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Rainfall pulses increased short-term biocrust chlorophyll but not fungal abundance or N availability in a long-term dryland rainfall manipulation experiment

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ABSTRACT

Microbial activity in drylands is mediated by the magnitude and frequency of growing season rain events that will shift as climate change progresses. Nitrogen is often co-limiting with water availability to dryland plants. This study investigated how microbes important to the nitrogen (N) cycle and soil N availability varied temporally and spatially in the context of a long-term rainfall variability experiment in the northern Chihuahuan Desert. Specifically, biological soil crust (biocrust) chlorophyll content, fungal abundance, and inorganic N were measured in soils adjacent to individuals of the grassland foundation species, *Bouteloua eriopoda*, and in the unvegetated interspace at multiple time points associated with experimental monsoon rainfall treatments. Treatments included 12 small weekly (5 mm) or 3 large monthly (20 mm) rain events, which had been applied during the summer monsoon for nine years prior to this study. Additionally, target plant C:N ratios were measured, and ^{15}N-glutamate was added to biocrusts to determine potential for nutrient transport to *B. eriopoda*. Biocrust chlorophyll was up to 67% higher in the small weekly and large monthly rainfall treatments compared to ambient controls. Fungal biomass was 57% lower in soil interspaces than adjacent to plants but did not respond to rainfall treatments. Ammonium and nitrate concentrations near plants declined through the sampling period but varied little in soil interspaces. There was limited movement of ^{15}N from interspace biocrusts to leaves but high ^{15}N retention occurred in the soils even after additional ambient and experimental rain events. Plant C:N ratio was unaffected by rainfall treatments. The long-term alteration in rainfall regime in this experiment did not change how short-term microbial abundance or N availability responded to the magnitude or frequency of rain events at the end of the growing season, suggesting a limited response of N availability to future climate change.

1. Introduction

Rainfall patterns in dryland ecosystems create temporal and spatial constraints on biological activity that affect nutrient cycling processes. Drylands are characterized by pulsed patterns of rainfall that drive biological activity, and the magnitude and frequency of rain events control the activation of soil and plant processes (Noy-Meir, 1973; Schwinning and Sala, 2004; Collins et al., 2014). Plants are sensitive to these dynamics and interact with microbes and physical processes integrating components of the nitrogen (N) cycle (Nielsen and Ball, 2015). Dry periods separating rain events limit the decomposition of soil organic matter, making nutrient availability an additional constraint on primary productivity (Collins et al., 2008). It is unclear, however, how changes in rainfall regimes that control this cascade of biological processes (Cook and Seager, 2013; Cook et al., 2015) will affect dryland soil microbial communities and N availability. Understanding how the size and frequency of rain events affects soil communities and nutrient availability is fundamentally important because drylands make up >40% of the earth's surface and support more than 38% of the world's population (Reynolds et al., 2007; Maestre et al., 2016).

The effects of rainfall events that vary in size and frequency on dryland microbial communities and their role in nutrient cycling are poorly resolved. Biological soil crusts (biocrusts) colonize bare soil interspaces between plants (Belnap et al., 2001) and are a major source of

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fixed N in dryland regions (Barger et al., 2016). Increases in rainfall frequency can damage biocrusts, altering their community composition (Ferrenberg et al., 2015) and structural properties (Faist et al., 2017). These changes can increase nitrification rates, shifting the balance between soil NH_4^+ and NO_3^- (Reed et al., 2012). Many organisms prefer ammonium as an N source to nitrate, which is easily lost from soil ecosystems through leaching and denitrification (Reed et al., 2012). In addition, plants can only use added N to support productivity if it is available to their roots. Rainfall regime shifts may strongly affect N dynamics in the microbe-soil-plant system because surface biocrusts are metabolically activated by small rain events while plants require greater infiltration into their rooting zone to activate photosynthesis (Huxman et al., 2004; Thomey et al., 2011; Petrie et al., 2016). Microbial communities with fungi are hypothesized to integrate biocrust and plant resources through nutrient translocation pathways. These hypothesized pathways enable resources to be exchanged during periods of demand and stored in a biotic pool (hyphae) when plants are inactive (Rudgers et al., 2018). Understanding rainfall size effects on fungal and biocrust abundance may further elucidate the role these organisms play in dryland water and N dynamics.

Significant uncertainty persists for rainfall effects on dryland N availability. Soil ammonium and nitrate concentrations have been observed to increase, decrease, or remain the same (Dijkstra et al., 2012; Bell et al., 2014; Nielsen and Ball, 2015; Morillas et al., 2015) immediately after moisture events. Long-term mineralization rates may be unaffected by soil moisture content (Yahdjian and Sala, 2010) or increase with heightened rainfall (Bell et al., 2014). These studies have focused on the effects of individual rain events, long-term changes in rainfall seasonality, or the amount of rainfall on N dynamics. The variability in their findings suggests the need to further assess the responses of dryland soil organisms and N pools to both single rain events and long-term shifts in rainfall regime.

This study assessed how biocrusts, fungi, and inorganic N pools within soil interspaces and the rooting zone respond to small, frequent or large, infrequent rain events, or ambient controls within a long-term rainfall variability experiment (Thomey et al., 2011). Evidence suggests that the number of rain events per day has increased, whereas the average size of events has decreased in the Southwestern US over the past 100 years (Petrie et al., 2014). On the other hand, climate models predict increased precipitation variability and more climate extremes in the future. Therefore, it is important to understand how ecosystem processes, such as soil N availability, will respond to potential changes in rainfall event size and frequency.

To understand these responses, this experiment addressed two questions. 1) How does rainfall event size affect dryland soil microbes and N availability under plant canopy and crust soils? It was predicted that the large, infrequent events would provide sufficient moisture for short-term biological activity but that biocrust and fungal biomass would decline during extended periods when surface soils were dry between rain events. It was also expected that small, frequent rain events would not support prolonged biological activity and could damage biocrusts that are sensitive to frequent drying and rewetting (Belnap et al., 2004). Inorganic N levels were predicted to remain lower near plants that assimilate these nutrients. Finally, large rain events were expected to remove more N by denitrification than small frequent events. 2) How does rainfall event size affect ^{15}N transport between biocrusts and plants and N integration by plants? The small, frequent events were expected to show the most movement, as multiple rain events could allow fungal hyphae to move the tracer through the soil solution. The ambient control was predicted to show the least tracer movement. Leaf C:N was also compared between treatments as an integrative measure of N in the plant and soil pools. It was hypothesized that plants in the large, infrequent regime would have access to more persistent soil deep moisture and incorporate more N than those in the small, frequent regime over the long term. These hypotheses were evaluated at a site that experienced nine years of experimental manipulation of size and frequency of rainfall events in the northern Chihuahuan Desert, USA. Accordingly, this study integrates short-term effects of rain events and dry periods with the long-term impacts of changes in rainfall regime.

2. Materials and methods

2.1. Study area

The study was conducted in the Sevilleta Long Term Ecological Research site in the Sevilleta National Wildlife Refuge (NWR) at the northern edge of the Chihuahuan Desert. Mean annual temperature and rainfall are 13.2 °C and 250 mm, respectively. Sixty percent of annual rainfall occurs during the summer monsoon from July through September (Báez et al., 2013). Soils are Typic Haplargids derived from piedmont alluvium, with basic pH (8.2+). Texture is 68.3% sand, 22.4% silt, and 9.2% clay, with 2% $CaCO_3$. Bulk density is 1.51 g cm^{-3}, soil porosity is 0.43 m^3 m^{-3}, total organic C is ~4.5 mg g^{-1} and mineralizable N is ~7 μg g^{-1} (Kieft et al., 1998). Grasslands are dominated by *Bouteloua eriopoda* (Torr.) Torr. (black grama) and transition into *Larrea tridentata* (DC.) Coville (creosote bush) shrublands to the south. Biocrusts are dominated by the cyanobacteria *Microcoleus vaginatus* (Vaucher) Gomont and *M. steenstrupii* Boye-Petersen (Fernandes et al., 2018).

Samples were collected in the Monsoon Rainfall Manipulation Experiment (MRME) located at 34° 20′20″ N, 106° 43′30″ W (Thomey et al., 2011), elevation = 1400 m. There are thirteen 9 m × 14 m plots fenced to reduce trampling and herbivory. Three plots are exposed to ambient rainfall only (control), five plots receive 20 mm of additional rainfall monthly in July, August, and September, and five plots receive 5 mm of additional rainfall weekly during those months. At the end of the growing season both treatments have received the same amount of added rain (60 mm). These treatments reflect two possible rainfall regimes that may emerge in arid regions as climate change progresses (Nielsen and Ball, 2015). Because rainfall additions began in 2007 (Thomey et al., 2011), the current study occurs within the context of 9 y of altered rainfall regimes. Each plot has a CS616 TDR probe (Campbell Scientific, Logan, UT) with data logger installed to record soil moisture in the top 15 cm (Collins, 2016a).

In each MRME plot, smaller 0.5 × 0.5 m quadrat locations were selected containing biocrusts and one target *B. eriopoda* grass tussock. In two of the ambient control plots, two quadrats were constructed at least 2 m apart to match the sample size of the 20 mm monthly and 5 mm weekly treatments. These quadrats were lined with aluminum flashing to a depth of 20 cm in June 2016, isolating the target plant and biocrust from the adjacent shallow soil. The flashing was intended to limit the diffusion of ^{15}N tracer (see 2.3).

2.1.1. Sample collection for biotic and abiotic responses

Sampling occurred from 31 August to September 25, 2016 (Fig. 1), after two months of rainfall regime manipulations had already occurred in that year. One 20 mm event and one 5 mm event occurred on 30 August, and three remaining 5 mm events occurred weekly thereafter. To identify immediate effects of rain events of different magnitude (water added from one 20 mm and one 5 mm event), samples were collected on 31 August, one day after all MRME plots received their relevant large or small rainfall treatment (hereafter, "Day 1"). To identify the effects of the different magnitude of events as soil moisture declined, the next samples were collected on 4 September, five days after the first rain event (hereafter, "Day 5"). Finally, to identify the effects of rainfall frequency with a dry period, samples were collected on 25 September, following a 26 day dry period in the 20 mm-addition plots and a 5 day dry period in the 5 mm-addition plots (total water added under both treatments over this time frame = 20 mm). Although all plots also received several small ambient rain events during the sampling period (Fig. 1), all but one of these rain events was <5 mm; they had

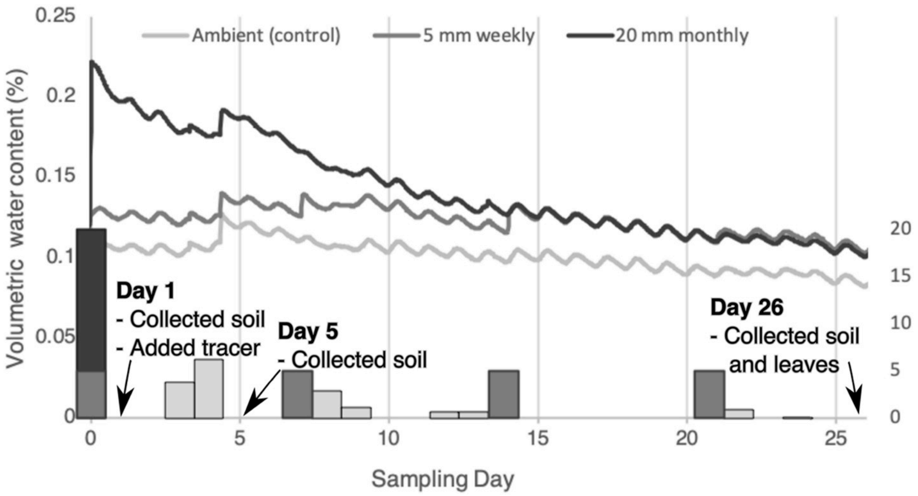

Fig. 1. Volumetric water content (%) in top 15 cm of soil (lines, left axis) and experimental rain additions and ambient rain events (bars, right axis), plus sample collection dates starting on August 30, 2016 (Sampling Day = 0). Note that plots had received this rainfall treatment during the summer monsoon (July–September) for 9 years prior to this study.

little effect on soil volumetric water content relative to the experimental water addition treatments.

Samples were collected from several locations on each of the sampling days. Soil was collected from the interspace away from the target grass in each quadrat (distance = 25 cm from grass), and rooting zone soil was collected adjacent to the plant base (distance = 0 cm from grass) on Days 1, 5, and 26. All soils were collected as a single core with a 1.90 cm diameter core to 10 cm depth. Soils were stored at −20 °C and processed within four months. Soils were subset for biocrust and fungal biomass measurements and for N availability. Leaves were collected on Day 26 and processed for ^{15}N and C:N (see 2.3).

2.1.2. *Biocrust and fungal biomass measurements*

Chlorophyll *a* concentrations were measured to determine how rainfall events affected biocrust photosynthetic capacity. Chlorophyll *a* was extracted from soil using dimethyl sulfoxide (Castle et al., 2011). Absorbance of the extracts at 750 and 665 nm was converted to μg chl*a* g^{-1} soil using equations developed by Ritchie (2006). One sample was missing from the 20 mm treatment on Day 5 and one on Day 26. Low absolute chlorophyll *a* concentrations were expected because samples were from 0 to 10 cm depth cores while most of the photosynthetic organisms are in the top 2 cm of soil. However, relative differences between rainfall treatments should be comparable.

To estimate fungal biomass, soil ergosterol concentrations were measured in three of the five replicate plots (due to budget and time constraints). Note that arbuscular mycorrhizal fungi do not produce ergosterol (Olsson et al., 2003) and thus are not detectable in this analysis. Ergosterol was extracted from soil using 0.8% KOH in methanol heated to 80 °C (Wallander et al., 2001). The ergosterol content of filtered extracts was determined using a high-performance liquid chromatograph (HPLC; Thermo Scientific Ultimate 3000, Waltham, MA, USA) with a C18 reversed phase column.

2.1.3. *Inorganic N measurements*

Soil ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were measured to determine how altered rainfall event sizes affected inorganic N availability. Ammonium and nitrate were extracted from soil with 2 M KCl. The filtered extracts were then processed with a Lachat Instruments QuickChem 8500 flow injector analyzer (Loveland, CO, USA) that used colorimetric methods to quantify ammonium and nitrate. Note that ^{15}N tracer was added on Day 1 to biocrusts (see section 2.3), meaning that N may have been detected above natural levels, especially at 25 cm from the plant. However, all plots received the same amount of additional N at the same time, allowing for comparisons of relative differences among treatments.

2.2. *Stable isotope tracer experiment and plant C:N*

On 31 August, one day after the rainfall addition events, 2 mL of 0.104 M^{15}N-glutamate (3.12 total mg N) was added to biocrusts 25 cm away from the grass tussock in each quadrat. A similar quantity of tracer was used in a previous stable isotope experiment at the Sevilleta NWR and is <1% of the N generally found in grass and biocrust biomass within an area the size of the quadrats (Green et al., 2008).

Stable isotope measurements were completed in three of the five replicates per rainfall treatment. These replicates were the same as those sampled for ergosterol. Plants were harvested and soil and leaf samples were collected for ^{15}N and percentage C and N values on Day 26. Average soil natural abundance values were obtained from four Day 1 cores that had been collected before the tracer was added ($\delta^{15}N = 5‰$). Soil subsamples were placed in silver capsules and fumigated in HCl for 24 h to remove inorganic carbonates (Harris et al., 2001). Soil samples were then packaged in tin capsules to improve combustion. Leaf tissues were ground using liquid N_2 and placed in tin capsules for analysis. Average leaf natural abundance values were obtained from *B. eriopoda* plants at a site near the MRME and used for the plants in this study ($\delta^{15}N = -0.8‰$). All samples were sent to the University of New Mexico Center for Stable Isotopes where they were run on an ECS 4010 Elemental Analyzer (Costech, Valencia, CA, USA) and a Delta V Isotope Ratio Mass Spectrometer (Thermo Scientific, Waltham, MA USA) to obtain weight percent C (%C), weight percent N (%N), and $\delta^{15}N$ values (precision <0.3‰). Plant molar C:N was calculated from the weight percentages and atomic masses.

2.3. *Statistical analysis*

All statistical analysis was completed using R (R Core Team, 2016). The lme4 (Bates et al., 2015) and car packages (Fox and Weisberg, 2011) were used for linear modelling. Average daily soil moisture was compared by day × treatment with plot as a random effect to account for repeated measures. Planned post-hoc comparisons of treatments were made within each day. Generalized linear mixed models were created for chlorophyll *a*, ergosterol, ammonium, and nitrate responses (all natural log transformed to improve normality of residuals) with plot included as a random effect. Main effects included rainfall treatment (ambient control, 20 mm event monthly, 5 mm event weekly), sampling day, and distance from the grass tussock in each quadrat (all as categorical variables) with all interactions. Post hoc comparisons with false discovery rate corrections (Benjamini and Hochberg, 1995) were used within sampling day if significant treatment and/or distance interactions existed.

For the stable isotope tracer experiment, the % recovery of tracer and excess ^{15}N in the plants and soils were calculated from the mass percent ^{15}N on Day 26 vs. natural abundance mass percent ^{15}N values (raw δ^{15}N presented in Figs. S2 and S3), the %N of each individual, and the dry sample mass. The dry mass of the soils was calculated using bulk density and the volume of the soil core. Models for ^{15}N enrichment for soils and leaves each included rainfall treatment, and soils included distance from plant. The model for C:N of leaves included treatment.

3. Results

Soil moisture was generally highest in the 20 mm monthly treatment (Fig. 1, treatment: $X^2 = 22.6$, $P < 0.001$), but the differences varied by day (day $X^2 = 12.5$, $P = 0.99$, treatment × day $X^2 = 84.9$, $P < 0.001$) such that for each of Days 1–8, the monthly 20 mm treatment was significantly higher than the weekly 5 mm (post-hoc $P < 0.05$) and ambient control (post-hoc $P < 0.05$), which were not significantly different from each other (post-hoc $P \geq 0.05$). For each of Days 9–13, the monthly 20 mm and weekly 5 mm events were not significantly different from each other (post-hoc $P \geq 0.05$) but both were significantly higher than the ambient control (post-hoc $P < 0.05$). For Days 14–26, there were no differences in treatment on any day (post-hoc $P \geq 0.05$). Soil moisture data for June through September 2016 are presented in Fig. S1.

3.1. *Biocrust chlorophyll and fungal ergosterol*

Soil chlorophyll content varied by rainfall treatment and distance from plant. Compared to control plots receiving ambient moisture alone, chlorophyll was >65% higher in plots receiving additional rainfall (Table 1, Fig. 2). Concentrations were 73% lower in the interspace (distance = 25 cm from the plant) than adjacent to the plant (distance = 0 cm). There was no effect of sampling date and no interactive effects among any predictors.

Fungal abundance did not change with rainfall treatment but was 57% lower in the interspace than adjacent to the plant (Table 1, Fig. 3). The magnitude of this effect varied slightly between sampling days ($P = 0.069$, Table 1). Interspace soils contained 63–66% less ergosterol than the plant-adjacent soils on Days 1 and 26, but only 34% less than plant adjacent soils on Day 5.

3.2. *Inorganic nitrogen*

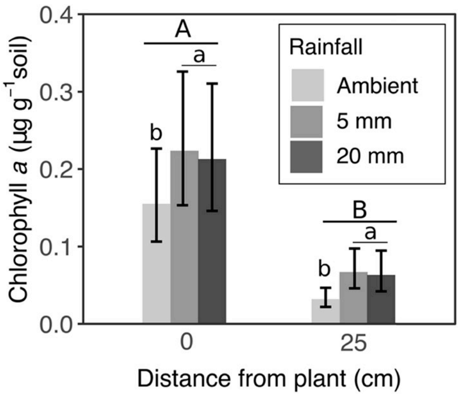

Fig. 2. Means ± 95% *CI* of chlorophyll *a* concentrations by distance from plant and experimental rainfall treatment (Ambient = control, Monthly = additional 20 mm monthly; Weekly = additional 5 mm weekly) across all sampling days. Uppercase letters show differences in distance from plant, and lowercase letters show differences in rainfall treatment (post hoc $P \leq 0.050$); there were no significant interactions between factors.

The rainfall treatments had a marginally non-significant effect on ammonium concentrations (Table 1, Fig. 4) with a trend that plots receiving the weekly 5 mm event had 4% less ammonium than the control plots exposed to ambient rainfall, while the plots receiving the monthly 20 mm event had 9% more ammonium than the ambient plots. Soil ammonium differed by distance from plant depending on sampling dates (Table 1). On Day 1 and 5 after the initial rain events, ammonium was 12% ($t_{56} = 1.93$, $P = 0.058$) and 30% ($t_{57} = 4.50$, $P < 0.001$; respectively) lower in the interspace (distance = 25 cm) than adjacent to the plant (distance = 0 cm), but ammonium declined by Day 26 such that there was no difference between 0 and 25 cm from the plant ($t_{56} = 0.63$, $P = 0.532$). This trend drove the overall decrease in ammonium by date, in which Days 1 and 5 had similar ammonium values ($t_{57} = -0.07$, $P = 0.944$), but Day 26 had 15% lower ammonium concentrations than on Day 1 ($t_{57} = 3.31$, $P = 0.002$).

The rainfall treatments had no effect on nitrate concentrations (Table 1, Fig. 4). However, as with ammonium, the amount of nitrate through time varied between microsites. Both microsites had generally similar nitrate concentrations on Day 1 (post hoc $t_{56} = -1.87$, $P = 0.066$) and Day 5 (post hoc $t_{56} = -1.30$, $P = 0.200$) after rain events, but by Day 26, the interspace (distance = 25 cm) had 168% more nitrate (post hoc $t_{56} = -4.69$, $P = <0.001$) than adjacent to the plant (distance = 0 cm), which reflected a decline in nitrate near the plant between Day 5 and 26.

3.3. *Transport of ^{15}N tracer and leaf C:N*

Soils showed considerable signs of enrichment adjacent to where the tracer had been added, with three samples having >93% of total added ^{15}N in the soil on Day 26, one sample having 11%, and the remaining 5 samples having less than 0.2%. The enrichment at the tracer addition point was higher than the enrichment in the soil at 25 cm away from the tracer addition point (maximum 0.1% of total added ^{15}N; $X^2 = 3.32$, $P =$

Table 1
Results from general linear mixed effects models testing for effects of rainfall treatment (ambient control, 20 mm monthly, 5 mm weekly), sampling day (Days 1, 5, and 26 after the initial experimental rain events), distance from plant (cm), and all interactions on biocrust chlorophyll *a* concentration (µg g^{-1} soil), fungal ergosterol abundance (µg g^{-1} soil), and soil ammonium and nitrate concentration (µg g^{-1} soil). *P* values ≤ 0.050 are shown in bold.

	df	Chlorophyll		Ergosterol		Ammonium		Nitrate	
		X^2	*P*	X^2	*P*	X^2	*P*	X^2	*P*
Rainfall	2	7.49	**0.024**	0.83	0.660	4.74	0.093	2.38	0.304
Sampling day	2	3.01	0.222	0.85	0.655	8.89	**0.012**	4.73	0.094
Distance from plant	1	6.72	**0.010**	14.59	**<0.001**	0.03	0.863	1.36	0.242
Rainfall × Sampling day	4	5.52	0.238	7.70	0.103	5.45	0.244	6.77	0.149
Rainfall × Distance from plant	2	0.47	0.789	2.22	0.329	2.54	0.281	0.56	0.754
Sampling day × Distance from plant	2	1.73	0.422	5.35	0.069	9.13	**0.010**	6.74	**0.034**
Rainfall × Sampling day × Distance from plant	4	4.83	0.305	5.99	0.200	5.11	0.276	2.75	0.601
Marginal R^2		0.46		0.56		0.35		0.36	

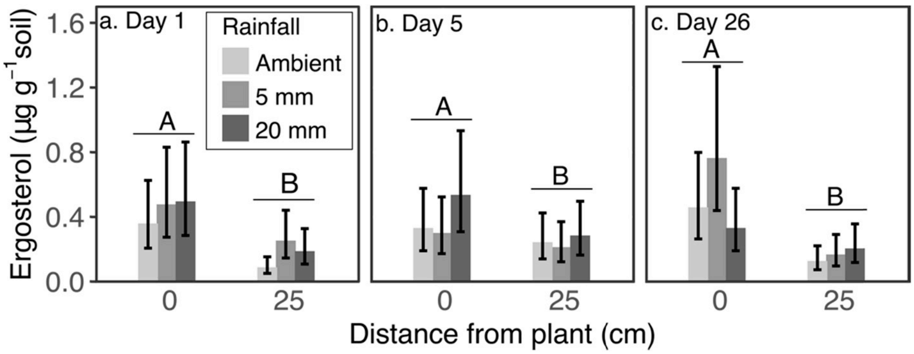

Fig. 3. Means ± 95% *CI* of ergosterol concentrations by distance from plant tussock and rainfall treatment (Ambient = control, Monthly = additional 20 mm monthly; Weekly = additional 5 mm weekly) on each sampling day (a. Day 1, b. Day 5, c. Day 26) after initial experimental rain events. Uppercase letters show significant contrasts between ergosterol levels at different distances from the target plant (post hoc $P \leq 0.050$).

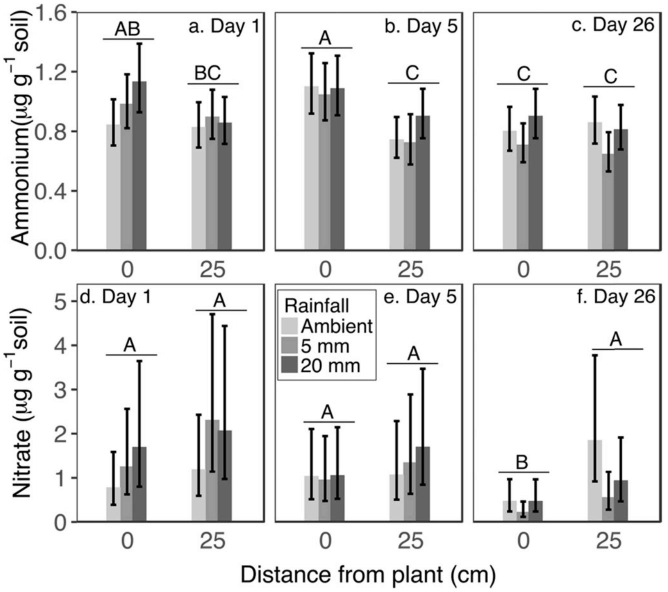

Fig. 4. Means ± 95% *CI* of ammonium (a. – c.) and nitrate (d. – f.) concentrations by distance from plant tussock and rainfall treatment (Ambient = control, Monthly = additional 20 mm monthly; Weekly = additional 5 mm weekly) on each sampling day (a. and d. Day 1, b. and e. Day 5, and c. and f. Day 26 after initial experimental rain events). Uppercase letters show significant contrasts between ammonium or nitrate levels at different distance by date combinations (post hoc $P \leq 0.050$).

0.068). There was no interaction or main effect of rainfall treatment on soil excess ^{15}N (rainfall: $X^2 = 0.01$, $P = 0.993$; interaction: $X^2 = 3.02$, $P = 0.991$).

There was no effect of rainfall treatment on ^{15}N excess in leaves, and no significant excess (intercept: $F_{1,6} = 0.01$, $P = 0.930$; rainfall: $F_{2,6} = 0.72$, $P = 0.524$) indicating minimal transfer of N from biocrusts to plants. However, one monthly 20 mm treatment plant had 5% of the tracer in leaves, and one weekly 5 mm treatment plant had 14% of the tracer in leaves, so with a larger sample size a difference could potentially have been detected. The remaining seven samples had <0.5% of tracer in leaves. There was no effect of rainfall treatment on leaf C:N ($F_{2,6} = 0.30$, $P = 0.749$) which averaged 55.8 ± 3.8 SE.

4. Discussion

Overall, the results indicate that N availability did not vary between rainfall treatments, suggesting that rainfall pulses differing in magnitude and frequency had little effect on N availability late in the growing season in this desert grassland. Although additions of any amount of rainfall increased soil chlorophyll *a*, the magnitude and frequency of rainfall additions had no effect. While including three substantially different rainfall regimes, the results do not reflect the hierarchy of rainfall responses suggested by some models in which different components of dryland soil ecosystems (e.g. biocrusts, soil bacteria and fungi, plants, and soil invertebrates) become active at different moisture thresholds (Collins et al., 2008; Nielsen and Ball, 2015) and produce, exchange, or use resources based on those thresholds.

The rainfall treatments had little effect on soil inorganic N concentrations which is surprising because available soil N is known to accumulate during extended dry periods in dryland ecosystems (White et al., 2004). Additionally, in dry soils, rain events can stimulate N mineralization by disrupting soil aggregates, improving the transport of organic substrates through diffusion, and increasing microbial mobility (Borken and Matzner, 2009). Dijkstra et al. (2012), observed a pulse of soil ammonium and nitrate availability in a Colorado semiarid grassland one day after a simulated rain event added in mid-July. In contrast, Bell et al. (2014) found no effect of large, monthly rain events added in June, July, and August on ammonium or nitrate levels at a Chihuahuan desert site in samples that were collected immediately before an August rain event. A previous study at the Sevilleta NWR found little effect of rainfall manipulations on soil enzyme activity but found a decrease in N availability from early to late in the growing season (Ladwig et al., 2015). There was no observed short-term response of nitrogen to rain events in the current study, potentially due to sampling at the end of the growing season and after multiple ambient and experimental rainfall additions. There was also no difference in available nitrogen among these rainfall treatments integrated over the entire growing season (2016 PRS probe data: rainfall $F_{2,10} = 1.07$, $P = 0.380$; Collins, 2016c). As a result, N dynamics in this system may be decoupled from individual rain events and could prove resistant to perturbations in rainfall regimes brought about by climate change.

Although fungal communities were expected to vary with rainfall regime, non-mycorrhizal fungal communities, measured by soil ergosterol, did not differ by treatment. Previous work has shown that the fungal communities in biocrusts and rhizospheres at the Sevilleta NWR were dominated by dark septate endophytes (Pleosporales, Ascomycota; Porras-Alfaro et al., 2008; Steven et al., 2014). Herrera et al. (2011) reported no differences in the abundance of root associated fungi between the monthly 20 mm and weekly 5 mm rain event treatments in this long-term experiment. Instead, water addition led to an increase in similarity among the fungal communities, irrespective of the size and frequency of precipitation events. Similarly, in a Chinese desert shrubland, the overall abundance of Ascomycota increased within days after a simulated rain event (Chen et al., 2019). However, the abundance of Ascomycota in the orders Pezizales (ectomycorrhizal) and Verrucariales (lichen-forming) decreased after two years of approximately weekly rain additions during the growing season (She et al., 2018), suggesting that long-term changes in communities may dampen short-term responses. Additionally, fungal sensitivity to rain events can vary between seasons. In an Arizona semiarid grassland, fungal community composition changed only when rain was added during the typically dry month of June, a manipulation that reduced fungal diversity and increased the abundance of the phylum Zygomycota (McHugh and Schwartz, 2015, 2016). Similarly, water additions had little impact on fungal abundance during monsoon season in piñon-juniper woodlands (Cregger et al., 2012). Fungal abundance also increased depending on antecedent moisture conditions in a northern California grassland (Hawkes et al., 2011). The lack of fungal abundance response to precipitation regime in this study may relate to long-term and seasonal aspects: rainfall regime treatments in the MRME experiment have occurred for multiple years during the summer monsoon, and samples were collected late in the growing season. This result also highlights the resilience of soil fungi to environmental change and their potential resistance to future shifts in rainfall regimes.

The results offered little support for rapid transport of N from biocrust to plants, contradictory to what was expected by the fungal loop hypothesis (Green et al., 2008; Rudgers et al., 2018). In a previous study conducted at the Sevilleta NWR, ^{15}N-glutamate and ^{15}N–NO_3^- were both translocated from biocrusts to individuals of *Bouteloua gracilis* (Willd. ex Kunth.) Lag. ex Griffiths, a species that responds rapidly to even small levels of N addition (Báez et al., 2007; Collins et al., 2010), at rates of up to 100 cm per day (Green et al., 2008). Aanderud et al. (2018) observed similar translocation rates through soil on the Colorado Plateau but detected little ^{15}N enrichment of plant leaves one day after a simulated 2 mm rain event. Given the gradual declines in inorganic N observed in this study near the rooting zone, plants with sufficient moisture may preferentially use available N in the rhizosphere rather than rely on transfers from biocrusts. Biocrust and fungal biomass and ammonium availability were elevated near plants, a result consistent with the "island of fertility" effect (Kieft et al., 1998; Ladwig et al., 2015; Aguilera et al., 2016; Ochoa-Hueso et al., 2018) that would reduce the efficiency of transfers from more distant biocrusts.

The gradual pace of rooting zone N consumption and limited incorporation of ^{15}N tracer may additionally be explained by the limited sensitivity of *B. eriopoda* to N inputs compared to *B. gracilis*. Subplots within the larger MRME rainfall treatments also received annual inputs of 5 g N m^{-2} starting in 2007, but aboveground production by *B. eriopoda* did not differ by rainfall regime or N fertilization treatment in 2016 (Rainfall $F_{2,20} = 335.5$, $P = 0.216$; Fertilizer $F_{1,20} = 95.4$, $P = 0.344$, Rainfall × Fertilizer $F_{2,20} = 9.41$, $P = 0.954$, Collins, 2016b). In a nearby site, Ladwig et al. (2012) found that production by *B. eriopoda* was lower while production by *B. gracilis* was higher on N addition plots (10 g N m^{-2}) compared to controls, perhaps because of competition with other species that were enhanced by fertilization. In this study, plant C:N ratios also showed no differences between ambient control, weekly 5 mm, or monthly 20 mm treatments, suggesting that individual plant N requirements may be decoupled from precipitation regime. This decoupling suggests that pulses in *B. eriopoda* carbon fixation following rain events (Thomey et al., 2014) may not significantly affect soil N pools, further illustrating how future changes in rainfall regime—and the timing of such pulses—may have little impact on soil N dynamics in this dryland. Data on leaf C:N ratios in response to rainfall pulse size are rare. In a pine plantation in China, needle C:N did not change with added rainfall during the first two years of experimental rainfall additions (Fan et al., 2017). In the current study, high rates of N uptake were expected because samples were collected at the end of the growing season when plants would be sequestering nutrients in preparation for the dormant season. Instead, plants were likely reallocating nutrients within tissues rather than incorporating new sources of N from these low N soils (Zak et al., 1994). Such reallocation may explain the relatively high average plant C:N observed in this experiment that could reflect storage of N in belowground tissues ahead of the dormant season.

Although biocrust photosynthetic capacity was expected to vary with rainfall treatment, there was an increase with water addition regardless of event size and frequency. There were no observed deleterious effects on biocrusts of altered rainfall frequency and drying-rewetting periods induced by multiple small rain events. This lack of response suggests either that weekly 5 mm events are large enough to maintain productivity or that ambient precipitation during the sampling period meant that the plots did not experience minimum moisture conditions (which averaged ~6% at this site during the study). Additionally, the microbial composition of biocrusts can shift due to long-term changes in rainfall regime (Fernandes et al., 2018; Fernandes et al., unpublished data), and may therefore compensate for effects of individual rain events of different sizes. Conversely, several studies in the Colorado Plateau suggest that long-term exposure to small, frequent rain events can reduce biocrust biomass (Belnap et al., 2004; Johnson et al., 2012). These results may be explained by composition differences in the biocrusts of the Chihuahuan Desert, dominated by cyanobacteria in the genus *Microcoleus* (Garcia-Pichel et al., 2013), compared to the Colorado Plateau where mosses are more common and especially susceptible to rainfall regime (Tucker et al., 2019). Although the photosynthetic potential did not differ between the two rain addition treatments, previous work has shown increased and prolonged soil respiration pulses with the 20 mm monthly treatment compared to the 5 mm treatment or controls (Vargas et al., 2012), indicating that carbon fixed may be allocated differently. Additionally, increased biocrust photosynthetic capacity did not appear to increase N fixation, as there was no effect of rainfall treatment on N availability. On the other hand, other pathways such as investment into extracellular polysaccharides (Mager and Thomas, 2011) could vary by rainfall regime and change the function of the biocrust.

Previous research has shown that year-to-year variation in precipitation can swamp effects of rainfall or nitrogen addition treatments on productivity in dryland ecosystems (Yang et al., 2019). Also unknown is if lag effects of prior year precipitation affected production responses in the observed time period (Sala et al., 2012; Bunting et al., 2017). Finally, given that the plants and microbes in each treatment have been acclimated to the altered conditions for nearly a decade, responsiveness to individual events may be dampened, as has been found for some plant physiological responses to warming treatments (Drake et al., 2016).

4.1. *Conclusions*

This study evaluated how microbial abundance and N availability responded to large and small rainfall events in the northern Chihuahuan Desert. While the addition of rainfall elevated biocrust chlorophyll *a*, the magnitude and frequency of rainfall events had no effect on fungal communities or N availability. Limited nutrient translocation was detected using stable isotope tracers, suggesting localized controls over N cycling under favorable soil moisture conditions. The pulse response to rain events by *B. eriopoda* (Thomey et al., 2014) is not sufficient to drive variation in N availability between treatments. Instead, the gradual decline in rooting zone N observed after the late season rain events applied in this study suggests that N dynamics vary over longer or shorter time scales than pulses of soil moisture following rain events. Overall, these findings suggest that long-term changes to rainfall regimes may have little impact on soil microbial activity immediately after rain events and during the dry periods that follow. Consequently, soil microbes and nutrient dynamics may be buffered to some extent from changes in rainfall regime that are predicted to occur in response to climate change.

Statement of authorship

JK conceived of study, collected and analyzed data. ES and RL assisted with the design and implementation of the field work, training for lab work, and data analysis. SC conceived of and ran the long-term manipulations and assisted with mentorship of JK. JK and ES wrote the manuscript and RL and SC contributed substantially to writing and editing.

Data accessibility statement

The data supporting the results are archived on EDI and can be found at https://doi.org/10.6073/pasta/573848e6e65f686686884670de506465.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107693.

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