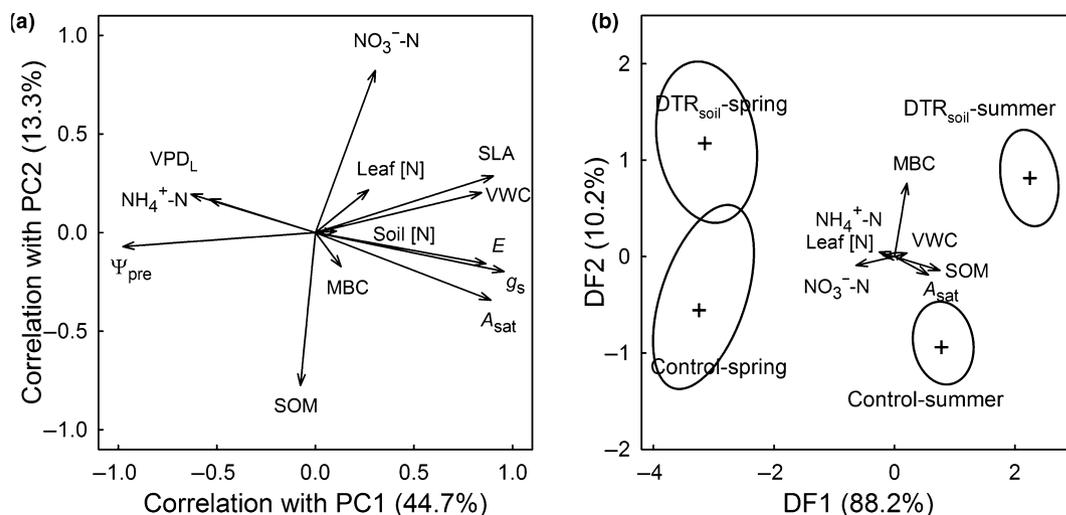


Fig. 8 Graphical representations of: (a) principal components analysis (PCA) with loadings of the plant (*Larrea tridentata*) and soil variables projected on the first two principal components (PC1 and PC2). The direction of any two vectors with one another and their lengths indicate the direction of the relationship of those variables and the strength of their relationship, respectively. Clockwise, the variables are: soil available NO_3^- -N, leaf N concentration (leaf [N]), specific leaf area (SLA), volumetric water content (VWC), total soil [N], leaf-level transpiration rates (E), stomatal conductance (g_s), leaf-level net photosynthetic rates at saturating light intensity (A_{sat}), soil microbial biomass C (MBC), soil organic matter content (SOM), xylem predawn water potential (Ψ_{pre}), soil available NH_4^+ -N, and leaf-to-air vapor pressure deficit (VPD_L). The percent of total variance explained by the portrayed relationships is 58%. (b) discriminant function analysis (DFA) with loadings (correlations) of a subset of plant and soil variables projected on the discriminant function (DF) axes. The first discriminant axis (DF1) explained most (88%) observed patterns, while the second discriminant axis (DF2) explained 10%. Treatment and season separations were along DF2 and DF1, respectively (i.e. seasonality had a stronger effect on patterns than treatment) and are represented by their centroids (+); centroids are surrounded by their 95% confidence ellipses. The correlations (loadings) of each variable with the DF axes are represented by vectors. The direction and length of any vector indicate the direction and strength, respectively, of that variable contributing to observed seasonal and treatment differences. Data were from spring and summer in 2007 and 2008. See legend (a) for variable descriptions.

Discussion

In support of our first two hypotheses, we found that a reduction in DTR_{soil} generated a twofold increase in soil MBC, a 42% increase in soil CO_2 efflux rates and a 16% reduction in soil NO_3^- -N availability throughout the experiment; soil available NH_4^+ -N was reduced by 18% in the third year only. Reductions in DTR_{soil} increased soil moisture up to 15% (a few days after a substantial rainfall), which contributed to higher CO_2 efflux rates. However, increased soil moisture did not affect MBC, which was significantly correlated with DTR_{soil} . We did not find support for our third hypothesis in that A_{sat} in *L. tridentata* was strongly regulated by g_s , but not affected by reductions in DTR_{soil} or soil available N over the 3 year period.

Impact of reducing DTR_{soil} on MBC and soil CO_2 efflux

Microbes commonly experience metabolic stress when exposed to high soil temperatures (Petersen & Klug, 1994; Zogg *et al.*, 1997). Although reductions in maximum soil temperature or increased soil moisture may

have reduced metabolic stress, we found no correlation between soil T_{max} and soil moisture with MBC. Moreover, MBC did not respond to a large rainfall pulse in summer of the third year. Instead, we found a weak, but significant negative correlation between DTR_{soil} and MBC, which suggests that DTR_{soil} is a regulator of MBC but not through effects on T_{max} or soil moisture.

Although we did not measure fungal biomass in our plots, soil fungi are the dominant microbial functional group in these Chihuahuan Desert soils (Collins *et al.*, 2008; Bell *et al.*, 2009; Clark *et al.*, 2009) and therefore, the largest contributor to MBC. Bell *et al.* (2008) observed that MBC response to rainfall events in a mid-elevation grassland at Big Bend National Park was lower in the spring than summer, reflecting higher relative abundances of fungi in the spring than summer. Moreover, Bell *et al.* (2008, 2009) found that environmental control of soil fungal activity was more tightly correlated with temperature and bacterial activity correlated with soil moisture. Subsequently, decreasing DTR_{soil} may disproportionately favor fungi over bacteria because of the more favorable temperature environment (Zak & Wildman, 2004).

In arid ecosystems, water is the primary environmental factor regulating microbial physiology and growth. In some instances, dramatically altered soil water potential may increase microbial turnover through osmotically induced mortality of soil microbial biomass (Bottner, 1985; Kieft *et al.*, 1987; Gordon *et al.*, 2008), subsequently followed by microbial proliferation. Despite this bust-and-boom response to rewetting of dry soils, total microbial biomass across seasons may not change in the long-term. We suggest that at longer time-scales, soil temperature including DTR_{soil} determines the maximum level of microbial biomass that can be sustained in an arid system.

Increases in MBC were proportionally greater than increases in CO_2 efflux, which suggests that reduced DTR_{soil} increased C use efficiency (i.e. CO_2 -C produced per unit MBC; Insam & Haselwandter, 1989; Anderson & Domsch, 2010). Increased C use efficiency could be a consequence of alterations in microbial community structure, which favors more energy efficient microbes such as fungi (Adu & Oades, 1978), or due to reduced respiration by the microbial community in response to reduced temperature variability (less stress), or some combination of these two processes.

Soil CO_2 efflux generally exhibits a strong positive relationship with temperature (Lloyd & Taylor, 1994; Cable *et al.*, 2011); however, this relationship is weakened when biological activity is constrained by water deficit (Kirschbaum, 2006; Yuste *et al.*, 2007; Lellei-Kovacs *et al.*, 2008). Indeed, we observed a strong positive correlation between soil CO_2 efflux and soil moisture and a weaker relationship with temperature. Following a large rainfall event of 29 mm at our site, soil CO_2 efflux was ca. 10 times greater than that observed in dry soils. Similarly, this effect has been widely reported in other field (Cui & Caldwell, 1997; Huxman *et al.*, 2004; Jarvis *et al.*, 2007; Inglima *et al.*, 2009) and laboratory studies (Agarwal *et al.*, 1971; Bottner, 1985; Kieft *et al.*, 1987; Fierer & Schimel, 2003; Butterly *et al.*, 2009) after dry soils received a significant pulse of water. Reductions in DTR_{soil} within arid systems may lead to significantly increased soil CO_2 efflux particularly following precipitation events or during longer periods of high soil water content.

Soil nutrients

The reduction in available soil N in response to decreasing DTR_{soil} was greatest in the third year, concomitant with the largest increase in soil MBC. Reductions in soil N availability have been observed during periods of increased MBC due to N immobilization (Doran *et al.*, 1998; Fosu *et al.*, 2007). We attribute the reduction in soil available N with decreased DTR_{soil} to

microbial processes and not utilization by *L. tridentata*. As the Chihuahuan Desert receives numerous small rainfall events <5 mm (Robertson *et al.*, 2010; Thomey *et al.*, 2011), these precipitation events trigger soil microbial activity including nutrient uptake, while plants require larger rainfall events to increase metabolic activity (Austin *et al.*, 2004; Schwinning & Sala, 2004). Moreover, leaf [N] and plant physiological activity were similar regardless of DTR_{soil} indicating that plant uptake of N remained unchanged. Alternatively, microbial-mediated reductions of soil available N could have also resulted from increased N volatilization during N transformations. N transformations, especially denitrification, may form a large source of N loss in desert systems (Peterjohn & Schlesinger, 1991). As these desert soils have low water-holding capacity and are often too dry to elicit metabolic activity, increased rates of gaseous N loss in treatment plots would occur only for a brief period after rainfall, during the period when a reduction in DTR_{soil} extended the window of adequate soil moisture.

Soil N loss can also occur via an abiotic pathway whereby rates of soil N loss accelerate with increases in soil temperatures (McCalley & Sparks, 2009). However, we suggest that this pathway was probably not the mechanism responsible for reduced soil N in the treatment plots as reduced maximum soil temperatures in these plots would have reduced N loss, and therefore have led to higher soil available N.

Both increased microbial immobilization of N and increased N volatilization probably contributed to reducing soil available N. However, we suggest that microbial immobilization played the larger role, as volatilization of N would have reduced total soil N. Instead, total soil N was either similar or higher in treatment plots compared with control plots.

Soil exchangeable NH_4^+ -N and NO_3^- -N levels showed different seasonal dynamics in response to edaphic conditions. We observed that NH_4^+ -N levels in dry soils with minimal soil CO_2 efflux rates had on average higher mean NH_4^+ -N compared with wet soils. This suggests that increased belowground activity from the soil microbial community and/or plant roots were responsible for observed declines of NH_4^+ -N (e.g. via microbial nitrification, microbial uptake or plant uptake), while during periods of low biological activity NH_4^+ -N accumulated. Other studies in semiarid and arid systems have similarly shown that inorganic N accumulates when drought limits biological activity (Stark & Firestone, 1995; White *et al.*, 2004). In contrast to NH_4^+ -N, there was no distinct pattern between NO_3^- -N availability and soil CO_2 efflux, suggesting that increased microbial immobilization of NO_3^- -N was temporally separated from subsequent higher rates

of microbial respiratory activity. Alternatively, during times of high microbial activity at optimum soil moisture denitrification dominated nitrogen dynamics.

Soil microbes function as both a source (decomposition) and sink (immobilization) for nutrients. In response to reduced DTR_{soil} , increased microbial biomass probably acted as a net sink for nutrients by immobilizing more N than it released via decomposition, and may have additionally promoted increased gaseous N loss during brief wet periods. Regardless of the mechanism, reductions in DTR_{soil} may limit primary production through microbial-mediated reductions of soil available N.

Plant physiology

Larrea tridentata physiology remained unaffected by reductions in DTR_{soil} . We hypothesized a reduction in A_{sat} as a result of microbial-mediated decreased available soil N. *Larrea tridentata* assimilates a greater proportion of NO_3^- -N than NH_4^+ -N (Schlesinger *et al.*, 2006; Jin & Evans, 2010), which is consistent with the greater relative abundance of NO_3^- -N compared with NH_4^+ -N in these Chihuahuan Desert soils. Interestingly, despite reductions in both forms of plant available N with reduced DTR_{soil} , we did not observe alterations in leaf [N]. Moreover, we found no relationship between leaf [N] and A_{sat} even at high plant water potentials. A weak or complete absence of the A vs. N relationship has been previously observed in *L. tridentata* (Mooney *et al.*, 1978; Lajtha & Whitford, 1989; Barker *et al.*, 2006). Strong correlations between g_s and A_{sat} and between Ψ_{pre} and g_s suggest that carbon assimilation in *L. tridentata* was predominantly driven by soil moisture and not DTR_{soil} .

Implications of reduced DTR_{soil} in semiarid systems

Arid and semiarid ecosystems are often slow to respond to environmental perturbation. Here, we demonstrated that it took 3 years for a reduction in DTR_{soil} to generate the largest increases in MBC and soil CO_2 efflux and the greatest decreases in soil available N; however, these belowground changes in C and N dynamics did not affect the physiological response of the dominant plant *L. tridentata*. While we found DTR_{soil} to positively affect MBC by reducing temperature stress, an extended period of adequate soil moisture after precipitation events probably interacted with reductions in temperature-related stress in increasing microbial activity and function. Increased MBC, soil CO_2 efflux and a lack of plant physiological response to reduced DTR_{soil} may have long-term consequences for C budgets within arid systems if soils increase ecosys-

tem C loss (respiration) without an equivalent ecosystem C gain (photosynthesis) (Huxman *et al.*, 2004). If these trends are maintained, our results suggest that arid systems will become greater C sources under conditions of reduced DTR_{soil} , which may consequently generate a positive feedback to rising global temperatures. However, longer-term studies are needed to assess whether belowground C input will eventually increase to sustain these higher rates of CO_2 efflux or whether observed increases were transitory. Ultimately, ecosystem models of N and C fluxes will need to account for these temperature-driven processes.

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