

JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2022JG006938

Key Points:

- Contrary to the pulse dynamics framework for drylands, plant available nitrogen did not pulse in response to monsoon rainfall
- Nitrogen availability increased over the growing season, particularly after small frequent rains that also stimulated microbial activity
- A shift to fewer, larger growing season rain events could reduce nitrogen availability and net primary production in desert grasslands

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

R. F. Brown,
rfbrown@unm.edu

Citation:

Brown, R. F., Sala, O. E., Sinsabaugh, R. L., & Collins, S. L. (2022). Temporal effects of monsoon rainfall pulses on plant available nitrogen in a Chihuahuan Desert grassland. *Journal of Geophysical Research: Biogeosciences*, 127, e2022JG006938. <https://doi.org/10.1029/2022JG006938>

Received 10 APR 2022

Accepted 3 JUN 2022

Author Contributions:

Conceptualization: Renée F. Brown, Scott L. Collins

Data curation: Renée F. Brown

Formal analysis: Renée F. Brown

Funding acquisition: Scott L. Collins

Investigation: Renée F. Brown, Scott L. Collins

Methodology: Renée F. Brown, Robert L. Sinsabaugh, Scott L. Collins

Project Administration: Renée F. Brown, Scott L. Collins

Resources: Robert L. Sinsabaugh, Scott L. Collins

Visualization: Renée F. Brown

Writing – original draft: Renée F. Brown, Scott L. Collins

Writing – review & editing: Renée F. Brown, Osvaldo E. Sala, Robert L. Sinsabaugh, Scott L. Collins

Temporal Effects of Monsoon Rainfall Pulses on Plant Available Nitrogen in a Chihuahuan Desert Grassland

Renée F. Brown¹ , Osvaldo E. Sala² , Robert L. Sinsabaugh¹ , and Scott L. Collins¹ 

¹Department of Biology, University of New Mexico, Albuquerque, NM, USA, ²School of Life Sciences, School of Sustainability, & Global Drylands Center, Arizona State University, Tempe, AZ, USA

Abstract Drylands are often characterized by a pulse dynamics framework in which episodic rain events trigger brief pulses of biological activity and resource availability that regulate primary production. In the northern Chihuahuan Desert, growing season precipitation typically comes from monsoon rainstorms that stimulate soil microbial processes like decomposition, releasing inorganic nitrogen needed by plant processes. Compared to microbes, plants require greater amounts of soil moisture, typically from larger monsoon storms predicted to become less frequent and more intense in the future. Yet field-based studies linking rainfall pulses with soil nutrient dynamics are rare. Consequently, little is known about how changes in rainfall patterns may affect plant available nitrogen in dryland soils, particularly across temporal scales. We measured daily and seasonal responses of soil inorganic nitrogen and related parameters to experimentally applied small frequent and large infrequent rain events throughout a summer growing season in a Chihuahuan Desert grassland. Contrary to long-standing theories around resource pulse dynamics in drylands, nitrogen availability did not pulse following experimental rain events. Moreover, large infrequent events resulted in significantly less plant available nitrogen despite causing distinct pulses of increased soil moisture availability that persisted for several days. Overall, nitrogen availability increased over the growing season, especially following small frequent rain events that also stimulated some microbial coenzymatic activities. Our results suggest that projected changes in climate to fewer, larger rain events could significantly impact primary production in desert grasslands by decreasing plant available nitrogen when soil moisture is least limiting to plant growth.

Plain Language Summary Deserts receive low amounts of rainfall, which limits nutrient availability and plant growth in these ecosystems. In the northern Chihuahuan Desert, monsoon rainstorms stimulate pulses of soil microbial activities that make essential nutrients like nitrogen available for plant growth during the summer growing season. Compared to microbes, plants require more water, typically from larger monsoon storms predicted to become less common and more intense in the future. However, little is known about how changes in rainfall patterns may affect nitrogen availability in desert soils. In this study, we measured soil inorganic nitrogen and related parameters in response to experimentally applied small frequent and large infrequent rain events throughout a summer growing season in a desert grassland. Contrary to long-standing ideas around desert ecological processes, nitrogen did not increase in days following experimental rain events, with large infrequent rains resulting in significantly less nitrogen available for plant use despite increasing soil water content. Overall, nitrogen availability increased over the growing season, especially in response to small frequent rains preferred by microbes. Our results suggest predicted changes in climate to fewer, larger rain events may reduce plant available nitrogen and consequently, plant growth in desert grasslands.

1. Introduction

Processes in arid and semi-arid ecosystems (i.e., drylands) are frequently characterized by a pulse dynamics framework, in which episodic precipitation events moisten dry soils, triggering brief pulses of biological activity and resource availability (Noy-Meir, 1973). Soil moisture pulses and consequent ecological responses are driven largely by the size and frequency of precipitation events. It is hypothesized that plants and soil microorganisms exhibit different sensitivities to pulses of soil moisture in these systems (Collins et al., 2014; Schwinning & Sala, 2004). While relatively small and infrequent rain events can activate microbially driven processes such as decomposition of soil organic matter (SOM) and nutrient mineralization in surface soils (Austin et al., 2004; Collins et al., 2008), larger or tightly clustered small rain events are typically necessary for deeper infiltration of soil moisture to trigger higher plant metabolism (Noy-Meir, 1973; Schwinning & Sala, 2004). Consequently, differences in rainfall size and frequency may create a scenario of asynchronous resource availability

in pulse-driven drylands, whereby plant and soil microbial processes are hypothesized to become temporarily uncoupled (Austin et al., 2004; Collins et al., 2014, 2008).

Nitrogen (N) is second to water as the most limiting resource for aboveground primary production in drylands (Austin et al., 2004; Yahdjian et al., 2011). Indeed, soils in water-limited ecosystems throughout the southwestern United States (US) contain especially low amounts of total available nitrogen (Zak et al., 1994). Most nitrogen in the soil is in the form of SOM and generally unavailable for direct assimilation by plants. Upon activation by episodic rain events, microbes decompose SOM, thereby liberating plant available nitrogen in the forms of ammonium ($\text{NH}_4^+\text{-N}$) and nitrate ($\text{NO}_3^-\text{-N}$). This pulse of microbially mediated nutrient mineralization that occurs in response to the wetting of dry soils, termed the “Birch effect,” frequently involves a rapid release of enzymes that facilitate nutrient acquisition from the surrounding environment, particularly if substrates are of low quality (Birch, 1958; Borke & Matzner, 2009; Robertson & Groffman, 2015). Enzyme expression is regulated by environmental signals, thus balancing microbial demand for limiting nutrients like nitrogen with the energetic costs associated with enzyme production (Sinsabaugh & Follstad Shah, 2012; Wallenstein & Weintraub, 2008; Xiao et al., 2018). However, during extended dry periods, irregular microbial activities, combined with little or no plant uptake (Austin et al., 2004; Birch, 1958; Borke & Matzner, 2009), can result in the accumulation of soil inorganic nitrogen (Augustine & McNaughton, 2004; White et al., 2004).

The Birch effect is most pronounced in arid (60–250 mm y^{-1}) and semi-arid (150–500 mm y^{-1}) regions that experience strong seasonal precipitation (Austin et al., 2004) like the predominantly warm and dry southwestern US where peak annual net primary production is driven by the North American Monsoon (Muldavin et al., 2008; Pennington & Collins, 2007). Historically this region has experienced frequent, but weak pulses of soil moisture throughout the summer monsoon, with rain events typically ranging from 2 to 5 mm in size and separated by brief intervening dry periods (Loik et al., 2004). Recent empirical analyses of meteorological data collected over the past century have revealed increasingly variable precipitation patterns throughout the southwestern US (Maurer et al., 2020; F. Zhang et al., 2021). In the northern Chihuahuan Desert, for example, rain event size has been decreasing, while the frequency of rain events, along with the prevalence of extreme wet and dry periods, has increased (Petrie et al., 2014). Regional climate models project further intensification of the hydrologic cycle, particularly during the summer monsoon (Diffenbaugh et al., 2008; Moustakis et al., 2021), with a higher occurrence of extreme precipitation events (Donat et al., 2016; Easterling et al., 2017, 2000) and prolonged dry spells (Bradford et al., 2020; Cook et al., 2021).

Future changes in rainfall patterns are likely to have significant consequences on the availability of limiting resources to primary production in drylands, especially if events become larger and more sporadic. Building on the pulse dynamics framework, the Threshold-Delay Nutrient Dynamics conceptual model suggests larger pulses of soil moisture not only stimulate primary production but also enable longer persistence of soil microbial activities and associated biogeochemical processes (Collins et al., 2008). Yet field-based studies investigating the temporal dynamics of plant available nitrogen in the context of altered precipitation regimes in drylands are not only uncommon but have also produced inconsistent results (Austin et al., 2004; Borke & Matzner, 2009; Epstein et al., 2019; Nielsen & Ball, 2015; Song et al., 2020). For example, small frequent rain events stimulated the greatest nitrogen mineralization rates throughout the growing season in Patagonian steppe (Yahdjian & Sala, 2010). In contrast, small frequent rain events resulted in the lowest mineralization rates and greatest losses of nitrogen in Chihuahuan Desert shrubland (Fisher et al., 1987). Yet, large infrequent rain events resulted in greater nitrogen losses in Patagonian steppe as well as piñon-juniper woodland in the southwestern US (Cregger et al., 2014; Yahdjian & Sala, 2010). On the other hand, large rain events resulted in greater mineralization rates in Colorado shortgrass steppe (Dijkstra et al., 2012; D. S. Schimel & Parton, 1986), as well as pulses of plant available nitrogen in the Great Basin and Colorado shortgrass steppe (Cui & Caldwell, 1997; Dijkstra et al., 2012). Yet a small rain event in Colorado shortgrass steppe stimulated a pulse of increased plant uptake that persisted longer than belowground processes (Dijkstra et al., 2012). Thus, a major knowledge gap exists with respect to how availability of the two most limiting resources for primary production in drylands will respond to future climate change.

To determine if nitrogen availability pulses in response to rainfall in a dryland ecosystem as predicted by the pulse dynamics framework, we examined the daily and seasonal responses of plant available nitrogen to rain events that differed in size and frequency throughout a summer monsoon in a northern Chihuahuan Desert grassland. We were specifically interested in addressing the following questions: (a) Does plant available nitrogen pulse in

response to monsoon rainfall, and if so, for how long? (b) How is plant available nitrogen affected by differences in rain event size and frequency? (c) How does the availability of nitrogen evolve over the growing season? (d) What are some potential drivers influencing nitrogen availability at the seasonal scale? To answer these questions, we measured soil inorganic nitrogen and related parameters in an existing rainfall manipulation experiment consisting of replicated treatment plots that receive a series of small frequent or large infrequent rain events throughout the summer growing season.

2. Materials and Methods

2.1. Site Description

This study was conducted during the 2014 summer monsoon (July–September) in a northern Chihuahuan Desert grassland dominated by black grama (*Bouteloua eriopoda*), a native shallow-rooted perennial C₄ grass. The Monsoon Rainfall Manipulation Experiment (MRME; 34.3441°N, 106.7272°W, elevation 1,604 m), located in the Sevilleta National Wildlife Refuge (NWR) in central New Mexico, USA, served as the experimental platform for this study. MRME was established in 2007 to investigate the effects of increased variability in monsoon rainfall on ecosystem processes in a desert grassland. In August 2009, a lightning-caused wildfire burned through the experiment.

MRME consists of thirteen 8 m by 13 m plots, all of which receive ambient precipitation throughout the year. Three plots serve as ambient controls, while the remaining 10 receive one of two experimentally applied rainfall addition treatments for 12 consecutive weeks during the summer monsoon (Thomey et al., 2011). “Small frequent” plots ($n = 5$) receive a 5 mm rainfall addition once per week ($n = 12$), whereas “large infrequent” plots ($n = 5$) receive a 20 mm rainfall addition once per month ($n = 3$). Thus, all rainfall addition plots receive the same amount of supplemental rainfall by the end of the summer monsoon (60 mm). Onsite storage tanks provide a reservoir for water obtained from a reverse-osmosis system. Treatments occur via raindrop-quality overhead sprinkler systems, which are applied shortly after dawn when winds are minimal and diurnal soil temperatures are at their lowest, thereby minimizing evaporative loss. Sensor arrays within each plot continuously record soil moisture as an integrated measurement of soil volumetric water content (SVWC) from 0 to 16 cm (CS616; Campbell Scientific Inc., Logan, UT, USA) as well as soil temperature at a depth of 8 cm (CS107; Campbell Scientific Inc.).

Growing season precipitation in the Sevilleta NWR is highly variable within and between years, originating primarily from localized convective thunderstorms driven by the North American Monsoon (Muldavin et al., 2008; Pennington & Collins, 2007). The summer monsoon is typically preceded by a 2-month period with high daytime temperatures and limited precipitation (Notaro et al., 2010). From 1990 to 2020, mean annual water year precipitation recorded at a nearby meteorological station (34.3592°N, 106.6911°W, elevation 1,600 m) was 233 ± 9.6 mm, with 118 ± 8.3 mm falling during the summer monsoon, while mean annual temperature was $13.7^\circ\text{C} \pm 0.0^\circ\text{C}$, with average monthly temperatures ranging from $25.4^\circ\text{C} \pm 0.2^\circ\text{C}$ in July to $1.3^\circ\text{C} \pm 0.3^\circ\text{C}$ in December (Moore, 2021). Atmospheric nitrogen deposition occurs at a rate of $0.2 \text{ g m}^{-2} \text{ yr}^{-1}$ (Báez et al., 2007). Soils are alkaline, with a pH of 8.5 ± 0.2 (Crenshaw et al., 2008), and are classified in the Turney loam series, formed by calcareous aeolian and alluvial deposits (Soil Survey Staff, 2019). Soil bulk density is 1.51 g cm^{-3} and porosity is 43% (Thomey et al., 2011; Vargas et al., 2012), with a texture distribution in the upper 20 cm consisting of 68% sand, 22% silt, and 10% clay, with <10% as CaCO₃ (Kieft et al., 1998).

2.2. Soil Collection

Dryland ecosystems are characterized by islands of fertility, where SOM, microbial ecoenzymatic activities, and nutrient availability are higher under and adjacent to plants compared to areas of unvegetated soil (Kieft et al., 1998; Ladwig et al., 2015; Schlesinger et al., 1990; Stursova et al., 2006). There is also some evidence that fungal hyphae can transport nitrogen fixed by biological soil crusts to plants located up to 1 m away (Carvajal Janke & Coe, 2021; Green et al., 2008). Prior to the summer monsoon we installed three soil collars (25.4 cm wide and 15 cm deep) per plot, each positioned around a randomly selected tussock of black grama to prevent plant roots and soil microbes from acquiring outside resources as well as to limit potential nitrogen losses through overland flow. We further reduced plant uptake of nitrogen, which is driven by transpiration, by clipping tussocks prior to

and throughout the summer monsoon so that we could more effectively detect pulses of soil inorganic nitrogen that would be available for plant use.

Rhizosphere soil samples (0–15 cm depth) were collected from within each soil collar using a 2.22 cm diameter hammer-head soil core sampler (AMS Inc., American Falls, ID, USA) during weeks in which both small frequent and large infrequent rainfall addition treatments were applied ($n = 3$). The first soil collections of each sampling period took place around sunrise, approximately 2 hr before rainfall addition treatments were applied (Sampling Day 0). Subsequent collections of soil occurred 1, 2, 3, 4, and 6 days following the rainfall addition treatments to assess pulse duration and associated responses. Intensive sampling campaigns occurred 3–9 July (sampling days J0–J6), 29 July to 4 August (A0–A6), and 26 August to 1 September (S0–S6) during the 2014 summer monsoon. Soil samples were bulked per plot and homogenized by gentle mixing in labeled quart-sized zip-top freezer bags that were immediately put on ice. Since collection, soil samples ($n = 234$) have been stored continuously at -20°C for subsequent laboratory analyses.

2.3. Nitrogen Availability

To measure plant available nitrogen, 10 g subsamples of wet mass soil were extracted following collection with 100 mL of 2M potassium chloride (KCl) solution containing 0.5 μg phenylmercuric acetate (PMA) for the analysis of extractable $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$. PMA was used as a preservative to prevent microbial transformation of nitrogen during the interval between soil collection and analysis. Gravimetric soil water content of each sample was determined using a second 10 g subsample of wet mass soil that was desiccated at 105°C for 24 hr and reweighed. After settling at room temperature for at least 24 hr, each clarified KCl sample was decanted through a Kimwipe into corresponding centrifuge tubes, which were then stored at 1.6°C for a period of no longer than 1 month. Each filtrate sample was analyzed for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ (as nitrite ($\text{NO}_2^-\text{-N}$) + $\text{NO}_3^-\text{-N}$) on a Technicon AutoAnalyzer II (Technicon Corp., Tarrytown, NY, USA) following previously described methods (Crenshaw et al., 2008; Kieft et al., 1998; White et al., 2004).

Plant Root Simulator (PRS®) probes (Western Ag Innovations, Saskatoon, Saskatchewan, CA) were buried within the rooting zone of a randomly selected, uncollared, and unclipped tussock of black grama in each plot on 2 July 2014 (Collins, 2020). PRS® probes mimic plant uptake using ion-exchange resin membranes and were used to provide an integrated estimate of plant available nitrogen over the summer monsoon. Upon removal on 10 October 2014, probes were rinsed in deionized water and shipped to the manufacturer, where they were subsequently analyzed for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$.

2.4. Microbial Ecoenzymatic Activities

To gain additional insight regarding the evolution of nitrogen availability over the summer monsoon, all soil samples were fluorometrically assayed to assess the potential hydrolytic activities of two nitrogen-acquiring enzymes. Given that the majority of soil organic nitrogen is contained in amino acids (peptides, proteins) and amino sugars (chitin, peptidoglycan), we measured the potential activities of leucyl aminopeptidase (LAP), which hydrolyzes leucine and other amino acids from the N-terminus of polypeptides, and β -1,4-*N*-acetylglucosaminidase (NAG), which degrades amino sugars contained in microbial cell walls to mobilize nitrogen (Sinsabaugh & Follstad Shah, 2012; Sinsabaugh et al., 2008; Zhou et al., 2013). Soil enzyme assays were performed following previously described methods that attempt to mimic the soil environment to approximate potential ecoenzymatic activities under natural conditions (e.g., Saiya-Cork et al., 2002; Stursova et al., 2006). Further methodological details are provided in the Supporting Information (Text S1 in Supporting Information S1).

2.5. Soil Organic Matter

To estimate the percentage of SOM contained in each sample as a proxy for substrate availability, we used the loss on ignition approach. Briefly, 10 g subsamples of wet mass soil were dried at 105°C for 2 hr, after which pre-ignition weights for each sample were determined. Dried soils were then placed in a muffle furnace and ignited for 2 hr at 360°C to oxidize organic matter to CO_2 while preventing the loss of CaCO_3 (H. Zhang & Wang, 2014). The percentage of organic matter in each sample was calculated as the difference between pre- and post-ignition weights divided by the pre-ignition weight.

2.6. Statistical Analyses

All data analyses were conducted using *R* version 3.6.3 (R Core Team, 2020). To assess the pulse response and duration of soil moisture (as SVWC), plant available nitrogen (as extractable $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$), and nitrogen-acquiring microbial ecoenzymatic activities (NAG, LAP) to experimental rainfall addition treatments over the summer monsoon, we used linear mixed effect models to perform repeated measures analysis of variance (ANOVA). Models were constructed using the *nlme* package in *R* (Pinheiro et al., 2020), where treatment, day, month, and their interactions represented fixed effects and plot was the random effect. Models also included a continuous first order autoregressive correlation structure to account for temporal autocorrelation. Seasonally integrated nitrogen supply rates measured by the PRS® probes were analyzed similarly using simplified models where treatment was the fixed effect and plot was the random effect. Response variables were natural log transformed to satisfy assumptions of normality (evaluated using Q-Q plots) and homoscedasticity (evaluated by plotting residuals against fitted values). Post-hoc Tukey's Honest Significant Difference pairwise comparisons were used to further investigate differences in treatment effects through time, which were considered statistically significant when $p \leq 0.05$.

To provide a more holistic understanding of how plant available nitrogen ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) and associated soil parameters (e.g., nitrogen-acquiring microbial ecoenzymatic activities, SOM) interact and respond to differences in rainfall size and frequency at the seasonal scale, we built a structural equation model (SEM) using the *lavaan* package in *R* (Rosseel, 2012). SEM is ideal for developing a system-level understanding of complex relationships in multivariate datasets through partitioning direct and indirect effects among variables, distinguishing the multiple pathways by which one variable can influence another, and estimating the strength of multiple effects (Eisenhauer et al., 2015). Spearman's rank order correlations of explanatory and response variables were conducted using the *rcorr* function in the *Hmisc* package in *R* (Harrell et al., 2020). Using a "weight-of-evidence" approach, significant correlations (Table S1 in Supporting Information S1; $p \leq 0.05$) aligning with a priori scientific knowledge informed the construction of a base model, which was further optimized by removing all non-significant paths ($p \geq 0.05$), followed by the stepwise addition of new paths based on relevant modification indices until the best model fit was achieved (Eisenhauer et al., 2015; Grace, 2020). Since we were specifically interested in the effects of both rainfall size and rainfall frequency on plant available nitrogen over the growing season, exogenous variables included experimental rainfall addition treatment size and frequency along with sampling month. Rainfall size and frequency were predicted to covary as treatments were not completely independent from each other. Rainfall size was specified as the amount of added rainfall per treatment event and rainfall frequency was specified as the total number of treatment events over the summer monsoon. Endogenous variables included soil moisture (as SVWC) and soil temperature averaged over the 24 hr preceding the end of each soil collection period (also predicted to covary), as well as SOM, LAP, and NAG. To satisfy assumptions of normality, SVWC, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and NAG activity were natural log transformed and LAP activity was rescaled. To assess goodness of model fit, we used the model Chi-square statistic (χ^2) and three approximate fit indices: root mean square error of approximation (RMSEA), comparative fit index (CFI), and standardized root mean square residual (SRMR). An SEM is considered to be well fitted to the data when the χ^2 statistic is insignificant ($p \geq 0.05$), $\text{RMSEA} \leq 0.05$ and its associated p -value ≥ 0.05 , $\text{CFI} \geq 0.95$, and $\text{SRMR} \leq 0.08$ (Grace, 2020; Kline, 2016).

3. Results

3.1. Pre-Treatment

Prior to experimental rainfall addition treatments (i.e., on J0, A0, and S0), SVWC ranged from $7.7\% \pm 0.3\%$ to $12.5\% \pm 0.7\%$, $\text{NH}_4^+\text{-N}$ from 1.91 ± 0.13 to $4.52 \pm 0.39 \mu\text{g N g}^{-1}$ soil, and $\text{NO}_3^-\text{-N}$ from 1.44 ± 0.09 to $2.44 \pm 0.35 \mu\text{g N g}^{-1}$ soil from July to September (Figure 1; Table 1). There were no significant *within-month* pre-treatment differences in SVWC. The only significant *within-month* pre-treatment differences in plant available nitrogen occurred in August, when availability of extractable $\text{NO}_3^-\text{-N}$ was significantly lower in the large infrequent treatment than in the small frequent treatment (Table 1).

Pre-treatment soil temperatures decreased as the season progressed, ranging from $32.2^\circ\text{C} \pm 0.1^\circ\text{C}$ in July to $28.5^\circ\text{C} \pm 0.2^\circ\text{C}$ in September. SOM content ranged from $1.64\% \pm 0.14\%$ in August to $1.75\% \pm 0.12\%$ in September. NAG activity ranged from $2.2 \pm 0.2 \text{ nmol hr}^{-1} \text{ g}^{-1}$ in July to $3.7 \pm 0.7 \text{ nmol hr}^{-1} \text{ g}^{-1}$ in September, while LAP

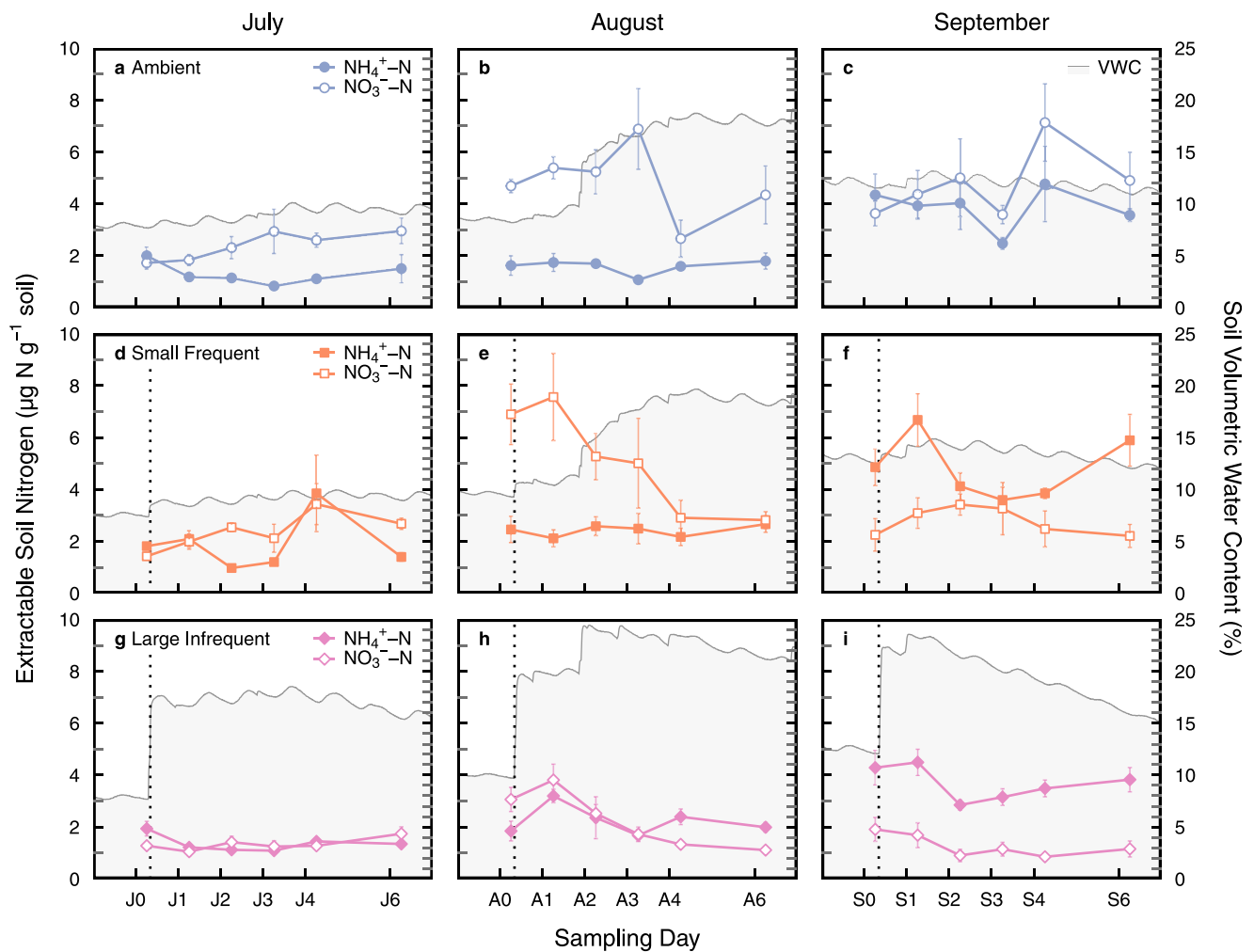


Figure 1. Soil nitrogen availability responses to experimental rainfall addition treatments over the summer monsoon. Rows represent rainfall treatments, with ambient treatments in blue (a–c), small frequent treatments receiving 5 mm of added rainfall once per week in orange (d–f), and large infrequent treatments receiving 20 mm of added rainfall once per month in pink (g–i). Columns represent months (July–September) during which the three sampling campaigns occurred. Points represent mean extractable soil nitrogen ($\mu\text{g N g}^{-1}$ soil; left y-axis) as $\text{NH}_4^+\text{-N}$ (closed circles) and $\text{NO}_3^-\text{-N}$ (open circles) measured each sampling day, with error bars indicating standard errors of the means. Gray lines and shading indicate soil volumetric water content (%; right y-axis) reported as continuous 15 min averages. Sampling days begin at the time soils were sampled, with dotted vertical lines (d–i) indicating the timing of rainfall addition treatments. Aboveground plant tissues were clipped at ground level prior to and throughout the summer monsoon to reduce nitrogen uptake.

activity ranged from $31.8 \pm 5.2 \text{ nmol hr}^{-1} \text{ g}^{-1}$ in September to $36.7 \pm 4.9 \text{ nmol hr}^{-1} \text{ g}^{-1}$ in August. There were no significant *within-month* pre-treatment differences in soil temperature, SOM content, or nitrogen-acquiring microbial ecoenzymatic activities over the summer monsoon (Table S2 in Supporting Information S1).

3.2. Pulse Response and Duration

Significant pulses of increased soil moisture availability were evident 1 day after large infrequent rainfall treatments (i.e., on J1, A1, and S1), persisting for the duration of each monthly sampling campaign (Figures 1g–1i; Table 1). While small frequent rainfall treatments also increased soil moisture availability throughout the summer monsoon (Figures 1d–1f), the only significant pulse occurred in July, which persisted for the duration of the sampling campaign (Figure 1d; Table 1). Over the 24 hr following the first rainfall addition events in July, SVWC increased 113.7% in response to the large treatment and 14.6% in response to the small treatment. By September, these increases had reduced in magnitude to 75.7% and 4.0% respectively. Yet despite these distinct pulses of increased soil moisture availability, plant available nitrogen never exhibited a significant pulse in response to any treatment in any month, except for $\text{NH}_4^+\text{-N}$ 1 day after the large rainfall treatment in August (Figure 1h; Table 1).

Table 1
Mean Pre- and Post-Treatment Soil Moisture and Extractable Inorganic Nitrogen Content Over the Summer Monsoon

	July		August		September	
	Pre-Trt _(J0)	Post-Trt _(J1)	Pre-Trt _(A0)	Post-Trt _(A1)	Pre-Trt _(S0)	Post-Trt _(S1)
Ambient						
SVWC	7.9 ± 0.5	8.0 ± 0.5 ^x	8.4 ± 0.4	8.6 ± 0.4 ^x	12.0 ± 0.5	11.9 ± 0.5 ^x
NH ₄ ⁺ -N	2.00 ± 0.33	1.18 ± 0.17	1.62 ± 0.37	1.74 ± 0.34	4.34 ± 0.80	3.93 ± 0.51
NO ₃ ⁻ -N	1.72 ± 0.24	1.84 ± 0.21	4.69 ± 0.26 ^{x,y}	5.39 ± 0.43	3.63 ± 0.48	4.37 ± 0.92 ^x
Small freq.						
SVWC	7.5 ± 0.9	8.6 ± 0.7 ^{††x}	9.5 ± 1.4	10.5 ± 1.4 ^x	12.9 ± 1.7	13.4 ± 1.6 ^x
NH ₄ ⁺ -N	1.82 ± 0.14	2.09 ± 0.32	2.46 ± 0.50	2.12 ± 0.33	4.86 ± 0.71	6.68 ± 1.00
NO ₃ ⁻ -N	1.43 ± 0.14	1.99 ± 0.29	6.90 ± 1.16 ^x	7.56 ± 1.68	2.25 ± 0.62	3.09 ± 0.59 ^{x,y}
Large infreq.						
SVWC	7.9 ± 0.3	16.8 ± 3.5 ^{†††y**}	17.1 ± 1.2 ^{xy*}	19.1 ± 3.0 ^{†††y**}	12.4 ± 0.7	21.8 ± 2.9 ^{†††y*}
NH ₄ ⁺ -N	1.94 ± 0.28	1.22 ± 0.13	1.85 ± 0.38	3.20 ± 0.26 [†]	4.29 ± 0.66	4.49 ± 0.50
NO ₃ ⁻ -N	1.28 ± 0.11	1.05 ± 0.16	3.06 ± 0.46 ^{y*}	3.81 ± 0.61	1.91 ± 0.46	1.69 ± 0.48 ^{y*}

Note. Summary of means ± standard errors of soil moisture and extractable soil inorganic nitrogen responses to experimental rainfall addition treatments (ambient, small frequent, large infrequent) during each monthly pre- and post-treatment sampling period. SVWC, soil volumetric water content (%); NH₄⁺-N, extractable soil ammonium (μg N g⁻¹ soil); NO₃⁻-N, extractable soil nitrate (μg N g⁻¹ soil); Pre-Trt, pre-treatment; Post-Trt, post-treatment; J, July; A, August; S, September. Subscripted values reflect the sampling day(s) within each sampling month with respect to the timing of the treatment event. For each variable, † indicates a significant pulse in soil moisture or nitrogen availability as determined by a significant difference in values between pre-treatment (i.e., J0, A0, and S0) and 1 day post-treatment (i.e., J1, A1, and S1), where †††p ≤ 0.001, ††p ≤ 0.01, and †p ≤ 0.05. For each variable (row) and sampling period (column), ^{x,y} indicates a significant within-month difference in value among treatments. For mean post-treatment values only (i.e., J1-6, A1-6, and S1-6), ^{a-z} indicates a significant between-month difference in value among treatments. In other words, different letters reflect significant differences among respective comparisons, where ***p ≤ 0.001, **p ≤ 0.01, and *p ≤ 0.05.

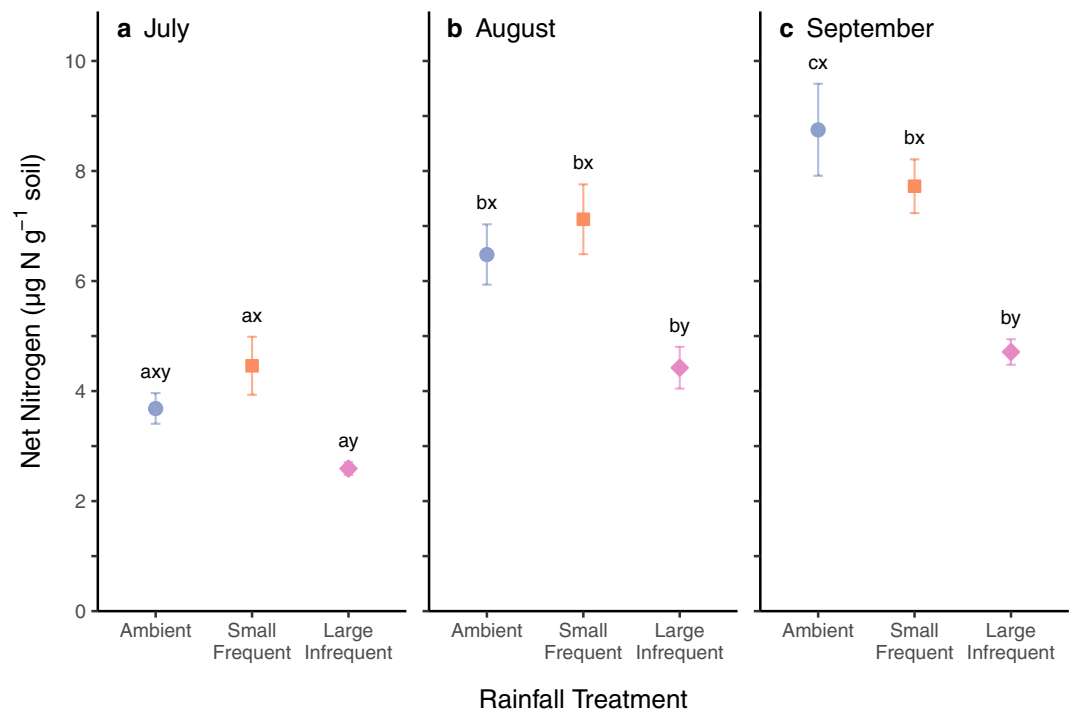


Figure 2. Net inorganic nitrogen ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$; $\mu\text{g N g}^{-1}$ soil) responses to rainfall treatments (ambient, small frequent, large infrequent) averaged across each monthly (July–September) post-treatment sampling period (i.e., J1-6, A1-6, and S1-6). $\text{NH}_4^+\text{-N}$, extractable soil ammonium ($\mu\text{g N g}^{-1}$ soil); $\text{NO}_3^-\text{-N}$, extractable soil nitrate ($\mu\text{g N g}^{-1}$ soil). For each treatment, ^{a-c} indicates a significant *between-month* difference in value. For each month, ^{x-z} indicates a significant *within-month* difference in value among treatments. In other words, different letters reflect significant ($p \leq 0.05$) differences among respective comparisons.

Similarly, nitrogen-acquiring microbial coenzymatic activities never pulsed in response to rainfall treatments over the summer monsoon (Table S2 in Supporting Information S1).

3.3. Rainfall Size and Frequency

Mean soil moisture availability during post-treatment sampling periods (i.e., J1-6, A1-6, and S1-6) was consistently highest following the large infrequent treatments (Figures 1g–1i), but this result was only significant in July (Table 1). There were no significant differences in post-treatment SVWC between the small frequent and ambient treatments in any month (Table 1).

Availability of net inorganic nitrogen ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) over post-treatment sampling periods was always significantly higher following the small frequent treatments than following the large infrequent treatments (Figure 2). Similarly, albeit not statistically significant, post-treatment availability of $\text{NH}_4^+\text{-N}$ was generally highest following small frequent treatments (Figures 1d–1f; Table 1). In contrast, availability of $\text{NO}_3^-\text{-N}$ was nearly always greatest in the ambient treatment (Figures 1b and 1c), particularly in comparison to the large infrequent treatments, which significantly reduced the availability of both $\text{NO}_3^-\text{-N}$ and net inorganic nitrogen over the season (Figures 1g–1i and 2; Table 1). Similarly, PRS® probe measurements of seasonally integrated net inorganic nitrogen supply rates were also lowest in response to the large infrequent treatments; however, these results were not statistically significant (Figure S1 in Supporting Information S1).

SOM content and LAP activity over post-treatment sampling periods were typically highest in the ambient treatments, while NAG activity was always highest following the small frequent treatments (Table S2 in Supporting Information S1). However, these trends were not significant. Post-treatment soil temperatures throughout the summer monsoon were consistently highest in the ambient treatments, but this trend was only significant during the first 24 hr following rainfall treatments (Table S2 in Supporting Information S1).

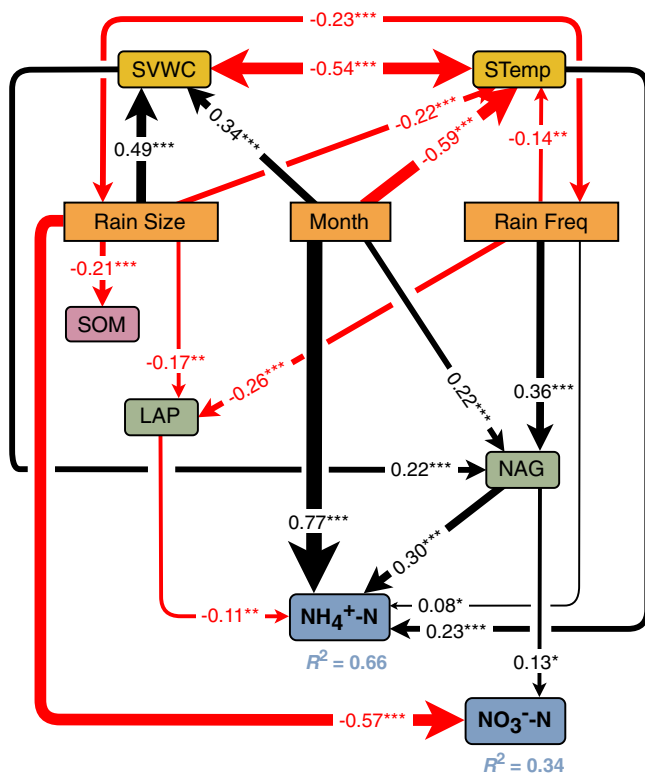


Figure 3. A structural equation model (SEM) depicting causal relationships among rainfall size and frequency (Rain Size and Rain Freq; orange), time (Month; orange) soil moisture and temperature (SVWC and STemp; yellow), soil organic matter (SOM; pink), nitrogen-acquiring eoenzymatic activities (LAP and NAG; green), and their respective influence on soil nitrogen availability ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$; blue) over the summer monsoon. Exogenous variables are enclosed in rectangular boxes and endogenous variables are enclosed in boxes with rounded corners. Line width and arrow size are proportional to the strength of each relationship, with single-headed arrows indicating directional effects and double-headed arrows linking covariates. Positive relationships are indicated by black lines, with negative relationships in red. Path coefficients, the sign of their effect (positive or negative), and significance level are noted along each path, where *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. R^2 values denote the proportion of variance explained by the model for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$. Additional variances explained by the model included SVWC ($R^2 = 0.35$), STemp ($R^2 = 0.41$), SOM ($R^2 = 0.04$), LAP ($R^2 = 0.08$), and NAG ($R^2 = 0.24$). Summary metrics indicate the model is well-fitted to the data: $\chi^2(22, n = 234) = 29.66, p \geq 0.05$; RMSEA = 0.04 with CI_{90} : (0.00, 0.07), $p \geq 0.05$; CFI = 0.99; SRMR = 0.04.

3.4. Seasonal Dynamics

Soil moisture availability increased over the summer monsoon in all treatments, with post-treatment SVWC ranging from $8.8\% \pm 0.2\%$ in the ambient treatment in July to $21.9\% \pm 1.0\%$ following the large treatment in August (Table 1).

Post-treatment availability of $\text{NH}_4^+\text{-N}$ increased consistently over the season (Table 1), ranging from $1.16 \pm 0.11 \mu\text{g N g}^{-1}$ soil in the ambient treatment in July (Figure 1a) to $4.83 \pm 0.38 \mu\text{g N g}^{-1}$ soil in response to the small frequent treatment in September (Figure 1f). Post-treatment availability of $\text{NO}_3^-\text{-N}$ was more variable, with the only consistent seasonal increases occurring in the ambient treatment, ranging from $2.53 \pm 0.22 \mu\text{g N g}^{-1}$ soil in July to $5.00 \pm 0.54 \mu\text{g N g}^{-1}$ soil in September (Figures 1a–1c; Table 1). Otherwise, $\text{NO}_3^-\text{-N}$ availability peaked in August, then declined significantly by September in response to both rainfall addition treatments (Figures 1d–1i; Table 1). Overall, post-treatment amounts of net inorganic nitrogen increased consistently over the season, ranging from $2.59 \pm 0.12 \mu\text{g N g}^{-1}$ soil in response to the large infrequent treatment in July to $8.75 \pm 0.84 \mu\text{g N g}^{-1}$ soil in the ambient treatment in September (Figure 2).

Seasonal trends in post-treatment SOM content and nitrogen-acquiring microbial eoenzymatic activities were largely insignificant (Table S2 in Supporting Information S1). While SOM content generally increased over the season regardless of treatment, LAP activity was more variable, generally increasing in the ambient treatment and declining in response to rainfall addition. Yet both rainfall treatments stimulated significantly greater NAG activity as the season progressed. Post-treatment soil temperatures in all treatments were significantly higher in July than in August or September (Table S2 in Supporting Information S1).

3.5. Drivers of Nitrogen Availability Over the Summer Monsoon

Our SEM was well fitted to the data ($\chi^2(22, n = 234) = 29.66, p \geq 0.05$; RMSEA = 0.04 with CI_{90} : (0.00, 0.07), $p \geq 0.05$; CFI = 0.99; SRMR = 0.04), explaining 66% of the variance in $\text{NH}_4^+\text{-N}$ availability and 34% of the variance in $\text{NO}_3^-\text{-N}$ availability over the summer monsoon (Figure 3). Time was the strongest driver of $\text{NH}_4^+\text{-N}$ availability (Figure 3), which increased significantly over the growing season in all treatments (Figure 1; Table 1). Increased NAG activity was identified as a significant driver of increased nitrogen availability (especially $\text{NH}_4^+\text{-N}$), whereas large rain events significantly reduced plant available nitrogen (specifically $\text{NO}_3^-\text{-N}$) throughout the season (Figures 1–3; Table 1). Similarly, large rain events drove the reduction of SOM content (Figure 3; Table S2 in Supporting Information S1); however, SOM was not identified as a driver of nitrogen availability or

nitrogen-acquiring microbial eoenzymatic activities in this study (Figure 3). NAG activity was stimulated by greater soil moisture availability, particularly from frequent rain events that also stimulated the availability of $\text{NH}_4^+\text{-N}$ (Figure 3; Tables 1 and S2 in Supporting Information S1). In contrast, LAP activity, which was stimulated by infrequent and smaller rain events, drove reductions in $\text{NH}_4^+\text{-N}$ availability (Figure 3; Table S2 in Supporting Information S1). Finally, while higher soil temperatures were identified as a driver of increased $\text{NH}_4^+\text{-N}$ availability at the seasonal scale (Figure 3), we found plant available nitrogen was lowest early in the summer monsoon when temperatures were hottest (Figures 1 and 2; Tables 1 and S2 in Supporting Information S1).

4. Discussion

We used a rainfall manipulation experiment to determine the pulse response and duration of plant available nitrogen following monsoon rain events that varied in size and frequency throughout a summer monsoon in a northern Chihuahuan Desert grassland. We also examined the evolution of plant available nitrogen over the growing season and attempted to identify some potential drivers that may be influencing seasonal nitrogen availability in this dryland ecosystem. Consistent with the pulse dynamics framework, we found large infrequent rain events always resulted in significant pulses of increased soil moisture availability that persisted for several days. Yet, contrary to our expectations, plant available nitrogen rarely pulsed in response to monsoon rainfall, regardless of event size or frequency, and declined significantly following large infrequent rain events. However, small frequent rain events were found to stimulate some microbial activities, which resulted in an overall increase of plant available nitrogen by the end of the summer monsoon.

In the pulse dynamics framework, rainfall stimulates pulses of increased biological activity and resource availability in dryland ecosystems (Noy-Meir, 1973). The Threshold-Delay Nutrient Dynamics model extends the pulse dynamics framework with the idea that larger rain events should result in greater soil moisture availability, thereby stimulating primary production in addition to soil microbial activities that regulate biogeochemical cycling (Collins et al., 2008). However, we found little to no evidence that either plant available nitrogen or nitrogen-acquiring microbial coenzymatic activities pulsed in response to our experimental rainfall treatments. Furthermore, whereas small frequent rain events stimulated some microbial activities that generally resulted in the greatest amounts of plant available nitrogen, large infrequent rain events significantly reduced nitrogen availability over the summer monsoon. Yet in other somewhat less water-limited ecosystems, short-lived pulses of plant available nitrogen have been observed within hours (Leitner et al., 2017) to 1–2 days (Cui & Caldwell, 1997; Dijkstra et al., 2012) following large rain events. Thus, the possibility exists we failed to capture short-duration pulsing events that may have occurred within hours of rainfall addition in our system—nitrogen that would have been rapidly immobilized by soil microbes or otherwise lost prior to the next sampling period.

Microbial activities tend to increase rapidly in response to the wetting of dry soils (Birch, 1958; Borken & Matzner, 2009). Indeed, we found NAG activity to be stimulated by increased soil moisture availability, particularly following small frequent rainfall treatments, which resulted in greater amounts of plant available nitrogen over the growing season. However, we did not find soil moisture availability to be a driver of LAP activity, which not only declined following rainfall treatments, but also reduced the availability of $\text{NH}_4^+\text{-N}$ when activity levels were high. Others too have found inconsistencies in microbial coenzymatic activity responses under greater soil moisture availability (J. P. Schimel, 2018). While nitrogen-acquiring coenzymatic activities were found to increase significantly in response to large frequent rain events over the growing season in a semi-arid Inner Mongolian steppe (Zhou et al., 2013), some meta-analyses have found increased precipitation only marginally stimulates nitrogen-acquiring coenzymatic activities across ecosystems globally (Sinsabaugh et al., 2008; Xiao et al., 2018). Fundamentally, a complicated relationship exists between nitrogen-acquiring microbial coenzymatic activities and nitrogen availability due to complexities in how microbial organisms respond to environmental changes (Burns et al., 2013; Sinsabaugh & Follstad Shah, 2012; Sinsabaugh et al., 2008). The methodology itself also presents an important limitation to interpretation in that laboratory assays measure “potential” coenzymatic activities using synthetic substrates in optimal conditions that include sufficient moisture (German et al., 2011; Wallenstein & Weintraub, 2008). Since results from laboratory assays are indicative of overall enzyme concentrations and not actual rates of in situ activities, they may not accurately reflect what happens under field conditions (Henry, 2012).

Low atmospheric deposition rates (Báez et al., 2007) combined with the low abundance of nitrogen fixers in biological soil crusts (Fernandes et al., 2018, 2022) suggest decomposition of SOM is the primary source of inorganic nitrogen in the northern Chihuahuan Desert. However, we did not find SOM to be a driver of either plant available nitrogen or nitrogen-acquiring microbial coenzymatic activities, nor did we find significant changes in SOM content over the growing season. Microbial biomass and coenzymatic profiles in dryland soils suggest strong processing of recalcitrant carbon compounds, making accumulation of SOM unlikely overall (Sinsabaugh et al., 2008; Waring et al., 2021). A recent meta-analysis focused on SOM in dryland ecosystems suggested that greater soil moisture availability preserves SOM from microbial attack (Plaza et al., 2018). Yet we found large rain events reduced SOM—a result consistent with long-term SOM dynamics in the northern Chihuahuan Desert (Hou et al., 2020).

Aside from microbial immobilization and plant uptake, nitrogen loss pathways common in desert soils include gaseous emissions, vertical leaching, and surface runoff. Losses to surface runoff are generally negligible in drylands like the Chihuahuan Desert (Peterjohn & Schlesinger, 1990; Turnbull et al., 2013), as overland flow typically only occurs on hillslopes and in response to extreme rain events (Borken & Matzner, 2009). Moreover, our use of soil collars to prevent soil microbes and plant roots from acquiring resources from their surrounding environment also precluded any potential losses of plant available nitrogen to surface runoff. We further minimized plant uptake by clipping aboveground biomass within each soil collar prior to and throughout the summer monsoon. Several theoretical and empirical studies have indicated that large infrequent rain events stimulate aboveground net primary production (ANPP) in drylands (e.g., Heisler-White et al., 2008; Hou et al., 2021; Knapp et al., 2008). However, in our study site (i.e., MRME), we have found large infrequent and small frequent rain events result in comparable amounts of ANPP (Thomey et al., 2011), indicating that losses of soil inorganic nitrogen following large infrequent rain events are not a consequence of differences in aboveground production. Furthermore, given that nitrogen availability increased over the growing season, it is unlikely that plant available nitrogen was lost to either surface runoff or plant uptake in this study.

Gaseous emissions via nitrification, denitrification, and ammonia volatilization are thought to account for the majority of nitrogen losses in drylands (Peterjohn & Schlesinger, 1990). Indeed, many studies have observed increased gaseous emissions following the wetting of dry soils consistent with the Birch effect (e.g., Leitner et al., 2017; McCalley & Sparks, 2009; Yahdjian & Sala, 2010). Leaching into deep soil horizons, on the other hand, has historically been considered an inconsequential loss pathway for nitrogen in drylands because like surface runoff, it typically only occurs following extreme rain events (Borken & Matzner, 2009; Peterjohn & Schlesinger, 1990). Yet, NO_3^- -N is particularly susceptible to leaching because of its high mobility in the soil (Reichmann et al., 2013; Robertson & Groffman, 2015; Song et al., 2020). Moreover, infrequent large rain events throughout the Holocene have resulted in substantial reservoirs of leached NO_3^- -N that have accumulated below the rooting zone throughout the southwestern US and are estimated to account for 4%–20% of the total soil nitrogen pool in the Chihuahuan Desert (Walvoord et al., 2003). Therefore, it is probable that some NO_3^- -N was leached beyond the rooting zone explored in this study following large infrequent rain events.

In general, losses of plant available nitrogen tend to increase and microbial coenzymatic activities tend to decline as soils become saturated (Austin et al., 2004; Borken & Matzner, 2009; Henry, 2012; J. P. Schimel, 2018). We found nitrogen availability declined significantly following large rain events. Furthermore, our SEM indicated large rain events were the strongest driver of reduced NO_3^- -N availability in this system, supporting similar findings in other dryland ecosystems (e.g., Cregger et al., 2014; Reichmann et al., 2013; Song et al., 2020; Yahdjian & Sala, 2010). We previously found soil respiration rates were greatest following large infrequent rain events in our study site (Thomey et al., 2011; Vargas et al., 2012), suggesting that rapid microbial consumption of available soil oxygen occurs under high soil moisture availability, potentially contributing to anoxic conditions. Several have established the relationship between soil moisture availability and soil microbial activities (Henry, 2012; Linn & Doran, 1984; Robertson & Groffman, 2015; Skopp et al., 1990). Microbial activities are minimal in dry soils, but as soil moisture increases, microbial activities also increase, and nitrification becomes the dominant transformation pathway. However, once water-filled pore space exceeds ~60%, microbial processes become inhibited by the lack of aeration in the soil and denitrification becomes the dominant pathway. Thus, reductions of NO_3^- -N following large rain events are likely also a consequence of denitrification as water-saturated soils reach an anoxic threshold in this northern Chihuahuan Desert grassland.

Meanwhile, high temperatures are known to stimulate biological transformations of nitrogen (Birch, 1958; Dai et al., 2020; Risch et al., 2019). Indeed, our SEM indicated that warmer soil temperatures stimulate NH_4^+ -N availability. Yet nitrogen availability was greatest towards the end of the summer monsoon when temperatures were cooler. This seemingly conflicting result is plausible because warmer temperatures tend to stimulate greater losses of nitrogen through gaseous emissions (Austin et al., 2004; McCalley & Sparks, 2009)—an effect that becomes more pronounced as soil moisture availability increases (Dai et al., 2020). Thus, it is likely early season reductions in nitrogen availability were a result of gaseous emissions when temperatures were highest.

Dryland ecosystems, which currently occupy 45% of the terrestrial land surface and account for 40% of global net primary production, are undergoing rapid expansion as a consequence of anthropogenic climate and land use changes (Burrell et al., 2020; Huang et al., 2017; Právělie et al., 2019). Meanwhile, climate models consistently predict greater intensification of the hydrological cycle, which could amplify asynchrony between microbial and

plant processes in these ecosystems. Our study provides further evidence that rainfall size and frequency simultaneously govern when plant and microbial processes are coupled by resource availability in drylands (Collins et al., 2008; Nielsen & Ball, 2015; Schwinning & Sala, 2004; Song et al., 2020). Overall, we found the greatest amounts of plant available nitrogen following small frequent rain events, which despite stimulating microbial processes, may not necessarily be sufficient to elicit plant responses. Consequently, a shift from the historical rainfall regime of frequent small events to fewer, larger events could substantially reduce the availability of soil inorganic nitrogen in northern Chihuahuan Desert grasslands, potentially lowering net primary production in these ecosystems.

5. Conclusions

The pulse dynamics framework suggests pulses of increased soil moisture availability stimulate pulses of biological activity and resource availability that control primary production in dryland ecosystems. However, field-based studies testing this framework in the context of altered precipitation regimes across temporal scales are rare. Evidence in support of the pulse dynamics framework has come primarily from leaf-level photosynthesis or soil respiration, often in response to a single rain event (e.g., Huxman et al., 2004; Pockman & Small, 2010; Sponseller, 2007; Thomey et al., 2014). In contrast, we found little evidence to support long-standing ideas regarding dryland ecosystem function in days following rain events or over the growing season. Nevertheless, our study provides further evidence that differences in the size and frequency of rain events can lead to the uncoupling of plant and microbial processes, which has important implications for net primary production in dryland ecosystems. Together, these results suggest that the pulse dynamics framework for drylands may operate on temporal scales that are either more rapid than the duration of a soil moisture pulse or apply to a narrower subset of moisture-driven processes (e.g., CO₂ flux) than previously thought.

Data Availability Statement

All data presented in this study, including soil inorganic nitrogen, microbial coenzymatic activities, soil organic matter, soil volumetric water content, and soil temperature have been archived in the Environmental Data Initiative Repository (EDI) under a Creative Commons Attribution 4.0 International (CC BY 4.0) license and can be found at <https://doi.org/10.6073/pasta/eabc9fe8e7bcfce33f6960ef50253caf> (Brown et al., 2022). Meteorological and PRS® data used in this study are also publicly available from EDI at <https://doi.org/10.6073/pasta/1cb-c37ae4d40b3844b5e4be9f6f18073> (Moore, 2021) and <https://doi.org/10.6073/pasta/a17b125176a9c24dbb-4caa760d2c9944> (Collins, 2020).

Acknowledgments

The authors thank Carl White for conducting the Technicon analyses, the Sevilleta Long Term Ecological Research program for logistical support, the University of New Mexico Sevilleta Field Station for additional logistical support and use of their facilities, and the U.S. Fish and Wildlife Service at the Sevilleta National Wildlife Refuge for permitting this study. The authors also appreciate the helpful comments from Shuli Niu and two anonymous reviewers on an earlier version of this manuscript. This research was supported by several grants from the US National Science Foundation to the University of New Mexico for Long Term Ecological Research, most recently under award number DEB-1655499, with additional support from DEB-1856383 for Long Term Research in Environmental Biology.

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