CrossMark

GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Seasonal microbial and nutrient responses during a 5-year reduction in the daily temperature range of soil in a Chihuahuan Desert ecosystem

Natasja C. van Gestel[1,2] · Nirmala Dhungana[2] · David T. Tissue[3] · John C. Zak[2]

Abstract High daily temperature range of soil (DTR_{soil}) negatively affects soil microbial biomass and activity, but its interaction with seasonal soil moisture in regulating ecosystem function remains unclear. For our 5-year field study in the Chihuahuan Desert, we suspended shade cloth 15 cm above the soil surface to reduce daytime temperature and increase nighttime soil temperature compared to unshaded plots, thereby reducing DTR_{soil} (by 5 °C at 0.2 cm depth) without altering mean temperatures. Microbial biomass production was primarily regulated by seasonal precipitation with the magnitude of the response dependent on DTR_{soil}. Reduced DTR_{soil} more consistently increased microbial biomass nitrogen (MBN; +38 %) than microbial biomass carbon (MBC) with treatment responses being similar in spring and summer. Soil respiration depended primarily on soil moisture with responses to reduced DTR_{soil} evident only in wetter summer soils (+53 %) and not in dry spring soils. Reduced DTR_{soil} had no effect on concentrations of dissolved organic C, soil organic matter (SOM), nor soil inorganic N (extractable $NO_3^- –N + NH_4^+ –N$).

Higher MBN without changes in soil inorganic N suggests faster N cycling rates or alternate sources of N. If N cycling rates increased without a change to external N inputs (atmospheric N deposition or N fixation), then productivity in this desert system, which is N-poor and low in SOM, could be negatively impacted with continued decreases in daily temperature range. Thus, the future N balance in arid ecosystems, under conditions of lower DTR, seems linked to future precipitation regimes through N deposition and regulation of soil heat load dynamics.

Introduction

Arid systems inherently experience high daily temperature range of air (DTR_{air}), but the variability and magnitude of soil surface temperatures on a daily basis are even more extreme as the daily temperature range of soil (DTR_{soil}) at the surface can vary over 40 °C (Hadley 1970; Nobel 1989). High DTR_{soil} has been shown to adversely impact microbial biomass (Biederbeck and Campbell 1973; van Gestel et al. 2011), microbial growth (Biederbeck and Campbell 1973) and function (Zhu and Cheng 2011). DTR_{air} has been decreasing globally since the 1950s because of minimum temperatures increasing at a faster rate than maximum temperatures (Vose et al. 2005); in deserts, the decreasing trend in DTR_{air} has been particularly strong (Zhou et al. 2009). How a decrease in DTR_{air}, and thus likely DTR_{soil}, will affect microbial processes in deserts is not known. In addition to high DTR_{soil}, arid systems also exhibit large seasonal differences in microbial dynamics and nutrient transformations that are linked to water availability (Austin

Communicated by Jason P. Kaye.

✉ Natasja C. van Gestel
natasja.van-gestel@nau.edu

[1] Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA

[2] Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA

[3] Hawkesbury Institute for the Environment, University of Western Sydney, Richmond, NSW 2753, Australia

Springer

et al. 2004; Bell et al. 2008; Collins et al. 2008; Parker and Schimel 2011). Large fluctuations in soil water potential (i.e. drying–wetting cycles), aside from influencing soil heat load dynamics, can promote microbial turnover, soil organic matter decomposition and mineralization (Kieft et al. 1987; Austin et al. 2004), resulting in temporary pulses of higher C and N compared to soils that are continuously wet (Austin et al. 2004). The fate of the microbial biomass pool is important because this pool dually functions both as a source and a sink of labile nutrients, and is thus linked to primary production.

We have a rudimentary understanding of the interaction between seasonal soil moisture levels and seasonal patterns of DTR_{soil} in regulating microbial biomass (including the immobilized N) and nutrient levels. We present data from a 5-year study in the Chihuahuan Desert that enabled us to examine the interplay between natural patterns in DTR_{soil} and seasonal moisture in influencing soil microbial biomass and nutrients. In the Chihuahuan Desert, which is a summer rainfall dominated system with a dry spring (Reynolds et al. 2004; Gutschick and Snyder 2006; Collins et al. 2008; van Gestel et al. 2011), DTR_{soil} is high in both seasons (van Gestel et al. 2011). In the dry spring, microbes are likely to be in a predominantly dormant state. Dormancy enables microbes to avoid adverse environmental conditions and can be achieved by producing endospores, cysts, and other propagules, or by reducing metabolic activity to a minimum level (Dion and Nautiyal 2008). Desert soil microbes tolerate temperature extremes better when they are dormant (Pointing and Belnap 2012). Therefore, microbes in spring should be less susceptible to daily temperature fluctuations compared to summer, when precipitation events are more frequent and microbes are in a higher state of activity.

Our previous field study (van Gestel et al. 2011) in the Chihuahuan Desert demonstrated that reducing DTR_{soil} down to 15 cm depth with maintenance of daily mean temperatures positively affected soil microbial biomass and reduced soil inorganic N (i.e. sum of extractable levels of $NH_4^+–N$ and $NO_3^-–N$), particularly during years when moisture was adequate for the microbial biomass to respond to imposed changes in DTR. However, some key issues remain unresolved, including whether: (1) microbial and nutrient responses to reduced DTR_{soil} differ between wetter seasons (summer) and drier seasons (spring); and (2) whether decreased soil inorganic N was a result of increased microbial N uptake. In this 5-year study, in order to address these key issues, we used a new shading design that elevated the shade cloth to reduce DTR_{soil} and maintained daily mean temperature while minimizing differences in soil moisture between control and shaded plots. We hypothesized that (1) a reduction in DTR_{soil} would increase soil microbial biomass and soil respiration rates to a greater degree in the warmer, wetter summer compared

with the cooler, drier spring, and (2) that increases in microbial biomass nitrogen (MBN) in response to DTR_{soil} would coincide with lower soil inorganic N.

Materials and methods

Study site and climate

The study site is located in the Chihuahuan Desert at Big Bend National Park in Texas (29.23°N, 103.17°W). Soils are loamy-skeletal hyperthermic Ustic Haplocalcids from the Corozones series (Cochran and Rives 1985), and are sparsely vegetated with *Larrea tridentata* ([DC] Cov.; creosotebush) which is the dominant shrub species. Mean annual air temperature is 19.4 °C (1981–2010; http://www.ncdc.noaa.gov), with average maximum air temperatures of 27.9 °C in spring and 33.7 °C in summer, and average minimum temperatures of 12.1 ºC in spring and 20.1 ºC in summer. Mean annual precipitation (MAP) is 342 mm (1983–2012). Average spring (March–May) rainfall is 17 % of MAP (59 mm) and 47 % of MAP (160 mm) in summer (June–August).

Since the 1950s, seasonal DTR_{air} has declined by 0.20 ºC/decade in spring and by 0.28 ºC/decade in summer http://www.ncdc.noaa.gov; Fig. 1), which emphasizes the importance of determining effects of reduced DTR_{soil} in these two seasons with distinct moisture patterns. The other two seasons exhibited a weak negative DTR_{air} trend
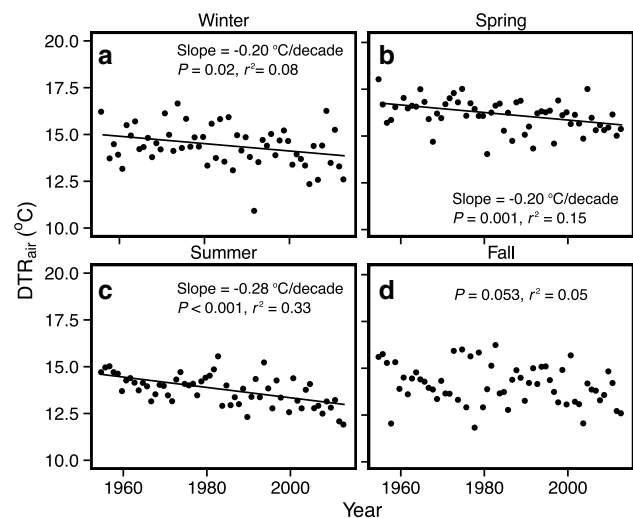

Fig. 1 Daily temperature range of air (DTR_{air}) averaged for **a** winter, **b** spring, **c** summer, and **d** fall, from 1955 to 2013 at Panther Junction, Big Bend National Park (http://www.ncdc.noaa.gov/; Panther Junction COOP ID 416792). Air temperatures are recorded at 1.5 m above the soil surface. Seasons are subdivided as follows: *Winter* December–February; *Spring* March–May; *Summer* June–August; *fall* September–November

(winter) or the trend was not significantly different from zero (fall; Fig. 1).

Experimental design and environmental monitoring

Soil temperature manipulation began in 2009 by elevating shade cloth (50 % white poly-ethylene fabric; Gempler's®, Madison, WI, USA) 15 cm above the soil surface in five plots (Fig. S1, supplementary material). The shade cloth was attached to a 4×3 m PVC frame and held in place with grommets and cable ties; an additional five 4×3 m plots served as controls (no shading). All plots are permanent. There is no visible cryptogamic presence at our gravelly site; if endolithic cyanobacteria are present (i.e. living inside rocks), we assume the shade cloth will have little direct effect on organisms that already live in the shade.

To capture the spring and summer seasons we collected soils in March, May, and July in 2009, and biannually thereafter (2010–2013) in March (spring) and August (summer) for a total of 11 sampling dates. On each sampling date, we collected 20 samples total (i.e. two samples per plot) from unvegetated shrub interspaces inside the plots. Soils were collected from the 0–15 cm soil layer with a hand shovel, sieved to 2 mm and kept at 4 ºC until analyzed (<1 week).

Air (at 1 m height) and soil temperatures were recorded every 30 min using HOBO® data loggers (H08-031-08 for air and HOBO® Pendants for soil; Onset Computer, Bourne, MA, USA). Soil temperatures were recorded near the soil surface at 0.2 cm depth to avoid direct sunlight and at 15 cm. Soil volumetric water content (VWC) was recorded every 2 h at 15 cm soil depth using EM-50 data loggers and EC-5 dielectric ECH2O probes (Decagon Devices, Pullman, WA, USA). We recorded VWC at 15 cm, because it is located within the 10–30 cm soil layer utilized by a variety of annual and perennial desert plants (Noy-Meir 1973).

Microbial biomass C and N

Soil microbial biomass C (MBC) and N (MBN) were assayed using field-moist soil within 2 days of collection using the chloroform-fumigation extraction technique (Brookes et al. 1985; Vance et al. 1987). Briefly, from each soil sample, we weighed 4 sub-samples on a 5-g dry weight equivalent basis. One pair was fumigated for 48 h with chloroform while the other pair was left un-fumigated. Soils were extracted with 50 ml of 0.5 M K_2SO_4. The solution was filtered using Whatman® Grade 43 filter paper and measured at 280 nm (Nunan et al. 1998) as well as analyzed via a TOC-TN analyzer (Shimadzu, Kyoto, Japan). The increase in extractable C and N in K_2SO_4 extracts in the fumigated set compared to the non-fumigated set were converted to MBC and MBN using a k_{EC} value of 0.45 (Vance et al. 1987; Joergensen 1996) and a k_{EN} factor of 0.54 (Jenkinson 1988), respectively. The K_2SO_4-extracted C in non-fumigated soils was used as a proxy for dissolved organic C (DOC) (Jones and Willett 2006; Zeglin et al. 2007). This proxy for DOC may include inorganic C (e.g., carbonates) and may thus overestimate actual DOC.

Nutrients, soil organic matter and gravimetric moisture

Extractable NH_4^+–N, NO_3^-–N (2 M KCl) and soil organic matter (SOM) were analyzed by Waters Agricultural Laboratories (Owensboro, KY, USA) within 5 days of collection. In addition to VWC, which best represents seasonal moisture patterns, we also measured gravimetric water content (GWC) to evaluate moisture conditions during the day of sampling. Our soils may contain gypsum and could lose water from the crystal structure. Therefore, we determined GWC by drying soils at 70 ºC until constant weight.

Soil CO_2 efflux

From March 2009 until March 2011, we measured soil respiration rates on the same day as soil sample collections. Soil CO_2 efflux was measured in each plot using the LI-6400 and attached soil respiration chamber (LI-6400-09; LI-COR, Lincoln, NE, USA), which was placed on permanently installed PVC collars. Measurements were taken within a 2-h window in the morning (0830–1030 hours) and we alternated between measuring control and DTR plots. The CO_2 drawdown–rise cycle was repeated three times and the computed CO_2 efflux values were averaged for each plot.

Statistical analyses

Statistics were performed in R (R Core Team 2013). First, we performed a mixed-model analysis of variance (ANOVA) using the 'lme' function (Pinheiro et al. 2012) with season, treatment, year and all pairwise comparisons (only DOC had a significant 3-way interaction) as fixed effects to determine whether soil variables (MBC, MBN, NH_4^+–N, NO_3^-–N, SOM, GWC, soil respiration) in spring responded differently to a reduction in DTR_{soil} compared to summer, and whether patterns were similar across years. For soil respiration, measured from 2009 until spring 2011, we omitted 2011 data because of historic severe drought that preceded the measurement. Because of non-independence of the data (plots were repeatedly sampled) we included plot ID as a random effect. We opted to use the model *without* temporal autocorrelation (using months since start of experiment as the time variable) because these models had lower AIC values.

Second, we used redundancy analyses (RDA; 'rda' function;) to determine whether the relationship between environmental conditions (DTR_{soil}, soil T_{max}, and soil moisture) and belowground responses differed between DTR plots and control plots. For this, we calculated the average environmental conditions during the 5-day period prior to each sampling date and related this to our suite of soil responses. We chose the 5-day window because antecedent conditions during the previous 5 days may be more important than current-day alone for a variety of desert ecological processes which can respond to abiotic factors at relatively short time scales (Ogle et al. 2015). Data were centered and scaled prior to running the RDA to account for differences in units and ranges. We performed a total of four RDA analyses, each with 30 observations per variable in spring and 25 in summer, by separating the dataset by season (spring and summer) and treatment (control and DTR plot). MBN data were excluded in the RDA because missing MBN data (in spring 2011) would have excluded the suite of other variables measured during that period in the RDA analyses. However, to address prediction 2, we examined whether the relationship between MBN and inorganic N differed between DTR plots and control plots. For this, we used a mixed-model analysis of covariance, where treatment was included as a fixed effect, plot ID as a random effect, and NO_3^-–N as the covariate. Variables were log-transformed when necessary to meet assumptions of homoscedasticity. Confidence intervals (CI) of the means are reported at the 2.5 and 97.5 quantiles (i.e. 95 % CI) following a bootstrap approach of 5000 iterations. The α-level was set at 0.1 to accommodate the high variability commonly observed in our ecosystem.

Results

Seasonal temperature and moisture during study period

The third year (2011) was an extreme drought year exhibiting the hottest air temperatures of the experimental period (air T_{mean} was 4.2 ℃ higher in spring and 3.3 ℃ higher in summer compared to the 30-year average of 20.5 ℃ and 27.1 ℃, respectively), while the other study years were similar to the 30-year average. Likewise, mean soil surface temperatures in control plots were highest in 2011 compared to the other study years due to a combination of high T_{max} and high T_{min}. Seasonal soil surface temperatures during the study period (with the exception of 2011) exhibited an average T_{min} of 15.0 ℃ and a T_{max} of 51.6 ℃ in spring, while summers were hotter, with an average T_{min} of 24.0 ℃ and a T_{max} of 60.4 ℃. Compared to these averages, 2011

had 2.6 ℃ higher T_{max} in both seasons, and T_{min} was 1.7 ℃ higher in both seasons, rendering 2011 the hottest year. However, the fifth year (2013) experienced the highest surface DTR_{soil} due to a combination of high T_{max} and lowest T_{min}, resulting in a DTR_{soil} of 41.2 ℃ in both seasons, compared to a DTR_{soil} of 35.5 ℃ in both seasons for the other years.

The 2011 drought affected 26 % of the contiguous USA (http://www.ncdc.noaa.gov), with no rainfall from September 2010 until late July 2011 (Fig. 2c). Typical for this desert, summer precipitation was usually higher than in spring (Fig. 2c), except in the fourth year (2012) when they were of similar magnitude in both seasons (ca. 110 mm). Highest seasonal precipitation was received in summer of 2010 [213 mm, mostly in June (61 mm) and July (129 mm)]. Continuous measurements of soil moisture (VWC), more indicative of seasonal moisture patterns, showed that generally soils were wetter in summer in summer [7.9 %; with 95 % confidence interval (CI) of 7.6–8.3 %] compared to spring (5.7 %; with 95 % CI of 5.5–6.0 %). However, spot measurements of soil moisture (GWC) during sample collection determined that soils collected in spring could be drier (2009), wetter (2010) or similar (2011–2013) to summer soils (Fig. 3).

Shading effects on the soil environment

With the exception of the extreme drought year (2011), the shade plots were cooler during the day and warmer during the night compared to control plots at 0.2 cm depth, but not at 15 cm depth. Henceforth, all references to soil temperatures (including DTR_{soil}) are for the 0.2 cm soil depth. The daytime reduction and nighttime increase of soil temperatures were equivalent in magnitude, thereby effectively reducing DTR_{soil} ($P < 0.001$) without altering T_{mean} ($P = 0.74$; Fig. 2a). In spring, shade plots experienced DTR_{soil} of 32.4 ℃ (−4.1 ℃ difference in DTR compared to control; Fig. 2b) and 30.6 ℃ in summer (−5.8 ℃ difference in DTR compared to control). From March until August 2011, during the severe drought, DTR_{soil} was greater or similar in shade plots compared to control plots. In the year of highest DTR_{soil} (2013), shading was effective in reducing DTR_{soil} by 4.0 ℃ on average (37.2 ℃ in DTR plots compared with 41.2 ℃ in control plots).

Temporal patterns of VWC (from data loggers) were the same between shaded and control plots ($P = 0.52$). Gravimetric water content (GWC), measured during soil collections only, was not affected by shading, except in 2009 (Fig. 3; Table 1; $P < 0.05$). Given that moisture differences were minimized between plot types we will henceforth refer to our shade plots as DTR plots.

Fig. 2 **a** Example of the effect of shade cloth on soil surface thermal regime over a 24-h period (midnight to midnight); values are averaged over the period July–December 2012. **b** Daily soil temperature range (DTR) measured in control and DTR$_{soil}$ reduction plots during 2009–2013. Values are presented as 5-day averages of the preceding 4 days and the current day. **c** Daily volumetric water content in control and DTR$_{soil}$ reduction plots in response to precipitation events from January 2009 through October 2013. Total spring (*spr*) and summer (*sum*) precipitation are indicated for each year
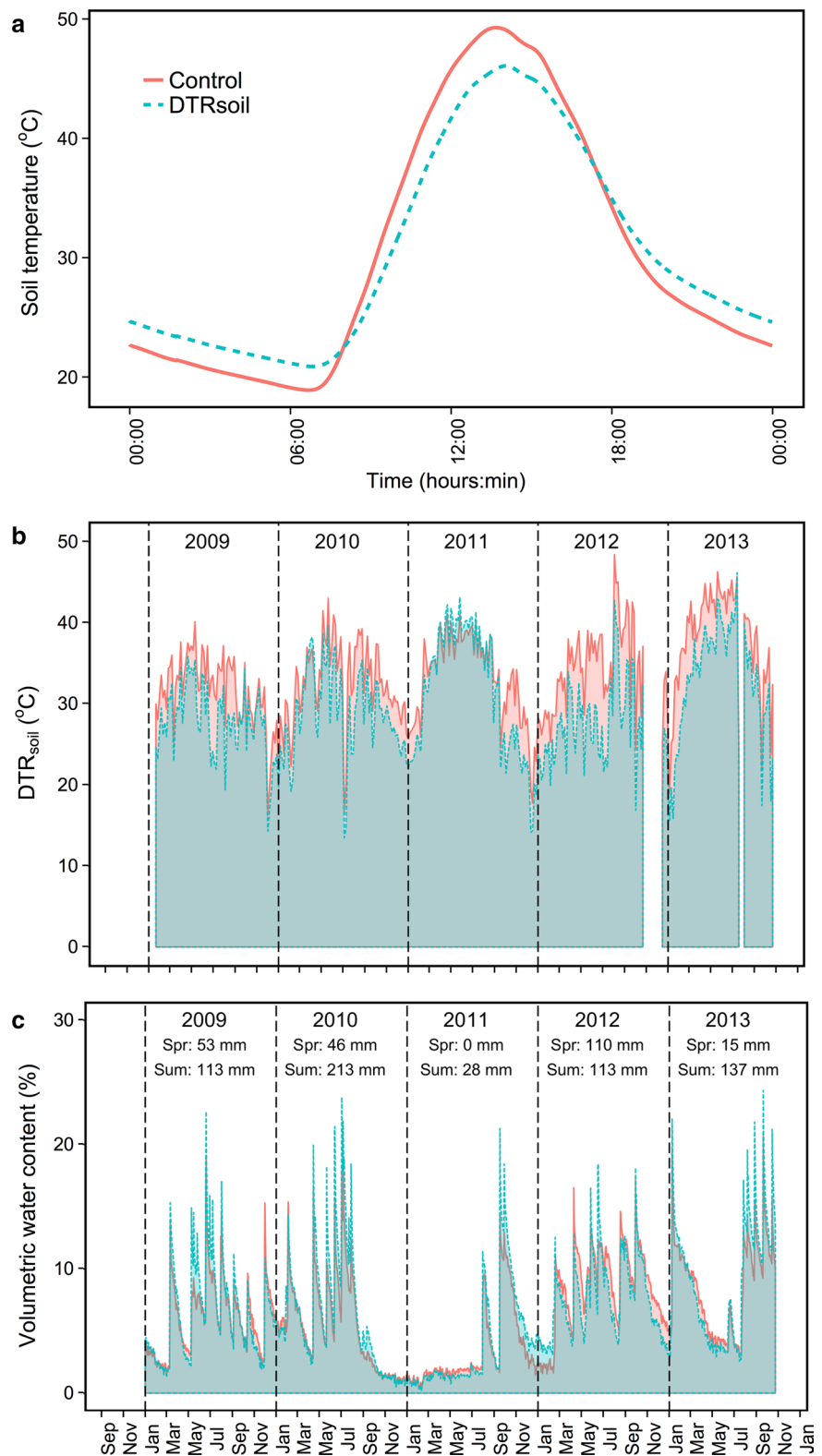
Soil microbial biomass C and N

The first 3 years (2009–2011) showed a more consistent pattern of higher MBC in DTR plots compared to control plots, with similar or lower MBC thereafter (Fig. 3a). This resulted in a wide CI of relative change in MBC from DTR plots compared to control plots, with 2–52 % (95 % CI) higher MBC in DTR plots compared to control plots in
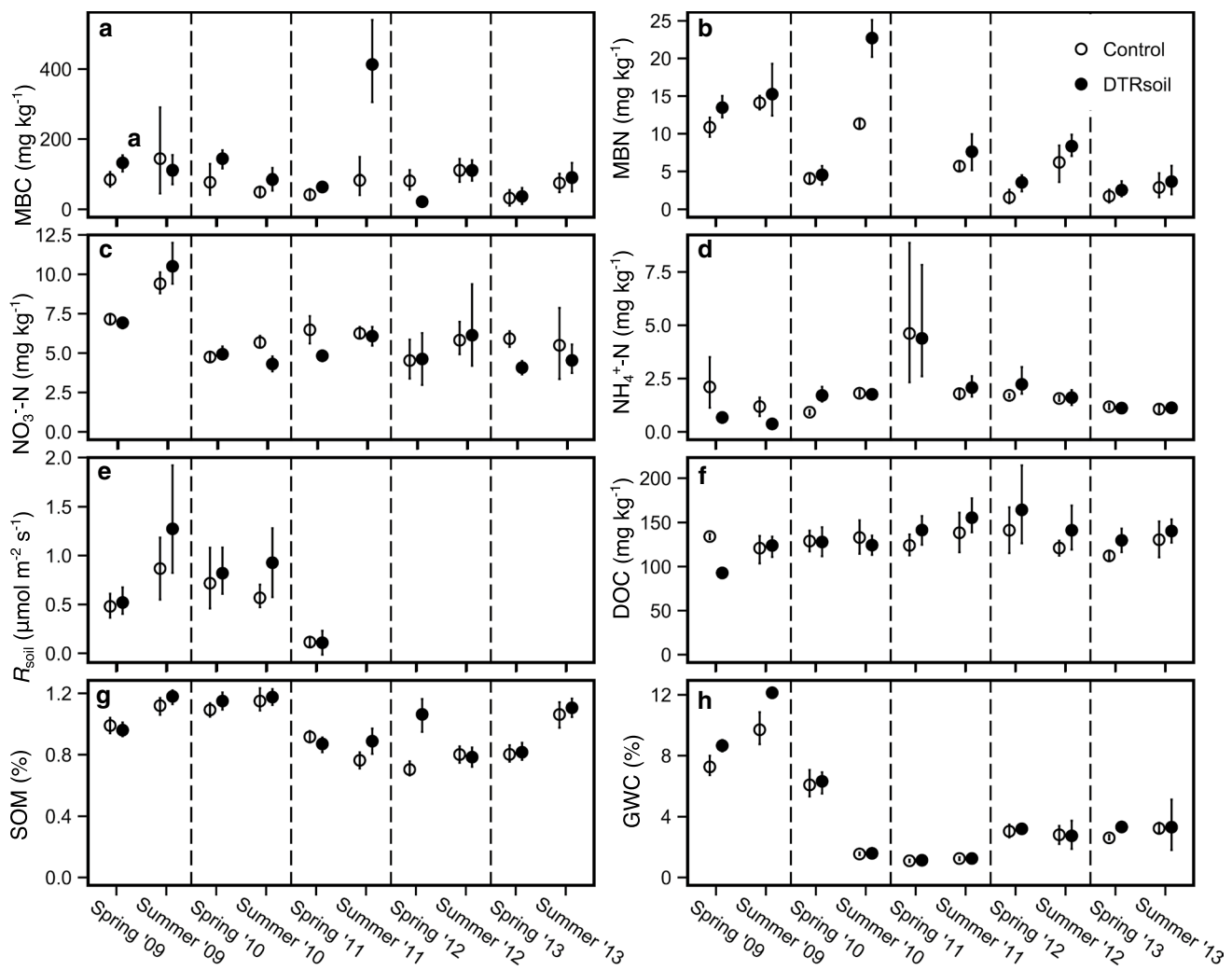
Fig. 3 Mean and 95 % CI (5000 bootstrap iterations) of the following soil variables during spring and summer of 2009–2013: **a** microbial biomass carbon (*MBC*), **b** microbial biomass nitrogen (*MBN*), **c** extractable NO_3^-–N, **d** extractable NH_4^+–N, **e** soil respiration rates (R_{soil}), **f** K_2SO_4–extractable dissolved organic carbon (*DOC*), **g** soil organic matter (*SOM*), and **h** gravimetric water content (*GWC*) at time of sampling. Non-overlapping CIs indicate that means are significantly different

spring, while these values were 17–150 % (95 % CI) in summer (Table 1). The upper CI of the summer response was largely driven by high MBC relative to control plots at the end of the extreme drought period, shortly after the first rainfall events, in summer 2011. In terms of seasonal patterns, MBC was higher, similar or lower in spring compared to summer, depending on year, but was overall 78 % higher (41–125 % CI) in summer (127 mg kg^{-1}) than spring (72 mg kg^{-1}; Table 1).

MBN showed a more consistent positive response to reduced DTR$_{soil}$ throughout the study period compared to MBC. MBN increased to a similar degree in spring (32 %; 10–51 % CI) and summer (43 %; 20–73 % CI) in response to reduced DTR$_{soil}$ (Fig. 3b). The strongest response occurred in summer of the second year (2010), when MBN was twofold higher in DTR plots

(22 mg kg^{-1}) compared to control plots (11 mg kg^{-1}; Fig. 3d; $P < 0.001$). There was a strong main effect of season ($P < 0.001$) on absolute MBN, with 85 % (62–111 % CI) higher MBN (comparable to summer MBC increases) in summer (9.8 mg kg^{-1}) compared to spring (5.3 mg kg^{-1}).

Inorganic soil N

There were no long-term positive or negative trends in extractable NO_3^-–N in response to reduced DTR$_{soil}$ (Fig. 3c). Rather, NO_3^-–N was highly variable, within and across years, with either similar or lower values in DTR plots compared to control plots. There was a marginally significant seasonal effect on overall NO_3^-–N, with 18 % (9–29 % CI) higher NO_3^-–N in summer (6.4 mg kg^{-1})

Table 1 Five-year seasonal data (period 2009–2013) of microbial biomass carbon and nitrogen (*MBC*, *MBN*), inorganic N, K$_2$SO$_4$ extractable dissolved organic C (C$_{K_2SO_4}$), gravimetric water content (*GWC*), soil organic matter (*SOM*) and soil respiration rates (R_{soil}) in control and DTR plots ($n = 5$)

Season/treatment	MBC (mg kg^{-1})	MBN (mg kg^{-1})	NH$_4^+$–N (mg kg^{-1})	NO$_3^-$–N (mg kg^{-1})	C$_{K_2SO_4}$* (mg kg^{-1})	GWC (%)	SOM (%)	R_{soil}^{a} (μmol m^{-2} s^{-1})
Spring								
Control	63 (54–75)	4.6 (4.4–4.7)	2.1 (1.5–3.0)	5.8 (5.5–6.1)	128 (118–139)	4.0 (3.9–4.1)	0.90 (0.87–0.92)	0.60 (0.42–0.85)
DTR$_{soil}$	80 (72–86)	6.0 (5.0–6.9)	2.0 (1.5–2.8)	5.1 (4.6–5.5)	131 (120–144)	4.5 (4.3–4.8)	0.97 (0.92–1.02)	0.67 (0.51–0.87)
Summer								
Control	92 (69–123)	8.0 (7.1–8.8)	1.5 (1.4–1.6)	6.5 (6.1–6.8)	129 (121–136)	3.7 (3.4–4.1)	0.98 (0.94–1.02)	0.72 (0.51–0.94)
DTR$_{soil}$	162 (121–206)	11.5 (9.9–13.1)	1.4 (1.3–1.5)	6.3 (5.5–7.2)	137 (125–151)	4.2 (3.8–4.6)	1.02 (0.98–1.08)	1.10 (0.73–1.58)
% Trt change								
Spring	26 % (2–52)	32 % (10–51)						12 % (−25–76)
Summer	75 % (17–150)	43 % (20–73)						53 % (−6–146 %)
% Change								
Summer vs. spring	78 % (41–125)	85 % (62–111)		18 % (9–29)		−7 % [−1–(−14)]	7 % (3–12)	43 % (1–102 %)
Mixed-model *P* values								
Treatment (T)	**0.04**	**0.02**	0.38	0.11	0.83	0.56	0.17	0.32
Season (S)	**0.001**	**<0.001**	0.75	**0.09**	0.20	**0.01**	**0.07**	**<0.001**
Year (Y)	**<0.001**	**<0.001**	**0.002**	**<0.001**	**0.01**	**<0.001**	**<0.001**	0.28
T × S	0.24	0.72	0.71	0.58	0.18	0.63	0.92	**0.05**
T × Y	**0.08**	0.19	**0.06**	0.29	**<0.001**	0.66	0.37	0.65
S × Y	**0.002**	0.36	0.47	0.26	0.51	0.33	0.91	**<0.001**

The percent change relative to control is shown when the main effect of treatment (T) or T × season were significant. Seasonal differences are shown as % change between summer and spring values when the season effect was significant. Values in parentheses represent the 95 % CI (5000 bootstrap iterations). *P* values were obtained using a mixed-model with treatment, season, year and all pairwise interactions as fixed effects, plot ID as the random effect. *P* values <0.1 are in bold

* Significant 3-way interaction

^{a} Soil respiration rates (R_{soil}) represent 2-year means for spring and summer (spring 2011 data were excluded)

compared to spring (5.4 mg kg^{-1}), corresponding to higher summer precipitation compared to spring (Fig. 2c).

There was high inter- and intra-annual variability in NH$_4^+$–N in response to reduced DTR$_{soil}$, which resulted in an overall (all years combined) non-significant effect of treatment on NH$_4^+$–N (Fig. 3d; Table 1). Furthermore, NH$_4^+$–N did not differ between spring and summer (1.7 mg kg^{-1} on average).

Soil CO$_2$ efflux rates, DOC and SOM

Although the main effect of treatment was not significant, there was a significant season × treatment interaction (Table 1) with higher soil CO$_2$ efflux rates in DTR plots compared to control plots in summer (+53 %), but not spring despite concurrent higher MBC in spring. In summer, higher soil CO$_2$ efflux rates coincided with either similar (2009) or higher MBC (2010). There was a significant main effect of season, with 43 % higher soil CO$_2$ efflux rates in summer compared to spring (Table 1); soil respiration rates depended strongly on moisture conditions (Fig. 3e, h), with lowest rates at 0.1 μmol CO$_2$ m^{-2} s^{-1} in

March 2011 due to lack of rainfall since September 2010, while a maximum rate of 2.5 μmol CO$_2$ m^{-2} s^{-1} was observed in moist soil in summer 2009.

There was no significant main or interactive effect of shading and season on overall K$_2$SO$_4$ extractable C (DOC; Table 1), but there was a significant treatment × year effect on DOC showing a pattern of DOC in DTR plots diverging from control plots starting in the third year (2011; Fig. 3f). SOM exhibited a seasonal trend with generally higher values in summer compared to spring (+7 %; 3–12 % CI; Table 1).

Redundancy analyses

Between 33 and 55 % of the variance in soil responses (MBC, NO$_3^-$–N, NH$_4^+$–N, DOC and SOM) were explained by the variance in T_{max}, DTR$_{soil}$ and soil moisture (Fig. 4a–d). Arrows in Fig. 4 are the scores that reflect the nature (angle of arrows) and strengths (lengths of arrows) of the relationships of the *explained* portion of the data. Variables can be related positively (arrows in same direction), negatively (arrows in opposite direction), or have

no correlation (arrows at right angles). Despite that control plots experienced higher soil temperatures than shade plots DTR_{soil}, not T_{max}, was a negative predictor of MBC in spring (Fig. 4a), while both temperature variables were a negative predictor of MBC in summer (Fig. 4c). In contrast, for DTR plots, neither temperature variables were predictors of MBC in spring (Fig. 4b), while in summer they were positive predictors of MBC (Fig. 4d). Another important predictor of MBC was VWC, with a generally positive relationship between the two across seasons and treatment.

Soil moisture was consistently an important positive predictor of NO_3^-–N regardless of season or treatment, while it generally was a negative predictor or not

correlated to NH_4^+–N. In contrast, DTR_{soil} was consistently a negative predictor of NO_3^-–N levels, but not an important predictor of NH_4^+–N except in spring control plots (Fig. 4a). Soil moisture was also important in modulating thermal regime, particularly in summer with higher soil moisture in summer resulting in a reduction in both T_{max} and DTR_{soil}.

For SOM, the predictors differed between seasons but the pattern was consistent regardless of temperature manipulation; in spring, soil T_{max} was a positive predictor of SOM, while in summer NH_4^+–N negatively correlated with SOM. No consistent pattern emerged in determining predictors for DOC.
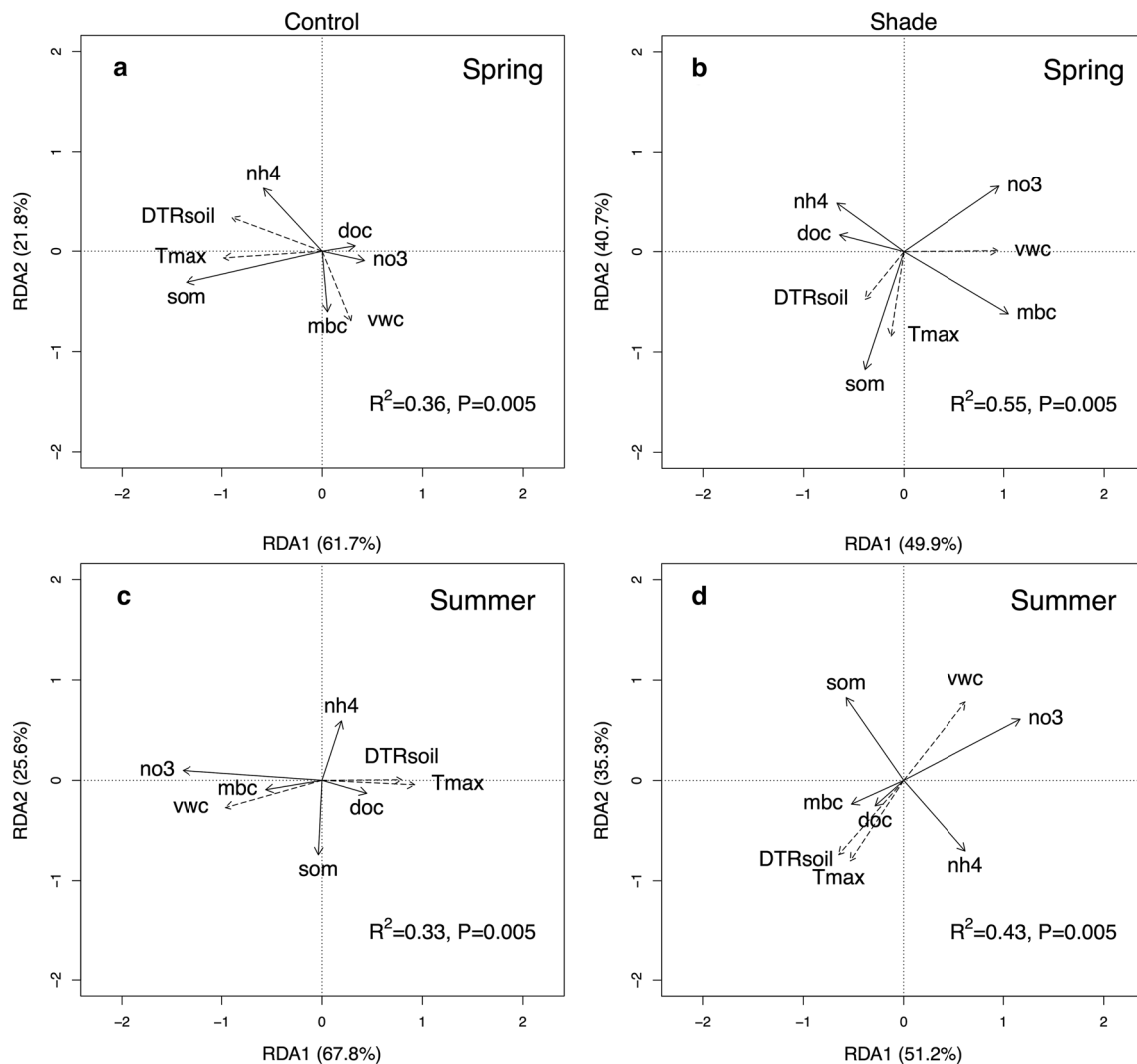

Fig. 4 Visual representation of redundancy analyses in spring for control **a** and shade plots **b**, and in summer for control **c** and shade plots **d**. The angle of the *two arrows* reflects the nature of the relationship between the variables (i.e. positive if in *similar direction*, negative if in *opposite direction*, and no relationship at *right angles*). *Arrow length* indicates the strength of that relationship. Explanatory variables (*dashed arrows*) are the 5-day average volumetric soil moisture (*vwc*), daily temperature range of soil (*DTR_{soil}*) and daily maximum soil temperatures (*T_{max}*) prior to soil collections. The response variables (*solid arrows*) are microbial biomass C (*mbc*), extractable NO_3^-–N and NH_4^+–N (*NO3, NH4*), soil organic matter (*som*), and dissolved organic C (*doc*)
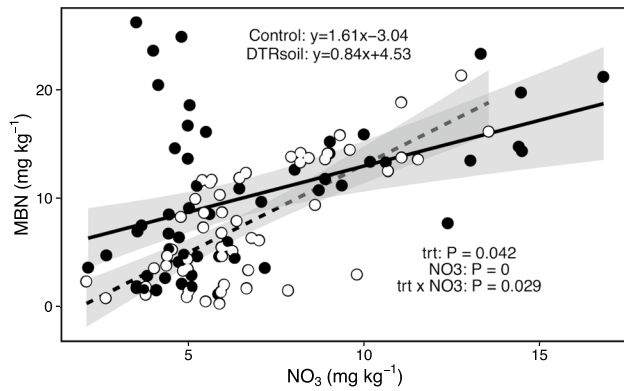
Fig. 5 Relationship between extractable NO_3^-–N and microbial biomass N (MBN) for control (*open*) and DTR plots (*closed*) during the 2009–2013 study period ($r = 0.53$). *Shaded areas* represent the 95 % confidence intervals of the *regression lines*. Results of a linear mixed-model analysis of covariance are presented

MBN and NO_3^-–N relationship

Pearson correlation analyses showed that MBN, soil moisture, and NO_3^-–N were positively inter-correlated (all $P < 0.001$), with a strong positive correlation between MBN and NO_3^-–N (Fig. 5; $r = 0.53$). Partial correlations showed that two pairwise combinations were significant ($P < 0.001$): (1) between NO_3^-–N and MBN ($r = 0.31$) after removal of moisture effects, and (2) between soil moisture and NO_3^-–N ($r = 0.60$) after removal of MBN effects.

We also found that DTR plots exhibited a different relationship between MBN and NO_3^-–N with higher MBN at lower NO_3^-–N levels than in control plots. This resulted in a significantly higher intercept for DTR plots compared to control plots (Fig. 5).

Discussion

A simultaneous decrease in soil T_{max} and increase in soil T_{min} (i.e. reduced DTR_{soil}) resulted in higher MBC in both seasons in the first 3 years but not in the final 2 years, while MBN more consistently showed an increase in response to reduced DTR_{soil}. Contrary to our hypothesis, the positive response of microbial biomass to decreased DTR_{soil} was similar in both spring and summer, and not limited to summer periods when soils are typically wetter and warmer than spring. Respiration rates, measured in both seasons for the first 2 years of the study, were strongly positively linked to ambient moisture (which was not affected by our treatment), with responses to DTR manipulation evident only in summer. Soil respiration was unaffected by DTR manipulation in spring despite concurrent higher MBC in DTR

plots compared to control plots. This suggests that reduced DTR_{soil} reduced the loss of C per unit of microbial biomass in spring. Our results are inconclusive regarding our second hypothesis because higher MBN coincided on occasion with lower inorganic N, but not always.

Responses to reduced DTR_{soil} in spring and summer

Microbes in dry grassland soils have been shown to still exhibit minimal activity (Xiang et al. 2008; Parker and Schimel 2011), suggesting that microbes can be metabolically active at extreme low moisture. For example, an important microbial group, the fungi, can produce hyphae throughout the dry summer season despite volumetric soil moisture content <5 % (Treseder et al. 2010). Fungi are the dominant microbial group in Chihuahuan Desert soils and more drought-tolerant than bacteria (Collins et al. 2008; Bell et al. 2009; Clark et al. 2009). We have no visible biocrust on the soil surface nor lichen on rocks, but do not rule out the presence of surface-dwelling photosynthetic organisms. We suspect soil respiration rates to be predominantly from non-photosynthetic soil microbes, because we sampled soils down to 15 cm in unvegetated shrub interspaces. Low, but positive soil respiration rates were observed during extended dry periods at our site, even during the 2011 drought, which suggests that microbes (most likely fungi) remained at low levels of metabolic activity, and, therefore, could have benefited from reduced DTR_{soil} despite seasonal differences in soil moisture status. Consistent with our previous study (van Gestel et al. 2011), the effect of shade cloth in increasing soil respiration rates was more apparent in wet soils. Consequently, in this study, CO_2 efflux rates were higher in DTR plots compared to control plots during the comparatively wetter summer and not in spring. In summer, MBC was either similar (2009) or higher (2010) in DTR plots during times when soil respiration was measured. Higher respiration without a concomitant increase in MBC suggests that in 2009 reduced DTR_{soil} enhanced activity of the soil microbes, while in 2010 higher CO_2 efflux rates in DTR plots reflected greater microbial biomass. A lack of respiration response to DTR manipulation treatment in spring, despite concurrent increases in microbial biomass, indicates that relatively less C was lost (i.e. lower soil respiration rates) per unit microbial biomass in response to reduced DTR_{soil}. Lower respiration rates per unit microbial biomass are an indication of higher carbon use efficiency (CUE; proportion of assimilated C used for building biomass). A possible, but untested, explanation for higher CUE in response to lower DTR_{soil} in dry spring soils is reduced 'energy spilling' compared to high DTR_{soil} (i.e. control plots). Energy spilling, suggested to increase with warming (Bradford 2013), is a mechanism whereby ATP is not used for growth or maintenance but is instead wasted

to increase survival (Russell 2007). Another plausible mechanism for higher CUE is lower maintenance energy costs, thereby increasing the proportion of energy used for growth. Energy demands for maintenance are assumed to vary with temperature (Alvarez et al. 1995; Sinsabaugh et al. 2013; but see Dijkstra et al. 2011). Alternatively, there could have been increases in abundances of members in the microbial communities with higher CUEs (e.g., bacteria vs. changes in the dominance of specific fungal phyla) that responded positively to lower DTR in spring. Regardless of the mechanism, the impact of changes in temperature (Allison et al. 2010; Dijkstra et al. 2011) and moisture (Herron et al. 2009) on CUE is still relatively unknown.

We hypothesized that higher MBN in response to reduced DTR_{soil} was due to increased N immobilization of inorganic N in soil. We reject this hypothesis as NO_3^-–N was either similar or lower in response to reduced DTR_{soil} and NH_4^+–N did not change. The positive relationship between MBN and NO_3^-–N reflected seasonal differences in soil moisture rather than treatment differences, with MBN and NO_3^-–N increasing with increasing soil moisture. If higher MBN was due to NO_3^-–N uptake, we would still expect a positive association between MBN and NO_3^-–N, but with values in DTR plots shifted relative to control plots to reflect higher MBN and lower NO_3^-–N than control plots. Higher MBN without a concomitant reduction in inorganic N could result from (1) faster N cycling due to treatment-induced shifts in gross N transformation rates (e.g., mineralization, ammonification, (de)nitrification, and gaseous N loss) such that production and subsequent removal of N negated each other (Jin and Evans 2007), or that (2) microbes have access to other sources of N, such as amino acids with fast turnover rates (Jones 1999; Jin and Evans 2007). We propose that future studies incorporate stable isotope pool dilution techniques to more accurately address the fate of N cycling in response to climate change factors.

Responses to natural seasonal variation in environmental conditions

Seasonal patterns in belowground dynamics, independent of our temperature manipulation, were distinct with higher MBN and MBC, SOM and higher soil respiration rates, in summer compared to spring. These findings were anticipated because drought in spring often limits physiological activity of microbes and reduces diffusion of nutrients, thereby further limiting metabolic activity (Robertson et al. 1997; Yuste et al. 2007). Furthermore, plant physiological activity is highest in summer (Robertson et al. 2009; Patrick et al. 2009), suggesting greater root exudation of carbon, which could increase microbial activity.

Along with higher summer MBN values, NO_3^-–N was also higher during the wetter summer season and lower during the drier spring, leading to a positive association between MBN and NO_3^-–N that is linked through precipitation. Perhaps improved hydrologic connectivity during the wetter summer months facilitated diffusion of NH_4^+–N to sites where nitrifier populations were present (Parker and Schimel 2011), such that nitrification rates increased NO_3^-–N levels. Alternatively, or in conjunction to improved hydrologic connectivity, perhaps rainfall events resulted in increased N deposition, as is often observed in our desert (Herrmann et al. 2000; Báez et al. 2007); according to the National Atmospheric Deposition Program (NADP) and Clean Air Status and Trends Network, our site receives 2.1 kg N ha^{-1} year^{-1} (1998–2013) in the form of wet and dry deposition, thereby potentially increasing N availability. In sum, precipitation events can modulate inorganic N by promoting physiological activity of the nitrifier populations, and more directly via increased deposition of N (Stursova et al. 2006), resulting in a positive relationship between MBN and NO_3^-–N.

Seasonal environmental predictors

The variance in temperature variables (T_{max} and DTR_{soil}) and soil moisture explained up to 55 % of the variance in microbial and soil conditions. Soil moisture was an important predictor of MBC regardless of treatment and season, while temperature variables (DTR_{soil} and T_{max}) differed in their relationship to MBC: in control plots, both temperature variables (particularly DTR_{soil}) and moisture were important predictors of MBC, while in DTR plots the temperature variables were either not predictors or positive predictors of MBC. This suggests that DTR plots lessened temperature stress on the microbial community and as such soil moisture was a more accurate predictor. DTR_{soil} has been shown to shape the temperature sensitivity of bacterial communities in these desert soils to a greater degree than seasonal temperatures, because bacteria living near the soil surface (0–5 cm; high DTR_{soil}) had a greater range of growth temperatures than those in the deeper 15–0 cm soil layer (lower DTR_{soil}); however, the temperature sensitivity of bacteria at both soil depths did not change from the cool season to the hot season (van Gestel et al. 2013). By reducing temperature stress associated with high DTR_{soil} in our study, we showed that DTR_{soil} does influence microbial biomass production in arid systems but is bounded by the extent of natural variability in this parameter. For example, in 2013, which experienced the highest values in natural DTR over the year, even our manipulations of DTR through shading were insufficient to promote a positive response in MBC. These results suggest that microbial response to DTR_{soil} for this arid ecosystem is a threshold-regulated

parameter. Perhaps the key to better understanding the role of DTR in soil and microbial processes is by determining when DTR becomes important in controlling soil and microbial processes and when it does not. While microbial biomass production and attendant nitrogen dynamics in arid ecosystems are primarily regulated by water, the magnitude of the microbial response to soil moisture will be dependent on DTR_{soil}.

Implications of reduced DTR_{soil}

Reduced DTR_{soil} enabled microbes to construct more biomass in spring and summer. It is unclear whether reduced DTR_{soil} resulted in faster soil N cycling rates, or whether alternate sources of N were used to generate higher MBN in response to a reduction in DTR_{soil}, but greater microbial biomass production can only be sustained if there are concurrent increases in N availability (through greater net N mineralization, N fixation or atmospheric N deposition). If increased MBN resulted only from faster internal N cycling (i.e. not through N fixation or atmospheric deposition), this could have a negative effect on desert productivity. In systems other than deserts (e.g., prairie grassland and arctic ecosystems), faster N cycling could enhance plant productivity (Schimel et al. 1990; Shaver et al. 1992), but in deserts the internal N source, the soil organic matter, is inherently very low. The dominant plant species, *Larrea tridentata*, had not altered their physiological activity in response to DTR_{soil} in our previous study at the site (van Gestel et al. 2011) and are, therefore, not likely to increase N input through litter. Thus, soil N may decrease in the longer term in this N-poor system. However, if microbes accessed external inorganic N from atmospheric deposition, then this could be a mechanism to increase soil fertility by reducing N losses from N volatilization (because N now resides in microbes and no longer susceptible to volatilization). High N volatilization in desert soils (McCalley and Sparks 2009) is a predominant pathway that leads to a nearly 80 % loss of incoming atmospheric N (Peterjohn and Schlesinger 1990). Thus, the future N balance under conditions of lower DTR seems linked to future precipitation regimes, through N-deposition or N fixation patterns and regulation of soil heat load dynamics.

Author contribution statement NCvG and JCZ conceived and designed the experiments. NCvG and ND conducted the field experiment and laboratory analyses. NCvG analyzed the data and created the figures. NCvG, DTT and JCZ wrote the manuscript.

References

Allison S, Wallenstein M, Bradford M (2010) Soil-carbon response to warming dependent on microbial physiology. Nat Geosci 3:336–340. doi:10.1038/NGEO846

Alvarez R, Santanatoglia OJ, Garcîa R (1995) Effect of temperature on soil microbial biomass and its metabolic quotient in situ under different tillage systems. Biol Fertil Soils 19:227–230. doi:10.1007/BF00336164

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235. doi:10.1007/s00442-004-1519-1

Báez S, Fargione J, Moore DI, Collins SL, Gosz JR (2007) Atmospheric nitrogen deposition in the northern Chihuahuan desert: temporal trends and potential consequences. J Arid Environ 68:640–651. doi:10.1016/j.jaridenv.2006.06.011

Bell C, McIntyre N, Cox S, Tissue D, Zak J (2008) Soil microbial responses to temporal variations of moisture and temperature in a Chihuahuan Desert Grassland. Microb Ecol 56:153–167. doi:10.1007/s00248-007-9333-z

Bell CW, Acosta-Martinez V, McIntyre NE, Cox S, Tissue D, Zak J (2009) Linking microbial community structure and function to seasonal differences in soil moisture and temperature in a Chihuahuan Desert grassland. Microb Ecol 58:827–842. doi:10.1007/S00248-009-9529-5

Biederbeck VO, Campbell CA (1973) Soil microbial activity as influenced by temperature trends and fluctuations. Can J Soil Sci 53:363–376

Bradford MA (2013) Thermal adaptation of decomposer communities in warming soils. Front Microbiol 4:1–16. doi:10.3389/fmicb.2013.00333

Brookes PC, Landman A, Pruden G, Jenkinson DS (1985) Chloroform fumigaton and the release of soil nitrogen—a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol Biochem 17:837–842. doi:10.1016/0038-0717(85)90144-0

Clark J, Campbell J, Grizzle H, Acosta-Martínez V, Zak J (2009) Soil Microbial community response to drought and precipitation variability in the Chihuahuan Desert. Microb Ecol 57:248–260. doi:10.1007/S00248-008-9475-7

Cochran RA, Rives JL (1985) Soil survey of Big Bend National Park: part of Brewster County. USDA-SCS in cooperation with the United States Department of Interior, National Park Service and Texas Agricultural Experiment Station. U.S. Government Printing Office, Washington DC

Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH (2008) Pulse dynamics and microbial processes in aridland ecosystems. J Ecol 96:413–420. doi:10.1111/j.1365-2745.2008.01362.x

Dijkstra P, Thomas SC, Heinrich PL, Koch GW, Schwartz E, Hungate BA (2011) Effect of temperature on metabolic activity of intact microbial communities: evidence for altered metabolic pathway activity but not for increased maintenance respiration and reduced carbon use efficiency. Soil Biol Biochem 43:2023–2031. doi:10.1016/j.soilbio.2011.05.018

Dion P, Nautiyal CS (2008) Microbiology of extreme soils. Springer, Berlin

Gutschick VP, Snyder K (2006) Water and energy balances within the Jornada Basin. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) Structure and Function of a Chihuahuan Desert Ecosystem, The Jornada Basin long-term ecological research site. Oxford University Press, New York, pp 176–188

Hadley N (1970) Micrometeorology and energy exchange in two desert arthropods. Ecology 51:434–444

Herrmann R, Stottlemyer R, Zak JC, Edmonds RL, Van Miegroet H (2000) Biogeochemical effects of global change on US national parks. J Am Water Resour Assoc 36:337–346. doi:10.1111/j.1752-1688.2000.tb04272.x

Herron PM, Stark JM, Holt C, Hooker T, Cardon ZG (2009) Microbial growth efficiencies across a soil moisture gradient assessed using 13C-acetic acid vapor and 15N-ammonia gas. Soil Biol Biochem 41:1262–1269. doi:10.1016/j.soilbio.2009.03.010

Jenkinson DS (1988) Determination of microbial biomass carbon and nitrogen in soil. In: Wilson J (ed) Adv nitrogen cycl agric ecosyst. CAB International, Wallingford, pp 368–386

Jin VL, Evans RD (2007) Elevated CO_2 increases microbial carbon substrate use and nitrogen cycling in Mojave Desert soils. Glob Change Biol 13:452–465

Joergensen RG (1996) The fumigation-extraction method to estimate soil microbial biomass: calibration of the k(EC) value. Soil Biol Biochem 28:25–31. doi:10.1016/0038-0717(95)00102-6

Jones DL (1999) Amino acid biodegradation and its potential effects on organic nitrogen capture by plants. Soil Biol Biochem 31:613–622. doi:10.1016/S0038-0717(98)00167-9

Jones DL, Willett VB (2006) Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. Soil Biol Biochem 38:991–999. doi:10.1016/j.soilbio.2005.08.012

Kieft TL, Soroker E, Firestone MK (1987) Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol Biochem 19:119–126

McCalley CK, Sparks JP (2009) Abiotic gas formation drives nitrogen loss from a desert ecosystem. Science 326:837–840. doi:10.1126/science.1178984

Nobel PS (1989) Temperature, water availability, and nutrient levels at various soil depths—consequences for shallow-rooted desert succulents, including nurse plant effects. Am J Bot 76:1486–1492

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

Nunan N, Morgan MA, Herlihy M (1998) Ultraviolet absorbance (280 nm) of compounds released from soil during chloroform fumigation as an estimate of the microbial biomass. Soil Biol Biochem 30:1599–1603. doi:10.1016/S0038-0717(97)00226-5

Ogle K, Barber JJ, Barron-Gafford GA, Bentley LP, Young JM, Huxman TE, Loik ME, Tissue DT (2015) Quantifying ecological memory in plant and ecosystem processes. Ecol Lett 18:221–235. doi:10.1111/ele.12399

Parker SS, Schimel JP (2011) Soil nitrogen availability and transformations differ between the summer and the growing season in a California grassland. Appl Soil Ecol 48:185–192. doi:10.1016/j.apsoil.2011.03.007

Patrick LD, Ogle K, Bell CW, Zak J, Tissue D (2009) Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics. Glob Change Biol 15:1214–1229. doi:10.1111/j.1365-2486.2008.01750.x

Peterjohn WT, Schlesinger WH (1990) Nitrogen loss from deserts in the southwestern United States. Biogeochemistry 10:67–79

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2012) nlme: Linear and nonlinear mixed effects models. R package version 3.1-104

Pointing SB, Belnap J (2012) Microbial colonization and controls in dryland systems. Nat Rev Microbiol 10:654. doi:10.1038/nrmicro2854

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004) Modifying the "pulse-reserve" paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141:194–210. doi:10.1007/s00442-004-1524-4

Robertson GP, Klingensmith KM, Klug MJ, Paul EA, Crum JR, Ellis BG (1997) Soil resources, microbial activity, and primary production across an agricultural ecosystem. Ecol Appl 7:158–170. doi:10.1890/1051-0761(1997)007[0158:SRMAAP]2.0.CO;2)

Robertson TR, Bell CW, Zak JC, Tissue DT (2009) Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland. New Phytol 181:230–242. doi:10.1111/j.1469-8137.2008.02643.x

Russell JB (2007) The energy spilling reactions of bacteria and other organisms. J Mol Microbiol Biotechnol 13:1–11. doi:10.1159/000103591

Schimel DS, Parton WJ, Kittel TGF, Ojima DS, Cole CV (1990) Grassland biogeochemistry—links to atmospheric processes. Clim Change 17:13–25. doi:10.1007/bf00148998

Shaver GR, Billings WD, Chapin FS, Giblin AE, Nadelhoffer KJ, Oechel WC, Rastetter EB (1992) Global change and the carbon balance of arctic ecosystems. Bioscience 42:433–441. doi:10.2307/1311862

Sinsabaugh RL, Manzoni S, Moorhead DL, Richter A (2013) Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. Ecol Lett 16:930–939. doi:10.1111/ele.12113

Stursova M, Crenshaw CL, Sinsabaugh RL (2006) Microbial responses to long-term N deposition in a semiarid grassland. Microb Ecol 51:90–98. doi:10.1007/s00248-005-5156-y

Treseder KK, Schimel JP, Garcia MO, Whiteside MD (2010) Slow turnover and production of fungal hyphae during a Californian dry season. Soil Biol Biochem 42:1657–1660. doi:10.1016/j.soilbio.2010.06.005

Van Gestel NC, Schwilk DW, Tissue DT, Zak JC (2011) 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. Glob Change Biol 17:3564–3576. doi:10.1111/j.1365-2486.2011.02479.x

Van Gestel NC, Reischke S, Bååth E (2013) Temperature sensitivity of bacterial growth in a hot desert soil with large temperature fluctuations. Soil Biol Biochem 65:180–185. doi:10.1016/j.soilbio.2013.05.016

Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass-C. Soil Biol Biochem 19:703–707

Vose RS, Easterling DR, Gleason B (2005) Maximum and minimum temperature trends for the globe: an update through 2004. Geophys Res Lett 32:L23822. doi:10.1029/2005GL024379

Xiang S-R, Doyle A, Holden PA, Schimel JP (2008) Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biol Biochem 40:2281–2289. doi:10.1016/j.soilbio.2008.05.004

Yuste JC, Baldocchi DD, Gershenson A, Goldstein A, Misson L, Wong S (2007) Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Glob Change Biol 13:2018–2035. doi:10.1111/j.1365-2486.2007.01415.x

Zeglin LH, Stursova M, Sinsabaugh RL, Collins SL (2007) Microbial responses to nitrogen addition in three contrasting grassland ecosystems. Oecologia 154:349–359. doi:10.1007/s00442-007-0836-6

Zhou L, Dickinson RE, Dai A, Dirmeyer P (2009) Detection and attribution of anthropogenic forcing to diurnal temperature range changes from 1950 to 1999: comparing multi-model simulations with observations. Clim Dyn 35:1289–1307. doi:10.1007/s00382-009-0644-2

Zhu BA, Cheng WX (2011) Constant and diurnally-varying temperature regimes lead to different temperature sensitivities of soil organic carbon decomposition. Soil Biol Biochem 43:866–869. doi:10.1016/j.soilbio.2010.12.021