ORIGINAL ARTICLE

Soil Microbial Responses to Temporal Variations of Moisture and Temperature in a Chihuahuan Desert Grassland

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Abstract Global climate change models indicate that storm magnitudes will increase in many areas throughout southwest North America, which could result in up to a 25% increase in seasonal precipitation in the Big Bend region of the Chihuahuan Desert over the next 50 years. Seasonal precipitation is a key limiting factor regulating primary productivity, soil microbial activity, and ecosystem dynamics in arid and semiarid regions. As decomposers, soil microbial communities mediate critical ecosystem processes that ultimately affect the success of all trophic levels, and the activity of these microbial communities is primarily regulated by moisture availability. This research is focused on elucidating soil microbial responses to seasonal and yearly changes in soil moisture, temperature, and selected soil nutrient and edaphic properties in a Sotol Grassland in the Chihuahuan Desert at Big Bend National Park. Soil samples were collected over a 3-year period in March and September (2004–2006) at 0–15 cm soil depth from 12 3 × 3 m community plots. Bacterial and fungal carbon usage (quantified using Biolog 96-well micro-plates) was related to soil moisture patterns (ranging between 3.0 and 14%). In addition to soil moisture, the seasonal and yearly variability of soil bacterial activity was most closely associated with levels of soil organic matter, extractable NH_4–N, and soil pH. Variability in fungal activity was related to soil temperatures ranging between 13 and 26 °C. These findings indicate that changes in soil moisture, coupled with soil temperatures and resource availability, drive the functioning of soil-microbial dynamics in these desert grasslands. Temporal patterns in microbial activity may reflect the differences in the ability of bacteria and fungi to respond to seasonal patterns of moisture and temperature. Bacteria were more able to respond to moisture pulses regardless of temperature, while fungi only responded to moisture pulses during cooler seasons with the exception of substantial increased magnitudes in precipitation occurring during warmer months. Changes in the timing and magnitude of precipitation will alter the proportional contribution of bacteria and fungi to decomposition and nitrogen mineralization in this desert grassland.

Introduction

Precipitation pulse sizes and corresponding soil moisture in arid ecosystems are discrete and highly variable events [1]. These discontinuous moisture pulses provide a window of opportunity for soil microbes, triggering mineralization for brief periods, and consequently releasing nitrogen and other minerals into the upper soil horizons [2–4]. However, primary producers in arid systems rarely benefit from brief moisture pulses, as plant growth is dependent not only on soil microbial activity, but also on other factors including the duration of the precipitation event, amount of soil water infiltration and subsequent soil moisture levels, and plant functional types [5, 6]. Consequently, short-term increases in soil microbial activity triggered by moisture pulses in arid systems will not typically correspond to subsequent increases in primary production on the same time scale. As decomposition and consequent mineralization can be stimulated by moisture pulses that are too brief to benefit primary producers [2, 7, 8], there is potential for soil

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nutrient pools to accumulate over time in desert soils and then become available to plants as heavier precipitation events occur. In addition, any accumulation of soil nutrients as a consequence of mineralization pulses caused by brief soil moisture pulses may subsequently influence microbial functional dynamics and consequently alter soil microbial community diversity.

Increased root and soil microbial respiration rates in response to isolated moisture pulses has been shown to occur in the Sonoran Desert at both Saguaro National Park and the Santa Rita experimental range outside Tucson, AZ, and in the northern Chihuahuan Desert at the Sevilleta National Wildlife Refuge in central New Mexico [9–11]. However, current understanding is incomplete as to how belowground microfloral dynamics in deserts functionally respond to environmental variation over a several-year period and how environmental variation might influence soil microbial biodiversity across arid landscapes [12–15]. Even less is known about how changes in soil microbial biodiversity will influence processes such as decomposition and mineralization rates in arid systems, and how ecosystem function will subsequently be affected as climate change results in altered precipitation patterns [15–20]. These questions are important to answer because available soil moisture is predicted to become increasingly variable in arid systems as a consequence of global climate change. Moreover, changes in plant productivity, root growth, and exudation patterns as a consequence of climate modifications are likely to significantly influence microbial diversity and activity [21–23]. These impacts will most likely occur through changes in soil organic matter levels, decomposition, and mineralization rates [24–29]. Thus, by evaluating microbial functional responses to current environmental patterns, potential impacts of climate change on soil microbial function can be addressed.

Assessment of carbon utilization patterns of soil microbial communities, as affected by soil moisture or temperature patterns, can provide some insights into microbial functional responses to environmental changes in arid regions. The Biolog procedure was introduced initially to identify bacterial functional differences between soil and water samples [30]. Zak et al. [31] used this procedure to measure soil bacterial functional diversity along a moisture gradient in the Chihuahuan Desert at the Jornada Long-Term Ecological Research site and reported considerable variation in the ability of bacterial communities to utilize different carbon substrates along the gradient. Zak et al. [32] later used this approach to examine bacterial carbon use along an extensive elevation gradient in the Chihuahuan Desert at Big Bend National Park. Using similar methodology, the FungiLog approach was then developed [33, 34] to determine saprophytic fungal functional diversity associated with decomposed plant material and soil. Although the

Biolog method is limited, as results cannot reflect accurately the carbon use potential of the bacterial community as a whole, the capacity of this approach for estimating microbial response patterns to various treatments, disturbance, or environmental conditions has been recognized [35, 36]. Employing these two methods, potential carbon usage of both saprophytic fungi and soil bacteria in response to temporal patterns of moisture and temperature in arid systems can be ascertained. Linking bacterial and saprophytic fungal carbon use to changes in soil moisture patterns, nitrogen availability, or soil temperature will be crucial for understanding consequences of changes in precipitation patterns on soil microbial dynamics in arid landscapes.

The objective of this research was to determine patterns of soil microbial and soil nutrient dynamics in a Chihuahuan Desert grassland at Big Bend National Park in response to temporal differences in environmental conditions with the goal of providing insight as to how global climate change predictions for this region will subsequently influence soil microbial activity and function and ultimately ecosystem process.

Materials and Methods

Site Description

This research was conducted in a Sotol Grassland site in the Pine Canyon Watershed [32], located in Big Bend National Park (BBNP), Texas. BBNP is located in the central region of the Chihuahuan Desert and is characteristic of the Chihuahuan Desert because of its many mountain ranges and diverse plant communities [37, 38]. Like the Chihuahuan Desert (taken as a whole), BBNP receives the majority of its rainfall in the summer months from moisture brought in by southeasterly winds blowing over from the Gulf of Mexico, with the least amount of precipitation occurring during winter months [39, 40]. Precipitation data collected at Big Bend's Panther Junction Visitor Center over the past 19 years shows the average winter rainfall (December–February) to be 55.9 mm, whereas the average summer rainfall (June–August) is 163.3 mm. The average total annual rainfall for BBNP over the past 19 years is 364 mm. Average daily air temperatures in BBNP range from ~10 °C in the winter months to ~32 °C in the summer (Fig. 1).

The research site for this study is located in the Sotol Grasslands in the Pine Canyon Watershed, which is situated on the northeast side of the Chisos Mountains (centrally located in BBNP). This desert grassland site is higher in elevation (1500–1678 m) than other components of the Chihuahuan Desert; consequently, climate is slightly wetter and cooler than for lower elevation grasslands in

Fig. 1 Average monthly precipitation (mm) for Panther Junction Visitor Center (elevation 1143 m) in Big Bend National Park (located in the Chihuahuan Desert) over the past 19 years (**a**) and daily maximum and minimum air temperatures (recorded at 1 m height) at the Sotol Grassland site in Pine Canyon (elevation 1550 m) in Bend N. P. (**b**). Temperatures were recorded every 36 min
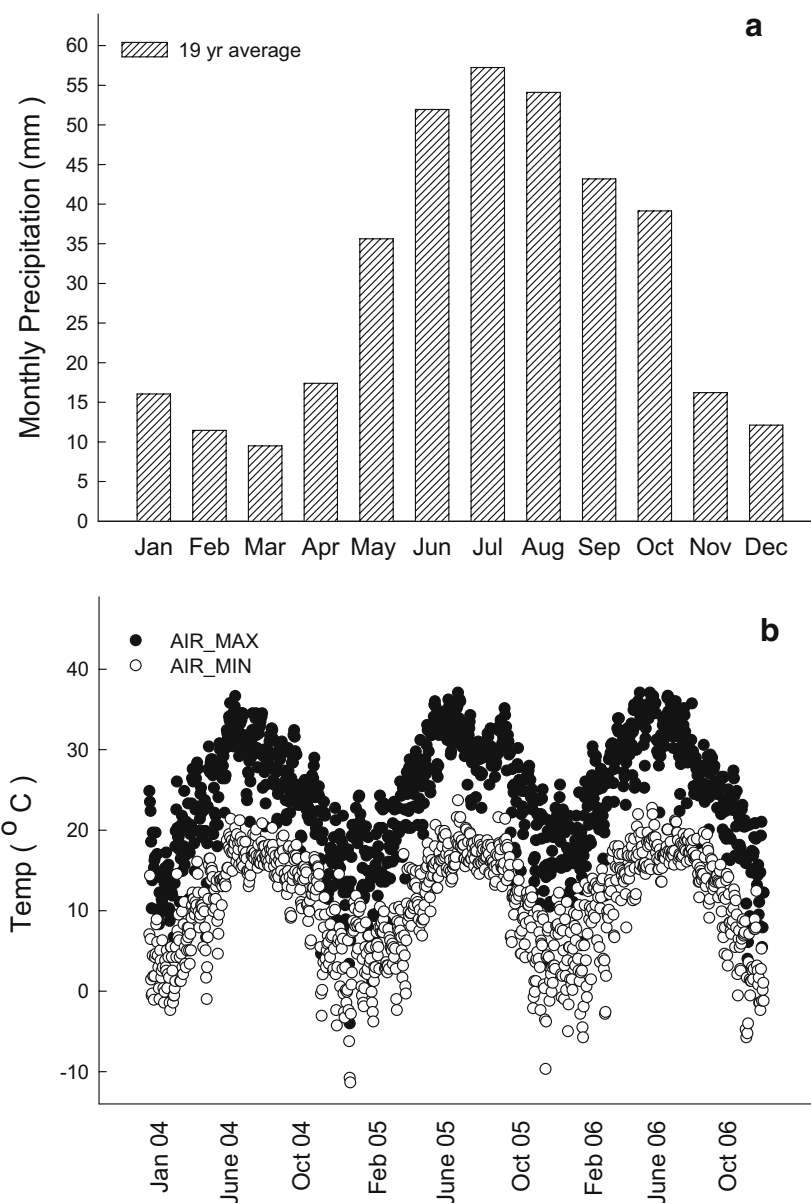
the Chihuahuan Desert. Dominant plants include sotol (*Dasylirion leiophyllium*), several species of prickly pear (*Opuntia phaeacantha*, *Opuntia engelmannii*, *Opuntia violacea*, and *Opuntia rufida*) and grama grasses (*Bouteloua capitola*, *Bouteloua curtipendula*, and *Bouteloua hirsute*). In general, desert grasslands are characterized as having the lowest biomass levels of any North American grassland type [41].

The Pine Canyon Sotol Grassland is located in a caldera (latitude: 29°5.86″ N; longitude: 103°14′13.54″ W), and the magma produced from the area is the major source forming the surrounding Chisos Mountains [42]. Soils in Pine Canyon typically have an extremely rock-strewn A-horizon with little to no litter layer that immediately overlays a fractured igneous bedrock foundation. This soil is described

as Lajitas-rock outcrop complex by USDA soil surveys [43, 44]. The soil texture throughout this site has been determined to be a sandy–loam (62% sand, 30% silt, 8% clay) by Waters Agricultural Laboratories, Inc. (Owensboro, KY).

Experimental Design

We established 12 3×3 m community plots to study long-term soil microbial and plant responses to seasonal patterns in precipitation. These community plots were constructed to uniformly encompass the three dominant plant species of the Sotol Grasslands in Pine Canyon (sotol, prickly pear, and grama grasses). Twenty-four soil samples (two per plot) were collected biannually in March and September for three consecutive years starting in 2004. These months were

chosen to represent the ends of the winter and summer seasons at BBNP, which are the two seasons predicted to experience the greatest shift in precipitation patterns due to global climate change in this region [45, 46]. Soil was collected from 0 to 15 cm depths and stored at 4 °C until use. All soils were analyzed within 2 weeks of collection.

Assessing the Potential Carbon Usage of Soil Microbes

Microbial functional responses to environmental conditions were assessed by analyzing potential carbon usage for both bacteria and fungi. To quantify bacterial responses, soil samples were diluted to 10^{-4} and inoculated into Biolog GN2 96-well microtiter plates containing 95 different carbon substrates following the Biolog method [30, 31, 36, 47]. Fungal functional responses were assessed by inoculating Biolog SFN2 96-well microtiter plates containing 95 different carbon substrates with a 20 ml inoculation mixture containing 50 mg SOM particles (ranging between 250 and 500 μm) following Soil Fungilog procedures. Soil organic matter particles were separated from the mineral soil fraction using the procedure as outlined by Sobek and Zak [34]. Functional responses for bacteria and fungi were quantified for total substrate activity and substrate richness after 72- and 120-h incubation periods. The 72- and 120-h incubation periods were chosen to allow for the most complete expression of microbial carbon use potential at the time of sampling [31, 34, 48]. Substrate activity refers to the sum of combined ability to utilize the different carbon substrates, whereas substrate richness refers to the number of wells (95 total wells) that have any level of carbon-use activity.

Nitrogen Dynamics

Exchangeable soil ammonium (NH_4–N) was determined via colorimetric assay and was extracted one day after the sample collection date using a 50-ml 2-M KCl solution from a 5-g field moist (oven dry equivalent) soil sample [49]. Levels of extractable NO_3–N were determined 1 day after the sample collection date by A&L Soil Laboratories (Lubbock, TX, USA) using ion-specific probes.

Potential Nitrogen Mineralization

Soil incubations were employed to evaluate seasonal changes in potential nitrogen mineralization patterns as described by Robertson et al. [27]. Ninety-six 250 mL soil chambers were incubated after each sampling period beginning in 2006. Forty-eight chambers were used to incubate soil for 40 days, with the second set of 48 chambers incubated over 80 days. Soils throughout all incubation periods were kept at (24 °C). Initial watering application increased soil moisture to near saturation (~20% soil moisture). Soils slowly dried over the

incubation intervals, and at the end of each incubation period, percent soil moisture was determined along with extractable soil NO_3–N and NH_4–N to assess net nitrogen mineralization rates, net nitrification rates, and relative percent nitrification [27]. Measurements of extractable NO_3–N and NH_4–N occurred as described above. Carbon to nitrogen ratios of initial, 40- and 80-day incubations were analyzed using a CE Elantech CHN analyzer (NCS 2500, Carlo Erba, Inc. Milan Italy) for samples collected in March and September 2006.

SOM

Soil organic matter (SOM) was estimated via loss-on-ignition method [50]. Soils were air-dried for 24 h, then placed in aluminum pans and oven-dried for an additional 24 h in a 60 °C drying oven. After drying for 24 h, approximately 10 g of soil was placed in a weighed porcelain crucible and then incinerated at 450 °C for 24 h. After incineration, samples were removed from the furnace and reweighed to determine ash weight remaining.

Microbial Biomass Carbon

Estimations of microbial biomass carbon (MBC) was accomplished using the chloroform fumigation and extraction method [51], in which two replicates from each soil sample were fumigated for 48 h, while another set of two replicates from each soil sample were not fumigated. Soil MBC was extracted using a 0.5-M K_2SO_4 solution from 5 g field moist (dry weight equivalent) soil sample and filtered using Fisherbrand-P2 fine-porosity filter paper. Extracted soil MBC was measured spectrophotometrically at 280 nm, and the difference between the extracted C in the fumigated and non-fumigated soils represents the microbial biomass C [52].

Environmental Parameters: Soil pH, Soil Moisture, and Air and Soil Temperatures

Soil pH was measured using a 2:1 paste extract [27]. Percent soil water content was measured at each sampling time by drying soils in a drying oven (60 °C for 48 h) [53]. Soil (15 cm depth) and air temperatures (1.0 m above soil surface) were collected using Onset Computer Corporation HOBO-H8 Pro Series data loggers at 36-min intervals [54]. For every sample period, average soil and air temperatures were calculated for 4 weeks before sampling occurred to represent environmental conditions critical for microbial response.

Statistical Analysis

The statistical approach used to assess significant differences in all observed parameters collected over the 3-year

Table 1 Pearson correlation matrix among environmental parameters measured in the Sotol Grasslands in Big Bend National Park

Independent variables	sm%	som	pH	NO_3–N	NH_4–N	Soil temp	Air temp
sm%	1.000						
som	0.018	1.000					
pH	−0.050	−0.037	1.000				
NO_3–N	**0.179**	**−0.208**	0.121	1.000			
NH_4–N	**0.217**	0.057	−0.102	0.089	1.000		
Soil temp	**0.373**	**−0.224**	0.053	**0.543**	−0.004	1.000	
Air temp	**0.385**	**−0.198**	0.071	**0.557**	0.011	**0.988**	1.000

sm%=soil moisture %, *som*=soil organic matter

Pearson correlation matrix indicates correlated variables used in multiple regression analysis for microbial and *in situ* nitrogen responses to soil properties and soil and air temperatures. Values in this matrix can range from −1.0 to 1.0, with 1.0 indicating perfectly correlated variables and −1.0 indicating perfectly negative correlations. Soil and air temperatures were the only environmental variables that were highly correlated. Significant correlations ($P \leq 0.05$) are indicated in bold. The sample size for each variable used for multiple regression analysis of microbial responses and *in situ* (initial) soil nutrient responses with the environmental variables listed above is N=144

period (soil pH, soil organic matter percentage, microbial biomass, available soil NH_4–N and NO_3–N, *in vitro* mineralized soil NH_4–N and NO_3–N, soil C:N, net nitrification, net mineralization, relative percent nitrification, and potential carbon usage for both bacterial and fungal communities) was repeated-measures analysis of variance (rmANOVA) using the consecutive sample dates as the within subject variable using the statistical software package SPSS 14.0 (Chicago, Il, USA). To determine microbial and soil nutrient responses to environmental conditions, stepwise multiple regression analysis was performed (SPSS 14.0, Chicago, Il, USA; [55]). The stepwise method was chosen because this technique provides, as the first step, a single-variable model that accounts for the most variation and then calculates successively more complex models. This approach allows for an examination of the relative contributions of each variable to the most parsimonious descriptive model. Biolog, Fungilog, and available soil NH_4–N and NO_3–N data was modeled as a function of environmental parameters to assess microbial response and available nutrient relationships to environmental and edaphic variables (Table 1). Levels of extractable NO_3–N and NH_4–N from *in vitro* incubations were modeled as a function of percent soil moisture and the inorganic nitrogen counterpart recorded at the end of the incubations using multiple regression analysis to detect any relationships between soil nitrogen levels and soil moisture (Table 2). Every R^2 statistic reported in this experiment is from the final significant model ($P \leq 0.01$) provided by the stepwise process. The stepping-method criteria entered any variable with the probability of $F \leq 0.005$ and removed any variable from the model $F > 0.01$. Pearson correlations (Tables 1 and 2) were examined to identify any highly correlated variables that might corrupt the models generated by the multiple regression analysis. Only two variables, soil and air temperature, were found to be highly correlated ($R > 0.80$). Statistical analyses were conducted with SPSS 14.0 (Chicago, Il, USA). The sample size for regression analysis for bacterial and fungal responses and initial (*in situ*) extractable soil nitrogen levels collected over the 3-year study (between 2004 and 2006) is 144. The sample size for regression analysis for *in vitro* nitrogen mineralization data collected from soil incubation methods was from March and September 2006 only; the sample size for these data is 192.

Results

Environmental Parameters

Over the 3-year period, average soil temperatures within each sample period closely matched average air temperatures during the same sampling period and were highly correlated throughout the study (R=0.98) (Fig. 2; Table 1). Soil and air temperatures in March were consistently lower than air and soil temperatures in September, with March temperature averages ranging from ~13–18 °C for soil

Table 2 Pearson correlation matrix for soil parameters during *in vitro* N-mineralization

Independent variables	NH_4–N	sm%	NO_3–N
NH_4–N	1.000		
sm%	−0.514	1.000	
NO_3–N	−0.678	0.577	1.000

sm%=soil moisture %

Pearson correlation matrix indicates correlated variables used in multiple regression analysis for in vitro soil incubations. Values in this matrix can range from −1.0 to 1.0, with 1.0 indicating perfectly correlated variables and −1.0 indicating perfectly negative correlations. Significant correlations ($P \leq 0.05$) are indicated in bold. The sample size for each variable used for multiple regression analysis of *in vitro* soil-N mineralization responses with the variables listed above is N=192

and ~13–16 °C for air. In September, temperature averages ranged ~24–26 °C for soil and ~23–26 °C for air. Monthly precipitation varied throughout the 3-year period, with 2004 receiving above average annual rainfall (567 mm), 2005 receiving average rainfall (329 mm), and 2006 receiving below average rainfall (273 mm; Fig. 2a). Soil moisture throughout the 3-year study was observed to be highly variable and contingent on the timing and magnitude of moisture, ranging between 3.0 and 12.0% (VWC). The first three sample periods (March 2004, September 2004, and March 2005) exhibited soil moisture values typical for these desert grasslands (6–8%; Fig. 2b). For the duration of the next two sampling periods (September 2005 through March 2006), this region experienced an extended drought; consequently, very low soil moisture levels (<4.0%) were recorded. The highest soil moisture (11.98%) was recorded in the final sample period of September 2006 as a consequence of heavy rainfall (>140 mm) received during the month before this sampling period (Fig. 2b).

Soil pH

Soil pH maintained relatively consistent acidic conditions (pH 5.9–6.2) throughout the study. Soils collected during the last year of the study appeared slightly less acidic than the previous 2 years; however, only September 2004 displayed significantly higher acidity levels ($P \leq 0.031$) than the last year of sampling (Fig. 3a).

SOM

Soil organic matter content tended to increase in March and decrease in September. However, this pattern was only significant in the first year ($P < 0.001$), whereas soil organic matter content over the last four sample periods, although exhibiting the same seasonal pattern observed in 2004, were not statistically significant (Fig. 3b).

Microbial Biomass Carbon

Microbial biomass carbon was relatively stable across season for the first 2 years of the study period, although MBC variability increased over time as annual precipitation decreased (Fig. 3c). MBC ranged from 218 µg g^{-1} in March 2004 to 335 µg g^{-1} in March 2006 to the highest amount (770 µg g^{-1}) recorded in September 2006. MBC levels recorded in September 2006 were significantly higher ($P \leq 0.003$) than MBC levels from all prior sample periods.

Fig. 2 Monthly precipitation for Panther Junction Visitor Center for 2004–2006 (a) and percent soil moisture, air temperature, and soil temperature for the Sotol Grasslands in Pine Canyon for 2004–2006 (b). Air temperatures (recorded 1 m from soil surface) and soil temperatures (recorded at 15 cm depth) represent average daily temperature for the month before soil sampling. Soil moisture values are expressed in mean± SE; N=24
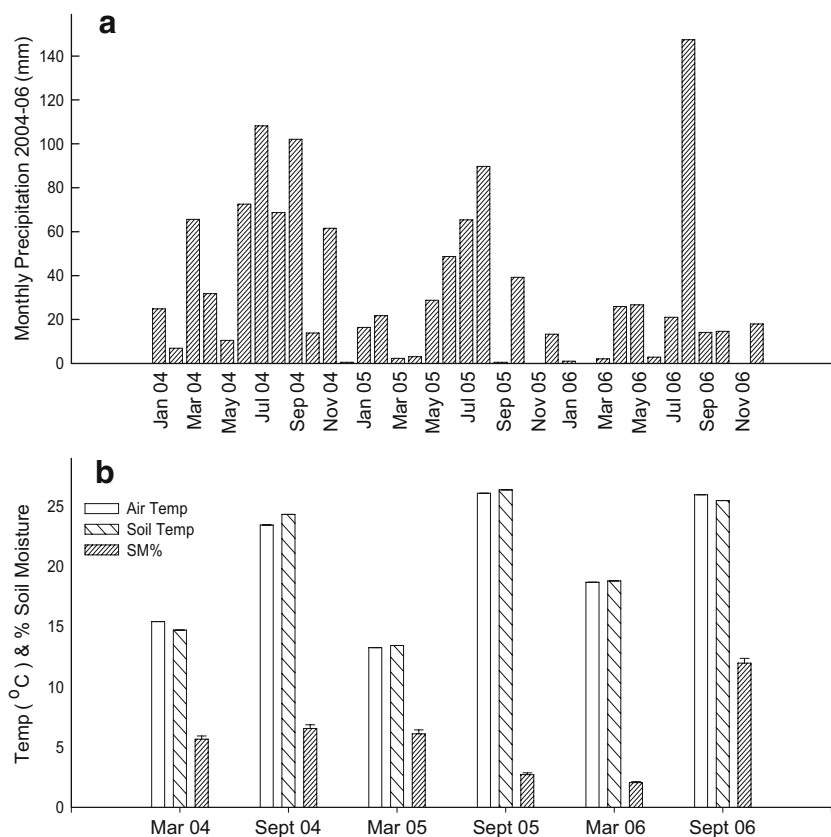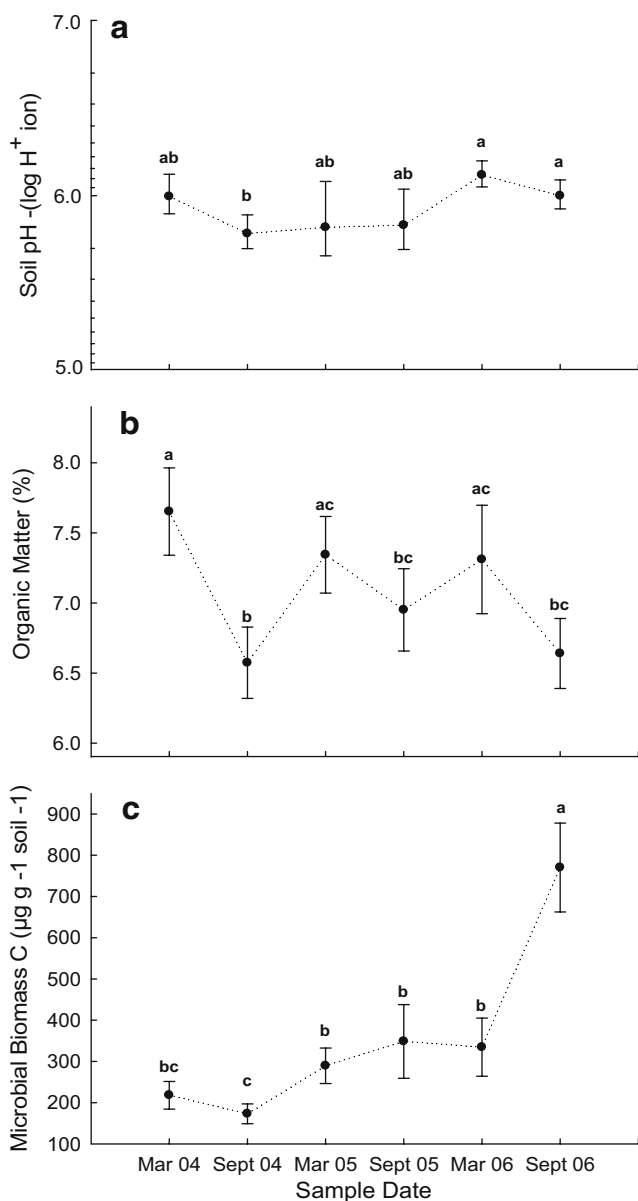
Fig. 3 Temporal changes in soil pH (**a**), soil organic matter (**b**), and microbial biomass carbon (**c**) for the Sotol Grasslands in Pine Canyon at Big Bend N.P. Values are mean±SE; N=24. *Letters above error bars* indicate significant difference at $P \leq 0.05$ using Fishers LSD post hoc tests

Nitrogen Dynamics

Extractable soil NH_4–N at the time of sampling ranged from 2.44 to 20.09 mg kg^{-1}, depending upon the sample period (Fig. 4a). The highest values were recorded during the last sample period in September 2006 when the highest percent soil moisture was recorded after an extended drought, and 2006 exhibited significantly higher levels of soil NH_4–N than the first 2 years ($P \leq 0.046$). Extractable soil NO_3–N at the time of sampling fluctuated temporally

with higher values recorded in September compared to March. Although these seasonal differences between March and September were observable throughout the study, this pattern was only significant ($P \leq 0.024$) over the last 2 years (Fig. 4b).

In determining soil NO_3–N dynamics in response to environmental conditions, air temperature (12–27 °C) was the sole predictor for seasonal and annual variability (R^2= 0.31; Table 3). For NH_4–N, a two-variable model was produced that included soil temperatures (13–27 °C) along with soil moisture as the two major determinants of seasonal and yearly variability (R^2=0.234; Table 3).

Nitrogen Mineralization

Soils collected in March and September 2006 displayed similar patterns with regard to how forms of inorganic nitrogen changed over time. Repeated measures ANOVA reported that in both sample periods, soil NH_4–N levels significantly decreased between the initial and 40-day incubation period (P<0.001; Fig. 5a–b). Levels of soil NH_4–N remained constant between 40- and 80-day incubations in March 2006 (P=0.068; Fig. 5a). In September 2006, NH_4–N levels significantly increased (although slight) between the 40- and 80-day incubation period (P< 0.001; Fig. 5b). Initial NH_4–N levels were relatively consistent over all incubations in both March and September 2006, as initial levels (~18.23 mg kg^{-1}) were not significantly different from one another (P=0.111; Fig. 5a–b). However, NH_4–N levels after the 40- and 80 – day incubations were significantly higher in March 2006 than in September 2006 ($P \leq 0.031$). Contrastingly, extractable soil NO_3–N levels over the duration of the incubation displayed dramatic and significant increases from initial levels in both March and September during the first 40 days of incubation (P<0.001). Ultimately, September NO_3–N levels were significantly higher by the end of the 80-day incubation period (P<0.001) than in March. The level of NO_3–N was significantly higher by the end of the 40-day incubation period in September 2006 when compared to the 40-day incubation period in March 2006 (P<0.001). Extractable NO_3–N levels peaked in September by the end of the 40-day incubation period and did not change significantly from the subsequent 80-day incubation. However, NO_3–N levels in March experienced significant increases between the 40- and 80-day incubation period (P<0.001; Fig. 5a–b), but were still lower than NO_3–N levels after the 40- and 80-day September incubations. Both forms of inorganic nitrogen were strongly related to soil moisture along with the inorganic nitrogen counterpart, and both soil NO_3–N and soil moisture accounted for much of the observed variation of extractable soil NH_4–N in the lab incubations (R^2=0.482; Table 3). Likewise, both soil NH_4–N and soil moisture
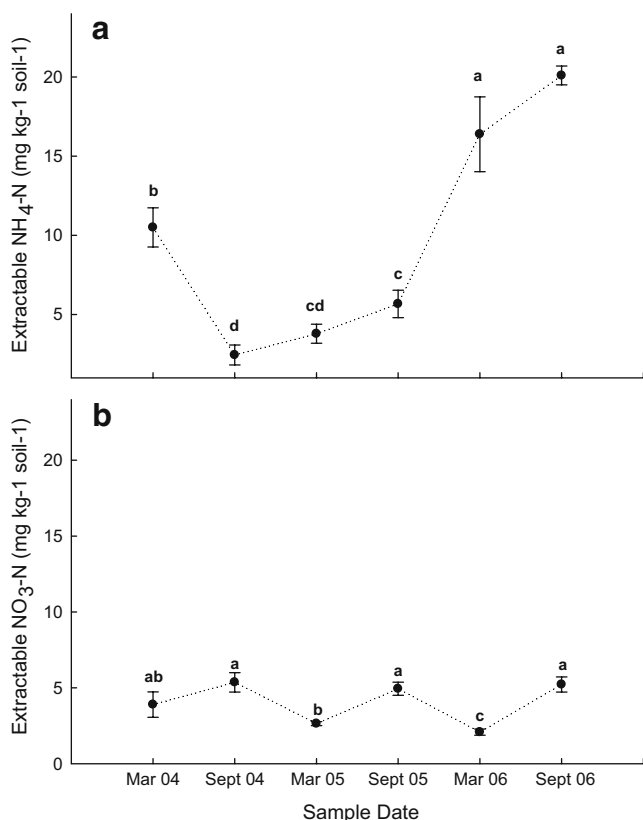
Fig. 4 Temporal patterns in extractable soil NH$_4$–N (**a**) and extractable soil NO$_3$–N (**b**) for the Sotol Grasslands in Pine Canyon at Big Bend N.P. Values are mean±SE; $N=24$. *Letters above error bars indicate significant difference at $P \leq 0.05$ using Fishers LSD post hoc tests*

accounted for the much of the observed seasonal variation of NO$_3$–N in the lab incubations ($R^2=0.531$; Table 3).

C:N Ratios

Soils collected in March and September 2006 displayed slightly different patterns with regard to how C:N dynamics

responded throughout the incubation periods (Fig 5c). In both sample periods, C:N ratios significantly decreased between the initial and 40-day incubation period ($P \leq 0.003$). C:N ratios remained constant between 40- and 80-day incubations in March 2006 ($P=0.439$), whereas C:N ratios between 40- and 80-day incubations in September 2006 continued to significantly decrease ($P=0.001$).

Net Nitrification, Net mineralization, and Relative Percent Nitrification

There were no significant differences in the daily rates of net nitrification between 40- and 80-day incubation periods in March 2006 (Fig. 6). Significant changes in daily rates of net nitrification were observed between the 0- to 40-day and the 0- to 80-day incubations in September 2006 (Fig. 6), as net nitrification/day after the 40-day incubation measured 1.98 mg kg^{-1} day^{-1}. By the end of the 80-day incubation period, these nitrification rates significantly dropped to 0.98 mg kg^{-1} day^{-1}, ($P<0.001$). Net nitrogen mineralization rates in March 2006 displayed similar patterns as net nitrification, as no significant increases occurred between the 40- and 80-day incubation periods. Likewise, September experienced significantly higher nitrogen mineralization rates than did March after the 40-day incubation period ($P \leq 0.001$). However, net mineralization rates dropped significantly by the end of the 80-day incubation period in September (40-day 1.52 mg kg^{-1} day^{-1} to 80-day 0.75 mg kg^{-1} day^{-1}) ($P \leq 0.001$). Relative percent nitrification throughout the March 2006 (0–40 day) incubation period increased nitrogen levels in the soil by 167% (Fig. 7a); however, by the end of the 80-day incubation period, relative percent nitrification significantly dropped to 44% of the first 40 days ($P<0.001$). Relative percent nitrification in September 2006 during the 0- to 40-day and 0- to 80-day incubations did not significantly differ (Fig. 7b), exhibiting an average of 133% for the two

Table 3 Regression model analysis of *in situ* soil nitrogen responses to environmental conditions and *in vitro* nitrogen mineralization responses during soil incubations in the Sotol Grasslands

Dependent variable	Model	Predictors	R	R square	Sig.
NO$_3$–N (*in situ*)	1	Air temp	0.557	0.305	<0.001
NH$_4$–N (*in situ*)	1	Soil temp	0.408	0.166	<0.001
	2	Soil temp, sm%	0.483	0.234	<0.001
NO$_3$–N (*in vitro* mineralization)	1	NH$_4$–N	0.678	0.46	<0.001
	2	NH$_4$–N, sm%	0.728	0.531	<0.001
NH$_4$–N (*in vitro* mineralization)	1	NO$_3$–N	0.678	0.46	<0.001
	2	NO$_3$–N, sm%	0.695	0.482	<0.001

sm%=soil moisture %

Multiple regression analysis indicated the relationship of how environmental factors influenced extractable levels of soil nitrogen and how available soil moisture and inorganic nitrogen counterparts influence potential nitrogen mineralization capabilities in the Sotol Grasslands across season and year; $P \leq 0.01$ for model inclusion. The sample size for each variable used for multiple regression analysis of *in situ* (initial) soil nutrient responses with the environmental variables listed above is $N=144$. The sample size for each variable used for multiple regression analysis of *in vitro* soil mineralization responses with the variables listed above is $N=192$
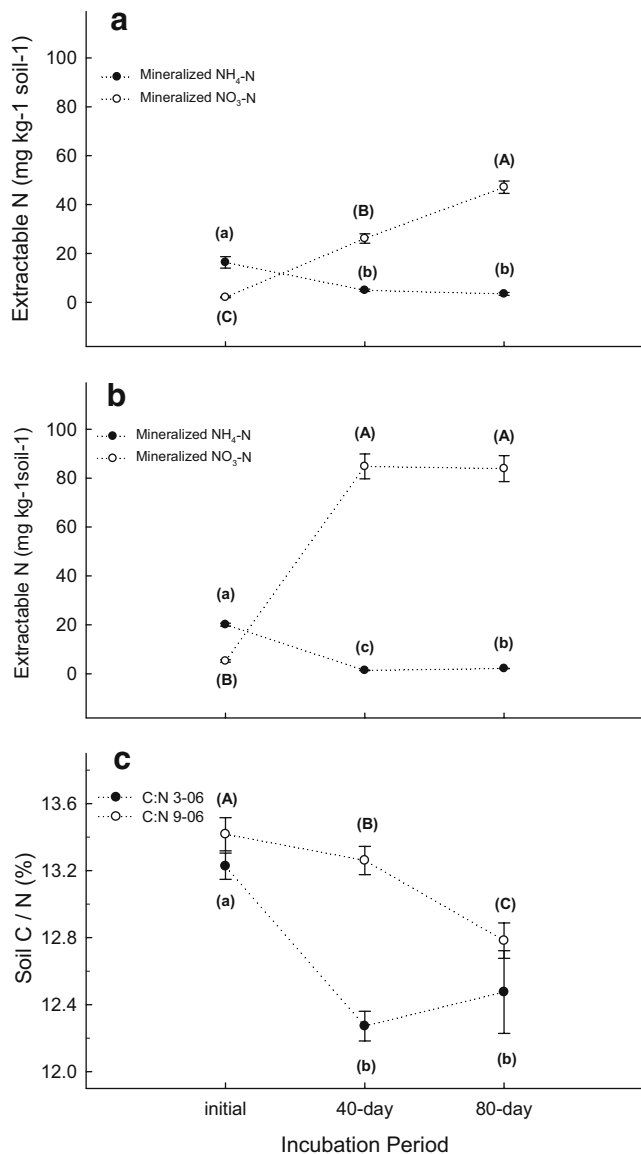
Fig. 5 Temporal influences in March 2006 (a) and September 2006 (b) on nitrogen mineralization patterns and C:N ratios (c) for soil collected from the Sotol Grasslands in Big Bend N.P, (for soils incubated throughout March and September 2006). Values are mean± SE; N=24. *Letters above error bars* indicate significant difference at P≤0.05 using Fishers LSD post hoc tests

periods. When comparing the two incubation intervals independently (0–40 vs 40–80 days), significant declines of relative percent nitrification (P<0.001) were observed during the 40- to 80-day incubation periods in both March and September from the first 0- to 40-day period to less than 100% (Fig. 7b).

Bacterial Carbon-Use Potential

Potential bacterial carbon usage, measured in terms of total substrate activity (BSA) and substrate richness (BSR), were variable across sample periods with the highest values recorded

in September 2006 (Fig. 8, 9). Lower values for BSA and BSR were associated with periods of low soil moisture. Temporal patterns in potential carbon usage by bacteria in the micro-wells were similar across incubation times. Higher values were recorded after the 120-h incubation (Fig 9a–b). Soil moisture was the dominant single parameter accounting for the seasonal and yearly variability of BSA after 72-h incubation (R^2=0.313; P<0.001; Table 4), whereas soil moisture, soil NH_4–N, and soil pH were related to carbon use patterns after 120-h incubations (R^2=0.446; P<0.001). Variation in BSR after the 72-hr incubation period was related to soil moisture and levels of soil NH_4–N (R^2=0.463; P<0.001) (Table 4). For BSR after 120-hr incubations, soil moisture, levels of soil NH_4–N, soil organic matter, and soil pH levels accounted for the most variation (R^2=0.515; P<0.001).

Fungal Carbon-Use Potential

Significant differences in total substrate activity (FSA) for the 72-h incubation periods were exhibited over all sample periods (P≤0.03; Fig. 8a). Overall substrate diversity (FSR) was significantly different throughout most of the study (September 2004–March 2006; P≤0.038; Fig. 8b); however, the first sample period in March 2004 and the last sample period in September 2006 were not significantly different from one another. Potential fungal carbon use followed temporal patterns of increased activity in March vs September coupled with annual precipitation levels; however, fungal activity dramatically increased in September 2006. Soil moisture and soil temperature accounted for most of the seasonal and yearly variability (R^2=0.388; P<0.001) in fungal substrate activity (FSA) after 72-h incubations (Table 4). For FSR after the 72-h incubation period, soil moisture and soil temperature were also significant (R^2=0.342; P<0.001; Fig. 8b; Table 4). Soil moisture was the only variable (R^2=0.118; P<0.001) that accounted for temporal variability in fungal substrate activity after the 120-h incubation.

Discussion

Environmental Parameters

The Chihuahuan Desert is unique in that it is the only North American Desert that receives the majority of it's annual precipitation exclusively in the summer months, with minor pulses contributing to annual net precipitation during the fall, winter, and spring months [38–40]. Annual precipitation and temperature patterns in the Sotol Grasslands in Pine Canyon at BBNP are relatively consistent with the Chihuahuan Desert as a whole. Over this 3-year study annual precipitation steadily declined, ranging from an

Fig. 6 Net nitrification and net mineralization rates using in vitro soil incubations (mean± SE; N=24) for soils collected in March and September 2006 from the Sotol Grasslands in Big Bend N.P. Incubation periods are indicated in *parenthesis*. *Letters above error bars* indicate significant difference at $P \leq$ 0.05 using Fishers LSD post hoc tests
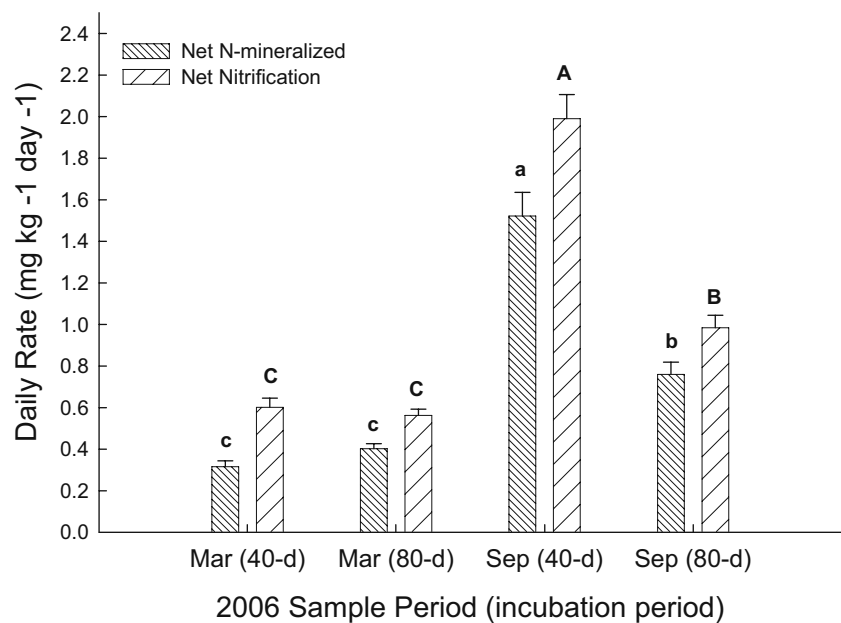
unusually wet year in 2004 (567 mm; 155% of the 19-year average), to average precipitation levels received in 2005 (329 mm; 90% of 19-year average), to drought-like conditions in most of 2006 (273 mm; 74% of 19-year average). The timing and magnitude of intra-seasonal precipitation in the Chihuahuan Desert is highly dynamic and varies greatly from year to year, as seasonal soil moisture variability reflects the timing and magnitude of precipitation, number of dry days between rain events, soil temperatures, and evapotranspiration rates [4, 56, 57]. The 2006 sampling year is a good example of how variable this system can be between years as this region experienced an extreme drought that started in late Fall in 2005 and continued throughout the first half of 2006, in which only 79 mm occurred between Jan–July 2006 (39% of historical averages for this period). Intense rainfall events occurred throughout August 2006. The total rainfall recorded for this month was 147.4 mm, which is 90% of historical rainfall received for the entire summer season (June, July, and August), producing 54% of the precipitation received in 2006.

Understanding soil microbial responses to soil moisture and rainfall is crucial to determine ecosystem responses to climate change. Soil microbes are typically the first responders to soil moisture pulses in arid systems and soil microbial functional capabilities in arid systems are directly linked to precipitation and resource availability [5, 8, 58]. The severe drought event that began in late 2005 and continued through mid-summer of 2006 allowed us to observe how soil microbes will respond to occurrences of extended drought periods accompanied by brief but intense precipitation events. These climate events are important to document because extreme drought patterns accompanied by increased magnitudes of brief precipitation events are predicted to

increase significantly throughout the 21st century in the arid regions of SW North America as reported by the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC; [45]). The stability of this desert grassland ecosystem as climate change occurs is likely to rely on the ability of soil microbes to function during these brief moisture windows of opportunity [3]. The dynamics of how properties such as soil pH, levels of soil NO_3–N and NH_4–N, and amounts of soil organic matter respond to these windows of opportunity can also greatly influence soil microbial dynamics in this ecosystem [56, 59].

Soil Carbon and Nitrogen Dynamics

When considering that the majority of precipitation occurs throughout the summer months in this region, the overall observed pattern of soil organic matter dynamics is similar to previous studies in which soil moisture dynamics (drying–rewetting) promotes loss of soil organic matter as it becomes more readily used by microbes as the primary source of nitrogen (via mineralization; [59–61]).

The soil organic matter patterns observed in this study suggest that the magnitude and timing of intra-seasonal precipitation is a key regulator for microbial ability to utilize soil organic matter. Our observations support this because regardless of 2005 receiving 50 mm more precipitation than 2006 by the end of the summer season, more soil organic matter was depleted in 2006, in which a few intense rainfall events occurred in August as opposed to the more frequent, less intense events throughout 2005. This suggests that soil microbes in this desert grassland are resilient to extended drought and seasonal resource depletions and are able to quickly respond to increases in soil moisture pulses as they occur.

Fig. 7 Temporal influences on relative percent nitrification using in vitro soil incubations for 0- to 40-day and 0- to 80-day incubations (**a**) and 0- to 40-day and 0- to 80-day incubations (**b**) for soils collected in 2006 from the Sotol Grasslands in Big Bend N.P (mean±SE; N=24). Incubation periods are indicated in *parenthesis. Letters above error bars* indicate significant difference at $P \leq 0.05$ using Fishers LSD post hoc tests. Relative percent nitrification is the ratio of net nitrification to net mineralization; ex: [%= $100 \times (N_{nitrification}/N_{mineralization})$]
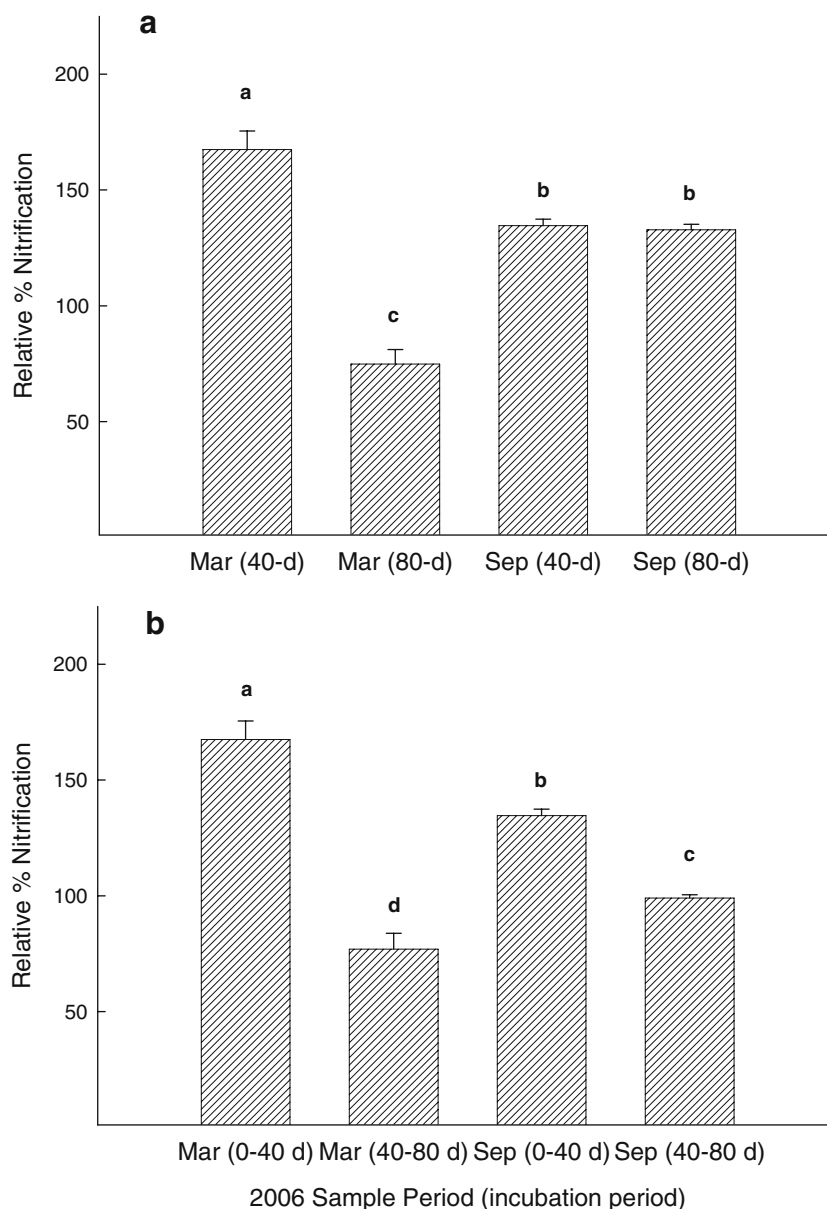
The nitrogen mineralization dynamics observed in this desert grassland further support these seasonal microbial activity patterns as nitrate levels were greater in September and lower in March, which inversely followed patterns in soil organic matter amounts. Moreover, levels of soil NO_3–N were negatively correlated with soil organic matter (R=−0.208). Both relative nitrification and nitrate levels significantly increased with moisture pulses, while soil NH_4–N levels declined, indicating that both soil moisture and temperature are key controlling factors regulating mineralization in this system [2, 60].

The *in vitro* potential N-mineralization patterns observed in this study were similar to results from previous semiarid grassland studies [2, 9], in which soil NH_4–N levels at the time of collection were consistently higher than soil NO_3–N levels at initial collection; while over time throughout the incubation periods, dramatic increases in NO_3–N levels were observed (with added moisture), while NH_4–N levels dropped dramatically over the same incubation period. Temporal differences in the rates of *in vitro* mineralization reflect the seasonal regulation of microbial metabolic potential, as both net nitrification and net mineralization rates in September far exceeded that of March. This indicates that above and beyond soil moisture, seasonal soil temperature is a second key regulating mechanism in this system influencing soil microbial functionality in this desert grassland by possibly down regulating soil microbial mineralization capabilities. Consequently, as seasonal tem-
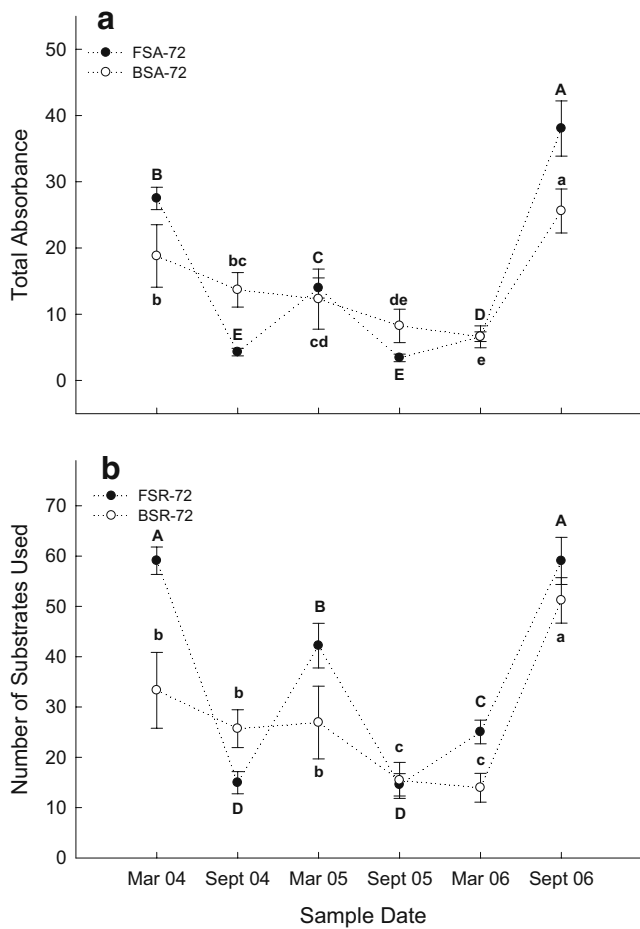
Fig. 8 Temporal response patterns of potential carbon use expressed as substrate activity (a) and total substrate richness (b) for soil bacterial and fungi from the Sotol Grasslands in Pine Canyon, Big Bend N.P., using Biolog and Fungilog procedures after 72-h incubations. Values are mean±S.E.; N=24. Letters above error bars indicate significant difference at P≤0.05 using Fishers LSD post hoc tests

peratures increase as predicted by global climate-change models, changes in precipitation, temperature, and soil moisture dynamics has the potential to greatly shift the soil microbial metabolic potential in this desert grassland system, which could, in turn, potentially alter the functionality of this ecosystem.

Microbial Parameters

Patterns in microbial biomass were observed to correspond with peaks in soil moisture levels. The dramatic shift in microbial responses from extreme drought to above average soil moisture in September 2006 demonstrates the resilience of the soil microbes in this system to remain viable enough during periods of drought to quickly respond to moisture windows of opportunity as they occur. Furthermore, these responses reveal how temperature regulates seasonal MBC, as the MBC levels in March (promptly after the winter season) are unable to respond to soil moisture availability,

but in September 2006, MBC does respond to moisture pulses regardless of prior temperature-stress conditions. Lower MBC levels recorded during the years with higher precipitation in 2004 and 2005 may suggest that microbial activity peaked earlier in the summer season with the earlier moisture pulses, thus depleting necessary resources. Another likely scenario is that microbial grazing by microfauna could be stimulated during the wetter years, which could reduce microbial biomass levels by the September sample collection period [62]. In addition, overall seasonal MBC levels in September were significantly higher than March, suggesting that soil temperatures could restrict microbial activity regardless of the availability of soil moisture and available soil nitrogen. Similar microbial biomass dynamics have been observed in previous studies in which increased soil microbial biomass carbon correlated with elevated soil moisture and nitrogen mineralization rates as available soil moisture was shown to stimulate microbial biomass
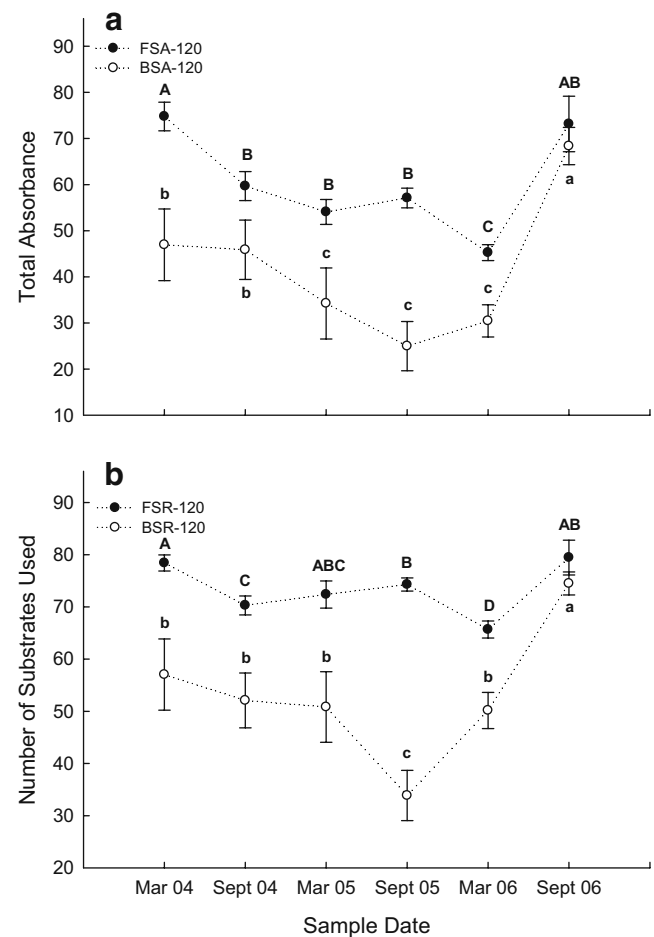

Fig. 9 Temporal response patterns of potential carbon use expressed as substrate activity (a) and total substrate richness (b) for soil bacterial and fungi from the Sotol Grasslands in Pine Canyon, Big Bend N.P., using Biolog and Fungilog procedures after 120-h incubations. Values are mean±SE; N=24. Letters above error bars indicate significant difference at P≤0.05 using Fishers LSD post hoc tests

Table 4 Regression analysis for bacterial and fungal carbon-use responses to environmental conditions in Big Bend NP

Dependent variable	Model	Predictors	R	R Square	Sig.
BSA 72-h incubation	1	sm%	0.560	0.313	<0.001
BSR 72-h incubation	1	sm%	0.652	0.425	<0.001
	2	sm%, NH_4–N	0.681	0.463	<0.001
BSA 120 h-incubation	1	sm%	0.600	0.36	<0.001
	2	sm%, NH_4–N	0.634	0.402	<0.001
	3	sm%, NH_4–N, Ph	0.668	0.446	<0.001
BSR-120 h-incubation	1	sm%	0.580	0.336	<0.001
	2	sm%, NH_4–N	0.659	0.435	<0.001
	3	sm%, NH_4–N, som	0.692	0.479	<0.001
	4	sm%, NH_4–N, som, pH	0.718	0.515	<0.001
FSA 72-h incubation	1	sm%	0.589	0.347	<0.001
	2	sm%, soil temp	0.623	0.388	<0.001
FSR 72-h incubation	1	sm%	0.436	0.190	<0.001
	2	sm%, soil temp	0.585	0.342	<0.001
FSA 120-h incubation	1	sm%	0.343	0.118	<0.001
FSR 120-h incubation	None				

sm%=soil moisture %, som=soil organic matter, BSA=bacterial substrate activity, BSR=bacterial substrate richness, FSA=fungal substrate activity, FSR=fungal substrate richness

Multiple regression analysis indicated the relationship of how environmental factors influenced bacterial and fungal carbon-use potential in the Sotol Grasslands across season and year; $P \leq 0.01$ for model inclusion. The sample size for each variable used for multiple regression analysis of bacterial and fungal responses with the environmental variables listed above is $N=144$

turnover in arid systems [63–66]. Other studies conducted by Kieft et al. and Van Gestel [61, 67] argue that osmotic shock can occur from intense rewetting of dry soils, resulting in cell lyses, from which remaining soil microbes can utilize labile organic carbon and nitrogen occurring from turnover. However, it is unclear to what degree microbial osmotic shock associated with precipitation events are responsible for observed patterns in microbial biomass and potential carbon usage in the soils of the Sotol Grasslands at BBNP. Potential carbon utilization dynamics for both fungi and bacteria displayed patterns that corresponded to seasonal and yearly soil moisture patterns over time; however, the responses to precipitation contrasted between bacteria and fungi. Bacterial substrate activity and substrate richness declined over much of the study directly tracking the annual declines in precipitation and soil moisture. These patterns suggest that bacterial carbon use is directly regulated by precipitation and subsequent soil moisture dynamics in this desert grassland.

Fungal carbon-use responses exhibited significant seasonal shifts with elevated early spring activity. Fungal abilities to use carbon substrates in this system demonstrated much weaker correlations to soil moisture over the 3-year study than did bacteria, as temperature was the major determinant of fungal carbon use. Zak and Wildman [68] indicated that despite soil temperature being a major environmental characteristic in desert ecosystems, the majority of soil fungi are adapted to a mesophilic lifestyle. Rather, saprophytic fungi have adapted life history strategies

that allow them to succeed through extreme heat conditions that exist in hot arid systems [3].

These carbon-use patterns demonstrate the resilience of soil bacteria and fungi to environmental stress in this arid system, as both soil bacteria and saprophytic fungal assemblages were able to quickly respond to substantial moisture windows regardless of prior environmental conditions. However, the activity of saprophytic fungi in this arid system declined with increased temperatures, as fungi were more active during early spring than late summer. The soil fungi during the summer months only respond to large precipitation events and subsequent available soil moisture increases, as was observed in September 2006 after intense rainfall events. Soil bacterial activity is highly responsive to levels of soil moisture, nitrogen, and soil organic carbon. Therefore, bacterial activity is tightly linked with soil carbon resulting from plant inputs and fungal activity (via decomposition and mineralization). Consequently, as increasing temperatures change soil moisture dynamics in this desert grassland, soil bacterial activity is likely to decline as well.

Although bacteria may be able to function more effectively than fungi at higher soil temperatures, global warming is likely to initiate declining windows of opportunity for both bacterial and fungal activity, which can ultimately lead to limited soil organic matter and soil nutrient levels in this system for above- and below-ground utilization. This observation presents a prospective scenario of how the environment regulates soil bacterial and fungal

species in this system, and how higher trophic dynamics in this arid system may be greatly disrupted by a change in climate. In this region, global climate change over the next 50 years is predicted to increase temperatures by 3–5 °C, which will consequently result in increased storm magnitudes and intra-seasonal climate variability, potentially altering current seasonal precipitation by as much as 25%. Changing moisture and temperature dynamics in this region are likely to greatly alter soil microbial activity, which could change the soil functional dynamics in this region by affecting both carbon and nitrogen cycling, ultimately disrupting above-ground processes, which has repercussions for both below- and above-ground microbe and plant successes.

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