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# Above- and belowground responses to environmental change in the northern Chihuahuan Desert

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# ABOVE- AND BELOWGROUND RESPONSES TO ENVIRONMENTAL CHANGE IN THE NORTHERN CHIHUAHUAN DESERT

by

**Renée Françoise Brown**

B.S. Biology, University of New Mexico, 2015
M.S. Biology, University of New Mexico, 2017

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Doctor of Philosophy**
**Biology**

The University of New Mexico
Albuquerque, New Mexico

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# DEDICATION

To the late Richard E. Martin
for encouraging my intellectual interests from a young age.

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## ABSTRACT

Drylands cover 45% of the terrestrial surface and are expanding rapidly due to anthropogenic drivers. Altered precipitation regimes, atmospheric nitrogen deposition, and wildfire will likely have significant consequences in these regions where ecological processes are limited by water and nitrogen. In this dissertation, I explored temporal dynamics of net primary production (NPP) and related above- and belowground processes under several environmental change drivers in the Sevilleta National Wildlife Refuge, central New Mexico, USA. Located in the northern Chihuahuan Desert, this region experiences strong seasonal precipitation patterns driven by the North American Monsoon, historically characterized by frequent small rain events hypothesized to benefit microbial processes, such as nitrogen mineralization. Climate models predict a shift to a more extreme precipitation regime characterized by fewer, but larger rain events hypothesized to benefit plant production. Yet, it remains unclear how drylands will respond to increased precipitation variability and other drivers of environmental change. To address this knowledge gap, I explored daily and seasonal responses of plant available nitrogen and related belowground parameters to altered rainfall size and frequency using a long-term rainfall manipulation experiment. Next, I explored long-term responses of aboveground NPP

(ANPP) and plant community composition to these altered rainfall patterns, along with chronic nitrogen enrichment. In contrast to long-standing ecological theories, small frequent rain events stimulated the greatest amounts of plant available nitrogen and ANPP, and when combined with nitrogen enrichment, led to the greatest shift in plant community composition following a wildfire. A more extreme growing season rainfall regime decoupled microbial and plant processes, and only when nitrogen limitation was alleviated did ANPP respond strongly to large infrequent rain events. Finally, I explored spatiotemporal impacts of precipitation, nitrogen enrichment, and a prescribed fire on belowground NPP (BNPP) and ANPP using sixteen years of annual measurements across a grassland-shrubland ecotone. Surprisingly, BNPP was largely unaffected by these drivers of environmental change and was not correlated with ANPP. Drylands are vastly understudied compared to other terrestrial ecosystems despite comprising the largest terrestrial biome. This research contributes important advances to understanding how dryland ecosystem structure and functioning may respond to future environmental change.

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## *Chapter 1*

# Introduction

Drylands are broadly defined as regions in which the aridity index (i.e., the ratio of mean annual precipitation to mean annual potential evapotranspiration) is less than 0.65 (Hoover et al., 2020; Huang et al., 2016, 2017; Maestre et al., 2012). Drylands cover 45% of the terrestrial surface, and are undergoing accelerated expansion worldwide as a consequence of anthropogenic climate and land-use change (Burrell et al., 2020; Huang et al., 2016, 2017; Prăvălie et al., 2019). Indeed, these characteristically water-limited ecosystems are disproportionately affected by large-scale climatic anomalies that intensify interannual variation in the terrestrial carbon sink (Ahlström et al., 2015; Houghton, 2000; Poulter et al., 2014). Yet, drylands are vastly understudied compared to other terrestrial ecosystems (Okin et al., 2015; D. S. Schimel, 2010), which limits our ability to predict how these regions might respond to future environmental change.

As a climate change hotspot, the southwestern United States (US) is exceptionally vulnerable to climatic variability and change (Biederman et al., 2017; Diffenbaugh et al., 2008; Friedlingstein et al., 2022). Over the past century, precipitation patterns have become increasingly variable throughout this dryland region (Maurer et al., 2020; F. Zhang et al., 2021), and growing season rain events driven by the North American Monsoon have become smaller and more numerous despite no overall change in total seasonal precipitation (Petrie et al., 2014). This empirical trend is counter to climate models that predict greater variation in precipitation patterns will occur throughout this region, characterized by an intensification of extreme precipitation events (Donat et al., 2016; Easterling et al., 2000, 2017; Moustakis et al., 2021) and prolonged dry spells

(Bradford et al., 2020; Cook et al., 2021), but little change in total annual precipitation (Gutzler, 2013). Increased precipitation variability within growing seasons and between years is likely to have significant consequences for dryland ecosystem structure and functioning, especially if rain events become larger and more sporadic. It is hypothesized that relatively small rain events can trigger microbially driven biogeochemical processes in surface soils (Austin et al., 2004; Collins et al., 2008), whereas larger rain events, which tend to infiltrate deeper into the soil profile where moisture persists longer, are typically necessary to initiate plant growth and production (Noy-Meir, 1973; Schwinning & Sala, 2004).

Net primary production (NPP) is a fundamental ecosystem service and key regulator of the global carbon cycle. Current knowledge around the patterns and controls of dryland NPP is based largely on aboveground measurements. For example, aboveground NPP (ANPP) is especially sensitive to changes in mean annual precipitation in water-limited ecosystems (Hsu et al., 2012; Huxman, Smith, et al., 2004; Knapp & Smith, 2001; Maurer et al., 2020). Yet, much less is known about the patterns and controls of belowground NPP (BNPP) despite being the main contributor to the largest terrestrial carbon pool (Janzen, 2004; Scharlemann et al., 2014; Sokol & Bradford, 2019) and estimated to represent a significant proportion of total NPP in dryland ecosystems (Gherardi & Sala, 2020). Limited evidence suggests ANPP and BNPP may exhibit dissimilar responses to drivers of environmental change; however, long-term empirical measurements of BNPP are exceedingly rare (Wilcox et al., 2017; Wu et al., 2011).

Nitrogen is second to water as the most important limiting resource for NPP in dryland ecosystems. In the southwestern US, low atmospheric nitrogen deposition rates (Báez et al., 2007), combined with a low abundance of nitrogen fixers in biological soil crusts (Fernandes et al., 2018, 2022) contribute to nutrient-poor soils in this region (Zak et al., 1994). Nitrogen deposition, which is strongly correlated with growing season precipitation (Báez et al., 2007), is increasing in many dryland regions as a consequence of anthropogenic activities (Fenn et al., 2003). However, not much is known about the temporal dynamics of nitrogen availability under altered precipitation regimes in dryland ecosystems (Austin et al., 2004; Epstein et al., 2019; Nielsen & Ball, 2015).

In addition to precipitation and nitrogen deposition, fire is also an important driver of vegetation change in drylands (Andela et al., 2013; Aslan et al., 2018; Hély et al., 2019). In the southwestern US, most natural, lightning-caused fires occur early in the summer when temperatures are high, humidity is low, and vegetation is dry (Parmenter, 2008). Fire is also commonly used as a management tool to counteract the early stages of woody shrub encroachment in desert grasslands (Archer et al., 2017; Hanan et al., 2021). However, there is some evidence to suggest that desert grasslands in the southwestern US may take up to a decade to recover from fires (Collins et al., 2017; Drewa & Havstad, 2001; R. J. Gosz & Gosz, 1996; Parmenter, 2008), which are projected to increase under future climatic change.

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 (Noy-Meir, 1973). Building upon the pulse dynamics framework, the Threshold-Delay Nutrient Dynamics (TDND) conceptual model hypothesized that small rain events stimulate microbially-mediated biogeochemical processes such as nitrogen mineralization (e.g., the "Birch effect"; Birch, 1958), whereas large events promote longer persistence of soil microbial processes in addition to stimulating NPP (Collins et al., 2008). In a variation on the theme, the bucket model hypothesized that large infrequent rain events stimulate greater rates of NPP compared to small frequent events in dryland ecosystems, due to deeper infiltration and longer persistence of soil moisture (Knapp et al., 2008).

With these hypotheses in mind, I studied the individual and combined effects of environmental change drivers on dryland ecological processes in the Sevilleta National Wildlife Refuge, central New Mexico, USA. The research described in Chapters 2 and 3 was conducted in a long-term monsoon rainfall manipulation experiment located in northern Chihuahuan Desert grassland. In Chapter 2, I examined daily and seasonal responses of plant available nitrogen and related belowground parameters (e.g., nitrogen-acquiring microbial ecoenzymatic activities, soil organic matter) to altered rainfall size and frequency throughout a summer monsoon under the pulse dynamics framework. In Chapter 3, I explored how these altered rainfall regimes, along with chronic nitrogen enrichment, influenced temporal dynamics of ANPP and plant community composition over a fourteen-year period under the bucket model framework. An unexpected lightning-caused wildfire provided the opportunity to also explore these dynamics during post-fire succession. In Chapter 4, I shift focus away from specific ecological theories to explore how drivers of environmental change influence spatiotemporal dynamics of ANPP and BNPP across a grassland-shrubland ecotone in the northern Chihuahuan Desert. Here, I used sixteen years of annual NPP measurements from three long-term research sites to explore how annual precipitation, chronic nitrogen enrichment, and a prescribed fire influence patterns of ANPP and BNPP across this dryland landscape.

Changes in precipitation, nitrogen deposition, and fire regimes are likely to have significant ecological consequences in dryland regions. My dissertation research, conducted in association with the Sevilleta Long Term Ecological Research program, aims to improve understanding around the temporal dynamics of dryland NPP and associated above- and belowground processes in the context of environmental change. Several dryland biomes representative of the southwestern US intersect within the Sevilleta NWR, making this a particularly unique location for studying ecosystem responses to environmental change (J. R. Gosz, 1993; R. J. Gosz & Gosz, 1996).

*Chapter 2*

# Temporal effects of monsoon rainfall pulses on plant available nitrogen in a Chihuahuan Desert grassland

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## 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 ecoenzymatic activities. Our results suggest 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.

**Keywords:** desert grassland, monsoon season, pulse dynamics, rainfall frequency, rainfall size, soil inorganic nitrogen

## 2.1 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., 2008, 2014).

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 ($NH_4^+$-N) and nitrate ($NO_3^-$-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; Borken & 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; Borken & 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 2-5 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., 2000, 2017) 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; Borken & 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: (1) Does plant available nitrogen pulse in response to monsoon rainfall, and if so, for how long? (2) How is plant available nitrogen affected by differences in rain event size and frequency? (3) How does the availability of nitrogen evolve over the growing season? (4) 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.

## 2.2 Materials and Methods

### 2.2.1 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 $C_4$ grass. The Monsoon Rainfall Manipulation Experiment (MRME; 34.3441° N, 106.7272° W, elevation 1604 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 ten receive one of two experimentally applied rainfall addition treatments for twelve 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 0-16 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 two-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 1600 m) was 233 ± 9.6 mm, with 118 ± 8.3 mm falling during the summer monsoon, while mean annual temperature was 13.7 ± 0.0 °C, with average monthly temperatures ranging from 25.4 ± 0.2 °C in July to 1.3 ± 0.3 °C in December (Moore, 2021). Atmospheric nitrogen deposition occurs at a rate of 0.2 g $m^{-2}$ $year^{-1}$ (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 $CaCO_3$ (Kieft et al., 1998).

### 2.2.2 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; Song et al., 2020; 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 one meter 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 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 two hours 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 July to 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.

### 2.2.3 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 $NH_4^+$-N and $NO_3^-$-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 hours and reweighed. After settling at room temperature for at least 24 hours, 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 one month. Each filtrate sample was analyzed for $NH_4^+$-N and $NO_3^-$-N (as nitrite ($NO_2^-$-N) + $NO_3^-$-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 $NH_4^+$-N and $NO_3^-$-N.

### 2.2.4 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 et al., 2008; Sinsabaugh & Follstad Shah, 2012; Xiaoqi 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). Soil slurries were prepared by adding 1.0 g dry weight equivalent soil to 125 mL of 50 mM sodium bicarbonate buffer ($NaHCO_3$; pH 8.2) to approximate ambient soil pH and homogenized to release enzymes bound to soil particles. Slurries were stirred continuously using a magnetic stirrer to maintain uniform suspension while aliquoting. For each assay, 200 µL aliquots of slurry were added to sixteen replicate wells in 96-well microplates and diluted with 50 µL of a 200 µM synthetic fluorogenic substrate (L-leucine-7-amido-4-methylcoumarin for LAP and 4-methylumbelliferyl-*N*- acetyl-b-D-glucosaminide for NAG) to measure the increase in fluorescence over a fixed incubation time. For each assay, additional 8-well replicates were used for quench correction (200 µL slurry plus 50 µL of a 10 µM reference standard) and as negative sample controls (200 µL slurry plus 50 µL $NaHCO_3$). Finally, each assay plate included additional 8-well replicates for blanks (250 µL $NaHCO_3$), negative standard controls (200 µL $NaHCO_3$ plus 50 µL reference standard), and negative substrate controls (200 µL $NaHCO_3$ plus 50 µL substrate). All slurries, substrate, reference standard, and buffer solutions were manually dispensed into black 96-well microplates using an 8- channel pipettor. Due to the large number of samples, soils were assayed in batches such that a unique replicate from each month, day, and treatment combination was included in each batch for a total of five batches. Batch effects were corrected prior to analysis using quantile normalization (Leek et al., 2010). Fresh substrate and standard solutions were made prior to running each batch and reference standards were prepared in methanol prior to diluting to improve solubility (Marx et al., 2001). Microplates were incubated at room temperature (1.5 hours for LAP and 3 hours for NAG), after which fluorescence was measured using a Synergy H1 microplate reader (BioTek, Winooski, VT, USA) using an excitation wavelength of 365 nm and an emission wavelength of 450 nm. Enzyme activities were calculated following German et al. (2011) and expressed as nmol of substrate converted per hour per gram of dry soil (nmol $h^{-1}$ $g^{-1}$).

### 2.2.5 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 (LOI) approach. Briefly, 10 g subsamples of wet mass soil were dried at 105 °C for two hours, after which pre-ignition weights for each sample were determined. Dried soils were then placed in a muffle furnace and ignited for two hours 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.

### 2.2.6 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 soil volumetric water content; SVWC), plant available nitrogen (as extractable $NH_4^+$-N and $NO_3^-$-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 (HSD) pairwise comparisons were used to further investigate differences in treatment effects through time, which were considered statistically significant when $p \leq .05$.

To provide a more holistic understanding of how plant available nitrogen ($NH_4^+$-N and $NO_3^-$-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). Structural equation modeling 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 2.1; $p \leq .05$) aligning with *a priori* scientific knowledge informed the construction of a base model, which was further optimized by removing all non-significant paths ($p \geq .05$), 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 hours 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, $NH_4^+$-N, $NO_3^-$-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 ($\chi^2$) 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 $\chi^2$ statistic is insignificant ($p \geq .05$), RMSEA $\leq .05$ and its associated $p$-value $\geq .05$, CFI $\geq .95$, and SRMR $\leq .08$ (Grace, 2020; Kline, 2016).

**Table 2.1** Spearman Correlation Matrix

| | Rain Size | Rain Freq | Month | SVWC | STemp | SOM | LAP | NAG | $NH_4^+$-N |
|---|---|---|---|---|---|---|---|---|---|
| Rain Freq | **0.219**$^{***}$ | | | | | | | | |
| Month | 0.000 | 0.000 | | | | | | | |
| SVWC | **0.450**$^{***}$ | -0.060 | **0.376**$^{***}$ | | | | | | |
| STemp | **-0.239**$^{***}$ | -0.121 | **-0.594**$^{***}$ | **-0.644**$^{***}$ | | | | | |
| SOM | **-0.196**$^{**}$ | -0.060 | 0.087 | 0.010 | -0.041 | | | | |
| LAP | **-0.207**$^{***}$ | **-0.268**$^{***}$ | -0.016 | 0.043 | 0.049 | **0.125**$^{*}$ | | | |
| NAG | 0.065 | **0.320**$^{***}$ | **0.313**$^{***}$ | **0.247**$^{***}$ | **-0.368**$^{***}$ | 0.093 | 0.017 | | |
| $NH_4^+$-N | 0.043 | **0.190**$^{**}$ | **0.750**$^{***}$ | **0.232**$^{***}$ | **-0.384**$^{***}$ | 0.097 | **-0.131**$^{*}$ | **0.470**$^{***}$ | |
| $NO_3^-$-N | **-0.572**$^{***}$ | -0.014 | **0.126**$^{*}$ | **-0.169**$^{**}$ | 0.079 | **0.138**$^{*}$ | 0.119 | **0.149**$^{*}$ | **0.133**$^{*}$ |

*Note*. Spearman's correlation coefficients used to a) infer causal relationships among rainfall addition treatment size and frequency, time (i.e., sampling month), and related parameters measured throughout the summer monsoon and b) inform construction of the structural equation model (SEM). Rain Size, rain event size; Rain Freq, rain event frequency; SVWC, soil volumetric water content; STemp, soil temperature; SOM, soil organic matter content; LAP, leucyl aminopeptidase activity; NAG, β-1,4-*N*-acetylglucosaminidase activity; $NH_4^+$-N, extractable soil ammonium; $NO_3^-$-N, extractable soil nitrate. The sample size for each variable is $n = 234$ (except for SOM, where $n = 233$). Significant correlations ($p \leq .05$) are bolded; asterisks denote significance level ($^{***}\ p \leq .001$, $^{**}\ p \leq .01$, $^{*}\ p \leq .05$).

## 2.3 Results

### 2.3.1 Pre-treatment

Prior to experimental rainfall addition treatments (i.e., on J0, A0, and S0), SVWC ranged from 7.7 ± 0.3 to 12.5 ± 0.7%, $NH_4^+$-N from 1.91 ± 0.13 to 4.52 ± 0.39 μg N $g^{-1}$ soil, and $NO_3^-$-N from 1.44 ± 0.09 to 2.44 ± 0.35 μg N $g^{-1}$ soil from July to September (Figure 2.1; Table 2.2). 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 $NO_3^-$-N was significantly lower in the large infrequent treatment than in the small frequent treatment (Figures 2.1e and 2.1h; Table 2.2).

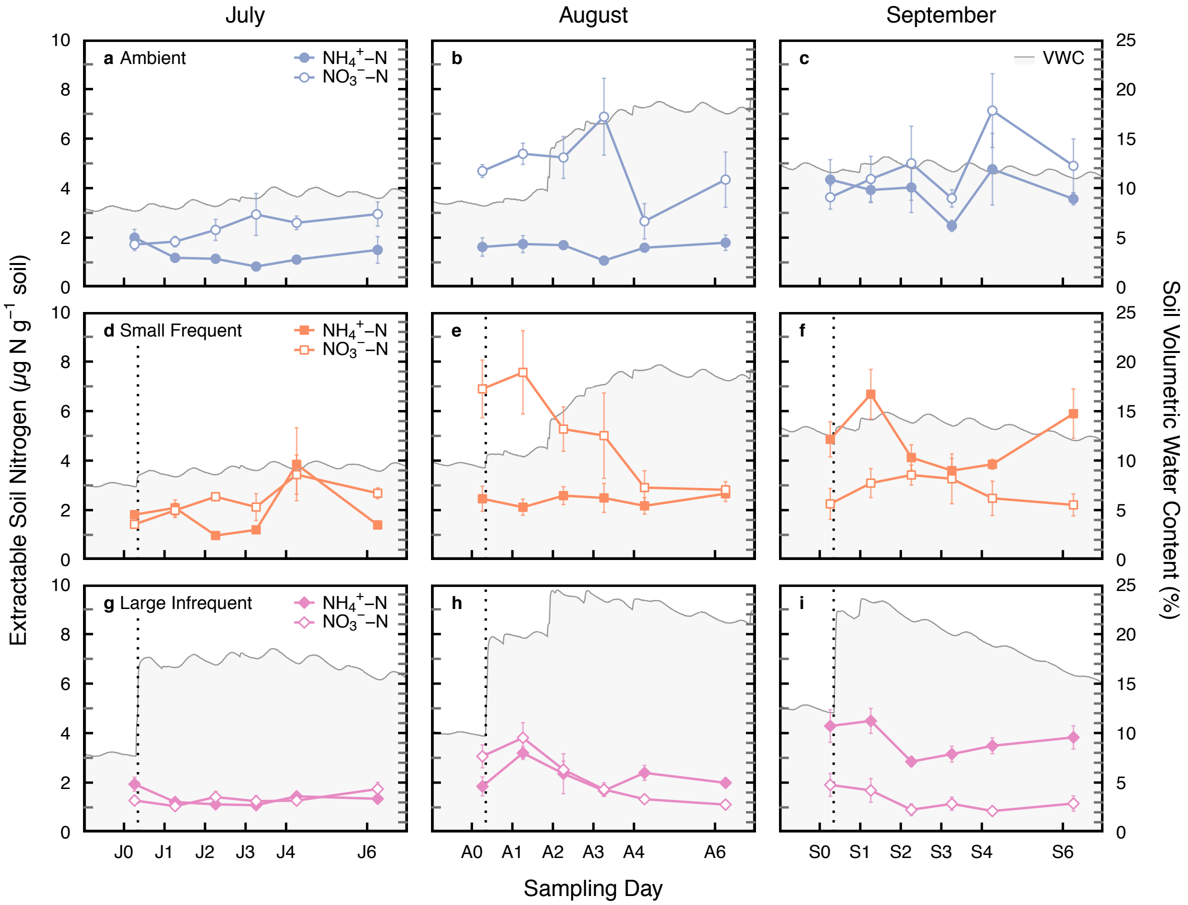

**Figure 2.1** Soil nitrogen availability responses to experimental rainfall addition treatments over the summer monsoon. Rows represent rainfall treatments, with ambient treatments in blue (a-c), small frequent treatments receiving 5 mm of added rainfall once per week in orange (d-f), and large infrequent treatments receiving 20 mm of added rainfall once per month in pink (g-i). Columns represent months (July, August, and September) during which the three sampling campaigns occurred. Points represent mean extractable soil nitrogen (µg N g$^{-1}$ soil; left y-axis) as $NH_4^+$-N (closed circles) and $NO_3^-$-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-minute 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.

**Table 2.2** Mean Pre- and Post-Treatment Soil Moisture and Extractable Inorganic Nitrogen Content over the Summer Monsoon

| | | **July** | | | **August** | | | **September** | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *Pre-Trt* $_{[J0]}$ | *Post-Trt* $_{[J1]}$ | *Post-Trt* $_{[J1\text{-}6]}$ | *Pre-Trt* $_{[A0]}$ | *Post-Trt* $_{[A1]}$ | *Post-Trt* $_{[A1\text{-}6]}$ | *Pre-Trt* $_{[S0]}$ | *Post-Trt* $_{[S1]}$ | *Post-Trt* $_{[S1\text{-}6]}$ |
| **Ambient** | SVWC | $7.9 \pm 0.5$ | $8.0 \pm 0.5^{x}$ | $8.8 \pm 0.2^{a,x}$ | $8.4 \pm 0.4$ | $8.6 \pm 0.4^{x}$ | $14.4 \pm 1.1^{b**}$ | $12.0 \pm 0.5$ | $11.9 \pm 0.5^{x}$ | $12.0 \pm 0.2^{a,b}$ |
| | $NH_4^+$-N | $2.00 \pm 0.33$ | $1.18 \pm 0.17$ | $1.16 \pm 0.11^{a}$ | $1.62 \pm 0.37$ | $1.74 \pm 0.34$ | $1.58 \pm 0.11^{b*}$ | $4.34 \pm 0.80$ | $3.93 \pm 0.51$ | $3.75 \pm 0.37^{c***}$ |
| | $NO_3^-$-N | $1.72 \pm 0.24$ | $1.84 \pm 0.21$ | $2.53 \pm 0.22^{a,x}$ | $4.69 \pm 0.26^{x,y}$ | $5.39 \pm 0.43$ | $4.90 \pm 0.53^{b**,x}$ | $3.63 \pm 0.48$ | $4.37 \pm 0.92^{x}$ | $5.00 \pm 0.54^{b**,x}$ |
| **Small Frequent** | SVWC | $7.5 \pm 0.9$ | $8.6 \pm 0.7^{\dagger\dagger,x}$ | $9.0 \pm 0.3^{a,x}$ | $9.5 \pm 1.4$ | $10.5 \pm 1.4^{x}$ | $15.4 \pm 1.1^{b***}$ | $12.9 \pm 1.7$ | $13.4 \pm 1.6^{x}$ | $13.6 \pm 0.7^{b**}$ |
| | $NH_4^+$-N | $1.82 \pm 0.14$ | $2.09 \pm 0.32$ | $1.91 \pm 0.35^{a}$ | $2.46 \pm 0.50$ | $2.12 \pm 0.33$ | $2.41 \pm 0.17^{b**}$ | $4.86 \pm 0.71$ | $6.68 \pm 1.00$ | $4.83 \pm 0.38^{c***}$ |
| | $NO_3^-$-N | $1.43 \pm 0.14$ | $1.99 \pm 0.29$ | $2.55 \pm 0.22^{a,x}$ | $6.90 \pm 1.16^{x}$ | $7.56 \pm 1.68$ | $4.72 \pm 0.61^{b**,x}$ | $2.25 \pm 0.62$ | $3.09 \pm 0.59^{x,y}$ | $2.89 \pm 0.29^{a,c*,y*}$ |
| **Large Infrequent** | SVWC | $7.9 \pm 0.3$ | $16.8 \pm 3.5^{\dagger\dagger\dagger,y**}$ | $17.1 \pm 1.2^{a,y*}$ | $9.9 \pm 1.0$ | $19.1 \pm 3.0^{\dagger\dagger\dagger,y**}$ | $21.9 \pm 1.0^{b*}$ | $12.4 \pm 0.7$ | $21.8 \pm 2.9^{\dagger\dagger\dagger,y*}$ | $20.2 \pm 1.0^{a,b}$ |
| | $NH_4^+$-N | $1.94 \pm 0.28$ | $1.22 \pm 0.13$ | $1.24 \pm 0.05^{a}$ | $1.85 \pm 0.38$ | $3.20 \pm 0.26^{\dagger}$ | $2.32 \pm 0.20^{b***}$ | $4.29 \pm 0.66$ | $4.49 \pm 0.50$ | $3.56 \pm 0.19^{c***}$ |
| | $NO_3^-$-N | $1.28 \pm 0.11$ | $1.05 \pm 0.16$ | $1.35 \pm 0.10^{a,b,y*}$ | $3.06 \pm 0.46^{y*}$ | $3.81 \pm 0.61$ | $2.10 \pm 0.25^{a,y**}$ | $1.91 \pm 0.46$ | $1.69 \pm 0.48^{y*}$ | $1.15 \pm 0.14^{b***,z***}$ |

*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 (%); $NH_4^+$-N, extractable soil ammonium (μg N $g^{-1}$ soil); $NO_3^-$-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, $^{\dagger}$ 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 one day post-treatment (i.e., J1, A1, and S1), where $^{\dagger\dagger\dagger}$ $p \leq .001$, $^{\dagger\dagger}$ $p \leq .01$, and $^{\dagger}$ $p \leq .05$. For each variable (row) and sampling period (column), $^{x\text{-}z}$ 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), $^{a\text{-}c}$ indicates a significant *between-month* difference in value among treatments. In other words, different letters reflect significant differences among respective comparisons, where $^{***}$ $p \leq .001$, $^{**}$ $p \leq .01$, and $^{*}$ $p \leq .05$.

Pre-treatment soil temperatures decreased as the season progressed, ranging from 32.2 ± 0.1 °C in July to 28.5 ± 0.2 °C in September. SOM content ranged from 1.64 ± 0.14% in August to 1.75 ± 0.12% in September. NAG activity ranged from 2.2 ± 0.2 nmol $h^{-1}$ $g^{-1}$ in July to 3.7 ± 0.7 nmol $h^{-1}$ $g^{-1}$ in September, while LAP activity ranged from 31.8 ± 5.2 nmol $h^{-1}$ $g^{-1}$ in September to 36.7 ± 4.9 nmol $h^{-1}$ $g^{-1}$ 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 2.3).

### 2.3.2 Pulse Response and Duration

Significant pulses of increased soil moisture availability were evident one day after large infrequent rainfall treatments (i.e., on J1, A1, and S1), persisting for the duration of each monthly sampling campaign (Figures 2.1g-2.1i; Table 2.2). While small frequent rainfall treatments also increased soil moisture availability throughout the summer monsoon (Figures 2.1d-2.1f), the only significant pulse occurred in July, which persisted for the duration of the sampling campaign (Figure 2.1d; Table 2.2). Over the 24 hours 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 $NH_4^+$-N one day after the large rainfall treatment in August (Figure 2.1h; Table 2.2). Similarly, nitrogen-acquiring microbial ecoenzymatic activities never pulsed in response to rainfall treatments over the summer monsoon (Table 2.3).

**Table 2.3** Mean Pre- and Post-Treatment Soil Temperature, Soil Organic Matter, and N-Acquiring Microbial Ecoenzymatic Activities Over the Summer Monsoon

| | | **July** | | | **August** | | | **September** | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *Pre-Trt* $_{[J0]}$ | *Post-Trt* $_{[J1]}$ | *Post-Trt* $_{[J1\text{-}6]}$ | *Pre-Trt* $_{[A0]}$ | *Post-Trt* $_{[A1]}$ | *Post-Trt* $_{[A1\text{-}6]}$ | *Pre-Trt* $_{[S0]}$ | *Post-Trt* $_{[S1]}$ | *Post-Trt* $_{[S1\text{-}6]}$ |
| **Ambient** | STemp | $32.0 \pm 0.1$ | $31.2 \pm 0.0^{x***}$ | $30.9 \pm 0.1^{a,x}$ | $30.6 \pm 0.0$ | $29.2 \pm 0.2^{x}$ | $26.7 \pm 0.5^{b***}$ | $29.1 \pm 0.1$ | $25.8 \pm 0.2^{x}$ | $26.8 \pm 0.4^{b***}$ |
| | SOM | $1.55 \pm 0.13$ | $1.71 \pm 0.11$ | $1.74 \pm 0.07$ | $2.20 \pm 0.76$ | $1.88 \pm 0.28$ | $1.86 \pm 0.10$ | $2.18 \pm 0.13$ | $2.00 \pm 0.24$ | $1.98 \pm 0.10$ |
| | LAP | $29.3 \pm 2.3$ | $43.0 \pm 10.3$ | $47.9 \pm 4.7$ | $47.6 \pm 13.1$ | $50.8 \pm 3.9$ | $50.4 \pm 3.6$ | $47.1 \pm 2.4$ | $43.2 \pm 10.5$ | $49.3 \pm 4.1^{x}$ |
| | NAG | $1.8 \pm 0.4$ | $2.1 \pm 0.3$ | $2.2 \pm 0.2$ | $1.9 \pm 0.2$ | $2.5 \pm 0.6$ | $2.3 \pm 0.2^{x}$ | $2.4 \pm 0.1$ | $2.6 \pm 1.3^{x}$ | $3.4 \pm 0.7$ |
| **Small Frequent** | STemp | $32.4 \pm 0.2$ | $29.2 \pm 0.4^{y**}$ | $29.8 \pm 0.2^{a,x,y}$ | $30.2 \pm 0.1$ | $26.5 \pm 0.4^{y***}$ | $25.5 \pm 0.3^{b***}$ | $28.5 \pm 0.2$ | $23.8 \pm 0.2^{y***}$ | $25.7 \pm 0.4^{b***}$ |
| | SOM | $1.90 \pm 0.12$ | $1.38 \pm 0.08$ | $1.70 \pm 0.10$ | $1.60 \pm 0.06$ | $1.77 \pm 0.12$ | $1.84 \pm 0.09$ | $1.69 \pm 0.15$ | $2.03 \pm 0.21$ | $1.74 \pm 0.08$ |
| | LAP | $31.7 \pm 7.6$ | $21.2 \pm 2.1$ | $34.9 \pm 3.4$ | $35.5 \pm 7.1$ | $38.5 \pm 14.2$ | $38.7 \pm 4.6$ | $36.5 \pm 9.1$ | $17.4 \pm 8.4$ | $31.2 \pm 3.0^{y*}$ |
| | NAG | $2.5 \pm 0.2$ | $2.4 \pm 0.3$ | $2.9 \pm 0.4^{a}$ | $3.5 \pm 0.9$ | $3.4 \pm 0.8$ | $5.7 \pm 0.7^{b***,y**}$ | $5.3 \pm 1.2$ | $5.5 \pm 1.0^{y*}$ | $4.9 \pm 0.5^{b**}$ |
| **Large Infrequent** | STemp | $32.1 \pm 0.3$ | $27.6 \pm 0.1^{z}$ | $28.5 \pm 0.2^{a,y*}$ | $30.8 \pm 0.1$ | $26.6 \pm 0.2^{y***}$ | $25.3 \pm 0.2^{b***}$ | $28.3 \pm 0.3$ | $24.3 \pm 0.1^{y***}$ | $25.1 \pm 0.3^{b***}$ |
| | SOM | $1.62 \pm 0.13$ | $1.49 \pm 0.14$ | $1.64 \pm 0.06$ | $1.46 \pm 0.18$ | $1.58 \pm 0.13$ | $1.71 \pm 0.07$ | $1.55 \pm 0.23$ | $1.84 \pm 0.15$ | $1.69 \pm 0.07$ |
| | LAP | $35.6 \pm 8.2$ | $40.9 \pm 6.8$ | $40.8 \pm 3.6$ | $31.4 \pm 7.6$ | $37.9 \pm 7.0$ | $38.6 \pm 3.5$ | $17.9 \pm 6.0$ | $28.9 \pm 4.7$ | $39.7 \pm 3.9^{x,y}$ |
| | NAG | $2.0 \pm 0.3$ | $1.9 \pm 0.2$ | $2.2 \pm 0.1^{a}$ | $1.9 \pm 0.1$ | $3.7 \pm 0.9$ | $4.4 \pm 0.4^{b***,y*}$ | $2.9 \pm 1.0$ | $4.1 \pm 1.5^{x,y}$ | $3.4 \pm 0.3^{b*}$ |

*Note.* Summary of means ± standard errors of soil temperature, soil organic matter, and nitrogen-acquiring microbial ecoenzymatic activity responses to experimental rainfall addition treatments (ambient, small frequent, large infrequent) during each monthly pre- and post-treatment sampling period. STemp, soil temperature (ºC); SOM, soil organic matter (%); LAP, leucyl aminopeptidase activity (nmol $h^{-1}$ $g^{-1}$); NAG, β-1,4-*N*-acetylglucosaminidase activity (nmol $h^{-1}$ $g^{-1}$); 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. There were no significant pulses of nitrogen-acquiring microbial enzymatic activities one day after treatment (i.e., on J1, A1, and S1). For each variable (row) and sampling period (column), $^{x\text{-}z}$ 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), $^{a\text{-}c}$ indicates a significant *between-month* difference in value among treatments. In other words, different letters reflect significant differences among respective comparisons, where $^{***}$ $p \leq .001$, $^{**}$ $p \leq .01$, and $^{*}$ $p \leq .05$.

### 2.3.3 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 2.1g-2.1i), but this result was only significant in July (Table 2.2). There were no significant differences in post-treatment SVWC between the small frequent and ambient treatments in any month (Table 2.2).

Availability of net inorganic nitrogen ($NH_4^+$-N + $NO_3^-$-N) over post-treatment sampling periods was always significantly higher following the small frequent treatments than following the large infrequent treatments (Figure 2.2). Similarly, albeit not statistically significant, post-treatment availability of $NH_4^+$-N was generally highest following small frequent treatments (Figures 2.1d-2.1f; Table 2.2). In contrast, availability of $NO_3^-$-N was nearly always greatest in the ambient treatment (Figures 2.1b and 2.1c), particularly in comparison to the large infrequent treatments, which significantly reduced the availability of both $NO_3^-$-N and net inorganic nitrogen over the season (Figures 2.1g-2.1i and 2.2; Table 2.2). 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 2.3).

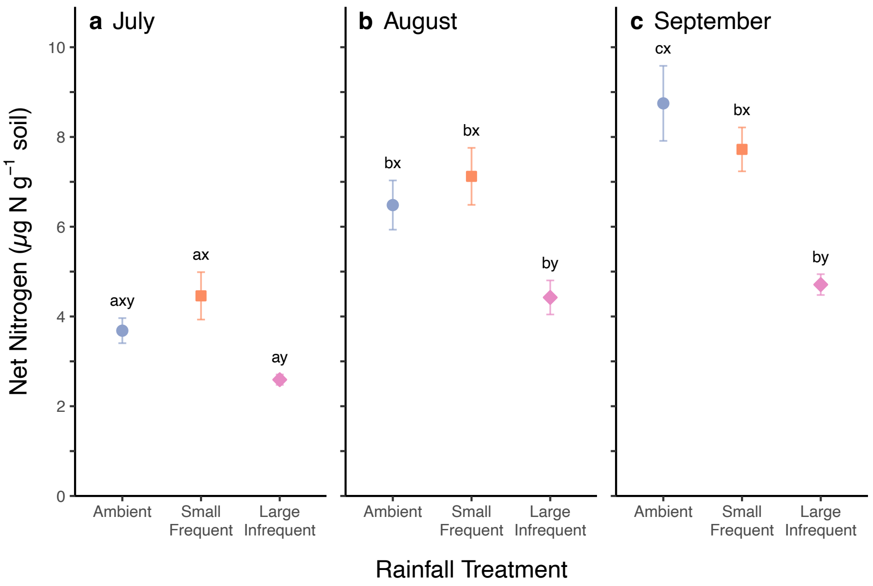

**Figure 2.2** Net inorganic nitrogen ($NH_4^+$-N + $NO_3^-$-N; μg N $g^{-1}$ soil) responses to rainfall treatments (ambient, small frequent, large infrequent) averaged across each monthly (July, August, September) post-treatment sampling period (i.e., J1-6, A1-6, and S1-6). $NH_4^+$-N, extractable soil ammonium (μg N $g^{-1}$ soil); $NO_3^-$-N, extractable soil nitrate (μg N $g^{-1}$ soil). For each treatment, $^{a\text{-}c}$ indicates a significant *between-month* difference in value. For each month, $^{x\text{-}z}$ indicates a significant *within-month* difference in value among treatments. In other words, different letters reflect significant ($p \leq .05$) differences among respective comparisons.

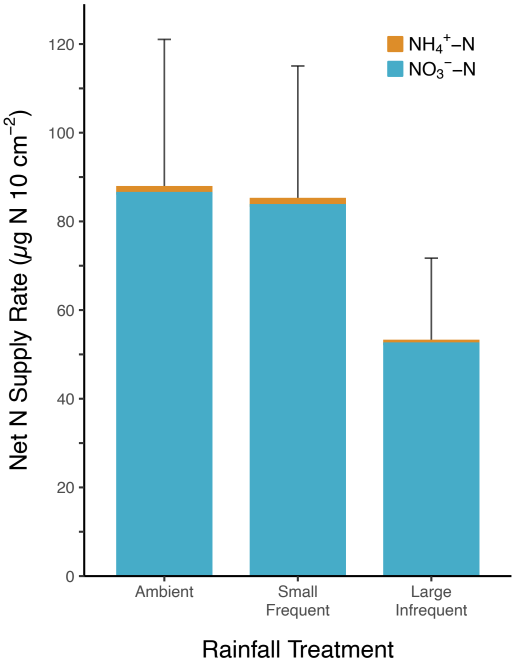

**Figure 2.3** Mean net inorganic nitrogen ($NH_4^+$-N + $NO_3^-$-N) supply rates (μg N 10 $cm^{-2}$) integrated across the summer monsoon (2 July 2014 – 10 October 2014) as measured by PRS® probes in each rainfall addition treatment (ambient, small frequent, large infrequent). Ammonium ($NH_4^+$-N) is represented in orange and nitrate ($NO_3^-$-N) in blue. Error bars indicate standard errors of the means. Results did not differ significantly at $p \leq .1$.

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 2.3). 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 hours following rainfall treatments (Table 2.3).

### 2.3.4 Seasonal Dynamics

Soil moisture availability increased over the summer monsoon in all treatments, with post-treatment SVWC ranging from 8.8 ± 0.2% in the ambient treatment in July to 21.9 ± 1.0% following the large treatment in August (Table 2.2).

Post-treatment availability of $NH_4^+$-N increased consistently over the season (Table 2.2), ranging from 1.16 ± 0.11 $\mu g$ N $g^{-1}$ soil in the ambient treatment in July (Figure 2.1a) to 4.83 ± 0.38 $\mu g$ N $g^{-1}$ soil in response to the small frequent treatment in September (Figure 2.1f). Post-treatment availability of $NO_3^-$-N was more variable, with the only consistent seasonal increases occurring in the ambient treatment, ranging from 2.53 ± 0.22 $\mu g$ N $g^{-1}$ soil in July to 5.00 ± 0.54 $\mu g$ N $g^{-1}$ soil in September (Figures 2.1a-2.1c; Table 2.2). Otherwise, $NO_3^-$-N availability peaked in August, then declined significantly by September in response to both rainfall addition treatments (Figures 2.1d-2.1i; Table 2.2). Overall, post-treatment amounts of net inorganic nitrogen increased consistently over the season, ranging from 2.59 ± 0.12 $\mu g$ N $g^{-1}$ soil in response to the large infrequent treatment in July to 8.75 ± 0.84 $\mu g$ N $g^{-1}$ soil in the ambient treatment in September (Figure 2.2).

Seasonal trends in post-treatment SOM content and nitrogen-acquiring microbial ecoenzymatic activities were largely insignificant (Table 2.3). 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.

### 2.3.5 Drivers of Nitrogen Availability over the Summer Monsoon

Our SEM was well fitted to the data ($\chi^2(22, n = 234) = 29.66, p \geq .05$; RMSEA = .04 with $CI_{90}$: (.00, .07), $p \geq .05$; CFI = 0.99; SRMR = .04), explaining 66% of the variance in $NH_4^+$-N availability and 34% of the variance in $NO_3^-$-N availability over the summer monsoon (Figure 2.4). Time was the strongest driver of $NH_4^+$-N availability (Figure 2.4), which increased significantly over the growing season in all treatments (Figure 2.1; Table 2.2). Increased NAG activity was identified as a significant driver of increased nitrogen availability (especially $NH_4^+$-N), whereas large rain events significantly reduced plant available nitrogen (specifically $NO_3^-$-N) throughout the season (Figures 2.1-2.3; Table 2.2). Similarly, large rain events drove the reduction of SOM content (Figure 2.4; Table 2.3); however, SOM was not identified as a driver of nitrogen availability or nitrogen-acquiring microbial ecoenzymatic activities in this study (Figure 2.4). NAG activity was stimulated by greater soil moisture availability, particularly from frequent rain events that also stimulated the availability of $NH_4^+$-N (Figure 2.4; Tables 2.2 and 2.3). In contrast, LAP activity, which was stimulated by infrequent and smaller rain events, drove reductions in $NH_4^+$-N availability (Figure 2.4; Table 2.3). Finally, while higher soil temperatures were identified as a driver of increased $NH_4^+$-N availability at the seasonal scale (Figure 2.4), we found plant available nitrogen was lowest early in the summer monsoon when temperatures were hottest (Figures 2.1 and 2.2; Tables 2.2 and 2.3).

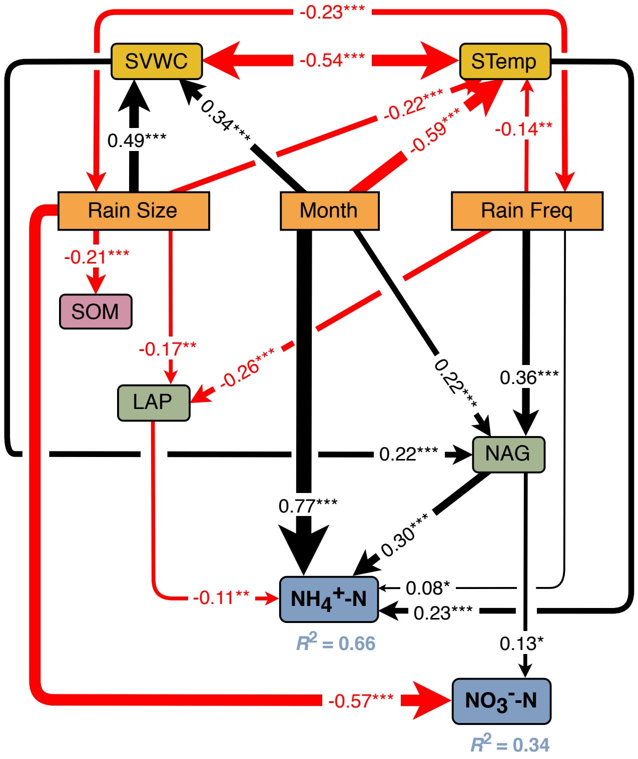

**Figure 2.4** A structural equation model (SEM) depicting causal relationships among rainfall size and frequency (Rain Size and Rain Freq; orange), time (Month; orange) soil moisture and temperature (SVWC and STemp; yellow), soil organic matter (SOM; pink), nitrogen-acquiring ecoenzymatic activities (LAP and NAG; green), and their respective influence on soil nitrogen availability ($NH_4^+$-N and $NO_3^-$-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 *** $p \leq .001$, ** $p \leq .01$, * $p \leq .05$. $R^2$ values denote the proportion of variance explained by the model for $NH_4^+$-N and $NO_3^-$-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: $\chi^2(22, n = 234) = 29.66$, $p \geq .05$; RMSEA = .04 with $CI_{90}$: (.00, .07), $p \geq .05$; CFI = 0.99; SRMR = .04.

## 2.4 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 ecoenzymatic 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 $NH_4^+$-N when activity levels were high. Others too have found inconsistencies in microbial ecoenzymatic activity responses under greater soil moisture availability (J. P. Schimel, 2018). While nitrogen-acquiring ecoenzymatic activities were found to increase significantly in response to large frequent rain events over the growing season in a semi-arid Inner Mongolian steppe (Xiaoqi Zhou et al., 2013), some meta-analyses have found increased precipitation only marginally stimulates nitrogen-acquiring ecoenzymatic activities across ecosystems globally (Sinsabaugh et al., 2008; Xiao et al., 2018). Fundamentally, a complicated relationship exists between nitrogen-acquiring microbial ecoenzymatic activities and nitrogen availability due to complexities in how microbial organisms respond to environmental changes 10/6/22 3:28:00 PM. The methodology itself also presents an important limitation to interpretation in that laboratory assays measure “potential” ecoenzymatic 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 ecoenzymatic activities, nor did we find significant changes in SOM content over the growing season. Microbial biomass and ecoenzymatic 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 ecoenzymatic 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 (WFPS) 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; Prăvălie 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.

## 2.5 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., $CO_2$ flux) than previously thought.

## 2.6 Acknowledgments

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## 2.7 Data Availability Statement

All data presented in this study, including soil inorganic nitrogen, microbial ecoenzymatic 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, Collins, et al., 2022). Meteorological and PRS® data are also publicly available from EDI at https://doi.org/10.6073/pasta/1cbc37ae4d40b3844b5e4be9f6f18073 (Moore, 2021) and https://doi.org/10.6073/pasta/a17b125176a9c24dbb4caa760d2c9944 (Collins, 2020).

## *Chapter 3*

# Long-term impacts of rainfall variability and nitrogen enrichment on net primary production in a Chihuahuan Desert grassland

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## Abstract

Anticipated intensification of the North American Monsoon in the southwestern United States is predicted to shift growing season rainfall patterns, historically characterized by frequent small rain events, to a more extreme precipitation regime consisting of fewer, but larger rain events. Moreover, atmospheric nitrogen deposition, which is strongly correlated with growing season rainfall, is increasing throughout this dryland region due to anthropogenic activities. Alterations in rainfall size and frequency, along with changes in nitrogen availability, are likely to have significant consequences for aboveground net primary production (ANPP) and plant community dynamics in dryland regions, where ecological processes are limited by water and nitrogen availability. The conceptual bucket model predicts a shift to fewer, but larger rain events would promote greater rates of ANPP in drylands by maintaining soil moisture availability above drought stress thresholds for longer periods during the growing season. However, only a few short-term studies have tested this hypothesis, and none have assessed the interaction between altered rainfall patterns and nitrogen enrichment. To address this knowledge gap, we conducted a fourteen-year study in which we experimentally altered rainfall size and frequency during the summer monsoon to investigate how changes in rainfall regimes, along with chronic nitrogen enrichment, impact ANPP in a northern Chihuahuan Desert grassland. Contrary to bucket model predictions, small frequent rain events promoted comparable rates of ANPP to large infrequent rain events in the absence of nitrogen enrichment. Only when nitrogen limitation was alleviated was ANPP greater under large infrequent rain events compared to small frequent events. Furthermore, nitrogen enrichment led to the greatest changes in plant community composition under the small frequent rainfall regime. Findings from our long-term experiment suggest dryland ecological processes are sequentially resource limited and that small frequent rain events have an important ecological role in these ecosystems.

**Keywords:** aboveground production, bucket model, fire, monsoon season, nitrogen fertilization, precipitation variability, rainfall frequency, rainfall size

## 3.1 Introduction

Precipitation patterns in the arid and semi-arid ecosystems (i.e., drylands) of the southwestern United States (US) have become increasingly variable within and between years over the past century (Maurer et al., 2020; F. Zhang et al., 2021). For example, growing season rain events driven by the North American Monsoon have become smaller and more numerous throughout the northern Chihuahuan Desert despite no overall change in total seasonal precipitation (Petrie et al., 2014). Yet, climate model projections for the southwestern US indicate intensification of the hydrologic cycle, particularly during the summer monsoon (Diffenbaugh et al., 2008; Moustakis et al., 2021), that will increase the occurrence of extreme precipitation events (Donat et al., 2016; Easterling et al., 2000, 2017) punctuated by longer dry spells between events (Bradford et al., 2020; Cook et al., 2021). Changes in rainfall size and frequency have important implications for dryland ecosystem structure and functioning (Collins et al., 2014; Schwinning & Sala, 2004). While relatively small rain events can trigger microbially-driven biogeochemical processes in surface soils (Austin et al., 2004; Belnap et al., 2005; Collins et al., 2008), larger rain events, which tend to infiltrate deeper into the soil profile where moisture persists longer, are typically necessary to initiate plant growth and production (Noy-Meir, 1973; Schwinning & Sala, 2004).

Grasslands are especially sensitive to changes in total growing season precipitation (Cleland et al., 2013; Hsu et al., 2012; Knapp & Smith, 2001), yet their responses to changes in the size and frequency of rain events during the growing season are less well understood. However, given the strong response of drylands to interannual variation in total precipitation (Sala et al., 2012; Unger & Jongen, 2015; Wilcox et al., 2017), within season changes in rainfall patterns are likely to also have significant consequences on dryland ecosystem structure and functioning, especially if rain events become larger and more sporadic. The conceptual bucket model (Knapp et al., 2008) predicts how terrestrial ecosystems will respond to a more extreme growing season precipitation regime characterized by fewer, but larger rain events. Inspired by soil hydrological models, the bucket model predicts that in drylands, infrequent large rain events would fill an empty 'bucket' represented by the uppermost soil layers where the maximum root biomass occurs, thereby maintaining soil moisture availability above drought stress thresholds for longer periods during the growing season. This contrasts with model predictions for mesic ecosystems, where extreme precipitation events would result in more frequent moisture deficits between rain events (e.g., Laseter et al., 2012). In other words, a shift to fewer, but larger rain events is predicted to benefit ecological processes in drylands, and negatively impact them in mesic systems.

Few studies have explored how alterations in rainfall size and frequency impact dryland ecological processes, such as aboveground net primary production (ANPP) or plant community composition, in the context of bucket model predictions (J. Liu et al., 2020; Unger & Jongen, 2015; Zeppel et al., 2014). Moreover, previous support of bucket model predictions in drylands has come from relatively short duration experiments (e.g., Heisler-White et al., 2008, 2009; Thomey et al., 2011). For example, in a two year study conducted in Chihuahuan Desert grassland, large infrequent rain events significantly increased soil moisture availability and ANPP of the dominant grass compared to small frequent rain events, although the magnitude of this response differed between years (Thomey et al., 2011). However, in mesic grasslands, more extreme rain events reduced ANPP, consistent with bucket model predictions (Heisler-White et al., 2009; Knapp et al., 2002), but had limited effects on plant community composition and structure (S. K. Jones et al., 2016). Nevertheless, short-term studies do not sufficiently capture long-term effects of altered precipitation regimes on ecosystem processes that might be expected from a future climate scenario (Beier et al., 2012).

Ecological responses to alterations in rainfall size and frequency are also likely to be influenced by additional factors, such as nutrient availability (Brown, Sala, et al., 2022; Jongen et al., 2014; Nielsen & Ball, 2015). Nitrogen is an important secondary limiting resource for ANPP in grassland ecosystems globally (Austin et al., 2004; Fay et al., 2015; Yahdjian et al., 2011). Yet it remains unclear how projected increases of atmospheric nitrogen deposition (Fenn et al., 2003), which is strongly correlated with growing season precipitation (Báez et al., 2007), will impact ANPP in drylands, especially under more variable precipitation regimes. Nitrogen enrichment has been found to increase ANPP in the Sonoran and Chihuahuan Deserts; however, this may only occur in years with above average precipitation (Hall et al., 2011; Ladwig et al., 2012). Changes in resource availability could also result in shifts in dryland plant community structure, which could underlie variation in ecosystem responses to increased precipitation variability (Avolio et al., 2014; Isbell et al., 2013; Wheeler et al., 2021).

Given that current empirical understanding of dryland ecosystem responses to altered precipitation regimes is based largely on short-term studies that potentially underestimate ecological consequences of future directional changes in climate, long-term studies are needed. To address this knowledge gap, we used a long-term (2007-2020) rainfall manipulation experiment to investigate how differences in monsoon rainfall size and frequency, along with chronic nitrogen enrichment, influence ANPP and plant community dynamics in a northern Chihuahuan Desert grassland. We were specifically interested in testing predictions made by the conceptual bucket model for drylands (Knapp, Beier, et al., 2008) to see if they held at the decadal scale. We asked 1) How does chronic nitrogen enrichment together with altered rainfall size and frequency impact community composition and ANPP over time? 2) Do infrequent large rain events consistently result in greater ANPP than frequent small rain events?

## 3.2 Materials and Methods

### 3.2.1 Study Site

This study was conducted over a fourteen-year period (2007-2020) in the Sevilleta National Wildlife Refuge (NWR), central New Mexico, USA. Domestic livestock were permanently excluded from the Sevilleta NWR in 1973 following more than a century of extensive cattle grazing (Parmenter, 2008; Rand-Caplan, 2006). The abundance of dominant grasses such as *Bouteloua eriopoda* has since recovered (Collins et al., 2020; Collins & Xia, 2015; Ryerson & Parmenter, 2001); however, these grasslands are periodically subjected to lightning-caused wildfires (Parmenter, 2008). Precipitation in this region exhibits high intra- and interannual variability, with growing season rainfall originating primarily from localized convective thunderstorms driven by the North American Monsoon (Muldavin et al., 2008; Pennington & Collins, 2007). The summer monsoon, which spans July through September, is typically preceded by a two-month period with high daytime temperatures and minimal precipitation (Notaro et al., 2010). Climate parameters in the Sevilleta NWR have been recorded continuously for over three decades by a spatially distributed network of automated meteorological stations (Moore, 2021). From 1990 to 2020, mean annual temperature recorded by the Deep Well station (34.3592°N, 106.6911°W, elevation 1600 m) was 13.7 ± 0.0 °C, with monthly temperatures ranging from 25.4 ± 0.2 °C in July to 1.3 ± 0.3 °C in December. Mean annual water year precipitation recorded over this same 31-year period was 233 ± 9.6 mm, with 118 ± 8.3 mm falling during the summer monsoon.

### 3.2.2 Experimental Design

The Monsoon Rainfall Manipulation Experiment (MRME; 34.3441°N, 106.7272°W, elevation 1604 m) was established in 2007 to investigate how changes in monsoon rainfall size and frequency affect ecosystem structure and functioning in a northern Chihuahuan Desert grassland. Vegetation is dominated by black grama (*Bouteloua eriopoda*), a native shallow-rooted perennial $C_4$ grass (Gibbens & Lenz, 2001; Thomey et al., 2011), with soils classified as Typic Haplocalcids formed by calcareous aeolian and alluvial deposits (Soil Survey Staff, 2019). Soil bulk density is 1.51 g $cm^{-2}$ and porosity is 43% (Thomey et al., 2011), with a texture distribution in the upper 20 cm consisting of 68% sand, 22% silt, and 10% clay, with <10% as $CaCO_3$ (Kieft et al., 1998). Atmospheric nitrogen deposition occurs primarily through wet deposition at a rate of 0.2 g $m^{-2}$ $yr^{-1}$, with 57% deposited as $NH_4$ and 43% as deposited as $NO_3$ (Báez et al., 2007).

Low rates of deposition together with a low abundance of nitrogen fixers in biological soil crusts (Fernandes et al., 2022) contribute to nutrient-poor soils in this site (Brown, Sala, et al., 2022).

MRME consists of thirteen 8 m by 13 m plots (Figure 3.1), with three plots serving as ambient controls, and the remaining ten receiving one of two experimentally applied rainfall addition treatments (*n* = 5 per rainfall treatment) for twelve consecutive weeks during the summer monsoon each year. Specifically, "small frequent" plots received a 5 mm rainfall addition once per week (*n* = 12), whereas "large infrequent" plots received a 20 mm rainfall addition once per month (*n* = 3), resulting in all rainfall addition plots receiving the same total amount of supplemental rainfall (60 mm) by the end of each monsoon season. Rainfall treatments were applied via raindrop-quality overhead sprinkler systems using reverse-osmosis water that was stored in onsite tanks. Ambient precipitation, received by all plots throughout the duration of this study, was measured continuously by a tipping bucket rain gage (TE525MM; Campbell Scientific Inc., Logan, UT, USA), with any missing or suspect data gap-filled from the nearby Five Points meteorological station (34.3350°N, 106.7293°W, elevation 1613 m; Moore, 2021). In August 2009, an intense lightning-caused wildfire burned through the experiment, consuming all aboveground vegetation. Following the wildfire, soil moisture sensors (CS616; Campbell Scientific Inc., Logan, UT, USA) were installed within the rooting zone (0-16 cm) of a randomly selected black grama tussock in each plot to provide continuous depth-integrated measurements of soil volumetric water content (SVWC).

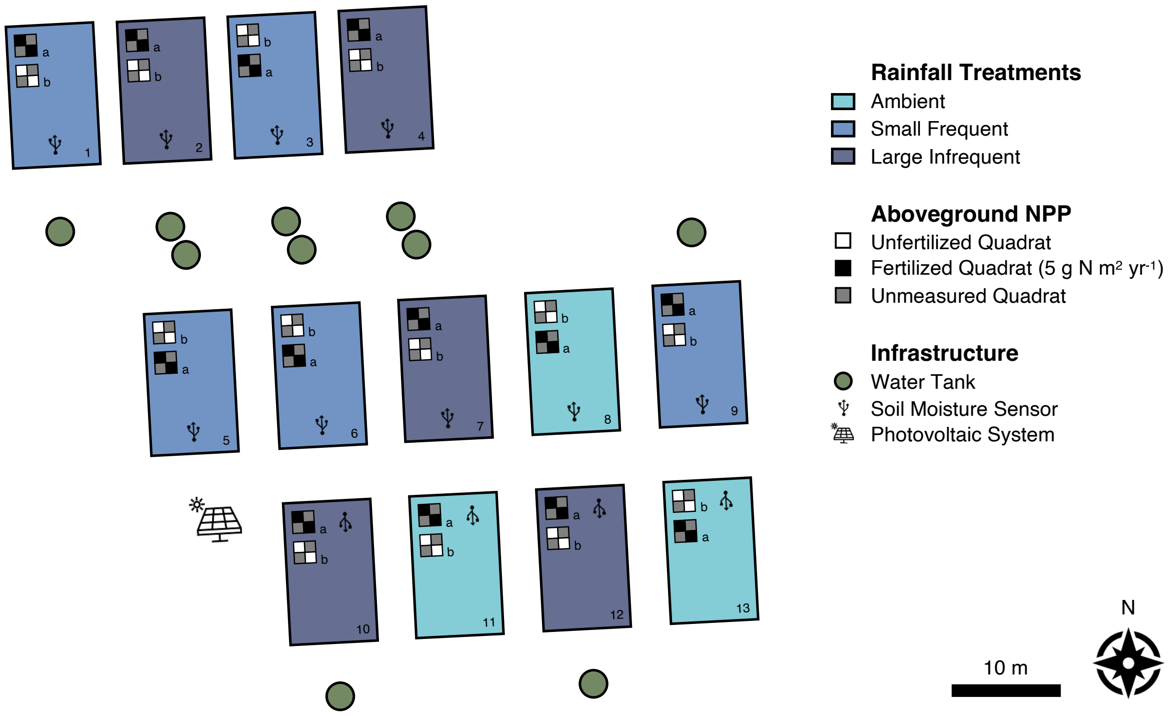

**Figure 3.1.** Simplified site layout of the Monsoon Rainfall Manipulation Experiment (MRME; 34.3441°N, 106.7272°W, elevation 1604 m), located in the Sevilleta National Wildlife Refuge, central New Mexico, USA. Labelled 8 m by 13 m plots (1-13) received one of two experimentally applied rainfall addition treatments ($n$ = 5 per rainfall treatment) for twelve consecutive weeks during the summer monsoon each year (2007-2020), with ambient controls in light blue, small frequent (5 mm weekly; $n$ = 12) in medium blue, and large infrequent (20 mm weekly; $n$ = 3) in dark blue. Two subplots within each plot (a, b) contain four 1 $m^2$ quadrats each. One subplot received 5 g N $m^2$ $yr^{-1}$, applied as ammonium nitrate ($NH_4NO_3$) each June prior to the summer monsoon, while the other subplot served as an unfertilized control. Aboveground net primary production (ANPP) measurements occurred annually in two unfertilized (white) and two fertilized (black) quadrats during the fall growing season. Water tanks provided an onsite reservoir for treatment water obtained from a reverse-osmosis system that was applied to treatment plots via overhead sprinkler systems (not shown). A photovoltaic system powered sensor instrumentation, which included a continuous depth-integrated (0-16 cm) measurement of soil volumetric water content (VWC) in each plot (2010-2020). A tipping bucket rain gage mounted adjacent to the photovoltaic system recorded ambient precipitation received by all plots year-round.

Aboveground NPP (ANPP) was measured during the fall growing season using a non-destructive allometric scaling approach based on height and cover measurements of individual plants (Muldavin et al., 2008). Species-level ANPP was estimated using linear regression models of weight-to-volume ratios, where intercepts were forced through the origin, developed from reference specimens harvested from adjacent areas (Rudgers et al., 2019). Measurements were recorded in two permanently located 1 $m^2$ quadrats within two 2 x 2 m subplots in each plot (Figure 3.1). One *fertilized* subplot received 5 g N $m^2$ $yr^{-1}$, applied as ammonium nitrate ($NH_4NO_3$) each June prior to the summer monsoon, while the other subplot served as an *unfertilized* control (Figure 3.1). Plant Root Simulator (PRS®) probes (Western Ag Innovations, Saskatoon, Saskatchewan, CA) were also buried within the rooting zone of a randomly selected black grama tussock in one *unfertilized* and one *fertilized* quadrat in each plot prior to the summer monsoon in most years (Collins, 2020). PRS® probes mimic plant uptake of nitrogen using ion-exchange resin membranes, providing a seasonally integrated estimate of plant available nitrogen. Following each summer monsoon, probes were retrieved, rinsed in deionized water, and shipped to the manufacturer where they were analyzed for ammonium ($NH_4^+$-N) and nitrate ($NO_3^-$-N).

### 3.2.3 Statistical Analyses

To assess the seasonal and overall effectiveness of rainfall treatments following the 2009 wildfire, repeated-measures analyses of variance (ANOVAs) were performed using mean daily SVWC averaged across each rainfall treatment between July and September of each year. Seasonally integrated nitrogen supply rates measured by PRS® probes were analyzed similarly using a linear mixed-effects model, where the rainfall and fertilization treatment combination was specified as a fixed effect and plot as a random effect.

To visualize interactive treatment effects on plant community composition over time, we constructed a Bray-Curtis dissimilarity matrix from Wisconsin double standardized square root transformed species-level abundances, measured as ANPP, followed by a three dimensional non-metric multidimensional scaling (NMDS) analysis using the *metaMDS* function in the *vegan* package in *R* (Oksanen et al., 2020). NMDS is considered the ordination method of choice for collapsing multidimensional ecological community data into reduced dimensional space, where species occurring in less than 10% of all observations were omitted prior to computing Bray-Curtis dissimilarities to reduce noise and improve interpretation (McCune & Grace, 2002). To determine if community composition differed significantly among treatments, we conducted permutational multivariate analyses of variance (PERMANOVAs) using the *adonis* function in *vegan*, with plot specified as a random effect using the strata parameter, followed by pairwise comparisons using the *pairwise.adonis2* function in the *pairwiseAdonis* package in *R* (Martínez Arbizu, 2020). Permutational multivariate analysis of dispersion (PERMDISP) within treatments was calculated using the *betadisper* function in *vegan*, followed by ANOVA and Tukey's HSD pairwise comparisons. Finally, the degree of community divergence among treatments was calculated with the *usedist* package in *R* (Bittinger, 2020).

To investigate treatment effects on ANPP over time, we constructed separate linear mixed-effects models for *unfertilized* and *fertilized* treatments, where the interaction between year and rainfall treatment was specified as a fixed effect. To examine impacts of the 2009 wildfire, additional linear mixed-effects models were constructed for ANPP of the dominant grass (black grama) and subdominant plant functional types (other grasses, forbs, and shrubs) found in MRME, where the interaction between burn status (i.e., pre- or post-fire) and treatment combination was specified as a fixed effect. Quadrat nested within subplot within plot was specified as the random effect in all ANPP models.

All data analyses were conducted using *R* version 3.6.3 (R Core Team, 2020). Linear mixed-effects models were constructed using the *nlme* package in *R* (Pinheiro et al., 2020) and included a continuous first-order autoregressive correlation structure to account for temporal autocorrelation. Response variables were either natural log or square root transformed prior to model runs 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 (HSD) pairwise comparisons were used to further investigate treatment effects on response variables, which were considered statistically significant when $p \leq .1$ to account for low replication.

## 3.3 Results

### 3.3.1 Soil Moisture and Nitrogen Availability

Ambient monsoon rainfall over this fourteen-year study exhibited high interannual variation, ranging from 42.7 mm in 2015 to 232.7 mm in 2013, with a coefficient of variation (CV) of 46% (Figure 3.2). Although average monsoon rainfall received over the study period was ~9% lower than the longer-term regional mean, treatments increased ambient monsoon rainfall by ~40% on average. Mean seasonal post-fire SVWC differed significantly among all rainfall treatments, ranging from 11.0 ± 0.1% in ambient to 12.7 ± 0.1% in small frequent to 14.1 ± 0.1% in large infrequent, with rainfall addition, regardless of treatment size or frequency, resulting in significantly higher SVWC compared to ambient in nearly all post-fire years (Figure 3.3). Fertilization resulted in significantly higher mean seasonally integrated net inorganic nitrogen ($NH_4^+$-N + $NO_3^-$-N) supply rates than unfertilized treatments regardless of rainfall treatment. However, large infrequent rainfall consistently resulted in less plant available nitrogen over the study period, especially in the absence of nitrogen enrichment (Figure 3.4).

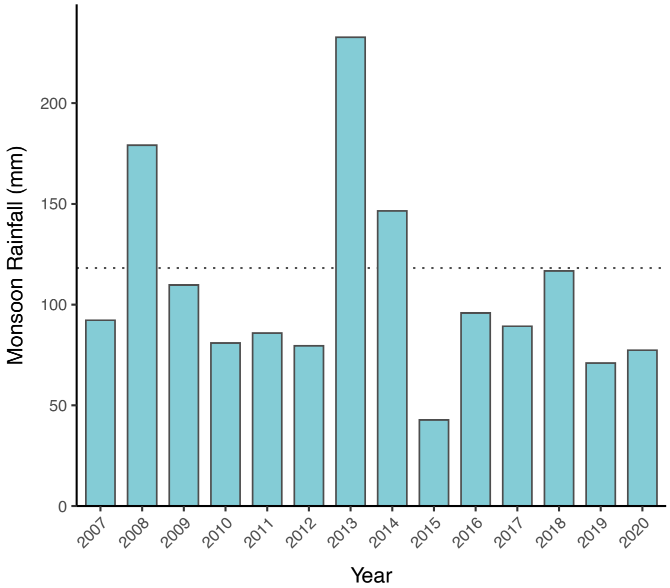

**Figure 3.2.** Total ambient summer monsoon (July-September) rainfall (mm) recorded in the Monsoon Rainfall Manipulation Experiment (MRME) over the fourteen-year study (2007-2020). All plots received ambient precipitation year-round, with rainfall addition treatments receiving an additional 60 mm each summer, either as small frequent (5 mm weekly; *n* = 12) or large infrequent (20 mm monthly; *n* = 3) events. The dashed line reflects the long-term (1990-2020) mean monsoon precipitation.

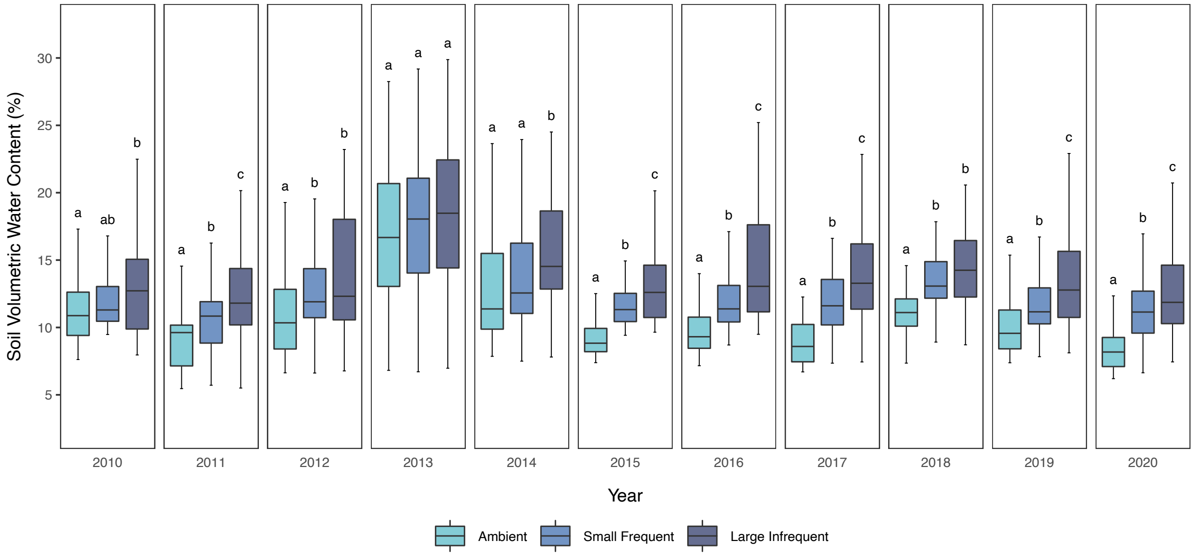

**Figure 3.3.** Mean daily-averaged summer monsoon (July-September) soil volumetric water content (SVWC) recorded in each rainfall treatment (ambient, small frequent, large infrequent) each year following the 2009 wildfire (2010-2020). Different letters indicate significant within-year treatment differences ($p \leq .05$). Pre-fire (2007-2008) SVWC was measured using a different methodology and reported previously by Thomey et al. (2011).

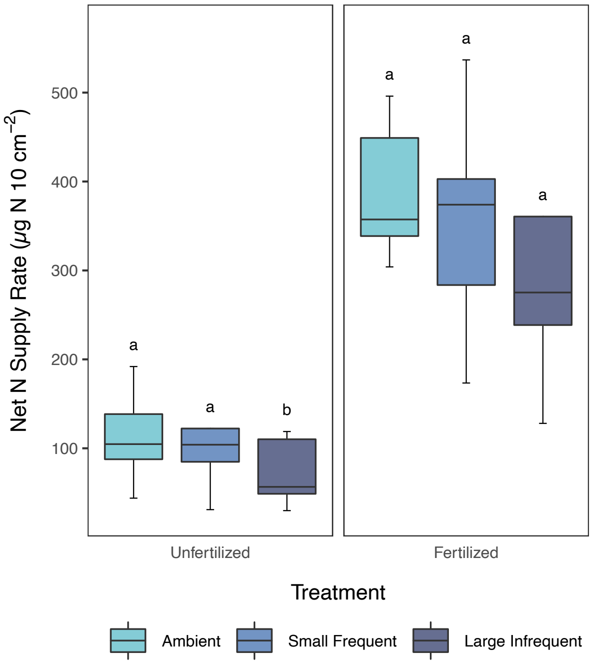

**Figure 3.4.** Mean seasonally integrated net inorganic nitrogen ($NH_4^+$-N + $NO_3^-$-N) supply rates (μg N 10 cm$^{-2}$) in unfertilized and fertilized (5 g N m$^2$ yr$^{-1}$) treatments within each rainfall treatment (ambient, small frequent, large infrequent) averaged across the nine years in which usable PRS® data were generated (i.e., 2007-2008, 2010, 2012-2016, 2019). Different letters indicate significant differences ($p \leq .05$) among rainfall treatments within fertilization treatments.

### 3.3.2 Plant Community Composition

The interactive effects of rainfall and fertilization treatments resulted in significant differences in plant community composition over the study period ($R^2 = .10, p \leq .001$), which were driven solely by fertilization treatments within each rainfall treatment ($.03 \leq R^2 \leq .08, p \leq .001$). With respect to post-fire recovery, the NMDS ordination (Figure 3.5) revealed a distinct temporal shift beginning in 2014, following an above-average monsoon in 2013 (Figure 3.3). Therefore, we focused additional analyses on the last seven years of the study (2014-2020) when vegetation was more stable over time. Interactive treatment effects during this period similarly resulted in significant compositional differences ($R^2 = .14, p \leq .001$), still driven solely by fertilization ($.04 \leq R^2 \leq .14, p \leq .001$), and resulting in significantly reduced black grama production and increased forb production, respectively. The greatest difference in community composition during 2014-

2020 occurred between the fertilization treatments in the small frequent rainfall treatment. Distances between fertilization treatment centroids ranged from .06 in ambient to .51 in the small frequent treatment, which was the only treatment comparison in which the communities exhibited significant temporal dispersion around the centroids (Figure 3.5b, $p \leq .01$).

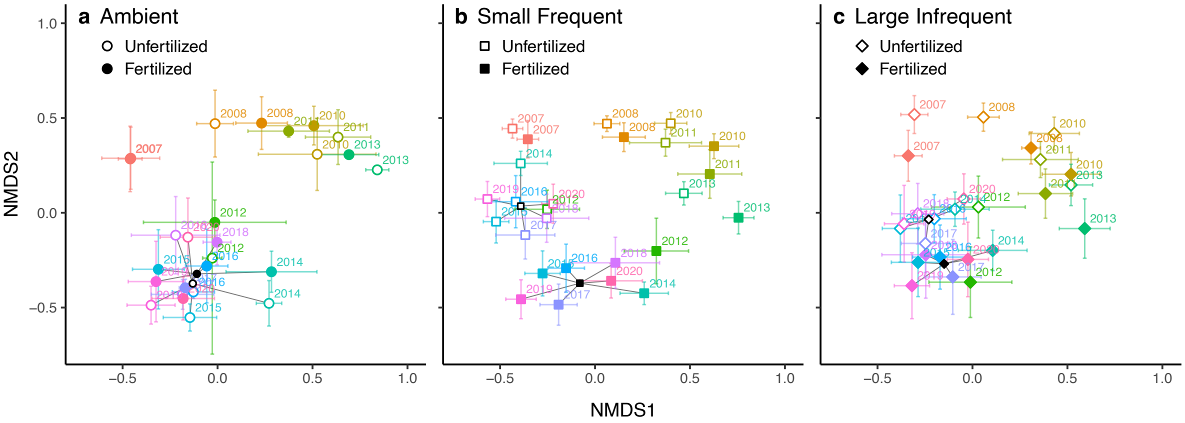

**Figure 3.5.** Non-metric multidimensional scaling (NMDS) ordination plots of a Bray-Curtis dissimilarity matrix visualized in two-dimensional space, where greater divergence in plant community composition is reflected by greater distances among points. Panels (a-c) reflect plant communities in unfertilized (open symbols) and fertilized ($5 \text{ g N m}^2 \text{ yr}^{-1}$; filled symbols) treatments within each rainfall treatment (ambient, small frequent, large infrequent). Colored symbols represent mean NMDS scores within each treatment combination, labelled by year (2007-2020), with error bars indicating standard errors of the means. Smaller white (unfertilized) and black (fertilized) symbols represent the centroids, or mean NMDS scores over the last seven years of the study (2014-2020; gray lines).

### 3.3.3 Aboveground Net Primary Production

Prior to the 2009 wildfire, the average proportion of ANPP attributed to the dominant species, black grama, ranged from 53% in the fertilized large infrequent treatment (Figure 3.6f) to 74% in the unfertilized large infrequent treatment (Figure 3.6e). Fire significantly reduced the proportion of black grama ANPP over the post-fire period in every treatment combination, ranging from 23% in the fertilized ambient treatment (Figure 3.6b) to 52% in the unfertilized large infrequent treatment (Figure 3.6e). Nitrogen enrichment negatively affected post-fire recovery of black grama, which exhibited significantly lower ANPP in all fertilized watering treatments compared to the pre-fire period (Figures 3.6b, 3.6d, and 3.6f). Consequently, the proportion of post-fire ANPP attributed to subdominant plant functional types tended to increase. Forbs were particularly responsive to nitrogen enrichment, exhibiting significantly higher ANPP in these treatments.

ANPP exhibited high interannual variation across all treatments over the study period (CV = 45%), with means ranging from 79.9 ± 12.4 g $m^{-2}$ $yr^{-1}$ in the fertilized ambient treatment to 147.3 ± 16.3 g $m^{-2}$ $yr^{-1}$ in the fertilized large infrequent treatment (Figure 3.7). In the absence of nitrogen enrichment, rainfall addition significantly increased ANPP over ambient conditions between 2011 and 2016, with the small frequent treatment resulting in significantly higher production over the entire study period, and particularly during the last seven years of the study (Figure 3.7a). In contrast, rainfall addition and fertilization together significantly increased ANPP over ambient conditions in most years, with the large infrequent treatment resulting in significantly higher production overall, and particularly during the last seven years of the study (Figure 3.7b). We also found greater separation among ANPP responses to rainfall treatments in the presence of nitrogen enrichment; however, the only statistically significant difference between the small frequent and large infrequent treatment occurred in 2016.

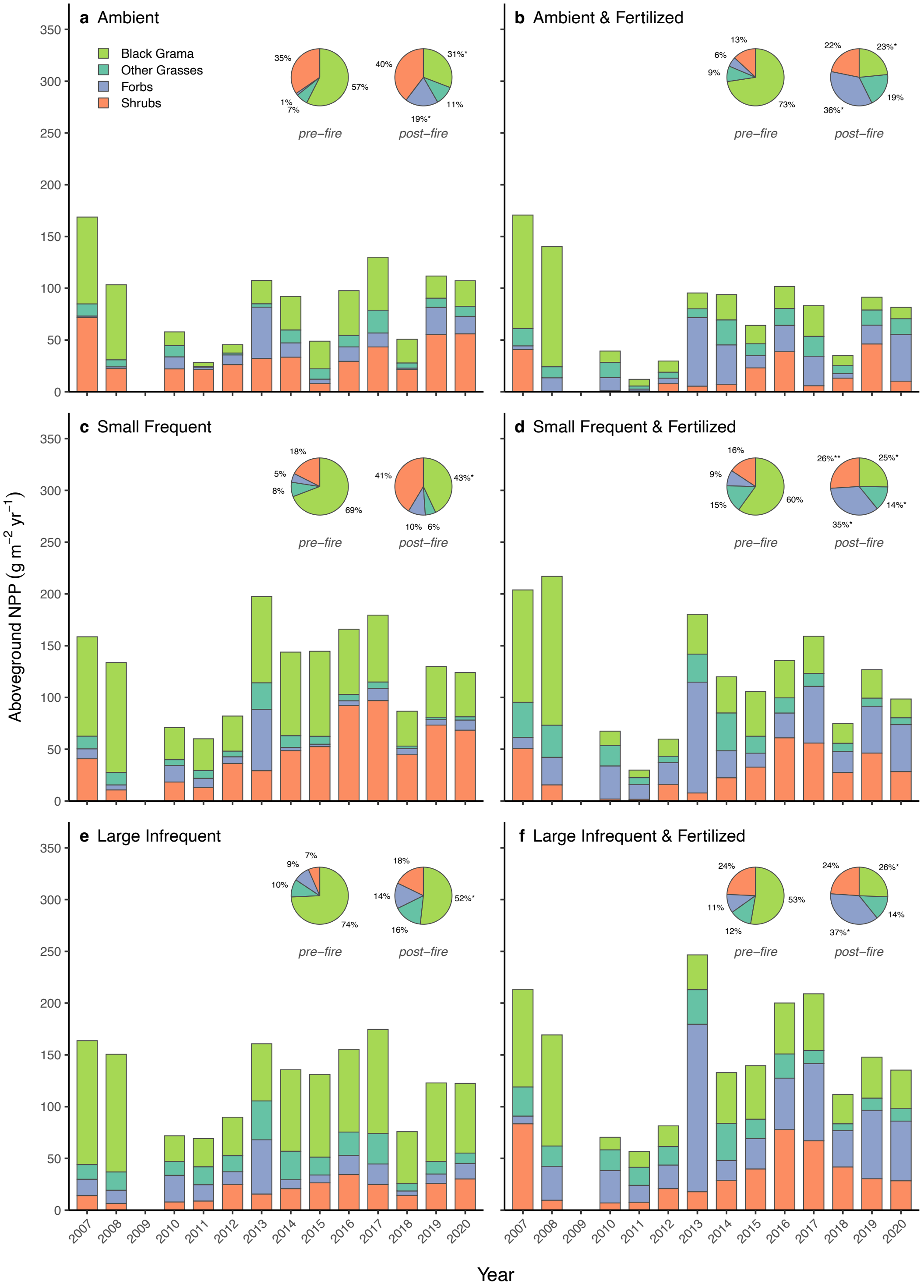

**Figure 3.6.** Mean fall season aboveground net primary production (ANPP; g m$^{-2}$ yr$^{-1}$) measured over the fourteen-year study (2007-2020), with rows representing rainfall treatments and columns representing fertilization treatments. Different colors reflect the proportion of ANPP contributed by the dominant grass (black grama, light green), along with other plant functional types (other grasses, dark green; forbs, blue; shrubs, orange) found in the site. No ANPP measurements were made in 2009 following a wildfire that burned through the experiment. Pie chart insets reflect the average proportion of ANPP contributed by each functional group before and after the 2009 wildfire, with significant post-fire differences ($p \leq .1$) indicated by asterisks.

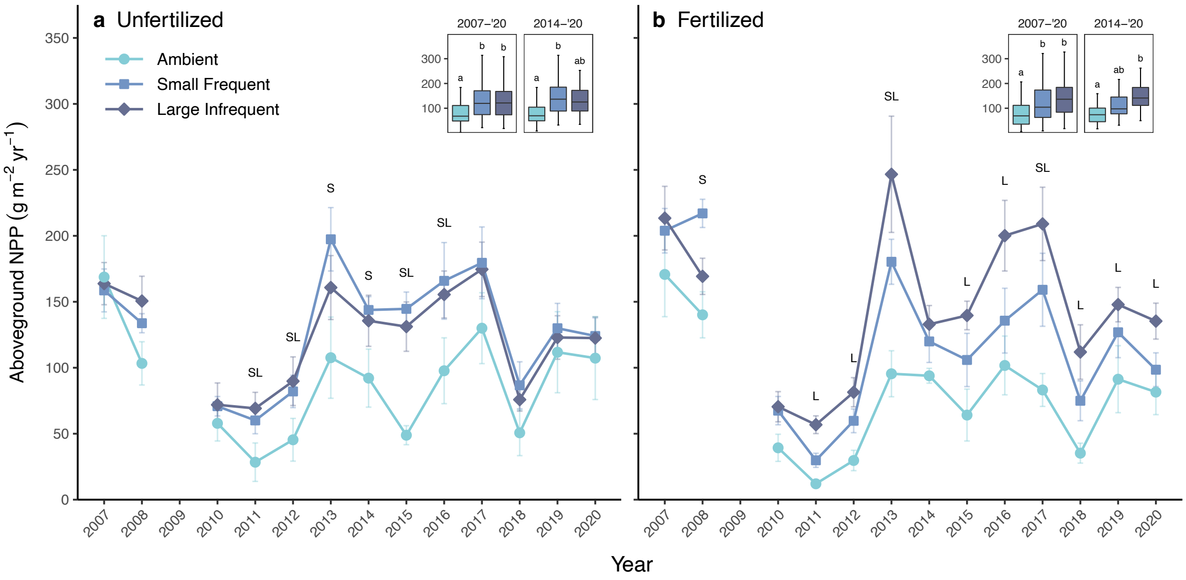

**Figure 3.7.** Mean fall season aboveground net primary production (ANPP; g $m^{-2}$ $yr^{-1}$) responses to rainfall and fertilization treatments over the fourteen-year study (2007-2020). Monsoon rainfall addition treatments are represented by different shades of blue, with ambient controls in light blue (circular symbols), small frequent (5 mm weekly) in medium blue (square symbols), and large infrequent (20 mm monthly) in dark blue (diamond symbols). All plots received ambient rainfall year-round. No ANPP measurements were made in 2009 following a wildfire that burned through the experiment. Symbols represent mean ANPP for each rainfall treatment by year, with error bars indicating standard errors of the means. Letters indicate significant within-year differences ($p \leq .1$) among rainfall treatments within each fertilization treatment, where "S" indicates a significant difference between the ambient and small frequent treatments, "L" between the ambient and large infrequent treatments, and "SL" between ambient and both rainfall addition treatments. Box plot insets reflect mean ANPP over the entire study (2007-2020) and over the last seven years of the study (2014-2020), with different letters indicating significant differences ($p \leq .1$) among rainfall treatments within the respective timeframe and fertilization treatment.

## 3.4 Discussion

The conceptual bucket model proposed by Knapp et al. (2008) predicts that under a more extreme precipitation regime consisting of fewer, but larger rain events, dryland ecosystems will experience reduced drought stress due to deeper infiltration and longer persistence of soil moisture, consequently resulting in greater rates of ANPP. This hypothesis has been supported by a few short-term experiments (Heisler-White et al., 2008; Knapp et al., 2002; Thomey et al., 2011) and modeling studies (Hou et al., 2021). That is, both approaches have found higher rates of ANPP under more extreme rainfall regimes in dryland ecosystems. Overall, our results correspond with the soil moisture component of the bucket model in that seasonal availability of soil moisture over the study period was greatest under large infrequent rain events. However, in contrast to bucket model predictions, large infrequent and small frequent rain events resulted in similar rates of ANPP on average over this fourteen-year experiment. Furthermore, large infrequent rainfall stimulated the greatest amounts of ANPP only when nitrogen limitation was alleviated. These results suggest northern Chihuahuan Desert grasslands are primarily water limited, with nitrogen being a strong secondary limiting resource, that together drive ANPP responses to within-season rainfall variability.

Previous tests of the bucket model in arid and semi-arid grasslands also revealed that a shift from current rainfall patterns to fewer, but larger rain events led to considerable increases in soil moisture availability (Heisler-White et al., 2008, 2009; Thomey et al., 2011). Soil moisture also persisted longer under large infrequent rain events, particularly earlier in the summer monsoon when soils are drier (Brown, Sala, et al., 2022), and in comparison to mesic grasslands (Heisler-White et al., 2009). The bucket model proposed that ecological responses to large infrequent rain events would be contingent on ambient precipitation amounts. In a revised conceptual bucket model, Thomey et al. (2011) proposed that interannual variability of ambient precipitation likely plays a role in the magnitude of production responses to these events, with greater responses expected in dry years than in wet years. Consistent with this hypothesis, we found that in all post-fire years where monsoon rainfall was close to or exceeding the long-term regional mean, soil moisture availability in one or both rainfall addition treatments was not significantly different from ambient conditions (i.e., 2013, 2014) or from each other (i.e., 2018).

Despite impacts on soil moisture availability, ANPP responses were inconsistent with bucket model predictions and some earlier studies (Heisler-White et al., 2008, 2009). Although supplemental monsoon rainfall significantly increased ANPP relative to ambient rainfall conditions, we found that in the absence of nitrogen fertilization, rates of ANPP under small frequent rainfall were often slightly higher than rates under large infrequent rain events. Only under nitrogen enrichment did we find responses that better aligned with the bucket model predictions that large infrequent rainfall stimulated the greatest amount of ANPP. In addition, we found greater separation in ANPP responses among rainfall treatments under nitrogen enrichment; however, this was only statistically significant in one year. One potential explanation for the different responses among studies is that our design layered experimental rain events onto ambient rainfall each year, whereas ambient events were excluded by Heisler-White et al. (2008, 2009). Thus, at the seasonal level, our treatments resulted in higher mean SVWC than Heisler-White et al. (2009).

Our study revealed that nitrogen enrichment, not differences in rainfall size and frequency, drove divergence in plant community composition over time, with the greatest divergence occurring between the unfertilized and fertilized treatments under the small frequent rainfall regime. While fire significantly reduced production of the dominant grass under all treatment combinations, nitrogen enrichment enhanced these losses while stimulating forb production. Chronic nitrogen enrichment has also been found to decrease the abundance of dominant native perennial $C_4$ grasses (Avolio et al., 2014; Isbell et al., 2013) and increase the abundance of forbs in mesic grasslands (Avolio et al., 2014), which led to an eventual decrease in ANPP under nitrogen addition in these grasslands. However, ANPP in our system remained consistently higher than ambient conditions over the entire study period, as found in a wide array of grasslands globally (Seabloom et al., 2021).

Previous studies in the Chihuahuan Desert have found black grama is limited primarily by water, but that this species responds more strongly to large rather than small rain events (Báez et al., 2007; Stephens & Whitford, 1993; Thomey et al., 2014). Yet, numerous studies have demonstrated the importance of small rainfall events for a variety of ecological processes in arid and semi-arid grasslands, including nitrogen availability (Brown, Sala, et al., 2022), diversity of biological soil crusts (Fernandes et al., 2022), lag effects on ANPP (Petrie, Collins, & Litvak, 2015), and production of dominant grasses (Sala & Lauenroth, 1982).

Wildfires are natural occurrences in the northern Chihuahuan Desert, but it can take up to ten years for the abundance of black grama to return to pre-burn levels (Drewa & Havstad, 2001; R. J. Gosz & Gosz, 1996; Parmenter, 2008). While it has been suggested recovery can be rapid under above average precipitation (Drewa et al., 2006), black grama production was still well below pre-fire levels in both rainfall addition treatments 11 years after the fire. Despite the lack of black grama recovery, total ANPP returned to pre-fire levels within four years under both rainfall treatments. Although all functional groups (other grasses, forbs, and shrubs) contributed to this response, forbs increased significantly in response to nitrogen addition under both rainfall regimes. This result contrasts with most nitrogen addition studies in which ANPP of grasses increase and forbs are either unaffected or decline with fertilization (You et al., 2017).

Regional climate models for the southwestern US predict a shift in growing season rainfall patterns, historically characterized by frequent small events, to a more extreme rainfall regime characterized by infrequent large events. In addition, atmospheric nitrogen deposition is predicted to increase as human populations continue to expand throughout this region (Fenn et al., 2003). Long-term manipulative experiments on the interactive effects of these drivers can improve our ability to predict how dryland ecosystems will respond to changes in rainfall size and frequency at decadal timescales. Our findings contribute further evidence that dryland ecological processes are sequentially resource limited and that small frequent rain events have an important ecological role in these ecosystems.

## 3.5 Acknowledgments

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## 3.6 Data Availability Statement

All aboveground net primary production and associated data presented in this study 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/04ca3bb840be58ed908a9dcb52fa8371 (Brown & Collins, 2022b). Meteorological and PRS® data used in this study are also publicly available from EDI at https://doi.org/10.6073/pasta/1cbc37ae4d40b3844b5e4be9f6f18073 (Moore, 2021) and https://doi.org/10.6073/pasta/a17b125176a9c24dbb4caa760d2c9944 (Collins, 2020).

*Chapter 4*

# As above, not so below: Long-term dynamics of net primary production across a dryland transition zone

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## Abstract

Drylands are key contributors to interannual variation in the terrestrial carbon sink, which has been attributed primarily to broad-scale climatic anomalies that disproportionately affect net primary production (NPP) in these ecosystems. Current knowledge around the patterns and controls of NPP is based largely on measurements of aboveground NPP (ANPP), particularly in the context of altered precipitation regimes. Limited evidence suggests belowground NPP (BNPP), a major input to the terrestrial carbon pool, may respond differently than ANPP to precipitation, as well as other drivers of environmental change, such as nitrogen deposition and fire. Yet long-term measurements of BNPP are rare, contributing to uncertainty in carbon cycle assessments. Here, we used sixteen years of annual NPP measurements to investigate responses of ANPP and BNPP to several environmental change drivers across a grassland-shrubland transition zone in the northern Chihuahuan Desert. We found chronic nitrogen enrichment stimulated ANPP, whereas a one-time prescribed burn reduced ANPP for nearly a decade. ANPP was positively correlated with annual precipitation across this landscape; however, this relationship was weaker within sites. Surprisingly, BNPP was largely unaffected by these factors, which suggests BNPP is driven by a different set of controls than ANPP. Although NPP generally exhibited similar trends among sites, temporal correlations between ANPP and BNPP within sites were weak. Our findings suggest belowground production cannot be inferred from aboveground measurements in dryland ecosystems. Improving understanding around the patterns and controls of dryland NPP at interannual to decadal scales is fundamentally important because of their measurable impact on the global carbon cycle. This study underscores the need for more long-term measurements of BNPP to improve assessments of the terrestrial carbon sink.

**Keywords:** aboveground production, belowground production, carbon cycle, Chihuahuan Desert, ecotone, fire, nitrogen enrichment, precipitation

## 4.1 Introduction

Drylands, which currently occupy 45% of the terrestrial land surface and account for 40% of global net primary production (NPP), are undergoing accelerated expansion worldwide as a consequence of anthropogenic climate and land-use change (Burrell et al., 2020; Huang et al., 2016, 2017; Prăvălie et al., 2019). These characteristically water-limited ecosystems are disproportionately impacted by large-scale climatic anomalies, such as the El Niño–Southern Oscillation, that contribute strongly to patterns of interannual variation in the terrestrial carbon sink (Ahlström et al., 2015; Houghton, 2000; Poulter et al., 2014). While other perturbations facing drylands, such as increased nitrogen deposition (Fenn et al., 2003), altered fire regimes (Aslan et al., 2018), and shrub encroachment (D'Odorico et al., 2012), also contribute to regional variation in the terrestrial carbon cycle (Keenan & Williams, 2018), considerably less is known about the longer-term implications of such disturbances in dryland ecosystems.

Despite being a key regulator of the global carbon cycle, current knowledge around the patterns and controls of dryland NPP is based largely on measurements of aboveground production, particularly in the context of altered precipitation regimes. Indeed, several broad-scale analyses have found aboveground NPP (ANPP) to be especially sensitive to changes in mean annual precipitation in water-limited ecosystems (Hsu et al., 2012; Huxman, Smith, et al., 2004; Knapp & Smith, 2001; Maurer et al., 2020). Yet, belowground NPP (BNPP) is the main contributor to soil organic carbon (Sokol & Bradford, 2019), which represents the largest terrestrial carbon pool (Janzen, 2004; Scharlemann et al., 2014). Consequently, BNPP represents a significant proportion of total NPP in dryland ecosystems (Gherardi & Sala, 2020). While limited evidence provided by recent meta-analyses suggests ANPP and BNPP may exhibit dissimilar responses to environmental change drivers, long-term empirical measurements of BNPP are exceedingly rare (Wilcox et al., 2017; Wu et al., 2011).

The predominantly arid and semi-arid ecosystems of the southwestern United States (US) have been especially impacted by climate change in recent decades (Friedlingstein et al., 2022), with high temporal and spatial variation in carbon storage capacity (Biederman et al., 2017). Recent studies have revealed precipitation patterns have become increasingly variable throughout this region (Maurer et al., 2020; F. Zhang et al., 2021), with climate models projecting greater intensification of the hydrologic cycle into the future (Diffenbaugh et al., 2008; Moustakis et al., 2021). However, precipitation alone cannot fully explain year-to-year variation in carbon cycle processes, particularly over local and regional scales (Lauenroth & Sala, 1992). Atmospheric nitrogen deposition, which is strongly correlated with growing season precipitation (Báez et al., 2007), is increasing in many dryland regions as a consequence of anthropogenic activities (Fenn et al., 2003). Although nitrogen is an important limiting resource for dryland ecosystem processes (Austin et al., 2004; Hooper & Johnson, 1999; Yahdjian et al., 2011), evidence from the Sonoran and Chihuahuan Deserts suggests nitrogen enrichment may only stimulate greater NPP in years with above average precipitation (Hall et al., 2011; Ladwig et al., 2012).

Fire is also a key driver of vegetation change in dryland ecosystems (Andela et al., 2013; Aslan et al., 2018; Hély et al., 2019; Humphrey, 1974). In particular, fire can counteract the early stages of woody shrub encroachment in desert grasslands (Junran Li et al., 2022; Ravi et al., 2009; Sankey et al., 2012; White, 2011), which has significant implications for regional carbon cycle dynamics (Archer et al., 2017; Barger et al., 2011). Indeed, the reduction of fine fuel loads caused by intensive livestock grazing is thought to be a primary driver of rapid shrub encroachment that occurred throughout the southwestern US in the 20th century (Archer et al., 2017; Grover & Musick, 1990; Van Auken, 2000, 2009). Consequently, fire is a common management practice for preserving pastoral economies in many dryland regions (Hanan et al., 2021).

Current understanding around the patterns and controls of dryland NPP at interannual to decadal scales is relatively poor, contributing to uncertainty in assessments of the terrestrial carbon sink (Friedlingstein et al., 2022; Keenan & Williams, 2018; Niu et al., 2017). To address this knowledge gap, we used sixteen years of data to explore temporal patterns of ANPP and BNPP in response to several key drivers of environmental change across a grassland-shrubland transition zone in the northern Chihuahuan Desert. We asked: (1) How do chronic nitrogen enrichment and fire affect temporal patterns of ANPP and BNPP *within* a site? (2) How does precipitation affect temporal patterns of ANPP and BNPP *within* and *among* sites? (3) How well are ANPP and BNPP correlated *within* and *among* sites?

## 4.2 Materials and Methods

### 4.2.1 Study Area

This study was conducted using sixteen years of data (2005-2020) from three long-term research sites situated along a grassland-shrubland transition zone in the Sevilleta National Wildlife Refuge (NWR), central New Mexico, USA (Figure 4.1). Here, Great Plains grassland dominated by blue grama (*Bouteloua gracilis*) transitions into Chihuahuan Desert shrubland dominated by creosote bush (*Larrea tridentata*) along a north-to-south gradient separated by a narrow ecotone of Chihuahuan Desert grassland dominated by black grama (*Bouteloua eriopoda*; J. R. Gosz, 1993; R. J. Gosz & Gosz, 1996). This dynamic region provides an ideal location for studying ecosystem responses to environmental change. Rapid encroachment of native $C_3$ evergreen shrubs into native perennial $C_4$ grasslands began in the mid to late 1800s throughout central and southern New Mexico, coinciding with the influx of large-scale cattle ranching (Gross & Dick-Peddie, 1979; Grover & Musick, 1990; Van Auken, 2000, 2009). After more than a century of historically high stocking rates and extensive overgrazing, domestic livestock were permanently excluded from the Sevilleta NWR in 1973 (Parmenter, 2008; Rand-Caplan, 2006). Unencroached grasslands have since recovered (Collins & Xia, 2015), but are periodically subjected to lightning-caused wildfires or prescribed management burns (Parmenter, 2008).

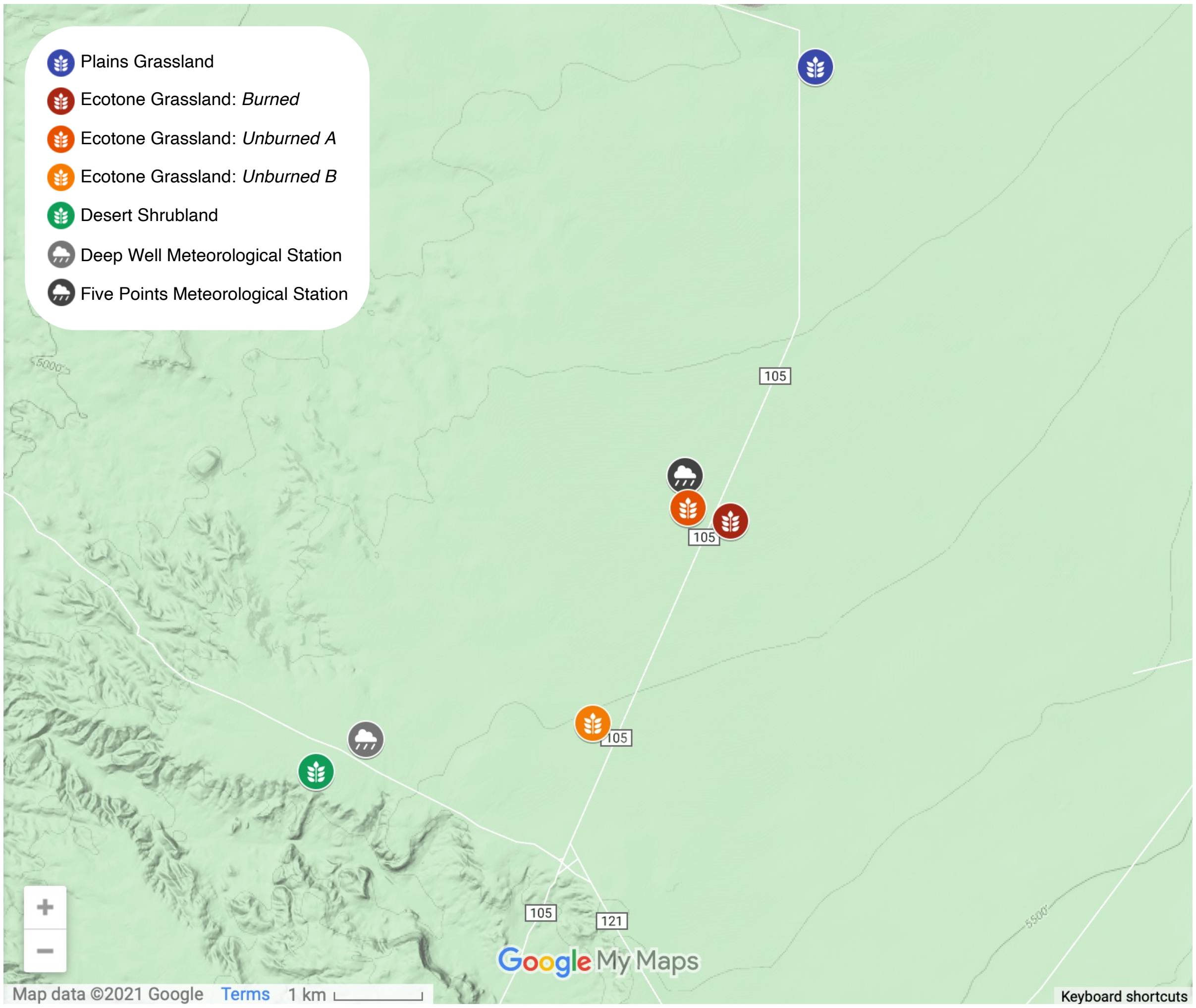

**Figure 4.1.** Map of the study area, with the top of the map aligning with the northern boundary of the Sevilleta National Wildlife Refuge. As defined by the legend, symbols correspond to the three long-term research sites (plains grassland, ecotone grassland, desert shrubland) and the two automated meteorological stations used in this study. The plains grassland site encompasses both *unfertilized* and *fertilized* treatments. The ecotone grassland site consists of an area *burned* by a prescribed management fire in 2003 and an *unburned* area (A) that was initially located across the road. Following a lightning-caused wildfire in 2009, aboveground quadrats were relocated to another *unburned* area (B) within the ecotone.

Soils in this region of the Sevilleta NWR are classified as Typic Haplocalcids formed by calcareous aeolian and alluvial deposits (Soil Survey Staff, 2019). Soil texture in the top 30 cm, where the majority of root biomass occurs (Gibbens & Lenz, 2001; Jackson et al., 1996; Kurc & Small, 2007; McCulley et al., 2004), consists of 60-68% sand, 22-30% silt, and 10% clay, with 10-15% as $CaCO_3$ (Kieft et al., 1998). A petrocalcic layer, ranging from 72-80 cm beneath the soil surface in Great Plains grassland to 26-29 cm in Chihuahuan Desert shrubland, further constrains moisture infiltration and rooting depth (Buxbaum & Vanderbilt, 2007; Gibbens & Lenz, 2001; Schenk & Jackson, 2002). Atmospheric nitrogen deposition occurs primarily through wet deposition at a rate of 0.2 g $m^{-2}$ $yr^{-1}$, with 57% deposited as $NH_4$ and 43% as deposited as $NO_3$ (Báez et al., 2007). Low deposition rates combined with a low abundance of nitrogen fixers in biological soil crusts (Fernandes et al., 2018, 2022) contribute to nutrient-poor soils throughout the region (Brown, Sala, et al., 2022; Zak et al., 1994).

Climate parameters in the Sevilleta NWR have been recorded continuously for over three decades by a spatially distributed network of automated meteorological stations (Moore, 2021) that include the Five Points station, located in the Chihuahuan Desert grassland and shrubland ecotone (34.3350°N, 106.7293°W, elevation 1613 m; Figure 4.1), and the Deep Well station, located in the Great Plains and Chihuahuan Desert grassland ecotone (34.3592°N, 106.6911°W, elevation 1600 m; Figure 4.1). From 1990 to 2020, mean annual water year precipitation (MAP) recorded by the Deep Well station was 233 ± 9.6 mm, with approximately 51% falling between July and September from localized convective storms driven by the North American Monsoon. Consequently, sporadic winter and spring precipitation together with monsoon rainfall create distinct spring and fall growing seasons in this region (Notaro et al., 2010). Mean annual temperature recorded over this same 31-year period was 13.7 ± 0.0 °C, with monthly temperatures ranging from 25.4 ± 0.2 °C in July to 1.3 ± 0.3 °C in December.

#### 4.2.1.1 Plains Grassland

In 1995, a long-term nitrogen fertilization experiment was established in a Great Plains grassland (34.4012°N, 106.6765°W, elevation 1562 m; Figure 4.1). This experiment consisted of twenty 5 m by 10 m plots with 10 *fertilized* plots receiving 10 g N $m^{-2}$ $yr^{-1}$ applied as ammonium nitrate ($NH_4NO_3$) each June prior to the summer monsoon, and the remaining 10 *unfertilized* plots serving as ambient controls (Ladwig et al., 2012). In 2004, four permanently located 1 $m^2$ quadrats were established within each replicate plot, enabling non-destructive measurements of seasonal ANPP (Rudgers et al., 2019; *see section 4.2.2*) in 80 quadrats at this site ($n_{ANPP}$ = 40 per treatment) until fall 2019 when measurements were reduced to two quadrats per plot ($n_{ANPP}$ = 20 per treatment). In fall 2004, root ingrowth donuts (Milchunas et al., 2005; *see section 4.2.3*) were installed in 20 plots ($n_{BNPP}$ = 10 per treatment), resulting in the first annual measurements of BNPP in 2005. Precipitation records for this site (hereafter referred to as plains grassland) were provided by the Deep Well meteorological station.

#### 4.2.1.2 Ecotone Grassland

In June 2003, a prescribed fire burned approximately 1200 ha encompassing the ecotone where Great Plains and Chihuahuan Desert grassland converge (Burnett et al., 2012). In 2004, seasonal measurements of ANPP began in 40 permanently located 1 $m^2$ quadrats in *burned* grassland (34.3583°N, 106.6878°W, elevation 1601 m; Figure 4.1) as well as in *unburned* grassland located ~35 m to the west across a firebreak (34.3586°N, 106.6911°W, elevation 1601 m; Figure 4.1), serving as ambient controls ($n_{ANPP}$ = 40 per treatment). In fall 2004, root ingrowth donuts were installed in the *burned* and *unburned* grasslands respectively ($n_{BNPP}$ = 10 per treatment), resulting in the first annual measurements of BNPP in 2005. In August 2009, a lightning-caused wildfire swept through the *unburned* grassland. Consequently, fall measurements of ANPP did not occur in these quadrats, which were later relocated to another area within the Great Plains and Chihuahuan Desert grassland ecotone that was unaffected by either the 2003 or 2009 fires (34.3363°N, 106.7019°W, elevation 1620 m; Figure 4.1). In spring 2010, seasonal measurements of ANPP were reduced ($n_{ANPP}$ = 30 per treatment) and in spring 2017, ANPP measurements were not collected. In spring 2019, seasonal measurements of ANPP ceased in *burned* grassland. Precipitation records for this site (hereafter referred to as ecotone grassland) were provided by the Deep Well meteorological station.

### 4.2.1.3 Desert Shrubland

In Chihuahuan Desert shrubland (34.3331°N, 106.7350°W, elevation 1611 m; Figure 4.1), seasonal measurements of ANPP began in 1999 in four permanently located 1 $m^2$ quadrats that were established within four 5 $m^2$ plots on the cardinal points along the perimeter of five 200 m diameter small mammal trapping webs (Muldavin et al., 2008; Parmenter et al., 2003). In spring 2004, seasonal measurements of ANPP were reduced to two quadrats per plot in each of the five webs ($n_{ANPP}$ = 40). In fall 2004, root ingrowth donuts were installed between two of the trapping webs ($n_{BNPP}$ = 10), resulting in the first annual measurements of BNPP in 2005. Precipitation records for this site (hereafter referred to as desert shrubland) were provided by the Five Points meteorological station.

### 4.2.2 Aboveground Net Primary Production

ANPP was determined using a non-destructive allometric scaling approach based on height and cover measurements of individual plants recorded in permanently located 1 $m^2$ quadrats in each of the three study sites during the spring (April-May) and fall (September-October) growing seasons (Muldavin et al., 2008). Species-level ANPP was estimated using linear regression models of weight-to-volume ratios, where intercepts were forced through the origin, developed from reference specimens harvested from adjacent areas (Rudgers et al., 2019). Annual ANPP per quadrat was calculated as the sum of peak seasonal (spring or fall) ANPP for each species.

### 4.2.3 Belowground Net Primary Production

Permanently located root ingrowth donuts (Milchunas et al., 2005) were used to estimate annual BNPP *within* each of the three sites from 0-30 cm in depth, where moisture infiltration is highest and most roots are concentrated (Gibbens & Lenz, 2001; Jackson et al., 1996; Kurc & Small, 2007; McCulley et al., 2004; Schenk & Jackson, 2002). Although all methods used to estimate BNPP have their biases (Neill, 1992; Tierney & Fahey, 2007; Xuhui Zhou et al., 2012), root ingrowth donuts provide reliable and repeatable comparative estimates of BNPP with minimal soil disturbance (Milchunas, 2009). Root ingrowth donuts were created by excavating a 20.3 cm diameter by 30 cm deep hole and lining the outer wall with 2 mm by 2 mm plastic mesh. Next, a 15.2 cm diameter by 30 cm tall polyvinyl chloride (PVC) cylinder was inserted into the center of the hole and filled with sandbags to hold it in place. Sieved soil was then added to the space between the PVC cylinder and the plastic mesh, creating a donut-shaped cylinder of root-free soil into which roots can grow. At the end of each subsequent fall growing season, this cylinder of soil was harvested and newly collected sieved root-free soil was used to reconstruct the root ingrowth donut for the next annual harvest. Following harvests, soils were passed through a 2 mm sieve and roots were floated in water for collection. Roots were subsequently dried at 60 °C for 48 hours and weighed. To calculate BNPP, root weights were divided by the area of the root ingrowth donut and scaled up to 1 $m^2$ to enable comparisons with ANPP (Diabate et al., 2018).

### 4.2.4 Statistical Analyses

In this study, we analyzed sixteen years of data (2005-2020), reflecting the period during which both ANPP and BNPP data were collected from all three sites. To determine *within*-site responses of ANPP and BNPP to nitrogen enrichment and fire in the plains and ecotone grasslands respectively, we constructed repeated measures linear mixed-effects models for each site using the *nlme* package in *R* (Pinheiro et al., 2020), where the interaction between year and treatment was a fixed effect and sampling location, which included an appropriate nesting structure to match the site design, was a random effect. Models also included a continuous first order autoregressive correlation structure to account for temporal autocorrelation. NPP data 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 (HSD) pairwise comparisons were used to assess differences in treatment effects over time, which were considered statistically significant when $p \leq .05$. Pearson correlations were used to investigate relationships between NPP and annual water year precipitation as well as between ANPP and BNPP *within* and *among* sites. All analyses were conducted using *R* version 3.6.3 (R Core Team, 2020).

## 4.3 Results

Mean annual net primary production over our sixteen-year study was generally low but exhibited moderate to high interannual variation (Figure 4.2; Table 4.1). ANPP ranged from 97.3 ± 8.9 g $m^{-2}$ in *burned* ecotone grassland to 142.6 ± 17.5 g $m^{-2}$ in *fertilized* plains grassland, which also had the highest temporal variability in ANPP (Table 4.1). BNPP was lower than ANPP in most years (Figures 4.2 and 4.5), ranging from 70.1 ± 11.2 g $m^{-2}$ in *burned* ecotone grassland to 86.1 ± 17.2 g $m^{-2}$ in *unfertilized* plains grassland. BNPP was also far less temporally and spatially consistent than ANPP. This was especially apparent in desert shrubland, where temporal variability in ANPP was relatively low (Figure 4.2c) but exhibited the highest temporal variability in BNPP compared to other sites (Figure 4.2f; Table 4.1).

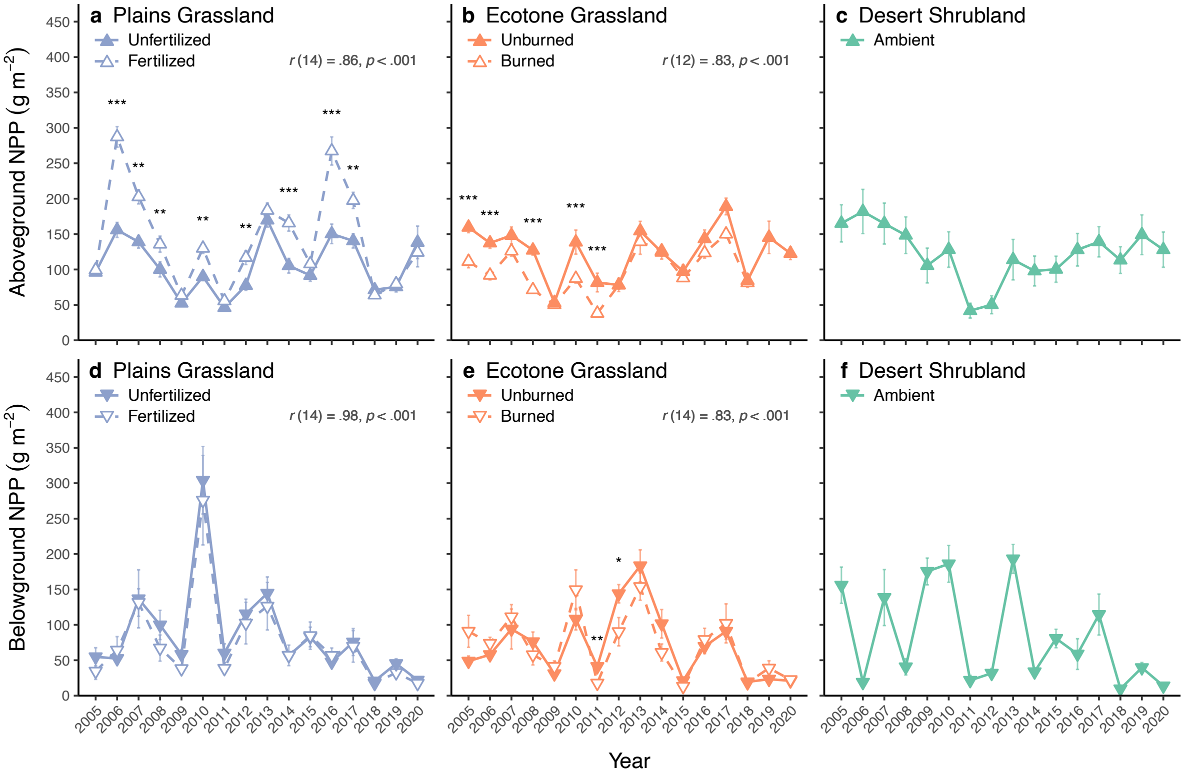

**Figure 4.2.** Sixteen years (2005-2020) of mean annual above- (a-c) and belowground (d-f) net primary production (NPP; $g\ m^{-2}$) in three long-term research sites situated along a grassland-shrubland transition zone, with plains grassland in blue, ecotone grassland in orange, and desert shrubland in green. Solid lines and filled points reflect NPP in the ambient controls *within* each of the three sites, whereas dashed lines and hollow points reflect NPP in the *fertilized* ($10\ g\ N\ m^{-2}\ yr^{-1}$) and *burned* (in 2003) treatments in the plains and ecotone grasslands, respectively. Error bars indicate standard errors of the means. Asterisks indicate significant *within*-site differences by year, where *** $p \leq .001$, ** $p \leq .01$, * $p \leq .05$. Pearson's $r$(df) and $p$-values reflect the strength and significance of the overall temporal correlation between treatments *within* the two grassland sites. Additional summary statistics are provided in Table 4.1.

| | | | Net Primary Production | | | | Precipitation | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Site** | **Treatment** | Mean ± SE | Min | Max | CV | $r$ | $R^2$ | $p$-value |
| | | | $g\ m^{-2}\ yr^{-1}$ | $g\ m^{-2}\ yr^{-1}$ | $g\ m^{-2}\ yr^{-1}$ | % | | | |
| **Aboveground** | Plains Grassland | *Unfertilized* | 106.2 ± 9.5 | 46.3 | 169.8 | 35.9 | .47 | .22 | = .067 |
| | | *Fertilized* | 142.6 ± 17.5 | 55.7 | 287.3 | 49.1 | .36 | .13 | = .177 |
| | Ecotone Grassland | *Unburned* | 124.1 ± 9.0 | 53.3 | 189.0 | 29.0 | **.60** | **.36** | **≤ .05** |
| | | *Burned* | 97.3 ± 8.9 | 38.1 | 150.0 | 34.1 | **.68** | **.46** | **≤ .01** |
| | Desert Shrubland | *Ambient* | 122.3 ± 9.6 | 41.9 | 181.9 | 31.4 | **.82** | **.66** | **≤ .001** |
| **Belowground** | Plains Grassland | *Unfertilized* | 86.1 ± 17.2 | 20.7 | 304.2 | 79.8 | -.12 | .01 | = .664 |
| | | *Fertilized* | 75.9 ± 15.9 | 17.4 | 276.0 | 83.9 | -.09 | .01 | = .727 |
| | Ecotone Grassland | *Unburned* | 70.7 ± 12.0 | 19.5 | 183.3 | 67.6 | .17 | .03 | = .541 |
| | | *Burned* | 70.1 ± 11.2 | 13.1 | 153.9 | 63.8 | .40 | .16 | = .121 |
| | Desert Shrubland | *Ambient* | 82.0 ± 16.8 | 9.6 | 193.1 | 82.2 | **.49** | **.24** | **≤ .05** |

**Table 4.1.** Summary of means ± standard errors (SE) of above- and belowground net primary production (NPP; g m$^{-2}$ yr$^{-1}$) over the sixteen-year study (2005-2020) *within* each site and treatment (also, see Figure 4.2). Minimum (min) and maximum (max) values reflect the lowest and highest NPP observed over the study, with coefficients of variation (CV; %) reflecting *within*-treatment interannual variability in NPP. Pearson's $r$ values indicate the strength and directionality of overall temporal correlations between NPP and water year precipitation, and $R^2$ values indicate the proportion of variance in NPP explained by precipitation (also, see Figure 4.4). Degrees of freedom (df) for Pearson's $r$ was 14, except for aboveground NPP in *burned* ecotone grassland, where df was 12. Significant relationships ($p \leq .05$) are in bold font.

## 4.1 How do nitrogen enrichment and fire affect temporal patterns of NPP *within* a site?

Annual nitrogen fertilization resulted in significantly greater ANPP in plains grassland in eight of the sixteen years (Figure 4.2a), with *fertilized* plains grassland exhibiting the greatest overall ANPP *among* all sites over our study period (Table 4.1). In contrast, BNPP was highly correlated between *unfertilized* and *fertilized* treatments in plains grassland and not significantly impacted by nitrogen fertilization (Figure 4.2d). Overall, ANPP was lowest in *burned* ecotone grassland (Table 4.1) following a one-time prescribed management burn, taking nine years to recover to unburned levels of production (Figure 4.2b). Like nitrogen fertilization in plains grassland, fire had little impact on BNPP in ecotone grassland, with the only significant differences between *unburned* and *burned* treatments occurring eight to nine years following the prescribed burn (Figure 4.2e).

### 4.2 How does precipitation affect temporal patterns of NPP *within* and *among* sites?

Precipitation over our sixteen-year study generally tracked the longer-term regional climate record (Figure 4.3). Mean annual water year precipitation recorded within our study region was 229.4 ± 9.5 mm, or ~2% less than the long-term mean. *Within* sites, ANPP was significantly correlated with annual precipitation in both *unburned* and *burned* ecotone grassland, but not in plains grassland (Figure 4.4a; Table 4.1). ANPP in desert shrubland exhibited the strongest *within*-site temporal correlation with annual precipitation (Figure 4.4a; Table 4.1). Desert shrubland was also the only site across the transition zone where BNPP exhibited a weak, but significant correlation with annual precipitation (Figure 4.4b; Table 4.1). Across the landscape, ANPP was significantly, but weakly correlated with annual precipitation (Figure 4.4a); however, we found no equivalent correlation between BNPP and annual precipitation *among* sites (Figure 4.4b).

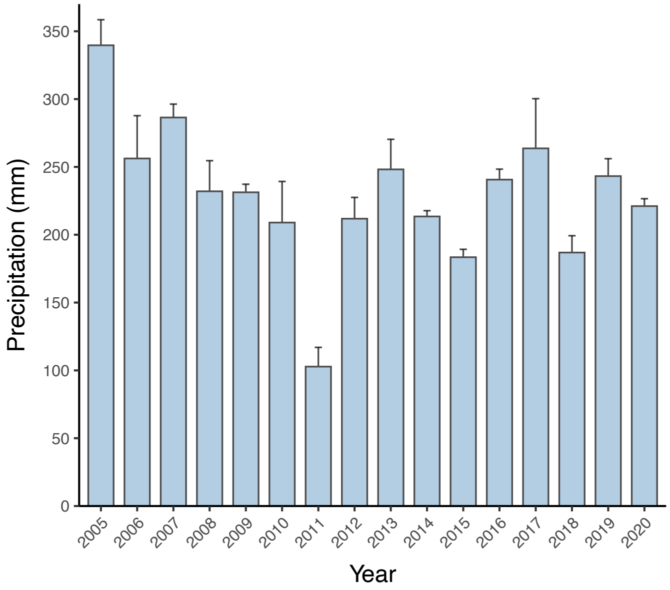

**Figure 4.3.** Mean annual precipitation (mm) per water year (October – September) recorded by both the Deep Well and Five Points meteorological stations during the sixteen-year study (2005-2020). Error bars indicate standard errors of the means.

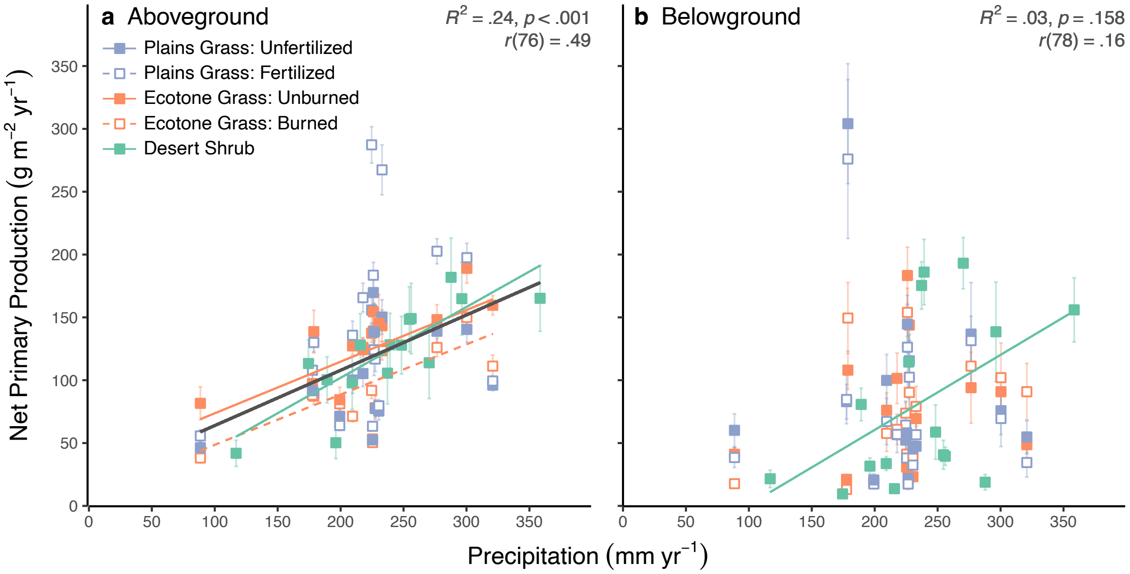

**Figure 4.4.** Relationships between (a) above- and (b) belowground net primary production (NPP; g $m^{-2}$ $yr^{-1}$) and water year precipitation (mm $yr^{-1}$) across a grassland-shrubland transition zone over the sixteen-year study (2005-2020), with plains grassland in blue, ecotone grassland in orange, and desert shrubland in green. Filled points represent ambient controls in all three sites, whereas hollow points represent *fertilized* (10 g N $m^{-2}$ $yr^{-1}$) and *burned* (in 2003) treatments in the plains and ecotone grasslands, respectively. Error bars indicate standard errors of the means. Solid linear regression lines reflect significant temporal correlations between NPP and precipitation *within* ambient controls, whereas dashed linear regression lines reflect significant temporal correlations *within* the *fertilized* and *burned* treatments (refer to Table 4.1 for corresponding *within* treatment statistics). $R^2$ values indicate the proportion of variance in NPP explained by precipitation *among* sites over time, with Pearson's $r$(df) and $p$-values indicating the strength and significance ($p \le .05$) of these relationships. Solid gray regression lines reflect significant correlations *among* sites over time.

### 4.3 How are above- and belowground NPP correlated *within* and *among* sites?

Overall, *within*-site temporal correlations between ANPP and BNPP were generally weak to non-existent except in *burned* ecotone grassland (Figure 4.5; Table 2). Across the landscape, we found ANPP to be significantly correlated *among* ambient controls in all three sites (i.e., *unfertilized* plains grassland, *unburned* ecotone grassland, and desert shrubland; Figure 6). In other words, ANPP generally exhibited similar trends *among* sites each year, with the strongest correlations occurring between the two grasslands as well as between ecotone grassland and desert shrubland. BNPP *among* ambient controls was not as well correlated at the landscape scale, with only the two grassland sites and the plains grassland and desert shrubland exhibiting similar significant trends (Figure 6).

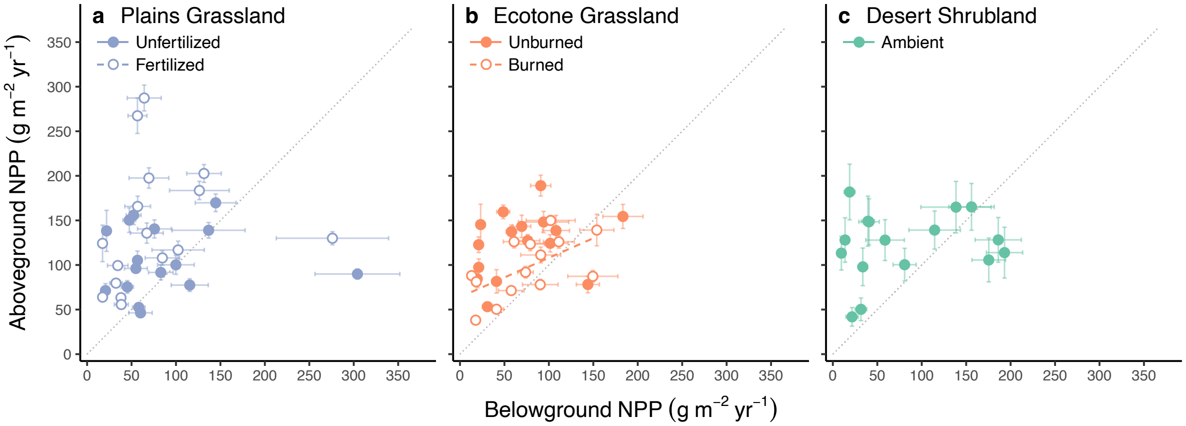

**Figure 4.5.** Relationships between above- and belowground net primary production (NPP; g m$^{-2}$ yr$^{-1}$) *within* sites across a grassland-shrubland transition zone over the sixteen-year study (2005-2020), with plains grassland in blue (a), ecotone grassland in orange (b), and desert shrubland in green (c). Filled points represent ambient controls in all three sites, whereas hollow points represent *fertilized* (10 g N m$^{-2}$ yr$^{-1}$) and *burned* (in 2003) treatments in the plains and ecotone grasslands, respectively. Error bars indicate standard errors of the means. Linear regression lines indicate significant ($p \leq .05$) *within*-site relationships (refer to Table 2 for corresponding summary statistics). Dotted gray lines indicate the 1:1 relationship between above- and belowground NPP *within* each site.

| **Site** | **Treatment** | ***r*** | ***$R^2$*** | ***p*-value** |
|---|---|---|---|---|
| *Plains Grassland* | *Unfertilized* | .05 | .00 | = .845 |
| | *Fertilized* | .20 | .04 | = .452 |
| *Ecotone Grassland* | *Unburned* | .31 | .10 | = .242 |
| | *Burned* | **.60** | **.36** | **≤ .05** |
| *Desert Shrubland* | *Ambient* | .21 | .04 | = .439 |

**Table 2.** Relationships between above- and belowground net primary production (NPP; g m$^{-2}$ yr$^{-1}$) over the sixteen-year study (2005-2020) *within* each site and treatment (also, see Figure 4.5). Pearson's *r* values indicate the strength and directionality of overall temporal correlations between above- and belowground NPP, and $R^2$ values indicate the proportion of variance in aboveground NPP explained by belowground NPP and vice versa. Degrees of freedom (df) for Pearson's *r* was 14, except for aboveground NPP in *burned* ecotone grassland, where df was 12. Significant relationships ($p \leq .05$) are in bold font.

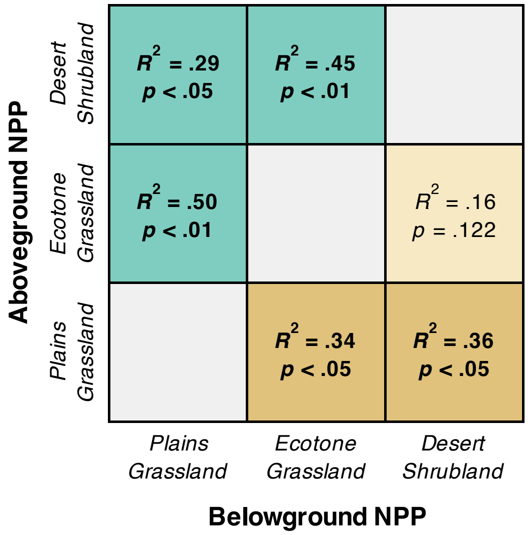

**Figure 6**. Relationships between above- (green) and belowground (brown) NPP *among* ambient controls in all three sites over the sixteen-year study (2005-2020). Pearson's *r*(df) and *p*-values indicate the strength and significance ($p \leq .05$) of these relationships, with significant relationships indicated by bold text and darker shading.

## 4.4 Discussion

We used sixteen years of empirical data to explore spatiotemporal dynamics of ANPP and BNPP across a grassland-shrubland transition zone in the northern Chihuahuan Desert. Characteristic of dryland ecosystems, NPP varied through time and space, with BNPP exhibiting consistently higher variation than ANPP. Chronic nitrogen enrichment tended to stimulate aboveground production, resulting in significantly greater ANPP in plains grassland during half of the years in our study, as well as the greatest overall ANPP across the landscape. In contrast, fire had strong negative impacts on ANPP in ecotone grassland, which took nine years to return to pre-fire levels of production following a one-time prescribed management burn. Although ANPP was significantly correlated with annual precipitation at the landscape scale, this relationship was less consistent within sites. BNPP was generally unaffected by any of the environmental change drivers we explored here, other than exhibiting a significant response to annual precipitation in desert shrubland. Moreover, we found the temporal relationship between ANPP and BNPP to be extremely weak overall.

The positive effects of nitrogen enrichment on ANPP were not surprising given that nitrogen is second to water as the most important limiting resource for ecological processes in dryland ecosystems (Austin et al., 2004; Yahdjian et al., 2011). Although previous studies have found Chihuahuan Desert grassland to be steadily encroaching northward into Great Plains grassland (Collins et al., 2020; Collins & Xia, 2015; Peters & Yao, 2012), others have shown nitrogen enrichment tends to favor plains grassland over desert grassland (Báez et al., 2007; Collins et al., 2010; Ladwig et al., 2012). Our results suggest that Great Plains grassland may respond favorably to increased rates of atmospheric nitrogen deposition in the future, potentially counteracting encroachment trends in this region. BNPP, on the other hand, was generally unaffected by nitrogen enrichment, extending earlier findings that nitrogen enrichment does not impact BNPP in this system (Ladwig et al., 2012). Our results also complement a few other short-term studies conducted in cold semi-arid grasslands of Inner Mongolia that found nitrogen enrichment had no impact on BNPP, even when water limitation was alleviated (Gao et al., 2011; Gong et al., 2015; Jiangzhou Li et al., 2011).

It has been hypothesized that as water availability becomes less limiting to dryland ecological processes, ecosystem sensitivity to precipitation decreases, and the limitation of other resources increases (Huxman, Smith, et al., 2004). However, plains grassland was the only site within our study area where ANPP was not significantly correlated with annual precipitation. Furthermore, we found no evidence to support the hypothesis that nitrogen limitation is alleviated only in years with above average precipitation (Ladwig et al., 2012). While outside the scope of this study, it is possible that the timing and magnitude of rain events may play an important role with respect to nitrogen limitation of NPP. Although rain events have become smaller and more frequent in this region over the past century, infrequent large rain events during the growing season significantly influence total precipitation amounts (Petrie et al., 2014), and have been found to significantly reduce plant available nitrogen that would otherwise be stimulated by small frequent events (Brown, Sala, et al., 2022).

A prescribed fire negatively impacted ANPP, but not BNPP, for nearly a decade in ecotone grassland where Chihuahuan Desert and Great Plains grasslands converge. Although fire is a common management practice in semi-arid grasslands, our results are consistent with earlier studies that found fire to have long-term detrimental impacts in Chihuahuan Desert grassland, which is an important source of forage grasses for wildlife in this region (Drewa & Havstad, 2001; R. J. Gosz & Gosz, 1996; Parmenter, 2008). Yet, whereas Chihuahuan Desert grassland is especially sensitive to fire, Great Plains grassland has been found to recover quickly (Collins et al., 2020; Ladwig et al., 2014; Parmenter, 2008). The susceptibility of this particular ecotone to fire has likely resulted in past fluctuations between grassland and shrubland states (Humphrey, 1974), influencing the carbon sequestration capacity of the dominant ecosystems in this region (Petrie, Collins, Swann, et al., 2015). While many have written about the broad scale implications of woody shrub encroachment (e.g., Archer et al., 2017; Barger et al., 2011; D'Odorico et al., 2012; Knapp et al., 2008), our study suggests that increased fire frequency, either from natural causes or as a management practice, could alternately shift this inherently dynamic region from Chihuahuan Desert grassland to Great Plains grassland. While fire has been found to reduce the establishment of young shrubs in this ecotone (Junran Li et al., 2022), our results together with previous work suggest prescribed fires are not an effective management strategy in natural semi-arid grasslands, particularly in the absence of grazing by domestic livestock (Z. Liu et al., 2022).

We found ANPP to be significantly correlated with annual precipitation in ecotone grassland, regardless of burn status, as well as in desert shrubland. Our results complement earlier findings that ANPP in both Chihuahuan Desert grassland and shrubland was positively correlated with annual precipitation (Muldavin et al., 2008). NPP in desert shrubland exhibited the strongest overall relationship with precipitation, which in the context of predicted increases in precipitation variability, has been shown to promote production in desert shrubland at the expense of desert grassland (Gherardi & Sala, 2015). Although a strong spatial relationship exists between mean annual ANPP and mean annual precipitation (Huxman, Smith, et al., 2004; Knapp & Smith, 2001; Sala et al., 1988), temporal relationships between ANPP and precipitation at local and regional scales are often much weaker and less predictable (Lauenroth & Sala, 1992; Maurer et al., 2020; Sala et al., 2012) as we also found in this study. A previous analysis found no correlation between ANPP and mean annual precipitation in our study area between 1999 and 2008 (Sala et al., 2012), which suggests the importance of long-term studies, especially in drylands where interannual variability in precipitation tends to be high. Surprisingly, BNPP did not exhibit a significant or consistent relationship with precipitation across this transition zone, despite limited evidence from other terrestrial ecosystems showing otherwise (Wilcox et al., 2015, 2017; Wu et al., 2011).

We found little evidence that BNPP was temporally correlated with ANPP within a site, consistent with earlier findings in this region (Burnett et al., 2012; Ladwig et al., 2012). Across the landscape, we found temporal variability in ANPP was generally higher in grasslands compared to shrubland, supporting earlier findings (Knapp & Smith, 2001). In contrast, temporal variation of BNPP was quite high in all sites, especially in desert shrubland, which exhibited some of the highest temporal variability in BNPP across the landscape. Although ANPP exhibited similar trends across the landscape, the spatial relationship between plains grassland and desert shrubland was weaker and somewhat less significant than relationships among the other sites. Given that plains grassland and desert shrubland were located furthest away from each other suggests there may be a distance limitation at which the spatial correlation of ANPP breaks down across this grassland-shrubland transition zone. However, while the strongest ANPP relationships occurred with sites closer to each other, this was not the case for BNPP, which was less temporally and spatially correlated overall.

Terrestrial ecosystems sequester nearly one-third of anthropogenic $CO_2$ emissions through NPP (Ahlström et al., 2015; Friedlingstein et al., 2022; Keenan & Williams, 2018). Given that dryland ecosystems are expected to comprise half of the terrestrial surface by the end of this century (Huang et al., 2016), improving understanding around the patterns and controls of NPP in these ecosystems is fundamentally important because of the measurable impact they have on the global carbon cycle. Our study uses the longest known dataset of empirical measurements of above- and belowground production in a dryland region to demonstrate that BNPP may be controlled by a different set of drivers than ANPP, and that the effects of environmental change may differentially affect dryland grasslands and shrublands. Consequently, estimates of carbon storage cannot be inferred from ANPP measurements. We found that BNPP exhibits greater temporal and spatial variation than ANPP, which likely contributes substantially to variation in the terrestrial carbon sink. This study underscores the need for additional long-term empirical measurements, particularly of BNPP, given that it represents the main source of soil organic matter for carbon storage and sequestration (Sokol & Bradford, 2019). Given that BNPP represents a significant proportion of total NPP in dryland ecosystems, changes in BNPP would undoubtedly result in profound effects on the terrestrial carbon sink.

## 4.5 Acknowledgments

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## 4.6 Data Availability Statement

All above- and belowground net primary production data presented in this study 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/6359b205829aa232f9479ac2e27eb503 (Brown & Collins, 2022a). Meteorological data used in this study are also publicly available from EDI at https://doi.org/10.6073/pasta/1cbc37ae4d40b3844b5e4be9f6f18073 (Moore, 2021).

## *Chapter 5*

# Conclusions

As noted in Chapter 1, the dryland ecosystems comprising the southwestern United States (US) are exceptionally vulnerable to climatic variability and change (Diffenbaugh et al., 2008). Historical evidence suggests that rain events have become smaller, but slightly more common in this region (Petrie, Collins, & Litvak, 2015); however, climate models consistently predict a future rainfall regime consisting of larger storms punctuated by longer dry intervals between rain events (Bradford et al., 2020; Donat et al., 2016; Moustakis et al., 2021). How ecological processes in dryland regions will respond to increased precipitation variability and other drivers of environmental change is uncertain. Some ecological theories have hypothesized that a shift in growing season precipitation to fewer, but larger rain events will enhance net primary production (NPP) and related processes in these sequentially water and nitrogen limited regions (Collins et al., 2008, 2014; Knapp, Beier, et al., 2008; Noy-Meir, 1973). Yet, field-based studies experimentally testing these predictions in the context of altered precipitation regimes and other drivers of environmental change across temporal scales are uncommon. In this dissertation, I addressed this knowledge gap by exploring the individual and combined effects of several environmental change drivers on NPP and related above- and belowground processes in the northern Chihuahuan Desert, central New Mexico, USA.

In Chapters 2 and 3, I used a long-term rainfall manipulation experiment in the Sevilleta National Wildlife Refuge (NWR) to explore the temporal dynamics of plant available nitrogen, aboveground NPP, and related above- and belowground processes in response to small frequent and large infrequent monsoon rainfall addition treatments. My findings, which contradict long-standing ecological theories regarding dryland ecosystem structure and functioning, highlight the ecological importance of small frequent growing season rain events in this black grama (*Bouteloua eriopoda*) dominated grassland. Furthermore, these results contribute to a growing body of evidence regarding the critical role that small rain events play in arid and semi-arid grasslands, not only with respect to soil microbial processes and nutrient availability (e.g., Fernandes et al., 2022; Yahdjian & Sala, 2010), but also plant physiological processes (e.g., Petrie et al., 2015; Sala & Lauenroth, 1982). A shift to a more extreme growing season precipitation regime characterized by fewer, but larger rain events is likely to decouple microbial and plant processes by inhibiting microbially driven biogeochemical processes and accelerating losses of plant available nitrogen that may consequently lower NPP in these regions.

In Chapter 3, I found that fall growing season aboveground NPP (ANPP) responded strongly to large infrequent monsoon rain events only when nitrogen limitation was alleviated by fertilization. While this result suggests a strong sequential limitation of water and nitrogen for overall ANPP in northern Chihuahuan Desert grasslands, post-fire recovery of the dominant grass, black grama, was significantly lower under nitrogen enrichment. In Chapter 4, annual ANPP in blue grama (*Bouteloua gracilis*) dominated Great Plains grassland was stimulated by nitrogen enrichment, but unlike in black grama dominated grassland, this response was not correlated with precipitation amount. While differential responses between these two grasslands may be due to differences in fertilization amount (i.e., 5 vs. 10 g N $m^2$ $yr^{-1}$) and the temporal scales explored (i.e., fall growing season ANPP and monsoon precipitation vs. peak annual ANPP and total annual precipitation), other studies in this region have found that blue grama responds more favorably to nitrogen enrichment than black grama (Báez et al., 2007; Collins et al., 2010; Ladwig et al., 2012). Blue grama also recovers much more rapidly after fire than black grama, which, consistent with Chapter 4 results, can take up to a decade to return to pre-fire levels of production (Collins et al., 2020; Ladwig et al., 2014; Parmenter, 2008). Previous studies in this region have found black grama is encroaching steadily northward into blue grama dominated grassland (Collins et al., 2020; Collins & Xia, 2015; Peters & Yao, 2012). Overall, my dissertation findings suggest that increased precipitation variability, nitrogen deposition, and/or fire frequency will negatively impact black grama, potentially reversing this trend.

Given the effectiveness of fire in combating the early stages of woody shrub encroachment (Junran Li et al., 2022), fire is a commonly used management tool to preserve pastoral economies in many dryland regions (Hanan et al., 2021). Yet, I found in Chapters 3 and 4 that fire negatively impacts ANPP in northern Chihuahuan Desert grasslands for up to a decade. These findings, which are consistent with earlier studies (Drewa & Havstad, 2001; R. J. Gosz & Gosz, 1996; Parmenter, 2008), contribute further evidence that prescribed fires are likely not an effective management strategy for preserving natural arid and semi-arid grasslands, particularly in the absence of grazing by domestic livestock (Z. Liu et al., 2022), as is the case in the Sevilleta NWR. Following recommendations made by others (e.g., Aslan et al., 2018; Jones et al., 2022), I encourage public land managers to consider an adaptive management approach with respect to wildfire mitigation and that they reduce the use of prescribed fires in arid and semi-arid grasslands, especially during periods of below average precipitation (Ladwig et al., 2014).

In Chapter 4, I found belowground NPP (BNPP) was not significantly affected by either chronic nitrogen enrichment or fire, which suggests BNPP may be controlled by a different set of drivers than ANPP. Furthermore, BNPP was not significantly correlated with mean annual precipitation across this northern Chihuahuan Desert grassland-shrubland transition zone, except in desert shrubland, dominated by creosote bush (*Larrea tridentata*). These findings contribute further evidence that dryland grasslands and shrublands may be differentially impacted by increased precipitation variability (Gherardi & Sala, 2015). Most notably, belowground NPP (BNPP) was not temporally correlated with ANPP at the site level over this sixteen-year study, which demonstrates belowground production cannot be inferred from aboveground production in dryland regions. Given that dryland regions contribute strongly to interannual variation in the terrestrial carbon sink (Ahlström et al., 2015; Poulter et al., 2014), combined with knowledge that BNPP is the primary contributor to the largest terrestrial carbon pool (Sokol & Bradford, 2019), these findings have important implications for the carbon sequestration capacity of dryland ecosystems under future environmental change.

Overall, my dissertation research contributes important advances to our understanding of dryland ecosystem structure and functioning. Although my research confirms that many ecological processes in these ecosystems are highly sensitive to changes in rainfall regimes both within and among growing seasons, many of these responses do not conform with established theory. Nitrogen availability did not pulse in response to individual rain events, as predicted by the pulse dynamics framework (Collins et al., 2008; Noy-Meir, 1973), and in contrast to the bucket model (Knapp et al., 2008), frequent small rain events increased ANPP as much as infrequent large events over the long term. Altogether, my findings emphasize the need for more long-term research to understand the drivers of aboveground, and especially, belowground processes in dryland ecosystems.

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