WHAT LIMITS DRYLAND ECOSYSTEMS? PATTERNS OF SOIL FERTILITY AND RESOURCE LIMITATION IN THE CHIHUAHUAN DESERT

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Dedication

To Analisa, for the love, friendship, and joy you bring into my life.

"*The history of every nation is eventually written in the way in which it cares for its soil*."

- Franklin D. Roosevelt

WHAT LIMITS DRYLAND ECOSYSTEMS? PATTERNS OF SOIL FERTILITY AND RESOURCE LIMITATION IN THE CHIHUAHUAN DESERT

by

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DISSERTATION

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Abstract

Human activities are substantially altering global resource cycles with widespread implications for biogeochemistry and ecosystem functioning globally. Drylands, regions where precipitation is outweighed by water losses, are especially sensitive to these large shifts in resource cycles due to their inherently low and variable resource availability. In these regions, resource availability and biological activity are often concentrated around plants – or fertile islands – and predominantly driven by pulses of water. However, our knowledge of the processes influencing biological productivity in drylands – patterns of soil fertility and resource limitation – remains lacking, and their unique biogeochemical and biological processes create difficulties in predicting dryland responses to global change. To improve our understanding of ecological function and biogeochemistry in drylands, I determine how patterns of soil fertility change across multiple spatial scales in the Chihuahuan Desert (Chapter 2), examine how soil nutrient pools change in response to changing resource availability (Chapter 3), explore how the plant community responses to resource addition treatments (Chapter 4), and investigate signatures of resource limitation in the microbial community and whether resource limitation constrains microbial function in this system (Chapter 5). This dissertation presents evidence of the inherent complexity of the biogeochemistry and ecology of these unique systems, demonstrating the urgent need to improve our understanding of the relationship between drylands and global biogeochemical cycles.

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BACKGROUND OF RESOURCE LIMITATION IN TERRESTRIAL SYSTEMS

The concept of nutrient limitation stems from the Law of the Minimum, formulated by Sprengel and popularized by Liebig (1840), which states that organismal growth is limited by the least abundant element relative to demands for growth. This definition, which was originally used for individual plants or species in agricultural settings is less directly applicable when applied directly to natural plant communities, because community responses are driven by multiple species and a range of environmental factors (Chapin et al. 1986). To detect nutrient limitation in natural systems, studies often employ experimental resource additions to detect nutrient limitation by measuring responses in biomass production, respiration, or internal nutrient concentrations (e.g. N:P ratios) (Koerselman and Meuleman 1996; Bracken et al. 2015; Chapin et al. 1986). However, recent studies have detected limitation in microbial communities by measuring investments into nutrient acquisition (Cui et al. 2023; 2021; Sinsabaugh et al. 2009). Community- and ecosystem-scale processes can significantly influence plant and microbial responses to nutrient addition treatments (Chapin et al. 1986; Cui et al. 2021), though microbial nutrient limitation remains complex and difficult to quantify or detect (Cui et al. 2023; Hobbie and Hobbie 2013).

An improved understanding of the implications of resource limitation is increasingly crucial as global resource cycles are dramatically shifting in response to anthropogenic activities (Penuelas et al. 2020; Vörösmarty and Sahagian 2000; Vitousek et al. 1997). Human activities have increased atmospheric CO_2 concentrations 10-100 times faster than pre-industrial rates (Falkowski et al. 2000), doubled reactive atmospheric N (Vitousek et al. 1997) – though recent evidence suggests terrestrial N supply is decreasing (Mason et al. 2022) – and increased P cycling by ~400% (Falkowski et al. 2000; Filippelli 2002), potentially altering resource limitation dynamics globally (Vitousek et al. 2010). These rapid changes to the cycling of key resources can impact systems in the Critical Zone, defined as Earth's outer layer where rock, soil, water, and air interact to support life. For example, shifts in precipitation regimes and nutrient availability can decrease the capacity of terrestrial systems to capture and store atmospheric carbon (Bailey et al. 2019; Kirkby et al. 2014; Tariq et al. 2024; Püspök et al. 2023), increase the variability of plant production (Bigio et al. 2025), or increase the production of greenhouse gases like nitric oxide (Homyak et al. 2016).

These same changes can also impact plant community composition by favoring more competitive species (Goldberg and Miller 1990; Tilman 1984; Harpole and Tilman 2007), which can result in woody plant encroachment (Archer et al. 2017; Van Auken 2009) or desertification (D'Odorico et al. 2013; Le Houérou 1996) in dryland regions, decrease species diversity (Harpole and Tilman 2007; Goldberg and Miller 1990), and diminish a system's capacity to provide ecosystem services (Egoh et al. 2018; Bengtsson et al. 2019). With large changes predicted to impact global resource cycles, it is becoming increasingly important to consider how the interactions between above- and belowground processes will shift. Soil moisture content often bridges processes across the Critical Zone by linking the above- and belowground (Cleverly et al. 2016), providing an opportunity to develop our understanding of how these processes interact to support life.

EFFECTS OF MULTIPLE RESOURCE LIMITATION IN TERRESTRIAL ECOSYSTEMS

Multiple resources (e.g. soil nutrients, water) can constrain biological activity (Gleeson and Tilman 1992; Eskelinen and Harrison 2015), and spatial and temporal variability in the availability of each can give rise to complex co-limitation or multiple resource limitation (Gleeson and Tilman 1992; Chapin et al. 1987; Bird et al. 2002). Serial limitation can occur when a second resource becomes limiting after an initial limitation is alleviated; however, this form of synergistic co-limitation differs from other interactive forms of limitation (Harpole et al. 2011). Multiple limiting factors can constrain activity at once either through interactive relationships between resources (Long et al. 2016; Cole and Heil 1981) or by limiting different species in the community (Harpole et al. 2011). Consequently, studies of multiple resource limitation should consider the interactive relationships that may exist between resources, as the contrast between serial limitation and multiple resource limitation can thus increase the unpredictability of community responses to resource limitation (Harpole et al. 2011; Saito et al. 2008).

Multiple resource limitation is globally widespread in plants (Du et al. 2020; Elser et al. 2007; Yahdjian et al. 2011) and microbes (Cui et al. 2021; 2025). Interactions between limiting resources can produce complex biological responses with compounding implications for the local ecosystem and global biogeochemical cycling. Resource limitation alters the cycling of key soil resources (carbon (C), nitrogen (N), and phosphorus (P)) by restricting biological activity (Elser et al. 2007; Hobbie and Hobbie 2013), reducing the decomposition of organic matter (Anjum and Khan 2021; Zhao et al. 2025), or altering organisms' capacity to acquire or use soil resources (Sinsabaugh and Moorhead 1994; Sinsabaugh and Follstad Shah 2012; Lajtha and Whitford 1989; Mooshammer et al. 2014) Thus, determining where, when, and how shifts in resource availability may interact to influence or limit ecosystem function is vital to the prediction and mitigation of the effects of anthropogenic shifts in resource availability on life-supporting processes in terrestrial ecosystems.

DRYLANDS ARE CHARACTERIZED BY RESOURCE SCARCITY

Drylands are water limited ecosystems where precipitation is typically less than potential evapotranspiration. Drylands are defined as regions with an aridity index < 0.65 (Hanan et al.

2021), where the aridity index is the ratio between precipitation (P) and potential evapotranspiration (PET), P/PET. Such regions have been estimated to cover around 40% of the earth's terrestrial surface and support over a third of the global population (Millennium Ecosystem Assessment 2005). Due to rising temperatures and increasing drought, drylands are expected to expand by about 10% by the end of the century (Feng and Fu 2013), raising the risk of land degradation and desertification while exposing a greater proportion of the human population to water scarcity, food insecurity, and adverse environmental conditions (D'Odorico et al. 2013; Millennium Ecosystem Assessment 2005b). Additionally, drylands play a dominant role in the global carbon cycle (Ahlström et al. 2015; Poulter et al. 2014), so climate-driven disturbances to these systems can decrease drylands' carbon sequestration capabilities and possibly lead to carbon losses and further land degradation (Hanan et al. 2021; Huang et al. 2016).

Drylands are characterized by extreme resource scarcity: in addition to low water availability, soil moisture, organic matter, and nutrients are present at low levels (Osborne, Bestelmeyer, et al. 2022; Jordaan et al. 2022a; Fransen et al. 2001). Biological activity and biogeochemical cycling are largely driven by water availability, and this produces complex and variable nutrient dynamics that are unique to drylands (Austin et al. 2004; Austin 2011). However, work on resource limitation in drylands has focused primarily on the role of water (Austin 2011), overlooking the potential of other mechanisms like nutrient limitation to influence soil processes and primary production. For example, soil organic carbon (SOC), N, and P pools are exceptionally small in dryland soils (Lal 2019; Serrano-Ortiz et al. 2012), resulting in soils with minimal nutrient availability, presenting a high possibility of nutrient limitation. While SOC formation has been shown to be water limited (Serrano-Ortiz et al. 2012), there is also evidence that the processes that form SOC (e.g. decomposition) are nutrient limited (e.g. Anjum and Khan 2021; Ramirez et al.

2012), necessitating an assessment of how multiple resource limitation (i.e. water and nutrient availability) might limit microbial function and SOC pools.

With such variable and complex patterns of resource availability, drylands are inherently variable across both space and time (Austin et al. 2004). Plant cover in drylands is low and typically organized into a bimodal pattern of vegetated and un-vegetated patches (Aguiar and Sala 1999). Vegetated patches are referred to as fertile islands or resource islands, as plants will enhance soil fertility under their canopies altering physical soil characteristics, increasing soil moisture and nutrient availability, or providing shade and shelter (Sala and Aguiar 1996; Schlesinger et al. 1990). With favorable soil conditions concentrated around large plants (Fitzpatrick et al. 2024), a large contrast exists between soils beneath plants and soils in the bare interspace. While the patchy vegetation pattern enhances primary productivity in these resource scarce environments, it may also drive the transition from grasslands to shrublands associated with desertification (Peters and Gibbens 2006; Schlesinger et al. 1990; Van Auken 2009). Similar to the patterns of spatial variability, the temporal variability in biological and biogeochemical activity are generally driven by pulses of water availability (Noy-Meir 1973; Collins et al. 2008). Pulses of soil moisture produce rapid biological responses including plant and microbial nutrient uptake, respiration and growth, and biogeochemical processes like denitrification or decomposition (Collins et al. 2008). Temporal variability in drylands is thus largely driven by the timing of rainfall; drylands often experience a rainy monsoon season with limited rainfall in the rest of the year, typically concentrating biological activity in the wet months (Maestre et al. 2016; Whitford and Duval 2019).

Despite widespread evidence of the influential role of water in biogeochemical cycling and biological activity in drylands, many questions remain about the relationship between water and soil nutrients and how their interactions might influence larger patterns of nutrient availability, microbial activity, and plant growth (Austin et al. 2004; Eldridge et al. 2024). Drylands are expected to experience increased warming and drought faster than global averages, highlighting their sensitivity to climate change (Scholes 2020). Rainfall has steadily declined in the last century while variability in precipitation has been growing (Rudgers et al. 2018), significantly impacting soil biogeochemistry, carbon storing capacity, and biological activity (Tariq et al. 2024; Bondaruk et al. 2025; Delgado-Baquerizo et al. 2013). We must improve our understanding of how multiple resources (e.g. water and nutrients) interact to drive dryland ecosystem function in order to better predict dryland responses to growing global change pressures.

DISSERTATION: PATTERNS OF SOIL FERTILITY AND RESOURCE LIMITATION IN DRYLAND ECOSYSTEMS

This dissertation aims to develop a thorough understanding of how soil fertility, multiple resource limitation, and interactions between biogeochemical cycles drive fundamental ecosystem function in the Chihuahuan Desert. All work was conducted within the Jornada Basin Long Term Ecological Research site in southern NM, USA. The Jornada Experimental Range (JER) and adjacent Chihuahuan Desert Research Center (CDRRC) lie within the Jornada del Muerto Basin, located at the northern extent of the Chihuahuan Desert (Figure 1.1). The Jornada Basin contains high levels of geomorphic and biotic diversity, enabling a comprehensive exploration of the relationship between geological and biological processes that drive ecosystem function in dryland systems (Monger et al. 2009; Peters and Gibbens 2006; Wondzell et al. 1996). Over the past century, the Jornada has undergone extensive vegetation changes from native grasslands to shrublands (Peters and Gibbens 2006) as a result of combined pressures from livestock grazing, increased drought (and variability of rainfall, see Rudgers et al. (2018)), and rising temperatures

(Archer et al. 2017; Bestelmeyer et al. 2015; Bock and Bock 1993; Yanoff and Muldavin 2008). A result of this transition to a shrub-dominated landscape, much of the vegetation in the Jornada follows a bimodal pattern with plant growth and biological activity concentrated around large shrubs, referred to as fertile islands (Schlesinger et al. 1990; Sala and Aguiar 1996; Fitzpatrick et al. 2024). I examine this bimodal landscape in Chapter 2, an observational study examining how the fertile island effect changes across multiple spatial scales to influence soil fertility. Then, by studying the biotic and biogeochemical responses to water and nutrient addition, chapters 3 through 5 address questions about the factors influencing nutrient availability, microbial activity, and plant growth in the Chihuahuan Desert.

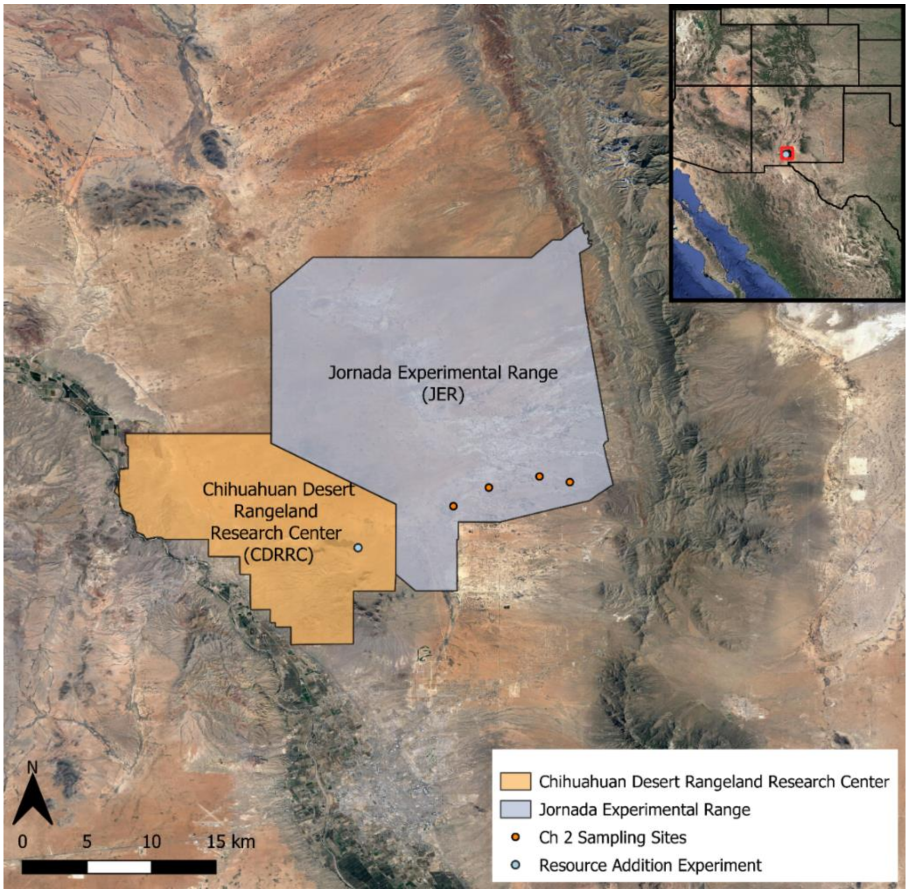

Figure 1.1. Map of study location. Jornada experimental range (JER) and Chihuahuan Desert Rangeland Research Center, Las Cruces, NM, USA, Northern Chihuahuan Desert.

CHAPTER SUMMARIES

Chapter 2 explores how patterns of soil fertility change across multiple spatial scales in the Chihuahuan Desert. In 2021, we collected soil samples to study the effects of physical soil characteristics on patterns of soil fertility across multiple spatial scales. Our goal was to compare how the magnitude of the fertile island effect varies across soil depths, local patch types (e.g. biocrust, grass, shrub), and geomorphic landforms to determine how physical soil characteristics and biological activity influence biogeochemical factors and biotic processes in drylands.

Chapters 3, 4, and 5 explore how a native grassland in the Chihuahuan Desert responds to additions of water, nitrogen, and phosphorus to answer questions about the influence of shifting resource availability on biogeochemical cycling and biological activity in arid regions. These chapters present results from a nitrogen and phosphorus fertilization and water addition experiment established in 2022 in a grassland dominated by black grama (*Bouteloua eriopoda*), a native perennial grass.

Chapter 3 tests the relationships between N, P, and water in the Chihuahuan Desert by increasing their availability independently and in combination with the objective of identifying individual and synergistic effects on soil nutrient pools. We asked which nutrient pools would be most affected by resource addition treatments and whether concurrent water additions would alter the effects of nutrient addition on biogeochemical responses to nutrient addition.

Chapter 4 investigates plant community responses to the addition of nutrients and water. We asked: 1) how plants respond to separate and combined additions of water, N, and P and whether different plant functional groups (e.g. native grasses, forbs, invasive grasses) respond differently to these treatments; and 2) whether treatment effects differ between years with typical climate conditions and years which are hotter and drier.

Chapter 5 discusses microbial responses to N, P, and water availability in seasons with and without plant activity. We asked: 1) how microbial stoichiometry shifts in response to resource addition; 2) whether shifts in microbial stoichiometry would coincide with shifts in nutrient demand or acquisition effort in the form of extracellular enzyme activity; and 3) if changes in plant-microbe interactions associated with seasonal changes would influence microbial responses (e.g. internal nutrient content and enzyme production) to resource addition.

Chapter 6 summarizes our findings and conclusions, synthesizing our research to suggest future research directions to investigate how resource limitation and changing soil fertility will influence drylands' responses to intensifying global change pressures.

Chapter 2: Multi-scale influences on the fertile island effect: Landscape-scale and patch-level processes drive patterns of soil fertility in the Chihuahuan Desert

ABSTRACT

Islands of fertility, patches of locally enhanced soil conditions, play a key role in increasing productivity in dryland regions. The fertile island effect (FIE) influences a range of variables including nutrient availability, soil moisture, and microbial activity. While most examinations of the FIE focus on islands created by perennial plants at local scales, the effect may vary across spatial scales and under cover types including shrubs, grasses, and biological soil crusts (biocrusts). This study explored differences in the FIE between soil depths across landforms and patch types for biogeochemical factors (nutrient availability) and biotic properties (microbial community structure, extracellular enzymatic activity). The FIE differed across landforms and soil depths, suggesting that soil geomorphology may play a major role in predicting soil fertility. Additionally, the FIE of enzymatic activity and available nutrients varied by patch type consistently across landforms, suggesting patch-scale processes influencing nutrient availability and acquisition are independent of landscape-scale differences. We show that biocrusts can have an FIE similar to that of shrubs and grasses, an underexplored control of variability and productivity in drylands. These findings necessitate further work to improve our understanding of how ecosystem processes vary across scales to influence patterns of productivity and soil fertility.

INTRODUCTION

Islands of fertility are an inextricable characteristic of drylands and a key driver of productivity in arid and semi-arid ecosystems (Aguiar and Sala 1999; Noy-Meir 1973; Sala and Aguiar 1996; Schlesinger et al. 1990). Fertile islands form through the concentration of resources (e.g. nutrients and water) below plant canopies, a result of biotic and abiotic processes that occur beneath plants, including the accumulation of nutrient-rich dust and plant litter, the modification of soil water holding capacity, and biological nitrogen fixation by symbiotic microbes associated with shrubs (Ridolfi et al. 2008; Sala and Aguiar 1996; Schlesinger et al. 1990). The concentration of resources creates a biological feedback where improved soil conditions promote growth in vegetated patches, further improving soil fertility compared to bare areas between plants (Charley and West 1975; Schlesinger et al. 1990). The formation of fertile islands and the biological feedbacks they create are well understood (e.g. Eldridge et al. 2024; Garner and Steinberger 1989; Li et al. 2017; Okin et al. 2015; Sala and Aguiar 1996); however, past work has mainly focused on fertile islands at the local plant scale despite evidence that soil fertility, and by extension the fertile island effect (FIE), may vary across multiple scales (Ding and Eldridge 2021; Duniway et al. 2022; Osborne, Roybal, et al. 2022).

The development of fertile islands and thus the magnitude of the FIE are mainly influenced at three spatial scales: (1) landscape-level (e.g. climatic, topographic, and edaphic properties), or at the local scales of (2) patch-level (e.g. dominant cover type within a patch), and (3) micro-site level (e.g. soil depth, areas with different microbial community composition) (Ding and Eldridge 2021; Ochoa-Hueso et al. 2018). At the landscape-scale, physical soil properties (e.g.. texture, calcite abundance) and other landscape factors (e.g., slope, elevation, runoff rates, dust or sediment accumulation) vary across landforms (Monger and Bestelmeyer 2006), which can considerably influence ecosystem properties that contribute to the FIE such as nutrient availability, soil moisture content, and vegetation cover and distribution (Buxbaum and Vanderbilt 2007; Lajtha and Schlesinger 1988a; McAuliffe 1994; Parker 1995; Rachal et al. 2012). At the local scale, patch-level (patch type) and microsite-level (soil depth) differences can also affect properties that influence the FIE including heterogeneity of soil nutrients, plant cover, and soil microbial community structure. Although past studies have examined the relationship between the FIE and variables including elevation (Thompson et al. 2005), aridity and patch type (Ding and Eldridge 2021), soil depth (Ma et al. 2024), and patch size (Fitzpatrick et al. 2024), it remains unclear how geomorphic context may influence the FIE and whether these large-scale changes in soil characteristics could influence the FIE at the patch-scale.

Additionally, the FIE is often considered only in the context of plants, as fertile islands are typically defined as islands formed by perennial plants (i.e. shrubs and grasses, see Ding and Eldridge 2021; Ma et al. 2024). However, biocrusts – soil surface aggregates containing communities of cyanobacteria, algae, lichens, mosses, and fungi (Pietrasiak et al. 2013; Weber et al. 2022) – can also enhance soil fertility between plant patches (Bowker et al. 2018; Maestre et l. 2024; Sepehr et al. 2022). Despite their importance to a range of ecosystem processes (e.g. Belnap et al. 2016), studies exploring the FIE often only consider biocrusts in relation to plants and not in isolation. Because they play a key role in many ecological processes (e.g nutrient and moisture content), biocrusts may act as fertile islands (or "mantles," as in Garcia-Pichel et al. 2003; Reed et al. 2019) regardless of plant presence to enhance dryland productivity. In biocrusts, the FIE may change at different scale than for plants, as microbial biomass is typically concentrated in the top few centimeters of soil, and the community composition of biocrusts can vary at the scale of centimeters and even millimeters (Garcia-Pichel et al. 2003; Steven et al. 2013).

This study aimed to compare how the magnitude of the FIE at two soil depths varies across spatial scales (landform and patch type) for both biogeochemical factors (e.g. nutrient availability) and biotic processes (e.g. microbial community structure, extracellular enzymatic activity). We hypothesized that, while the size of the FIE would vary across patch types and soil depth, landform-driven differences would be the largest due to significant edaphic differences between landforms. We also hypothesized that the effect size of most variables would be positive for all patch types, though shrubs would have the largest effect sizes, as plant canopy size generally exhibits a positive relationship with soil resource availability (Fitzpatrick et al. 2024).

METHODS

Study Site

This study was conducted in the Jornada Experimental Range (JER) in southern New Mexico, USA, at the northern extent of the Chihuahuan Desert. Mean annual precipitation in the area is 23 cm, with about 52% of precipitation occurring during the summer monsoon (July 1 - September 30) (Greenland et al. 1997). Air temperatures range from a monthly average maximum of 36ºC in June to an average minimum of 13ºC in January (Greenland et al. 1997). The JER was historically dominated by black grama (*Bouteloua eriopoda*) grassland but has been transitioning to shrubland in response to factors like grazing and extreme drought in the last 50-150 years (Peters and Gibbens 2006).The JER has twenty-two unique soil types, each having high inorganic carbon (calcium carbonate) content and little to no organic matter, distributed across twenty-four distinct geomorphic units (Gile et al. 1981; Monger 2006).

Sites were selected on four distinct geomorphic units (landforms hereafter) along the basin’s piedmont slope, based on the classification described in Monger (2006): (1) Alluvial Flat - the lowest topographic landform on the slope, characterized by alluvial sediments brought in by sheet floods from upslope; (2) Erosional Scarplet - a lower portion of piedmont slope with arcuate ridges of quartzose sand deposits derived from the basin floor. Our study focused on the sandy ridges; (3) Fan Piedmont - the dominant landform on the piedmont slope, largely comprising coalescent alluvial deposits; (4) Alluvial Fan Remnant – the topographically highest landform on the piedmont slope, often containing petrocalcic horizons (see Figure 2.1a for spatial distribution of sampling sites and Table 2.1 for physical soil properties of each landform). Within each landform, three representative patches of four patch types were selected: (1) shrub – below a tarbush (*Flourensia cernua*) plant canopy; (2) grass – beneath an individual of the dominant grass at each site, tobosa grass (*Pleuraphis mutica*) or bush muhly (*Muhlenbergia porteri*); (3) biocrust – soil with a distinct biocrust layer in the plant interspace; and (4) interspace – bare, uncrusted soil (Figure 1b).

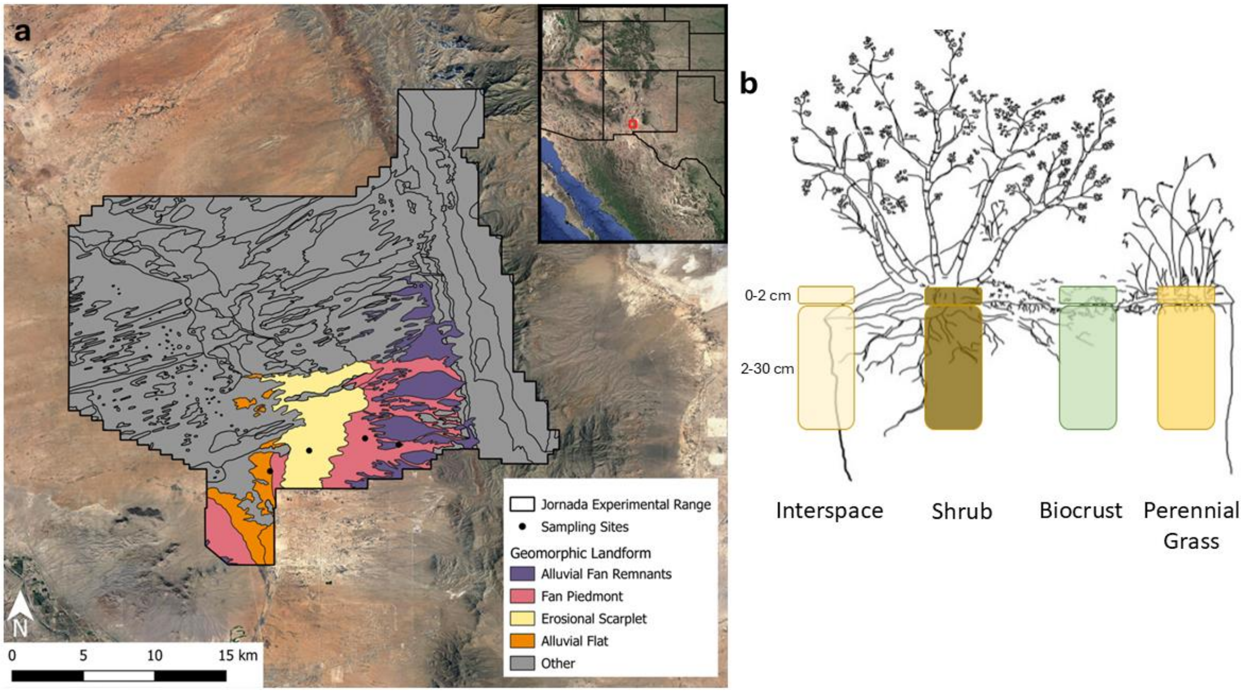

Figure 2.1. a) Map of the study's sampling sites (shown as black points) along the piedmont slope with the four sampled landforms colored. b) On each landform, three replicates of each of the four patch types were selected, and soil samples were collected at two depths (0-2 cm and 2-30 cm). Figure 2.1b created by Megan S. Stovall.

Table 2.1: Mean values of physical soil qualities at each sampling scale. A multiway ANOVA was used to detect significant differences in each variable across landforms, patch types, and soil depths. See Table S2.1 for significant effects.

Landform	Patch Type	Soil Depth (cm)	Gravel (%)	Sand (%)	Silt (%)	Clay (%)	Percent Saturation	Soil pH	EC (dS/m)	% Calcite
Alluvial Flat	Shrub	0-2	0.09	42	55	3	51	7.23	2.81	2.16
		2-30	0	21	70	9	29	7.47	0.87	1.97
	Grass	0-2	0.01	46	51	3	49	7.20	1.20	1.79
		2-30	0	20	71	8	29	7.37	0.64	1.65
	Biocrust	0-2	0	20	71	9	32	7.33	0.73	1.6
		2-30	0	20	72	8	28	7.43	0.51	2.05
	Interspace	0-2	0	20	74	6	34	7.40	0.67	1.97
		2-30	0	19	72	8	30	7.30	1.42	1.94
Erosional Scarplet	Shrub	0-2	0.60	54	44	2	24	7.47	0.97	0.64
		2-30	1.29	29	64	8	22	7.47	0.84	1.84
	Grass	0-2	0.05	59	39	1	33	7.20	0.93	1.23
		2-30	0.36	34	58	8	22	7.34	0.62	1.63
	Biocrust	0-2	0.34	29	65	6	22	7.40	0.67	1.42
		2-30	4.32	18	72	9	25	7.40	0.43	2.94
	Interspace	0-2	0.01	87	13	0	17	7.60	0.47	0.35
		2-30	0.41	30	62	9	20	7.50	0.45	1.54
Fan Piedmont	Shrub	0-2	3.27	57	41	2	24	7.47	0.86	1.77
		2-30	11.96	28	66	6	29	7.47	0.65	3.32
	Grass	0-2	0.03	64	35	1	35	7.20	1.27	1.40
		2-30	11.27	45	52	3	28	7.33	0.99	2.09
	Biocrust	0-2	1.03	42	55	3	26	7.43	0.68	2.13
		2-30	20.49	37	58	5	27	7.50	0.82	3.20
	Interspace	0-2	19.44	40	54	5	21	7.57	0.46	1.83
		2-30	6	29	65	6	29	7.53	0.50	4.03
Alluvial Fan Remnant	Shrub	0-2	7.16	51	46	2	23	7.70	0.75	4.21
		2-30	15.34	38	57	5	26	7.73	0.74	5.21
	Grass	0-2	2.55	64	34	1	27	7.43	1.05	2.72
		2-30	4.78	52	44	3	26	7.70	0.47	3.44
	Biocrust	0-2	11.70	55	43	1	25	7.40	0.63	2.13
		2-30	66.64	49	48	3	23	7.57	0.54	4.19
	Interspace	0-2	37.98	45	49	6	18	7.60	0.48	3.25
		2-30	19.37	34	60	6	25	7.67	0.37	4.12

Soil Sampling

Samples were collected in June 2021 using sterile soil sampling techniques. At each patch within a site, we used a 6 cm diameter corer to collect five soil cores to a depth of 2 cm within a 25 cm2 area. These surface cores were combined into one composite sample representing each patch at each site. This sampling depth was chosen to reflect the typical thickness of topsoil including biological soil crusts in this system. Subsurface (2-30 cm) soil samples (representing a general Bw horizon) were collected from soil pits excavated at the same locations as surface samples at the edge of the plant canopy. Soil pits were 100 cm by 50 cm wide for shrubs and 50 cm by 50 cm for grasses. For biocrust and interspace patches, pits were 25 cm by 25 cm. Pits extended to a depth of 30 cm or the top of the caliche, whichever was shallower. Pits reached caliche at two interspace patches on the Alluvial Fan Remnant. Subsurface soils were collected from the soil profile as a composite sample from a depth of 2 cm to 30 cm, focusing consistent sampling within a 25 cm wide area. Soil samples were transported in a cooler to a 4 ºC cool room for storage until processing.

Laboratory Analyses

Physical Soil Analysis

The fine earth fraction (< 2 mm) was obtained by removing litter and gravel and passing soil aggregates through a 2 mm sieve. After sieving, gravel was weighed and compared against total sample weight to determine gravel content. The fine earth fraction was homogenized and split using sterile techniques in a laminar flow hood for soil microbial, chemical, physical and nutrient analyses.

We determined soil pH and electric conductivity (EC) using the saturated paste method using 150-200 g of soil depending on texture via an Oakton Cole-Palmer pH/CON 510 Benchtop Meter (Vernon Hills, IL, USA) (U.S. Salinity Laboratory Staff, 1954). Soil texture was assessed using a Malvern Mastersizer 2000 laser diffractometer (Malvern Instruments Ltd., Worcestershire, UK). Soil particle size distribution was calculated as the percentage of three sizes: sand (2.0 – 0.063 mm), silt (0.063 – 0.002 mm), and clay (< 2 mm), with gravel > 2 mm. Total soil carbon was determined using a LECO SC632 Sulfur/Carbon Determinator (LECO Corporation, MI, USA). Soil inorganic carbon content was determined using a pressure calcimeter (Sherrod et al. 2002; Sparks 2009) – soil was acidified in a sealed bottle and the resultant CO_2 was quantified based on the pressure change. Organic carbon content was determined as the difference between total and inorganic soil carbon.

Microbial Community Analysis

A 20 g subsample was sent to Ward Laboratories, Inc. (Kearney, NE, USA) for microbial biomass and composition determination by the Phospholipid Fatty Acid (PLFA) method as described in Quideau et al. (2016) within 2 weeks of sample collection (Findlay 2004). The Shannon Diversity Index, an index of functional group diversity of the microbial community, was calculated using the "vegan" package in RStudio Version 12.1.402 (Oksanen et al. 2022).

Extracellular Enzymatic Potential Activity

Potential activity of ten extracellular enzymes (Table 2.2) was measured using methods modified from Saiya-Cork et al. (2002) and McLaren et al. (2017). One gram of soil was blended with modified universal buffer (pH = 7.75), and slurries pipetted onto 96-well microplates along with fluorescing, 4-methylumbelliferone (MUB) tagged substrates. Assays were incubated at 20 °C for 3.5 h with half-hourly measurements, ensuring activity was measured in the linear range of the reaction. Sample fluorescence (i.e. cleaved substrate) was read at 360 nm excitation, 460 nm emission (BioTEK Synergy HT microplate reader; BioTek Instruments Inc., Winooski, VT, USA).

Soil Nutrient Analysis

Available nitrate (NO_3^-) and ammonium (NH_4^+) were determined by extracting 5 g of soil with 25 mL of 0.5 M potassium sulfate and shaking for 2 hours before filtering through glass filter paper. Extracts were analyzed using colorimetric microplate assays with a vanadium (III) chloride assay for nitrate (Doane and Horwáth 2003) and a Berthelot Reaction assay for ammonium (Rhine et al. 1998). Available phosphate (PO_4^{3-}) was extracted using 30 mL of 0.5 M sodium bicarbonate (pH=8.5) added to 5 g of soil and shaken for 16 hours before filtering (Olsen 1954). Biologically based phosphorus (BBP) pools were measured using the method outlined by DeLuca et al. (2015). Briefly, this method uses four extractants to emulate strategies used by plants or microbes to access P: 0.01 M calcium chloride - P available in soil pore water; 0.01 M citric acid - P sorbed to clay or weakly bound to the soil matrix made accessible through organic acids released by plant roots and microbes; 1 M hydrochloric acid - P strongly bound to mineral surfaces and locked in mineral lattice (e.g. pedogenic carbonate) which is less biologically accessible, and 0.2 EU/mL phosphatase - labile organic P available through enzyme hydrolysis. Extractions were conducted in parallel by shaking 0.5 g of each sample in 10 mL of each extractant for 3 hours before centrifuging at 2500 rpm for 2 minutes and filtering. Phosphate in extracts was analyzed using colorimetric microplate assays (BioTEK Synergy HT microplate reader; BioTek Instruments Inc., Winooski, VT, USA) with a malachite green assay (D'Angelo et al. 2001).

Numerical and Statistical Analyses

The fertile island effect (FIE) size was calculated using the Relative Interaction Index (RII) (Equation 2.1; Armas et al. 2004) to represent the magnitude of the difference between a fertile island patch and bare interspace soil between plants as described in Ding and Eldridge (2021) and Ochoa-Hueso et al. (2018):

$$\mathrm{RII} = (X_p - X_i)/(X_p + X_i) \qquad (2.1)$$

where X_p is the value of the biotic (e.g. microbial biomass) or abiotic (e.g. available nutrients) variables for the patch type of interest and X_i is the value of the same attribute in the interspace soils from the same site and soil depth. RII ranged from -1 to 1, where positive values showed increased soil fertility compared to interspace soils, and negative values reflected a decrease in the variable relative to the interspace. We calculated the RII for each cover type and soil depth combination, considering the RII to be significantly positive or negative when the mean plus or minus one standard error (SE) did not intersect zero.

We aggregated closely related variables based on the biogeochemical processes to which each variable was most closely related (Table 2.2) and calculated the mean RII of the selected variables for each sample. The FIE of each aggregated group was analyzed using a multi-factor ANOVA with the main factors of landform, patch type, and soil depth. In the presence of multi-factor interactions, aggregated variables were separated by factor and analyzed using a one-way

ANOVA followed by a Tukey's HSD post-hoc test. Plots were made using the "ggplot2" package in R Version 12.1.402 (Posit team, 2024; Wickam, 2016). Assumptions of normality were tested using the Shapiro-Wilk Test. When needed, variables were transformed to meet the assumptions; figures present untransformed data.

Table 2.2: Aggregated variables and abbreviations. When possible, variables were aggregated based on most closely related biogeochemical or biological processes. Microbial biomass, microbial diversity, occluded P, and organic matter were not closely related to any other variables and were thus separated into distinct categories.

Group	Variables Included	Abbreviation
Carbon Acquiring Enzymes	A-1,4-glucosidase β-1,4-glucosidase β-1,4-xylosidase β-D-1,4-cellobiosidase	C-acq
Nitrogen Acquiring Enzymes	β-1,4-N-acetyl-glucosaminidase Leucine amino peptidase	N-acq
Phosphorus Acquiring Enzymes	Phosphodiesterase Acid Phosphatase	P-acq
Oxidative Enzymes	Phenol oxidase Peroxidase	Oxi
Microbial Biomass	Total Microbial Biomass	Total MB
Microbial Diversity	Microbial Shannon Diversity Index	Shannon Div
Readily Available Nutrients	Olsen-P K_2SO_4 extractable NO_3^-, NH_4^+, and PO_4^{3-}	Avail. Nutrients
Nutrients Accessible with Biological Effort	Citric acid extractable phosphate Enzyme extractable phosphate	Biol. Effort
Occluded P	HCl extractable PO_4^{3-}	Occl. P
Organic Matter	Organic Carbon	Org. C

RESULTS

Physical and chemical soil characteristics

Soil particle size varied across all spatial scales (landform, patch type, and soil depth; Table 2.1). For most variables related to particle size, there was a significant interaction between all three spatial scales (Table S2.1). Generally, gravel and sand content were lowest and silt and clay highest at the basin floor (Alluvial Flat); these increased or decreased respectively up the piedmont slope. Gravel content was marginally higher in the unvegetated soils while soils beneath grasses and shrubs had higher sand content and lower silt and clay content than the other patch types for three out of four landforms. Surface soils had higher gravel, silt, and clay but lower sand content than subsurface soils.

Differences in soil EC varied at all spatial scales, with the multi-way ANOVAs revealing a significant three-way interaction between landforms, patch types, and soil depths (Tables 2.1, S2.1). EC in surface soils was generally higher than in subsurface soils beneath shrubs and grasses but not in biocrust and interspace patches. In surface soils, EC was significantly higher below all cover types compared to interspaces. The magnitude of these differences largely depended on landform. In subsurface soils, EC below shrubs, grasses, and biocrusts was higher than interspace soils in upland landforms, and this difference decreased downslope. In the Alluvial Flat, the EC in subsurface soils in all vegetated patches was lower than in interspace soils. Soil pH ranged from 7.20 to 7.47. pH was elevated at the top of the piedmont slope (Alluvial Fan Remnant) compared to the other landforms. pH was similar across patch types and soil depths.

Landscape-scale variations in the fertile island effect

There was a significant landform effect or an interaction between landform and another factor for the FIE of all aggregated variables except organic carbon (Figures 2.2 and 2.3, Tables S2.2 and S2.3). Landform effects interacted with soil depth for microbial diversity, N-acquiring enzymes, oxidative enzymes, available nutrients, unavailable nutrients, and nutrients requiring biological effort.

The FIE of total microbial biomass was smaller at the bottom of the piedmont slope (Alluvial Flat and Erosional Scarplet) than the upper slope (Fan Piedmont and Alluvial Fan Remnant). Similarly, the FIE of microbial diversity in surface soils was around zero in lower landforms and significantly higher at the top of the slope. In subsurface soils, microbial diversity had a negative or zero FIE across all landforms.

The FIE of both C- and P-acquiring enzymes was smallest at the bottom of the piedmont slope (Alluvial Flat), with no difference between the other three landforms. The FIE of N-acquiring enzymes followed the same trend but only in subsurface soils. In surface soils, the FIE of N-acquiring enzymes was elevated in the middle of the piedmont slope (Erosional Scarplet and Fan Piedmont) compared to the top and bottom of the slope (Alluvial Flat and Alluvial Fan Remnant). The FIE of oxidative enzymes in surface soils was positive in the Erosional Scarplet, negative in the Fan Piedmont, and absent at the top and bottom of the slope. In subsurface soils, oxidative enzymes showed little to no FIE across all landforms. In surface soils, available nutrients and biologically acquired nutrients exhibited a positive FIE in all landforms except at the top of the slope, where biologically acquired nutrients had a negative FIE. The FIE of HCl-extracted P was positive in the Erosional Scarplet and negative in all other landforms. In subsurface soils, all forms of nutrients followed a similar trend – the FIE was about 0 in the Alluvial Flat and Fan Piedmont, less than or around 0 in the Erosional Scarplet, and positive at the top of the slope (Alluvial Fan Remnant).

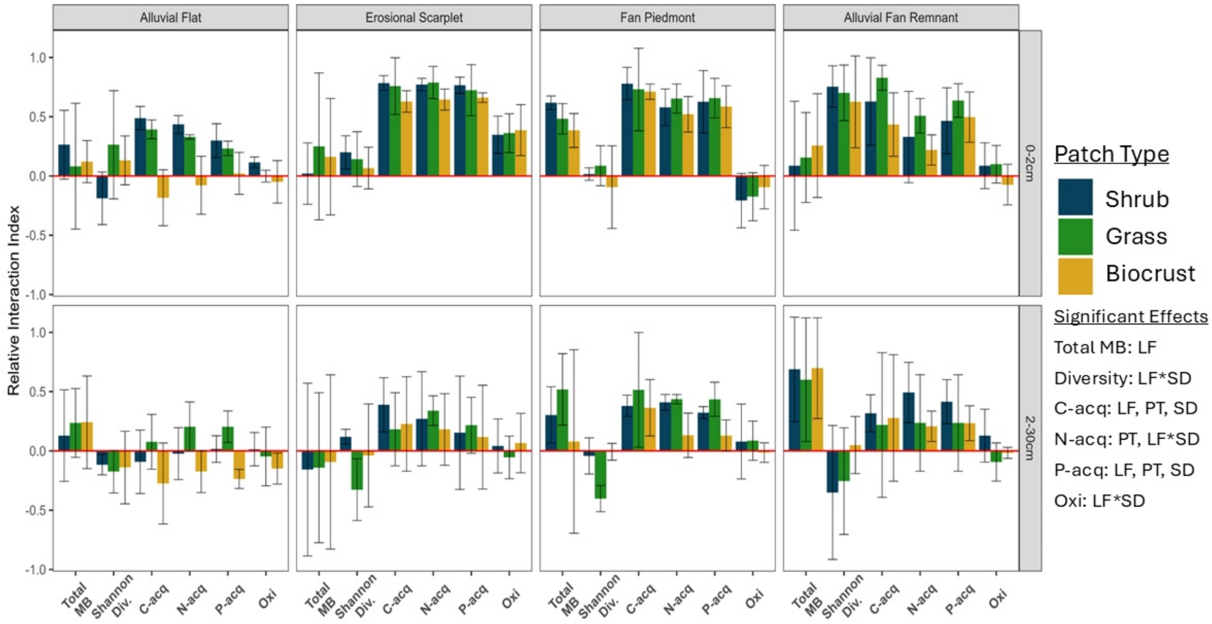

Figure 2.2. Differences in the fertile island effect for variables related to microbial community activity across geomorphic landforms, patch types, and soil depths. The fertile island effect is displayed as the Relative Interaction Index (RII), described in Equation 1. Bar height represents the mean of replicates (n=3) within a sampling site, and error bars show one standard error. RII is considered either positive or negative if the mean +/- SE does not intersect 0. Significant ANOVA effects ($p<0.05$) are displayed alongside the figure legend: LF is landform, PT is patch type, and SD is soil depth. Interactive effects are displayed as two factors joined with an asterisk.

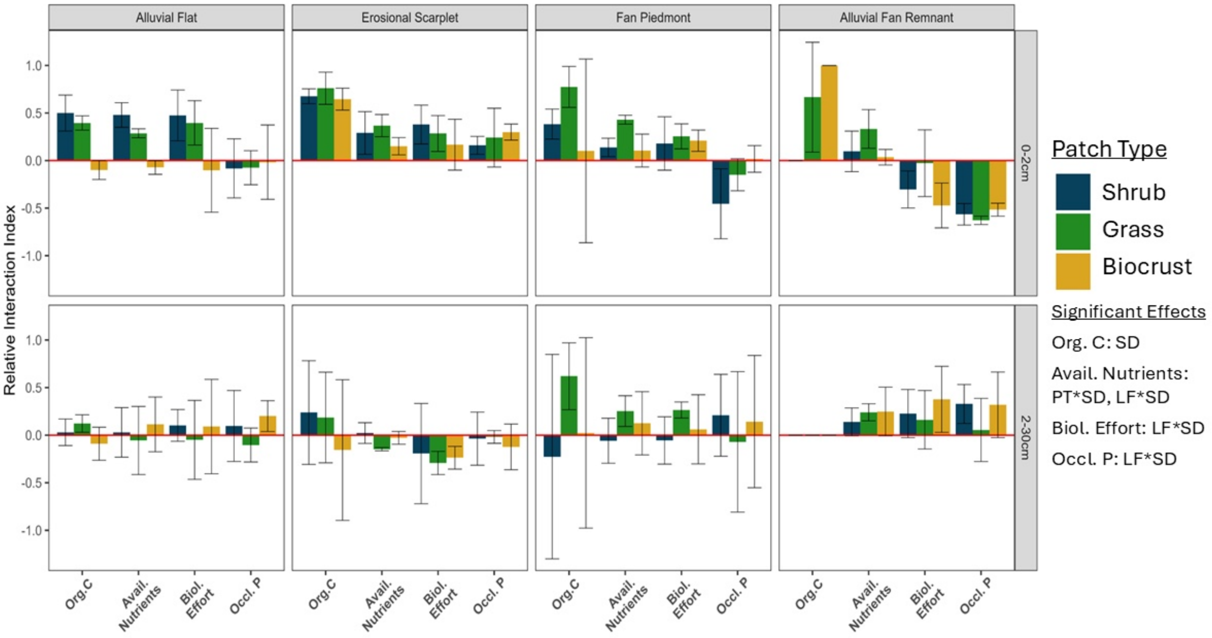

Figure 2.3: Differences in the fertile island effect for variables related to nutrient availability and soil organic matter across geomorphic landforms, patch types, and soil depths. The fertile island effect is displayed as the Relative Interaction Index (RII), described in Equation 1. Bar height represents the mean of replicates (n=3) within a sampling site, and error bars show one standard error. RII is considered either positive or negative if the mean +/- SE does not intersect 0. Significant ANOVA effects ($p<0.05$) are displayed alongside the figure legend: LF is landform, PT is patch type, and SD is soil depth. Interactive effects are displayed as two factors joined with an asterisk.

Patch-level variations in the fertile island effect

Patch-level effects were present only for C-, N-, and P- acquiring enzymes and available nutrients (Figures 2.2 and 2.3 – Significant Effects). Although the FIE of C- and P-acquiring enzymes showed an effect of patch type, post-hoc analysis did not show significant differences between patch types. The FIE of N-acquiring enzymes was suppressed beneath biocrusts compared to shrubs and grasses.

The patch-level effect on the FIE of available nutrients interacted with soil depth (Figure 2.3 – Significant Effects). The effect of patch type was only evident in surface soils, where the FIE of available nutrients below biocrusts was smaller than that of shrubs and grasses.

Microsite-level variations in the fertile island effect

Soil depth only significantly affected C- and P-acquiring enzymes and organic C (Figures 2.2 and 2.3 - Significant Effects) independent of other spatial scales. The FIE of organic C was larger in surface soils than subsurface soils. C- and P-acquiring enzymes had a similar trend, where the FIE was on average higher in surface soils than subsurface soils.

DISCUSSION

We examined the magnitude of the fertile island effect (FIE) on a range of biogeochemical and microbial variables at two soil depths (0-2 cm and 2-30 cm) across multiple patch types (shrub, perennial grass, biocrust) in four landforms which varied in age and geomorphology. Our results reinforce the prevalence of the FIE in dryland ecosystems – metrics of soil fertility were generally higher below shrubs, grasses, and biocrusts compared to bare interspace soils. However, the size of the FIE varied considerably across spatial scales, revealing distinct trends at each scale. These trends varied between response variables, suggesting that the magnitude and importance of the FIE may ultimately depend on a variety of biogeochemical and biological processes acting at vastly different spatial scales.

We found that the presence or size of the FIE is mainly influenced by variability in physical soil properties like texture at the landscape and microsite scales. Meanwhile, multiple patch types had a significant impact on nutrient availability and access, and differences in the FIE between patch types were consistent across the landscape. Although landform-level effects had a substantial impact on soil fertility as hypothesized, soil depth was similarly important, illustrating the highly variable nature of dryland soils, which can vary both across the landscape and within 2 cm in a soil profile. Surprisingly, the FIE was similar between biotic patch types for many response variables, with soils from biocrusts and grasses sometimes exhibiting an effect equal to or larger than shrubs, and these patch-specific effects influenced the FIE independently from the effects of landforms and soil depths.

The fertile island effect is widespread across spatial scales

While patterns in the FIE varied across the spatial scales considered here, measured variables generally exhibited a positive FIE across all landforms in all or most patch types (Figures 2.2 and 2.3). Our results reinforce and expand our current understanding of the FIE (Eldridge et al. 2024; Garner and Steinberger 1989; Ochoa-Hueso et al. 2018). First, all biotic patch types (including biocrusts) typically had enriched soil (e.g. elevated soil nutrients), elevated soil microbial activity (enzymatic activity, microbial biomass), more available soil moisture, and increased organic matter across all landforms compared to bare interspace soils. Additionally, the coarser soils below grasses and shrubs compared to unvegetated patches shows that vegetation stabilizes the soil and captures dust particles, especially larger particles like sand. Lastly, the FIE was more apparent in surface soils (0-2 cm), though it was also observed in subsurface soils (2-30 cm) depending on landform and patch type. The elevated FIE in surface soils reflects the concentration of microbial activity and plant roots close to the soil surface; unsurprisingly, biological activity was generally higher where soil fertility was higher (Gibbens and Lenz 2001; Kirschner et al. 2021; Taylor et al. 2002).

Occluded P presents a notable exception to the trend of a positive FIE. Occluded P exhibited a positive FIE in both surface and subsurface soils in only one landform (Erosional Scarplet for surface and Alluvial Fan Remnant for subsurface), and the FIE of occluded P was either absent or negative in all other landforms. The negative FIE in surface soils under all cover types compared to the interspace reflects the variety of effects that plants and biocrusts can have on nutrient cycling (Delgado-Baquerizo et al. 2014; Hobbie 1992; Maestre et al. 2024). P is made unavailable through leaching to deeper soils or sorption to pedogenic carbonate in the soil; these processes may be increased in interspace soils where plants and microbes are not actively cycling the available P (Belnap 2011; Guppy et al. 2005). As a result, this “stagnant” P may be more vulnerable to occlusion and leaching, thus decreasing P availability. The lack of a significant FIE on Occluded P in subsurface soils in these landforms may show a comparably small influence of plant and microbial activity on P cycling compared to surface soils. As droughts and heat waves increase in frequency and severity, the increased occlusion of available P due to decreased biological demand could degrade dryland soil fertility, causing significant negative feedbacks in P cycling in arid regions.

The soil-geomorphic template influences the magnitude of the fertile island effect

Geomorphology is the primary long-term control in structuring dryland landscapes and developing into units of similar soil properties and ecological conditions designated as the soil-geomorphic template, a conceptual framework predicting vegetation, animal, and microbial community composition and structure (Monger 2006; Monger and Bestelmeyer 2006). Under the soil-geomorphic template, biotic processes are influenced by variation in soil properties (e.g. texture, salinity), topography (e.g. elevation, aspect), microclimate, and parent material. Accordingly, the soil-geomorphic template considers many factors directly relevant to soil fertility including water, nutrients, root development, and plant anchorage, and may help predict patterns of soil fertility in dryland systems as suggested in our study.

Due to their proximity (<10 km between sites), our study sites had similar climate, parent material, and dominant vegetation types; consequently, differences in topography and soil properties (e.g. particle size, soil moisture) likely explain much of the variation between sampling sites. Lower elevation landforms typically had a gentle slope and fine-textured soils while higher elevations had a steeper slope and gravelly, coarser-textured soils. Although soil texture class did not change dramatically across the landscape (soils ranged from silty loam at the base of the slope to sandy loam at the top), sand and gravel contents did increase substantially with elevation, indicating the role of geomorphology in determining soil texture (Table 2.1). However, biotic processes can also alter texture, evidenced by coarser soils beneath shrubs and grasses compared to unvegetated patches (Table 2.1). This effect is the strongest at the bottom of the slope with finer soil texture, possibly because wind would be strongest at low elevations, thus increasing the trapping of coarse sediments by plants and biocrusts, while the weak effect at the top of the slope indicates that coarse sediments accumulate regardless of vegetation or biocrust presence.

Soil texture directly influences an array of ecosystem processes including water and nutrient availability, microbial activity, plant survival and recruitment, and C storage (Osborne et al. 2022; Silver et al. 2000; Veblen et al. 2022). However, we found that regardless of texture or topography, soil salinity (measured as electrical conductivity, Table 2.1), a proxy for water availability in such water-scarce environments, was higher in surface soils beneath plants than in unvegetated soils in all landforms. The consistency of this effect indicates plants' ability to increase water availability and improve soil conditions beneath their canopies across a range of geomorphic conditions (Fitzpatrick et al. 2024; Sala and Aguiar 1996). The increased salinity beneath plants may also stem from hydraulic lift, wherein plant roots bring potentially saline water from lower soil layers to the soil's surface (Armas et al. 2010; Caldwell et al. 1998). Additionally, the accumulation of litter and sediment beneath plants can increase decomposition, further explaining the elevated electrical conductivity in vegetated patches (Anjum and Khan 2021; Stavi et al. 2019; Xu et al. 2016). While vegetation's effect on soil moisture persisted regardless of landform, the magnitude of the effect varied: the difference in salinity between vegetated and unvegetated patches was greatest at the valley floor where water availability is often highest, increasing accumulation around plants (Table 2.1). That the effect of vegetation can vary dramatically across landforms implies that landscape position plays a role in determining the strength of the FIE.

Variations in the FIE of both biogeochemical and microbial factors were observed across the landscape, which may be explained in part by processes comprising the soil-geomorphic template. The FIE of variables related to microbial activity (i.e. biomass, diversity, enzymatic activity) were generally highest at the top of the piedmont slope and lowest at the valley floor (Figure 2.2). However, nutrient availability generally exhibited the opposite trend, with a larger FIE in fine-textured soils at the bottom of the slope, though FIE was generally positive across all landforms (Figure 2.3). Additionally, the FIE of microbial activity and available nutrients was positive in both coarse and fine soils, indicating higher levels of each below fertile islands compared to interspace soils, but differences between fine and coarse soils were more pronounced for microbial activity than nutrient availability. The contrast between microbial activity and nutrient availability illustrates that fertile islands may differentially affect different biogeochemical processes depending on their geomorphic context. Naturally, factors not considered in this study such as heterogeneity of local precipitation, grazing intensity, or time since patch formation likely contribute to the observed trends (Allington and Valone 2014; Ridolfi et al. 2008; Schlesinger et al. 1990). The soil-geomorphic template provides a framework in which to consider and potentially predict how patterns of soil fertility may vary across a range of geomorphic conditions.

Patterns in the fertile island effect across patch types are consistent across landforms

Islands of fertility are typically defined as vegetated patches, often shrubs or grasses, that improve soil conditions below their canopies (Allington and Valone 2014; Schlesinger et al. 1990) while biocrusts in this context are typically only considered alongside vegetation (e.g. Ding and Eldridge 2021). We provide evidence that unvegetated patches with pronounced biocrust cover can exhibit a FIE of similar strength to that of grasses and shrubs across key metrics of soil fertility. This finding necessitates further investigation into the ability of biocrusts to act as fertility islands (or “mantles,” see Garcia-Pichel et al. 2003) independently from vegetation. Proposed mechanisms explaining the origins of fertile islands often center on the initial establishment of the shrubs that in time become an island (see Ridolfi et al. 2008; Sala and Aguiar 1996); our study contributes to a growing body of evidence that the formation of fertile island may be supported in part by facilitation from biocrust communities (e.g. Sepehr et al. 2022).

Despite the widespread landform effects on the FIE and the differences in physical soil characteristics between landforms, the effects of patch type on the FIE remained consistent across the landscape. Patch type effects on the FIE were limited to variables related to nutrient availability and acquisition (available nutrients and extracellular enzymatic activity), and these effects were largely unaffected by landform-level differences (Figures 2.2 and 2.3). The lack of an interactive effect between landforms and patch types on the FIE of available nutrients and enzymatic activity suggests that large, landscape-scale differences in soil properties do not affect the patch-level biological processes influencing nutrient availability and acquisition. Plants and biocrusts can act as ecosystem engineers to modify and improve soil conditions (van Breemen and Finzi 1998; Xiao et al. 2022), and the microbial community may play a similar role through the use of extracellular enzymes. Consequently, plant and microbial activity may be more influential than landscape-scale processes in producing the patch-scale patterns described in this study.

However, patch-level effects on the FIE of available nutrients did differ across soil depths. The interactive effect between patch type and soil depth on available nutrients may be explained partly by the difference in soil depths that different organisms can access. Microbes are typically concentrated in the soil surface (topsoil) or around roots while plant roots can extend deeper into the soil profile (Garcia-Pichel et al. 2003; Gibbens and Lenz 2001; Kirschner et al. 2021). Thus, microbial uptake may be a dominant form of nutrient uptake in the top 2 cm of all patch types – but especially biocrusts – while uptake by plant roots and associated microbes may be dominant in deeper soils beneath grasses and shrubs. Our findings stress the importance of patch type, as each patch type can distinctly influence the FIE regardless of geomorphological context. The patch types considered in this study exhibited a positive FIE across many response variables and vastly different spatial scales, and the effect was often comparable between patch types, indicating that shrubs, grasses, and biocrusts can all similarly affect soil fertility.

CONCLUSION

Our findings provide evidence that interactions between soil geomorphology and soil fertility vary across spatial scales while also demonstrating that biogeochemical processes are differentially affected by geomorphology depending on both biotic and abiotic processes. This new understanding of the relationship between geomorphology and soil fertility necessitates a more interdisciplinary approach to studying patterns of productivity in dryland ecosystems. Including the influences of processes acting on the fertile island effect - and thus productivity – at a range of spatial scales will help improve models of dryland productivity and land-cover change. Additionally, our results show that biological soil crusts may also act as fertile islands; expanding our perception of fertile islands to include biocrusts in addition to perennial plants may reveal novel insights into the factors driving this key dryland phenomenon. These findings necessitate further work to improve our understanding of how ecosystem processes vary across scales to influence patterns of soil fertility and productivity.

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AUTHOR CONTRIBUTION STATEMENT

Dylan J. Stover: Writing – original draft preparation, review and editing, Investigation, Visualization, Data Curation. **Lixin Jin:** Writing – review and editing, Methodology, Investigation, Funding acquisition, Data Curation. **Nicole Pietrasiak:** Writing – review and editing, Methodology, Investigation, Data Curation. **Jennie R. McLaren:** Writing – review and editing, Methodology, Data Curation, Supervision.

DATA AVAILABILITY STATEMENT

Data are available from the Environmental Data Initiative (EDI) repository at https://doi.org/10.6073/pasta/9085a63e6ff1e310f13784b6fa0f8616.

Chapter 3: Dryland biogeochemistry is not solely driven by water: The effects of nitrogen, phosphorus, and water additions on soil nutrient availability in a Chihuahuan Desert grassland

ABSTRACT

Water, nitrogen, and phosphorus are essential to biological activity, but cycling and availability of these resources are changing globally in response to human activities and climate change. Dryland regions are especially vulnerable to large changes in resource availability. To understand how these large global shifts will affect dryland biogeochemistry, we conducted a factorial resource (water, N, and P) addition experiment to identify individual and interactive relationships that exist between these key resources. We examined a variety of soil nutrient fractions ranging from readily available to occluded pools to determine how each fraction responded to resource additions and whether water additions would alter effects of nutrient addition treatments. Unsurprisingly, we found that N and P additions resulted in respective increases in readily available N and P pool. We also found that water and P additions both drove changes in soil N cycling by increasing the capacity for biotic N uptake. Conversely, soil P was not strongly affected by independent N or water additions, though adding both N and water together decreased soil P, possibly by increasing uptake and pushing the system toward P limitation. These results underscore the importance of water availability to dryland biogeochemistry, but they also demonstrate the ability for soil nutrients to interact independently from water. Our work contributes to the growing evidence of the importance of P availability in balancing N inputs and losses in dryland ecosystems, potentially regulating the production of greenhouse gases like NO_X or N_XO. Future work should continue to explore this relationship to better understand the role of dryland regions in global biogeochemical cycles.

INTRODUCTION

Water, nitrogen (N), and phosphorus (P) are essential resources for biological activity, but these global resource cycles are shifting in response to human activities and climate change (Penuelas et al. 2020; Vitousek et al. 1997; Mahowald et al. 2008). Drylands, which play a major role in global biogeochemical cycles and primary productivity (Poulter et al. 2014; Ahlström et al. 2015; Field et al. 1998; Hanan et al. 2021; Mahowald et al. 2008), may be especially sensitive to shifts in these biogeochemical cycles due to their naturally low and variable resource availability (Jordaan et al. 2022b; Osborne, Bestelmeyer, et al. 2022). For example, drought risk is rapidly increasing in drylands (Seager et al. 2007; Cook et al. 2015) and precipitation regimes are becoming increasingly variable in these regions (Rudgers et al. 2018), with drought projections showing large geographic differences across the drylands of North America (Bradford et al. 2020).

Alongside changing precipitation regimes, human activities including agriculture and fossil fuel combustion have drastically altered global biogeochemistry. Human activity has doubled the rate of terrestrial N accumulation and significantly increased atmospheric concentrations of N_2O and NO_x gases (Vitousek et al. 1997; Galloway et al. 2003), though recent evidence suggests that N availability is decreasing in terrestrial systems globally (Mason et al. 2022). Even small shifts in N availability can have large ecological effects in drylands (Sinsabaugh et al. 2015). Increasing aridity decreases total soil N (Delgado-Baquerizo et al. 2013; Plaza et al. 2018; Jordaan et al. 2022b), but atmospheric N deposition will also continue to increase as human activities expand in drylands (Vitousek et al. 1997; Sinsabaugh et al. 2015), necessitating a deeper understanding of how dryland soils respond to shifting N concentrations. Lastly, P bioavailability is a function of temperature and water availability, so the rise in extreme heat waves and droughts across dryland regions can diminish the already restricted P supply by increasing aeolian P losses and promoting mineral occlusion of available P (Belnap 2011).

There is significant evidence that these global cycles are linked (Zhang and Mao 2025; Austin et al. 2004; Osborne, Bestelmeyer, et al. 2022; Delgado-Baquerizo et al. 2013), and the anthropogenic changes in all three are likely to produce unexpected interactive changes where shifts in one resource cycle can produce subsequent shifts in another. This is clearly apparent with the water cycle, which typically drives nutrient cycling in dryland systems (Austin and Sala 2002; Noy-Meir 1973; Brown et al. 2022). Increased water supply promotes biological activity, which could increase the accumulation of soil N through biological N fixation but also increase gaseous N losses by stimulating processes such as denitrification or volatilization (Hartley and Schlesinger 2000; Ramond et al. 2022a; Hartley and Schlesinger 2002; Homyak et al. 2016). Conversely, dry conditions can slow the release of mineral-bound P by decreasing biological activity that solubilizes soil P through the production of extracellular phosphatase enzymes or organic metabolites (de-Bashan et al. 2022; Belnap 2011). The N and P cycles also interact; for example, N fixation – a very energy-intensive process – requires sufficient P availability (Postgate 1982; Tierney and Wurzburger 2024; Reed et al. 2007) while the production of P-acquiring phosphatase enzymes is dependent in part on N availability (Sinsabaugh and Follstad Shah 2012; Sinsabaugh and Moorhead 1994). Additionally, the co-precipitation of ammonium and phosphate ions in soil improves the retention of bio-available N and P, increasing soil fertility (Adams 2015; Grunes 1959; Wei et al. 2024). The inherent relationships between the cycling of critical resources raises the question of how simultaneous shifts in these three resource cycles may interact to alter soil nutrient availability in resource-scarce environments such as drylands.

We tested the relationships between N, P, and water in the Chihuahuan Desert by increasing their availability independently and in combination with the objective of identifying individual and synergistic effects of shifting N, P, and water availability on soil nutrient pools. We hypothesized that: 1) readily available nutrient pools (e.g. available P, soluble P, NO_3^- and NH_4^+) would be most impacted by N and P additions because the processes that occlude these nutrients occur on a much longer timescale than this experiment encompassed; 2) because of its importance to nearly all biogeochemical processes, water would impact most – if not all – nutrient pools; and 3) the effects of N and P additions would interact, although at a lesser scale than the nutrient-water interaction.

METHODS

Study Site

We conducted our study from May 2022 to February 2025 in the Jornada Basin Long Term Ecological Research site (Jornada) in southern New Mexico, USA at the northern extent of the Chihuahuan Desert (latitude 32.511 N, longitude 106.799 W). Mean annual precipitation in the area is 247 mm, with about 53% of precipitation occurring during the summer monsoon (July 1 - September 30) (Greenland and Anderson 1997). The average monthly maximum temperature ranges from 36°C in June to 13°C in January (Greenland and Anderson 1997). The study site was located in a native grassland dominated by black grama (*Bouteloua eriopoda*) with a mix of purple three-awn (*Aristida purpurea*), needle grama (*Bouteloua aristidoides*), and introduced Lehmann's Lovegrass (*Eragrostis lehmanniana*) with annual forbs (including silverleaf nightshade (*Solanum elaeagnifolium*) and Palmer's Amaranth (*Amaranthus palmeri*)), shrubs (honey mesquite (*Prosopis glandulosa*), creosote bush (*Larrea tridentata*), longleaf jointfir (*Ephedra trifurca*)) and cactus (*Opuntia* sp.) interspersed throughout the site. The JER was historically dominated by black grama grassland but has been transitioning to shrubland in response to factors like grazing and extreme drought in the last 50-150 years (Peters and Gibbens 2006).

We employed a full factorial experimental design with water-, N-, and P-addition as the main factors and 8 replicates of each treatment for a total of 64 randomly assigned plots. Plots were 2 m x 2 m in size, located at least 5 m away from other plots and offset from each other along the slope to avoid runoff between plots. Plots were located at least 5 m from mesquite shrubs to avoid any effect from nitrogen fixation associated with leguminous plants. We fertilized the plots in late June of each year, before the monsoon season began. N was added as 10 $g/m^2/yr$ of ammonium nitrate (NH_4NO_3) to minimize the soil acidification effect (Lines-Kelly 1992). P was added as 5 $g/m^2/yr$ of calcium dihydrogen phosphate hydrate ($CaH_4O_8P_2$). Fertilizers were dissolved in 1 L of water before being applied to the plots using a fertilizer sprayer. The equivalent of 8 mm of precipitation in water was added by hand weekly throughout the 12-week monsoon season each year for a total of 96 mm of water per year, approximately 75% of average historical monsoon rainfall.

Sample Collection

We collected soil samples from 0 – 10 cm soil depth in 2022, 2023, and 2024 using a 2.54 cm diameter soil auger. We collect samples at three time points throughout the growing season: 1) Peak Season (PS) – mid-August, with high growing activity; 2) Peak Biomass (PB) – early- to mid-November, with low growing activity and biomass just beginning to senesce; 3) Winter (W) – late January to early February, with low plant activity and biomass already senesced.

Laboratory Analysis

Bulk Soil Analysis

We passed each sample through a 2 mm sieve and removed plant material by hand before sub-sampling for subsequent analyses. We measured soil pH in each plot in PB of Year 1, PS of Year 2, and W of Year 3 using the saturated paste method with 15 g of soil in 30 mL of water via a Fisherbrand benchtop pH meter (accumet AB315, Fisher Scientific, Waltham, MA, USA). We measured total C and N using a combustion elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA, USA) after drying and grinding the soils to a consistent particle size and packing them in tin capsules for analysis. We determined total P for each plot in PS of Years 1 and 3 using the EPA 3051A digestion method and ICP-OES analysis (Brigham Young University, Provo, UT, USA). We calculated soil bulk density as the soil volume divided by dry soil weight for soil cores of known volume collected within each plot.

Soil Nutrient Analysis

We extracted 5 g of soil in 25 mL of 0.5M potassium sulfate (K_2SO_4) to measure available nitrate (NO_3^-) and ammonium (NH_4^+). Samples were shaken for 2 hours then vacuum filtered through glass filter paper. To measure available phosphate (PO_4^{3-}), we extracted 5 g of soil in 30 mL of 0.5M sodium bicarbonate ($NaHCO_3$) for 16 hours before filtering (Olsen 1954).we measured biologically important P fractions using the biologically based phosphorus (BBP) method from DeLuca et al. (2015). This method emulates strategies employed by plants and microbes to acquire P through four parallel soil extractions: 0.01 M calcium chloride ($CaCl_2$-P) – P available in soil pore water; 0.01 M citric acid (Citrate P) – P sorbed to clay or weakly bound to soil particles made accessible through organic acids released by plant roots and microbes; 0.2 EU/mL phosphatase (Enzyme P) – labile organic P available through enzyme hydrolysis; and 1 M hydrochloric acid (HCl-P) – P strongly bound to mineral surfaces and locked in mineral lattice (e.g. pedogenic carbonate) which is less biologically accessible. These extractions were conducted in parallel by shaking 0.5 g of each sample in 10 mL of each extractant for 3 hours before centrifuging at 2500 rpm for 2 minutes and filtering.

We analyzed soil extracts with colorimetric microplate assays (BioTEK Synergy HT microplate reader; BioTek Instruments Inc., Winooski, VT, USA), using a vanadium (III) chloride assay for nitrate (Doane and Horwáth 2003), a Berthelot Reaction assay for ammonium (Rhine et al. 1998), and a malachite green assay for phosphate (D'Angelo et al. 2001).

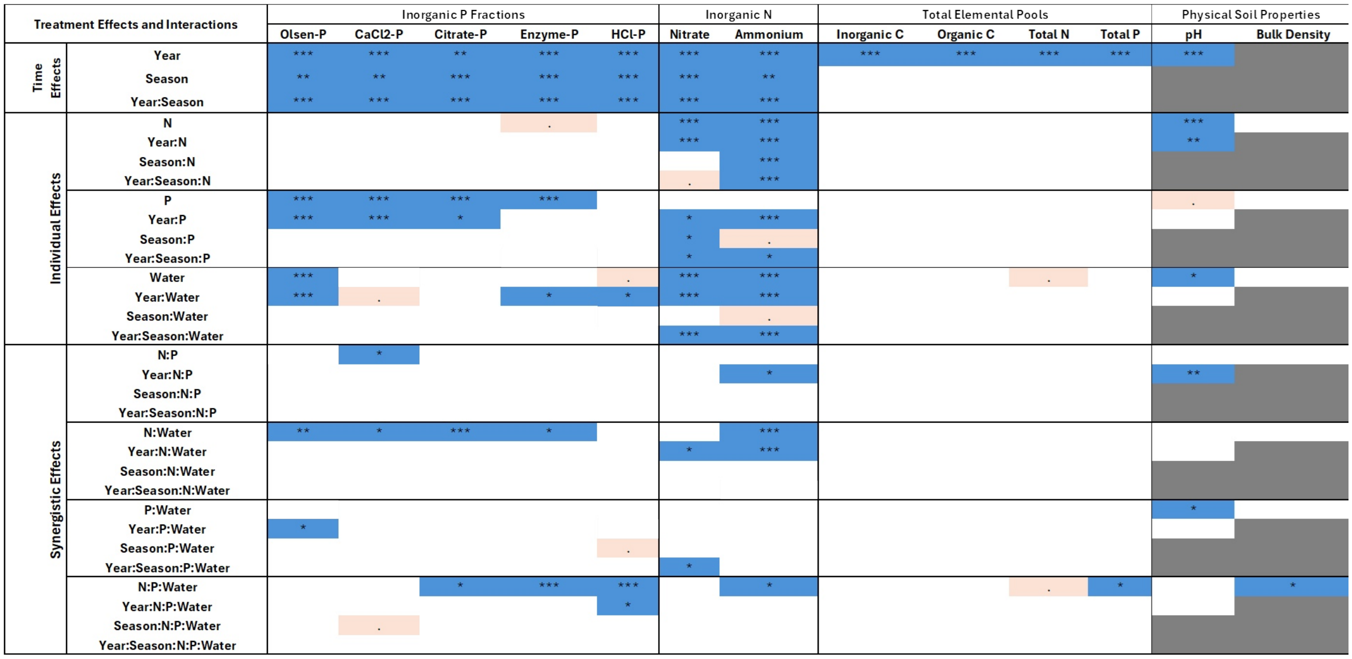
Statistical Analysis

We tested for differences in soil nutrient responses to treatments across years and seasons using a multi-way ANOVA with N, P, water, season, and year as the main factors with effects considered significant at $p < 0.05$. N, P, and water were treated as binary dummy variables, where Control plots = (0, 0, 0), N addition plots = (1, 0, 0), P addition plots = (0, 1, 0), water addition plots = (0, 0, 1), and mixed treatments plots were the respective combination of these terms. We tested assumptions of normality using the Shapiro-Wilk Test. When needed, we used a log-transformation to meet assumptions of normality but present untransformed data in the figures. We used the "dplyr" package in R Version 12.1.402 (Posit team 2024; Wickham et al. 2019) for data analysis and the "ggplot2" and "ggthemes" packages to create plots (Arnold 2024; Wickham 2016).

RESULTS

Seasonal and annual changes in soil nutrient pools

All nutrient pools exhibited a significant interaction between season and year (Figure 3.1, Table S3.1). pH varied by year, and season independently, and total C, N, and P varied significantly by year (Figure 3.1, Table S3.2, Table S3.3). Soil bulk density did not vary with time (Figure 3.1, Table S3.3).



Treatment Effects and Interactions		Inorganic P Fractions					Inorganic N		Total Elemental Pools				Physical Soil Properties	
		Olsen-P	CaCl2-P	Citrate-P	Enzyme-P	HCl-P	Nitrate	Ammonium	Inorganic C	Organic C	Total N	Total P	pH	Bulk Density
Time Effects	Year	***	***	**	***	***	***	***	***	***	***	***	***	▨
	Season	**	**	***	***	***	***	**					▨	▨
	Year:Season	***	***	***	***	***	***	***					▨	▨
Individual Effects	N				.		***	***					***	
	Year:N						***	***					**	▨
	Season:N							***					▨	▨
	Year:Season:N						.	***					▨	▨
	P	***	***	***	***								.	
	Year:P	***	***	*			*	***						▨
	Season:P						*	.					▨	▨
	Year:Season:P						*	*					▨	▨
	Water	***				.	***	***			.		*	
	Year:Water	***	.		*	*	***	***						▨
	Season:Water							.					▨	▨
	Year:Season:Water						***	***					▨	▨
Synergistic Effects	N:P		*											
	Year:N:P							*					**	▨
	Season:N:P												▨	▨
	Year:Season:N:P												▨	▨
	N:Water	**	*	***	*			***						
	Year:N:Water						*	***						▨
	Season:N:Water												▨	▨
	Year:Season:N:Water												▨	▨
	P:Water												*	
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	Year:Season:P:Water						*						▨	▨
	N:P:Water			*	***	***		*			.	*		*
	Year:N:P:Water					*								▨
	Season:N:P:Water		.										▨	▨
	Year:Season:N:P:Water												▨	▨

Figure 3.1. A multiway ANOVA was used to detect significant ($p < 0.05$) differences in each variable across Years, Seasons, and Treatment Effects (N, P, and Water). Blue boxes denote significant effects, with * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Pink boxes denote marginal effects ($0.05 < p < 0.10$). Grey boxes denote factors that were not included for those variables. See Tables S3.1, 3.2, and 3.3 for ANOVA results.

Notable seasonal and annual trends were observed in multiple variables. Both nitrate and ammonium decreased to nearly 0 g/m^2 in Winter 2022, but this pattern did not repeat in the following years (Figure 3.2). Olsen-P and $CaCl_2$-P remained relatively stable throughout 2022 and 2023, only changing substantially in 2024 (Figure 3.3a). In 2022, Citrate-P increased substantially from Peak Biomass to Winter, a trend not seen in the other two years (Figure 3.3a). Enzyme-P remained stable in 2022 and 2023, though it decreased slightly in Winter 2022; in 2024 only, Enzyme-P increased significantly from Peak Season to Peak Biomass before dropping to nearly 0 g/m^2 in the Winter (Figure 3.3a). HCl-P dropped significantly during our Peak Biomass sampling in 2023 only (Figure 3.3b). Total P was only measured in 2022 and 2024 and did not change between years (Figure 3.3c). The HCl-P pool was smaller than Total P in 2022, but the two pools were about equal in 2024 (Figure 3.3c). Lastly, soil pH was highest in 2024 (Figure S3.1).

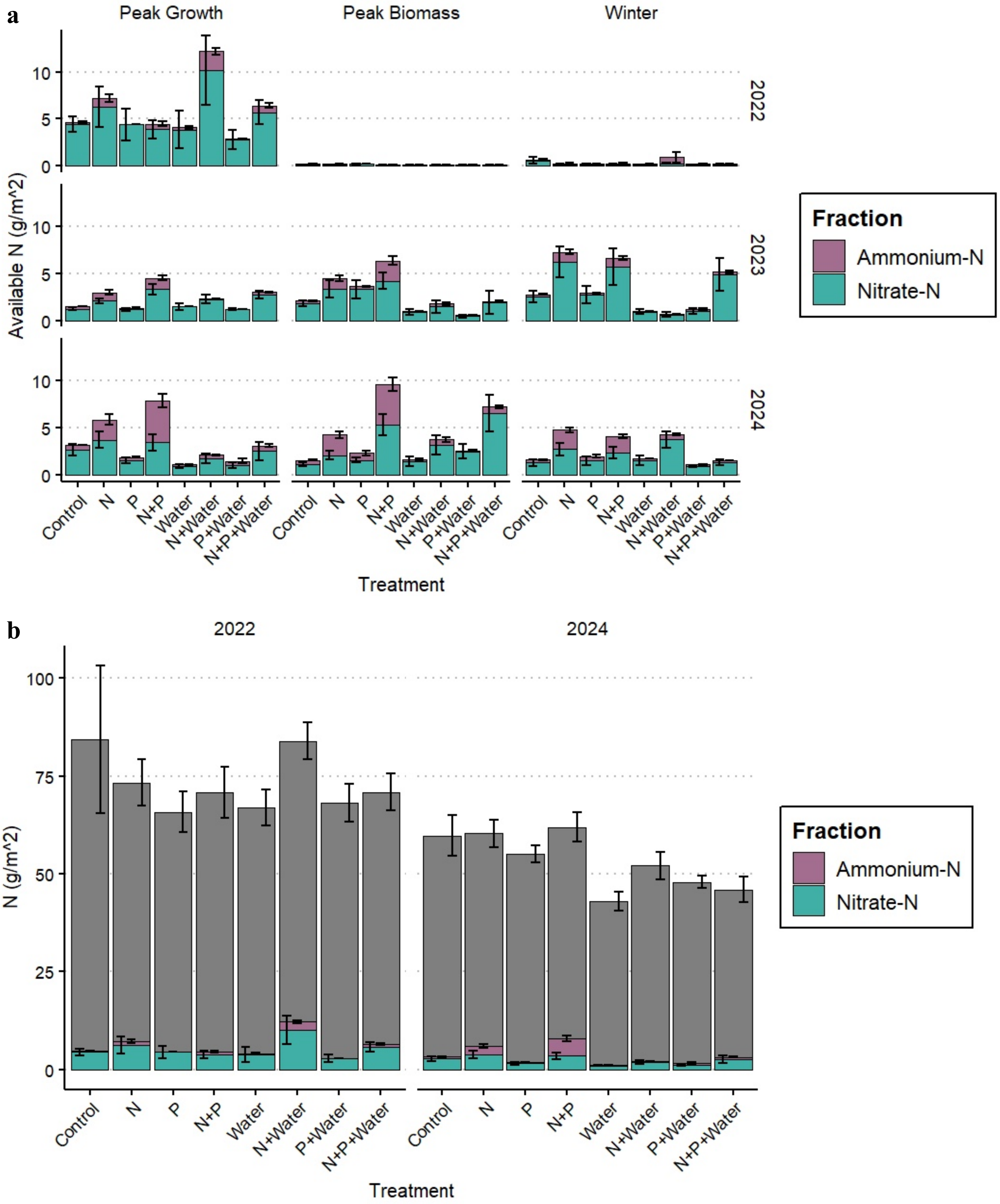
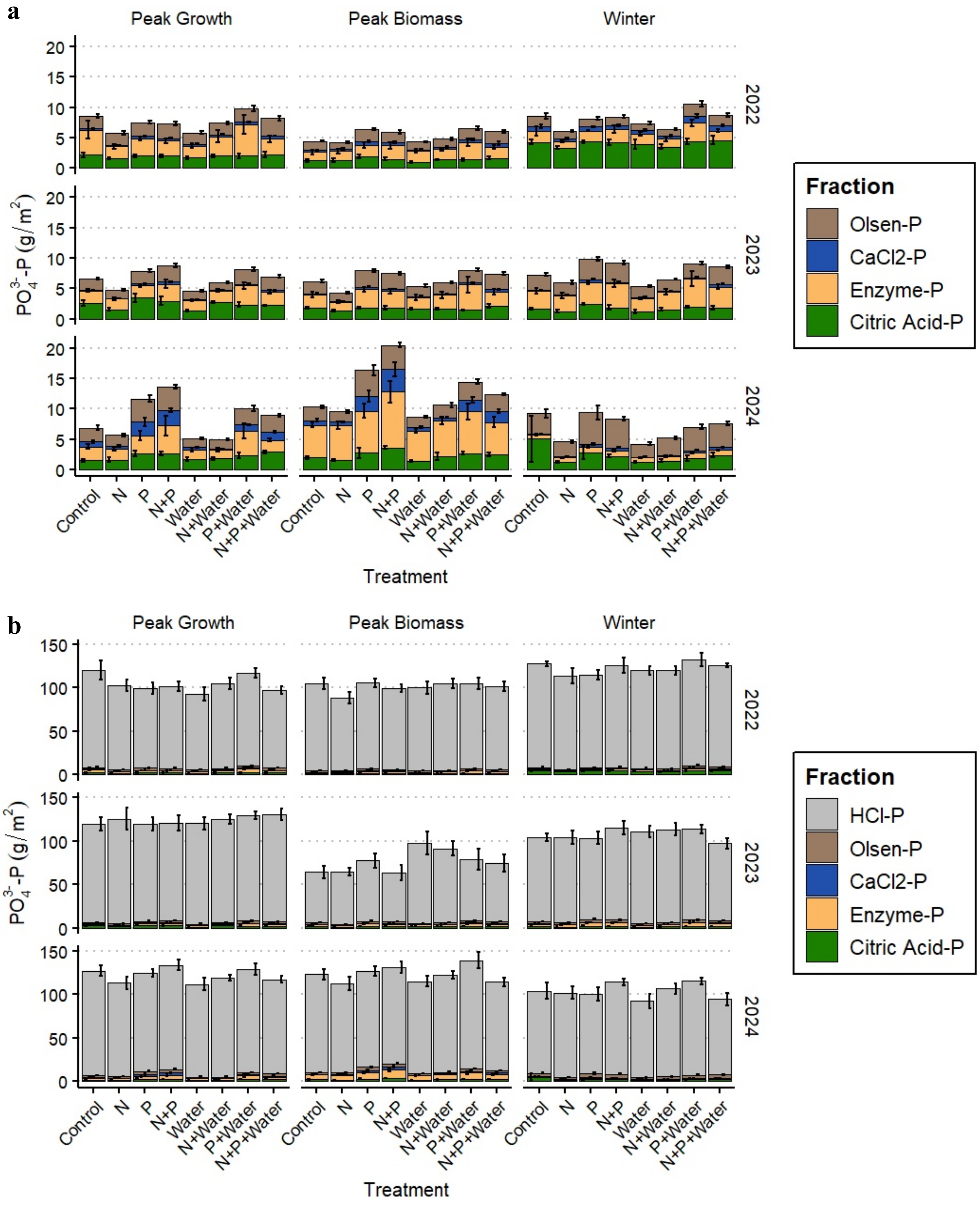


Figure 3.2. a) Shifts in available soil N fractions – Ammonium (NH_4^+) and Nitrate (NO_3^-) – in response to resource addition treatments across years and seasons. See Figure 1 for significant ANOVA effects. Error bars show the mean value ± 1 SE. b) Total N (grey bars) and available soil N responses to resource addition. See Figure 1 for significant ANOVA effects. Error bars show the mean value ± 1 SE.


a
Peak Growth
Peak Biomass
Winter
2022
2023
2024
PO_4^{3-}-P (g/m^2)
0
5
10
15
20
Control
N
P
N+P
Water
N+Water
P+Water
N+P+Water
Treatment
Fraction
Olsen-P
CaCl2-P
Enzyme-P
Citric Acid-P
b
Peak Growth
Peak Biomass
Winter
2022
2023
2024
PO_4^{3-}-P (g/m^2)
0
50
100
150
Control
N
P
N+P
Water
N+Water
P+Water
N+P+Water
Treatment
Fraction
HCl-P
Olsen-P
CaCl2-P
Enzyme-P
Citric Acid-P

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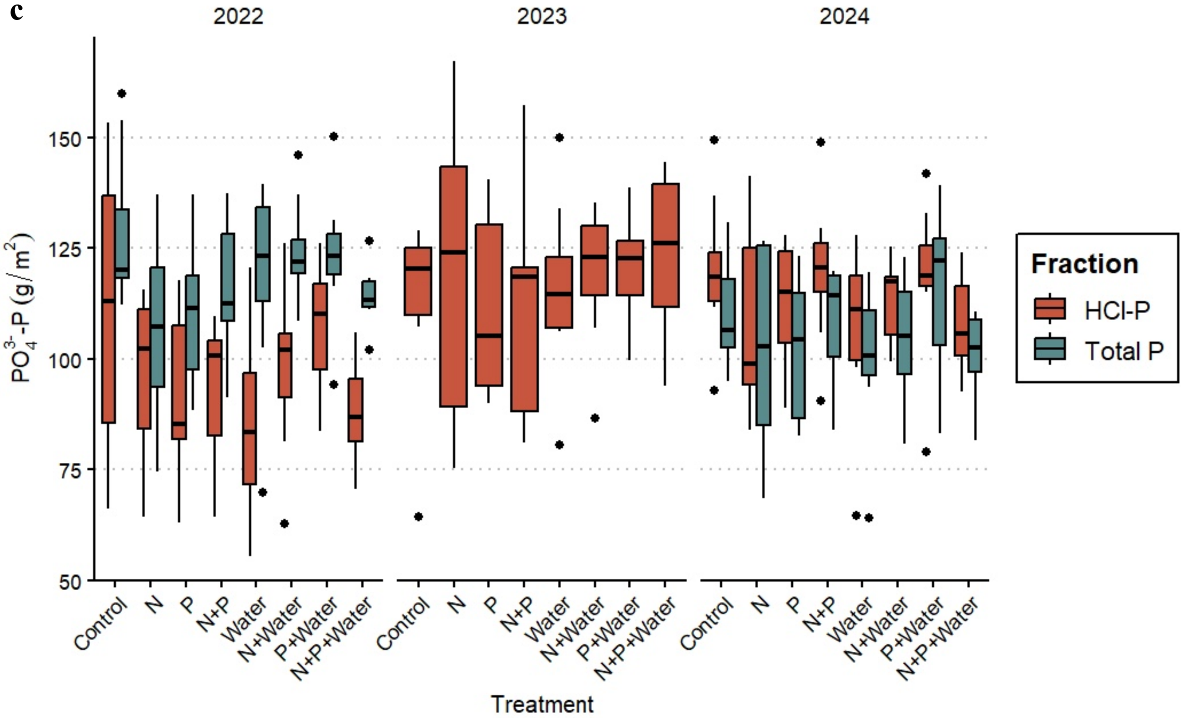

Figure 3.3. a) Shifts in bioavailable P Fractions (Olsen-P – available P; $CaCl_2$-P – soluble P; Citrate-P – weakly bound inorganic P; Enzyme-P – phosphatase accessible organic P) in response to resource addition across years and seasons. See Figure 1 for significant ANOVA effects. b) Bioavailable P fractions and occluded inorganic P (HCl-P) in response to resource addition across years and seasons. See Figure 1 for significant ANOVA effects. c) HCl-P and total P in response to resource addition across years. Data displayed are from the Peak Growth sampling point each year. Total P was collected only in 2023 and 2024. See Figure 1 for significant ANOVA effects.

Individual Treatment Effects

Organic C and organic N were the only variables measured for which there was no synergistic treatment response. Water addition caused a significant decrease in organic C, and this effect varied by year (Figure 3.4); total N decreased marginally ($p < 0.10$) in response to water addition (Figure 3.2b). All other measured variables exhibited significant interactions between treatments.

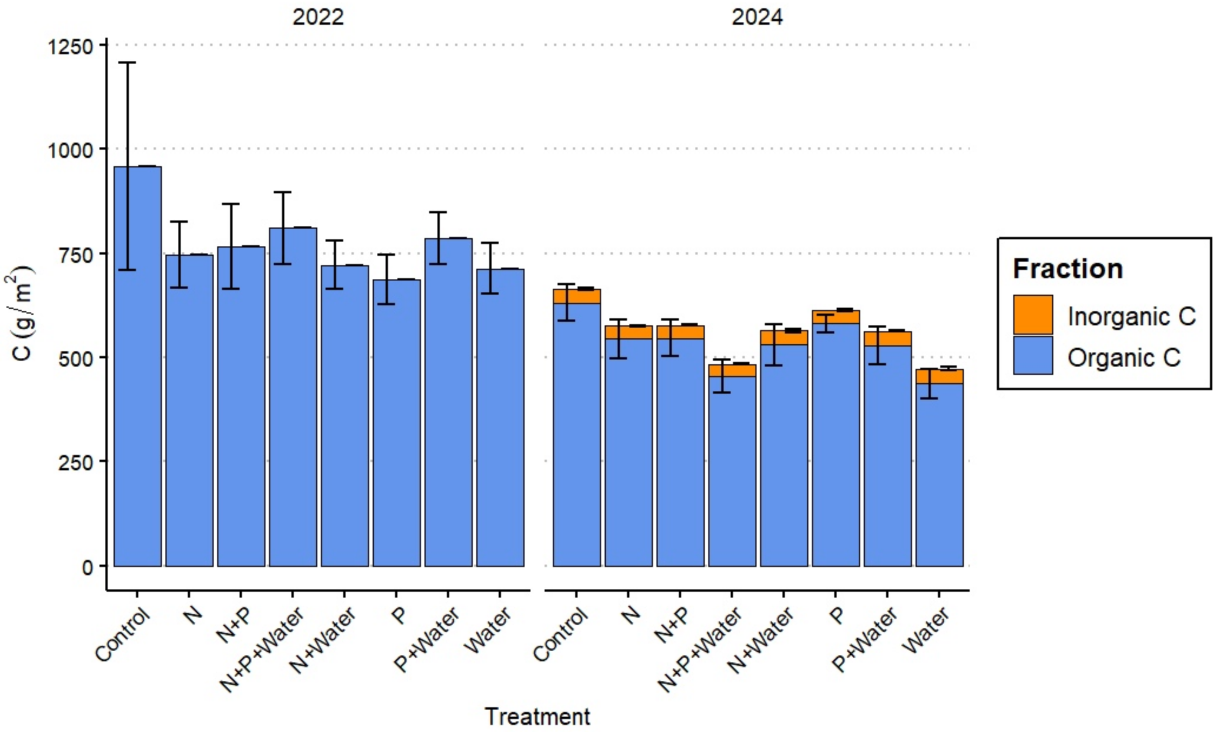

Figure 3.4. Shifts in inorganic and organic C in response to resource addition. Samples were analyzed for inorganic and organic C in 2022 and 2024 only. See Figure 1 for significant ANOVA effects.

Nitrogen-Phosphorus Interactions

N and P additions interacted to significantly increase $CaCl_2$-P and ammonium and shift soil pH independent of water addition (Figure 3.1, Table S3.1). In 2023 and 2024, $CaCl_2$-P typically increased with P addition and ammonium increased with N addition. Concurrent N and P additions generated a larger increase in both $CaCl_2$-P and ammonium than either treatment individually (Figure 3.3a). Because pH was only measured in one season per year, pH responses are only considered across years. In 2024, N addition significantly decreased soil pH while this effect was only observed in 2023 when N and P were added together (Figure S3.1).

Water-Nutrient Interactions

Water-Nitrogen Interactions

Olsen-P, $CaCl_2$-P, and nitrate had a significant N x Water interaction (Figure 3.1, Table S3.1). This interactive effect was consistent through time for the P fractions but varied by year for nitrate. Adding N and water together led to a decrease in each P fraction which did not occur when adding either resource alone (Figure 3.3). Nitrate increased with the addition of N and decreased with the addition of water; when added together, there was little change in this pool compared to the control plots (Figure 3.2). Notable deviations in this pattern occurred in Winter 2023 when N + Water decreased nitrate levels more than water alone, and in both Peak Biomass and Winter 2024 when N+Water produced a larger increase in nitrate than N alone.

Water-Phosphorus Interactions

Nitrate, Olsen-P, and soil pH had a significant P x Water interaction, which varied by year and season for nitrate and by year for Olsen-P (Figure 3.1). Adding P or water alone led to a decrease in nitrate but adding both together led to a larger decrease in nitrate than adding either resource individually except in Peak Biomass 2024, which showed a small increase from this treatment (Figure 3.2a). In 2023 and 2024, Olsen-P increased with P addition and decreased with water addition; when added together, these effects produced little response. pH increased in response to P and water addition (Figure S3.1).

Water-Nitrogen-Phosphorus Interactions

Citrate-P, Enzyme-P, HCl-P, ammonium, Total P, and soil bulk density had a significant interaction between N, P, and Water, and this interaction was consistent across years except for HCl-P (Figure 3.1). $CaCl_2$-P had a marginal interaction between these three factors, which varied seasonally. P addition generally increased Citrate-P, while N and water additions only influenced this fraction when added together. While Enzyme-P sometimes increased after P addition and decreased after N or water addition, concurrent N and P additions led to higher enzyme-P levels than either treatment independently; conversely, adding water, N, and P together negated the N + P effect. HCl-P slightly decreased in response to water in 2022, remained stable in response to treatments in 2023, and decreased slightly in response to the N and N+P+Water treatments in 2024 (Figure 3.3b). Adding either nutrient without water appeared to decrease total P, which was most apparent in 2022 (Figure 3.3c). Ammonium typically increased after N addition, and this effect was magnified when N and P were added together. Water did not have a significant independent effect, but it diminished the effect of N and P additions. In 2022, water, N, and P additions separately and together decreased the HCl-P pool relative to Total P, whereas these pools were about equal in 2024 regardless of treatment (Figure 3.3c). In both 2023 and 2024, the P+water treatment increased soil pH, but this effect was absent when adding N, P, and water together (Figure S3.1). Soil bulk density was slightly lower in plots that received the N+P+Water treatment (Figure S3.2).

DISCUSSION

We conducted a factorial nitrogen (N), phosphorus (P), and water addition experiment in the northern Chihuahuan Desert to explore how resource additions interact to alter soil nutrient pools. We found large fluctuations in all soil nutrient pools attributable to seasonal and annual variability, highlighting the importance of temporal heterogeneity in arid regions (Felton et al. 2021; Wang et al. 2022; Rudgers et al. 2018; Noy-Meir 1973) and emphasizing the need for further work to understand how temporal variability changes soil nutrient pools (Brown et al. 2022; Austin et al. 2004). Despite the significant temporal trends, resource additions generated significant responses across all nutrient pools. N and P additions resulted in respective increases in available

N and P fractions while the two treatments sometimes interacted to produce a larger effect than either individually. We also found that P additions significantly affected available N pools while N additions only affected P fractions when added in conjunction with water (Figure 3.1, Figure 3.3a), suggesting that the effects of N addition are more dependent on water than those of P addition. This study provides much needed clarity about how soil nutrient cycling in drylands responds to shifting resource availability and how these shifts may interact to produce unexpected responses across soil nutrient pools.

Soil nutrient pools are highly variable across time

Drylands are extremely heterogeneous, both spatially and temporally, due to their variable weather and patchy, bimodal vegetation patterns consisting of vegetated patches – or islands – interspersed among patches of low plant cover (Schlesinger et al. 1990; Aguiar and Sala 1999; Garner and Steinberger 1989). Over the three years of the study, our site experienced large swings in precipitation and temperature (Table S3.4). We attempted to minimize the effects of inter-annual variability in precipitation with a water addition treatment (70% of historical average monsoon precipitation) that was expected to provide sufficient water across treatments over the course of each growing season. However, 2023 and 2024 experienced drier- and hotter-than-average summers, receiving only 38.6% and 29.2% of average monsoon rainfall and experiencing 59 and 45 days, respectively, during the 90-day monsoon with a maximum temperature above 36 ^{o}C (Table S3.4; Greenland and Anderson 1997). In 2023, the temperature exceeded 36 ^{o}C on 41 consecutive days compared to 15 and 12 in 2022 and 2024, respectively (Table S3.4). These hot and dry conditions may have counteracted our experimental considerations by causing a large portion of the added water to evaporate before it could be used. Thus, in the face of extreme heat and severe drought, much larger amounts of water are likely necessary to provide sufficient water to substantially alter biogeochemical cycling.

These large climatic shifts along with the high heterogeneity of dryland soils produced large temporal variation in soil nutrient availability, where every nutrient pool measured exhibited a significant interaction between Years and Seasons (Figure 3.1, Table S3.1). This interactive effect meant that seasonal trends in each nutrient pool were not consistent across years. The citrate-P and N pools best demonstrate this – in Winter 2022 when the site received a large amount of rainfall, weakly-bound citrate-P increased (Figure 3.3a), while available N dropped to nearly zero (Figure 3.2a), but these patterns were not exhibited in the other two years of the experiment. This trend can be attributed to the high biological activity tied to high water availability, which would deplete available N through uptake and gaseous emissions (Homyak et al. 2016; Hartley and Schlesinger 2000; Yang et al. 2011) and increase the citrate-P fraction by increasing both plant litter production (Noy-Meir 1973; L. Wang et al. 2022; Cleverly et al. 2016) and the subsequent decomposition rate of that plant litter (Zhao et al. 2025; Bigio et al. 2025), ultimately transforming more P into this one pool. Even total C and N decreased over the 3 years of the experiment (Figure 3.4), likely due to decreased organic inputs in drought years with little vegetation.

Factors in addition to varying precipitation are likely responsible for seasonal and annual variation in multiple nutrient pools (Austin 2011). For example, the enzyme-accessible P fraction increased significantly after the growing season only in 2024 while the less available HCl-P fraction dropped significantly after the 2023 growing season before recovering in the next season, signaling large swings in the distribution of soil P across both years and seasons even in years that were consistently hot and dry. Further, residual P – the difference between HCl-P and total P (Crews et al. 1995) – was significantly smaller in 2024 than at the beginning of the experiment while total P remained stable (Figure 3.3c). The residual, unavailable P pool appeared to decrease over the course of the experiment, suggesting that the residual pool may be transformed into less occluded forms while remaining in the system on the scale of a few years regardless of water availability. While water availability is often assumed to drive temporal variation in drylands (Epstein et al. 2019; Wang and Collins 2024), factors other than water were also responsible for temporal variation in our results, underscoring the importance of a broad range of factors in driving both seasonal and annual trends in biogeochemical cycles.

Direct and indirect effects of nutrient addition on N and P availability

Even with strong temporal trends in soil nutrient availability, treatment effects significantly influenced soil fertility. N and P additions generated respective increases in N (Figure 3.2) and P (Figure 3.3) availability. Because we added N and P in readily available forms, we expected the available pools to be most affected. As expected, P effects were focused in the readily available Olsen-P and $CaCl_2$-P fractions, though this was most evident in 2024 (Figure 3.3a). Conversely, the N treatment effect was more consistent on ammonium (NH_4^+), which more than doubled after fertilization while the more readily available nitrate (NO_3^-) saw only modest increases after N addition (Figure 3.2a). N was added as ammonium nitrate (NH_4NO_3), so a concurrent increase in both pools was plausible; however, nitrate is rapidly processed or taken up by plants and microbes while ammonium is typically more stable and long-lived in the soil . Thus, a large portion of the added nitrate was likely removed or lost from the soil too rapidly to be detected in our sampling.

In addition to the expected N and P treatment effects on their respective available pools, our results also show that P additions can directly alter N availability (Figure 1). The effect of P addition on N availability was inconsistent, however, with P addition increasing, decreasing, or not altering N pools depending on the year and season (Figure 1, Figure 2). P addition has been shown to stimulate N uptake or denitrification, potentially decreasing soil availability (Bracken et al. 2015; Reed et al. 2007; Xia et al. 2023; Cole and Heil 1981), but it can also promote N mineralization, which could increase soil availability (Chen et al. 2016; Achat et al. 2010). The lack of a clear and continuous individual P effect exemplifies the large temporal shifts in biological demand and biogeochemical supply in dryland systems, where biological activity is closely tied to water availability (Austin et al. 2004; Noy-Meir 1973). Nevertheless, P additions consistently changed both pools of available N measured, showing the dependence of N availability on P supply.

While nutrient additions produced significant individual effects, the addition of both N and P together also produced consistently synergistic effects. N addition increased ammonium availability and P addition had little to no effect on ammonium; however, adding N and P together led to a larger increase in ammonium than N addition alone (Figure 2a). This interactive effect was also evident in the readily available $CaCl_2$-P pool and the higher effort enzyme-P pool in 2024 (Figure 3a). Ammonium and phosphate co-precipitate in soil when added together, which helps retain both nutrients in the soil by preventing leaching or other forms of loss (Adams 2015; Grunes 1959; Wei et al. 2024). Additionally, ammonium decreases the P sorption capacity of calcareous soils like those in our study site (Wei et al. 2024), which would help the fertilizer P remain in the easily soluble $CaCl_2$-P fraction. Organic P may have accumulated in the enzyme-P pool as a result of the increased supply of readily-available P forms after P addition, reducing the need to access this pool by investing in enzyme production (Sinsabaugh and Follstad Shah 2012; Cui et al. 2023).

Water is a major – but not absolute – driver of nutrient cycling

Our results demonstrate the important role water plays in nutrient cycling, but we also present evidence that soil nutrient responses to shifting nutrient availability (i.e. nutrient addition) are regulated, not driven, by water. Both water and P influenced soil N availability separately, and their interaction was temporally varied and limited to just effects on nitrate (Figure 1). Further, addition of either resource decreased soil N, meaning that both water and P independently stimulated removal of N from the soil, either through uptake or loss. This result is expected of water, as increased water availability would decrease soil nutrient levels through increased uptake stimulated by the favorable soil moisture conditions (Cortina et al. 2013; Hu and Schmidhalter 2005). However, the direct effect of P addition must mean that increases in P supply stimulate losses or removal of soil N in drylands regardless of water availability.

There is no clear consensus whether P limits plant growth in drylands (Belnap 2011; Lajtha 1987; Lajtha and Klein 1988; Lajtha and Schlesinger 1988b), though past studies have found that P does not limit microbial respiration or productivity (Choi et al. 2022; McHugh et al. 2017); this result supports other work suggesting that P may indirectly limit production through the limitation of other processes (e.g. ATP production, see Wu et al. 2010; Balemi and Negisho 2012). P addition has been shown to increase both N mineralization (Munevar and Wollum II 1977; Xia et al. 2023; Chen et al. 2017) and microbial N uptake (Bracken et al. 2015). Our results suggest that P deficiency limits processes related to N cycling (e.g. biological N fixation, nitrification, ammonification, and uptake) that remove available N from the soil. Additionally, N losses outweighed N inputs under P addition, emphasizing the importance of soil P to processes that decrease levels of available N in the soil.

Unlike soil N availability, which was altered by both water, N, and P additions, soil P fractions were resistant to independent changes in water and N availability. N did not directly affect any P fractions, and water significantly affected only a few P fractions, which were all involved in higher order interactions, particularly with N, making it difficult to quantify water’s individual effect on soil P supply (Figure 3.1). Despite the lack of strong individual effects, adding N and water together significantly affected all P fractions except for the strongly occluded and stable HCl-P. Separate N and water additions sometimes reduced specific P fractions (mainly citrate-P), but that effect was negated when adding them together. Water and N additions can independently stimulate nutrient uptake, explaining the observed decrease in soil P; conversely, adding both together could increase both nutrient uptake and P transformation from less available fractions (e.g. organic or occluded), balancing inputs and losses from the available pools. The interaction between N and water additions can be explained by a combination of a few factors. The co-precipitation of ammonium and phosphate (Adams 2015) or acidification by the N fertilizer and increased soil moisture (Jordaan et al. 2022b; Lines-Kelly 1992) could lead to higher rates of P uptake, P mineralization, and dissolution of mineral-bound P. Alternatively, if P scarcity limits N cycling as discussed earlier, the increased water and N availability could decrease the reliance on soil P for N acquisition.

This study has detailed the complex pair-wise interactions that exist between water, N, and P in drylands. A main goal of this study was to determine whether shifts in all three resources could interact to alter soil nutrient availability. Three-way ANOVA interactions between N, P, and water were present only in “high-effort” nutrient pools that are accessed through additional biotic processing like root exudation (citrate-P, enzyme-P, HCl-P, and ammonium; Figure 3.1). This interaction highlights the complex nutrient cycling dynamics present in resource-scarce drylands, as these pools appear to be altered only by large-scale shifts in all three essential resources used here. Processing ammonium into nitrate or producing organic acids and extracellular enzymes is energetically expensive (Li et al. 2020; Ström 1997; Sinsabaugh and Moorhead 1994; Lynch et al.

2005; Wang and Lambers 2020), and our results indicate that this energetic cost might be too high to consistently access these pools without additional water, N, and P.

In general, our results highlight the complex biogeochemical cycling dynamics present in dryland systems. Water plays a major role in nutrient cycling, especially of N, but this role is not pervasive or all-encompassing, since water did not directly affect most P fractions unless added in tandem with N. The observed changes in soil nutrient levels after resource addition can be traced to a few causes: biogeochemical processes like leaching and solubilization (Wei et al. 2024; R. Wang et al. 2022; Mehnaz et al. 2019) or biological responses stimulated by the favorable conditions created by resource addition (e.g. increased biological activity; Brown et al. 2022; Austin et al. 2004; Harpole et al. 2011; Hooper and Johnson 1999)). Water is a key factor driving changes in both the N and P cycles (Jordaan et al. 2022b; Austin et al. 2004), so it is no surprise that water altered the effect of N and P additions in most cases. However, our study shows that water is not the sole driver of nutrient cycling in this system, as N and P cycling also interacted to produce complex and unexpected effects on soil fertility.

CONCLUSION

Water, N, and P cycling dynamics are rapidly shifting in drylands in response to anthropogenic activities and climate change (Vitousek et al. 1997; Osborne, Bestelmeyer, et al. 2022; Scholes 2020; Austin et al. 2004; Brown et al. 2022). While our findings underscore water's importance to soil nutrient cycling in drylands, we show that changes to resources beyond water can also affect soil nutrient responses, and interactions between soil nutrients can also significantly influence soil fertility independent of water. We show that P may limit processes related to N cycling while the opposite is not true without sufficient water. Our work contributes to the growing evidence of the importance of P availability in balancing N inputs and losses in dryland ecosystems, potentially regulating the production of greenhouse gases like NO_X or N_XO. Future work should continue to explore this possibility to better understand the role of dryland regions in global biogeochemical cycles.

ACKNOWLEDGEMENTS

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AUTHOR CONTRIBUTION STATEMENT

Dylan J. Stover: Writing – original draft preparation, review and editing, Investigation, Methodology, Visualization, Formal Analysis, Project Administration, Data Curation. **Anthony J. Darrouzet-Nardi** - Writing – review and editing, Funding Acquisition, Conceptualization, Visualization. **Jennie R. McLaren:** Conceptualization, Funding Acquistion, Writing – review and editing, Methodology, Project Administration, Data Curation, Supervision.

DATA AVAILABILITY STATEMENT

Data will be made publicly available when the manuscript is published.

Chapter 4: Can drought benefit native grasses? Grassland responses to resource additions on a natural drought gradient in the Chihuahuan Desert

ABSTRACT

Healthy grasslands provide essential ecosystem services, but these systems are globally threatened by degradation from factors like overgrazing, invasive species, and climate change. Grasslands are especially vulnerable in drylands, where nutrient limitation due to these regions' inherently scarce soil nutrients poses an additional risk. To determine how grasslands respond to shifts in resource availability, we conducted a factorial resource addition experiment in the Chihuahuan Desert. Additionally, a severe drought during the experiment provided the opportunity to investigate how increasing aridity alters the plant community and its responses to resource addition. We asked: 1) how plants respond to separate and combined additions of water, N, and P and whether different plant functional groups (e.g. native grasses, forbs, invasive grasses) respond differently to these treatments; and 2) whether treatment effects differ between years with typical climate conditions versus years which were hotter and drier. We found that water was the only resource limiting plant growth, though N and P affected species diversity. Native grasses appeared to benefit most from watering, but the invasive Lehmann lovegrass was greatly reduced during the drought years while native grasses persisted and recovered after the drought ended. Understanding the implications of climate change and other key global change pressures for plant communities in these increasingly vulnerable ecosystems will be essential to future efforts to preserve and restore grasslands in dryland regions.

INTRODUCTION

Grasslands provide a myriad of ecosystem services, but the degradation of grasslands globally has greatly diminished their capacity to provide these services (Chen and Costanza 2024; Mueller et al. 2014; Zhao et al. 2020). Healthy grasslands provide erosion control (Fu et al. 2011; Bengtsson et al. 2019), improve soil moisture conditions (Macleod and Ferrier 2011) and improve carbon sequestration capacity (Lal 2019) while also increasing biodiversity (Scasta et al. 2016; Bock and Bock 1992) and facilitating human activities like livestock and agriculture (Egoh et al. 2018; Kemp and Michalk 2007). Drylands (regions where potential evaporation outweighs precipitation (Middleton and Thomas 1997)) cover nearly half of the global land surface (Millennium Ecosystem Assessment 2005) and also account for nearly half of global grasslands (Squires et al. 2018), making these regions especially important to our understanding of the causes and consequences of grassland decline globally.

Native grasslands in southwestern North America have been greatly diminished in the last 100 years (Weltzin et al. 1997). Throughout the Chihuahuan Desert, native grass species, such as black grama (*Bouteloua eriopoda*), once covering over 36 million hectares across the southwestern United States, have decreased substantially (Wright and Streetman 1958). For example, black grama grass experienced a loss of nearly 80% of basal area from 1915 to 1979 (Gibbens and Beck 1988) and an 85% reduction in dominance by 1998 (Peters and Gibbens 2006) in the Jornada Basin at the northern end of the Chihuahuan Desert in southern New Mexico. This decline is a result of many interacting factors including grazing – historically by livestock and both native (e.g. javelina) and non-native wildlife (e.g. oryx) (Reynolds et al. 2007; Archer et al. 2017; Bock and Bock 1993) – drought (Ohlert et al. 2025; Luo et al. 2025), and competition with shrubs (e.g. mesquite, creosote) or introduced grasses (Van Auken 2009; Pierce et al. 2019; Buerdsell and Lehnhoff

2023). The compounding effects of these factors has been shown to complicate native grass restoration and conservation and increase their vulnerability to degradation (Verwijmeren et al. 2014; Koerner and Collins 2014; Heitschmidt et al. 2005). The loss of grasslands in drylands decreases their ability to provide ecosystem services and reduces their resilience to future environmental pressures (Tariq et al. 2024; Egoh et al. 2018; Bengtsson et al. 2019). Improving our understanding of how desert grassland communities may respond to future environmental conditions will thus inform predictions of the broader impacts of global change in drylands.

Drylands are expected to undergo multiple global changes including warming, increases in both the frequency and severity of droughts (Bradford et al. 2020; Huang et al. 2017; Scholes 2020), and substantial changes in nutrient cycling and availability (Osborne, Bestelmeyer, et al. 2022; Austin 2011), necessitating a consideration of how natural plant communities will respond to global change when planning native grassland restoration efforts in these systems. Intensive land-use in arid and semi-arid regions (e.g. grazing, agriculture) has decreased soil water holding capacity and increased evaporative water losses and surface runoff (Vörösmarty and Sahagian 2000). Simultaneously, precipitation in drylands is becoming both more limited and increasingly variable (Bradford et al. 2020; Rudgers et al. 2018). Increased drought and aridity sharply decrease grass cover, productivity, and forage production for cattle in drylands (Buerdsell et al. 2022; Garbowski et al. 2020; Khumalo and Holechek 2005; Luo et al. 2025; McIntosh et al. 2019) while the effects of increased variability in precipitation patterns differs across the plant community based on interspecific differences (Rudgers et al. 2018; Garbowski et al. 2020). For example, black grama is a slow-growing, perennial C4 grass that primarily reproduces vegetatively, as favorable soil moisture conditions for seed germination are becoming increasingly rare (Moreno-de las Heras et al. 2016; Peters 2000). Conversely, Lehmann lovegrass (*Eragrostis lehmanniana*) is a major invasive grass in the Chihuahuan Desert, partly because of its rapid growth and prolific seed production in both wet and dry conditions (Frasier and Cox 1994). With changes to precipitation regimes and intensifying competition from invasive grasses, black grama restoration is expected to become more challenging as aridity increases (Peters 2002).

In addition to alterations to the water cycle, human activities are rapidly altering global biogeochemical cycles (Penuelas et al. 2020; Peñuelas et al. 2013; Vitousek et al. 1997). Human activity has altered the global C cycle (Bhatti et al. 2005), doubled the rate of terrestrial N accumulation and significantly increased atmospheric concentrations of N_2O and NO_x gases (Vitousek et al. 1997; Galloway et al. 2003; Penuelas et al. 2020), though recent evidence suggests that N availability is decreasing in terrestrial systems globally (Mason et al. 2022). Likewise, human activities (e.g. phosphate extraction, fertilizer application) have rapidly accelerated the transfer of P from the lithosphere (Yuan et al. 2018). Shifting resource availability (e.g. experimental nutrient addition) may alter the plant community composition or relative species abundance because plant species (e.g. native vs invasive grasses) can respond differently to shifting nutrient levels (Fransen et al. 2001; Clark and Tilman 2008; Xia and Wan 2008). Additionally, soil nutrient availability has been shown to limit plant growth (Chapin et al. 1986; Elser et al. 2007; Du et al. 2020) and interact with changing precipitation regimes (Bondaruk et al. 2025; Chapin et al. 1987; Wheeler et al. 2021; Yahdjian et al. 2011) in many ecosystems, making multiple resource limitation another potential process driving plant responses to global changes (Harpole et al. 2011; Rastetter and Shaver 1992). Many nutrient limitation studies in drylands have shown little to no plant response to nutrient addition (e.g. Lajtha and Schlesinger 1986; Holguin et al. 2025; Stephens and Whitford 1993). Studies showing positive plant responses to nutrient addition have most often included a concurrent water addition (Lajtha and Whitford 1989; Fisher et al. 1988; Gutierrez et al. 1988; Harpole et al. 2007), as nutrient limitation is often only exhibited when water availability is high (Bondaruk et al. 2025; Yahdjian et al. 2011; Yang et al. 2011; Hooper and Johnson 1999), demonstrating the strong relationship between water availability and nutrient limitation.

To preserve and restore native grasslands threatened by global change in the Chihuahuan Desert, we must develop our understanding of how the plant community interacts with naturally scarce resources (e.g. water and nutrients) and how interspecific interactions drive plant responses to shifting resource availability, rising temperatures, and increasing aridity. We asked how different plant functional groups (e.g. native grasses, forbs, invasive grasses) respond to separate and combined additions of water, N, and P. We hypothesized that growth of all plant functional groups would mainly be limited by water availability, and that nutrients would positively affect plant growth when water was present in sufficient amounts, indicating co-limitation or serial limitation by water and nutrients (Harpole et al. 2011). Our study site experienced a severe drought and heat wave in the second and third years of the experiment (Table 4.1), so we opportunely asked whether treatment effects differed between typical years and unusually hot, dry years. We hypothesized that plants would be more responsive to the watering treatment in the dry years, and nutrient-driven responses would be less apparent when water availability was lower.

METHODS

Study Site

This study site (latitude 32.511 N, longitude 106.799 W) was located on New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC) in southern New Mexico, USA, adjacent to the Jornada Experimental Range (JER). Average temperatures range from around 26 ºC in July to 4 ºC in January (Wainright 2006). Mean annual precipitation in the area is

247 mm, with about 53% of precipitation occurring during the summer monsoon (July 1 - September 30) (Greenland et al. 1997; Wainright 2006). The site was on the eastern slope of Mt. Summerford's alluvial fan collar (Monger 2006), and soils were classified as coarse-loamy, mixed, thermic Typic Haplargids. Livestock grazing has been excluded from this site since before 1936, though wild grazers (e.g. javelina and oryx) are commonly observed in the area.

The study site was in a native grassland dominated by black grama (*Bouteloua eriopoda*) with purple three-awn (*Aristida purpurea*), needle grama (*Bouteloua aristidoides*), introduced Lehmann's Lovegrass (*Eragrostis lehmanniana*), and annual forbs (including silverleaf nightshade (*Solanum elaeagnifolium*) and Palmer's Amaranth (*Amaranthus palmeri*)). Woody plants (honey mesquite (*Prosopis glandulosa*), creosote bush (*Larrea tridentata*), longleaf jointfir (*Ephedra trifurca*)) and prickly pear cactus (*Opuntia* sp.) were present throughout the site. When establishing our study plots, we designated plot locations to exclude woody plants from all plots and limit prickly pear cactus cover to a maximum of 10% within any plot.

Experimental Design

We conducted a factorial nitrogen, phosphorus, and water addition experiment from May 2022 to February 2025 to explore biogeochemical (Chapter 2), microbial (Chapter 3), and plant community responses to shifting resource availability. We added N, P, and water individually and in all possible combinations to determine individual and interactive effects of each, with 8 replicates per treatment. For nutrient addition treatments, we added nitrogen as 10 g ammonium nitrate (NH_4NO_3) per square meter per year and phosphorus as 5 g calcium dihydrogen phosphate hydrate ($CaH_4O_8P_2$) per square meter per year. For water addition treatments, we added eight mm of water by hand weekly throughout the 12-week monsoon season (July – September) each year for a total of 96 mm of added water per year. Each study plot was 2 m x 2 m in size and separated from all other plots by a minimum of 5 m and offset from each other along the slope to avoid runoff between plots.

Plant Community Composition

We measured total plant cover in each year of the experiment using a 1 m by 1 m quadrat divided into 25 equal squares, each representing 1% total of the 2 x 2 m plot, placed in the center of each plot, measuring a total of 25% of each plot. We measured species cover within each experimental plot in early October each year, after the end of the annual monsoon period but before plant senescence began. To calculate relative plant cover for each plot, we divided each cover value by the sum of all cover for that plot. To conserve native perennial grasses, we did not destructively harvest above-ground biomass to determine net primary productivity. Instead, we use plant cover as a measure of plant abundance to test effects of resource additions on plant growth.

Plant Tissue Nutrient Content

We measured shifts in plant tissue stoichiometry on leaf samples collected in early October of 2023 and 2024 from each experimental plot, after the end of the monsoon but before plant senescence began. We collected a minimum of 10 leaves from native grasses *(Bouteloua eriopoda*, *Aristida purpurea*, *Bouteloua aristidoides),* exotic Lehmann Lovegrass (*Eragrostis lehmanniana*), and annual forbs (*Amaranthus palmeri*, *Solanum elaeagnifolium*, *Croton pottsii* mostly) whenever they were present. Because of extreme drought and heat in these years, plant cover was minimal, which limited plant sampling efforts. Plant leaves were dried and ground using a mortar and pestle before analysis. When the plant material collected was insufficient to analyze species separately, we combined samples within functional groups within a single plot. If the combined amount was still insufficient for our analyses, we combined samples from the same functional group from plots that received the same experimental treatment. Subsamples were taken from dried and ground samples for elemental analysis.

Total C and N concentrations of leaf samples were determined using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen, GER). We measured leaf P concentration with a dry-ash digestion – 0.1 g of dried and ground samples of leaves were digested with 1 mL of 6 M hydrochloric acid. P content in digested samples was analyzed as phosphate (PO_4^{3-}) using a malachite green colorimetric microplate assay (BioTek Synergy H1 Multimode Reader; D'Angelo et al. 2001).

Statistical Analysis

We tested for differences in treatment effects on plant cover, diversity, and plant C, N, and P content across years and functional groups (native grasses, forbs, and introduced grass) using a multi-way analysis of variance (ANOVA) with N, P, water, functional group, and year as the main factors. When sample sizes were unbalanced, we used a Type II ANOVA to determine significant ANOVA effects. Effects were considered significant at $p < 0.05$ and marginal at $0.05 < p < 0.10$. N, P, and water were treated as binary dummy variables, where Control plots = (0, 0, 0), N addition plots = (1, 0, 0), P addition plots = (0, 1, 0), water addition plots = (0, 0, 1), and mixed treatments plots were the respective combination of these terms.

Assumptions of normality were tested using the Shapiro-Wilk Test. When needed, data were log-transformed to meet assumptions of normality. Data were analyzed using the "dplyr," "car," and "emmeans" packages in R Version 12.1.402 (Lenth 2025; Posit team 2024; Wickham et al. 2018, Fox & Weisberg 2019) and plots were made using the "ggplot2," "ggthemes," and "corrgram" R packages (Arnold 2024; Wickham 2016; Wright 2006).

RESULTS

Overarching Climate Conditions

Temperature and precipitation were considerably different across the three years of the experiment (Table 4.1). Year 1 was an average year with temperatures and rainfall aligning with historical averages. Years 2 and 3 were hotter and drier, with significantly more days above the historical maximum temperature and significantly less rainfall across both the monsoon season and the full year compared to historical averages.

Table 4.1: Changes in climate throughout the experiment. Average Annual Precipitation is 230mm, and average Monsoon Precipitation is 119.6mm. A heat wave is defined as consecutive days above the historical average maximum temperature of 36 ºC.

Year	Days above 36ºC	Longest Heat Wave	Total Monsoon (Jul-Sep) Precipitation (mm)	Total Monsoon Precipitation / Avg. Total Monsoon Precipitation	Total Annual Precipitation (mm)	Total Annual Precipitation / Avg. Annual Precipitation
2022	44	15	123.4	1.032	234.5	1.020
2023	72	54	46.2	0.386	112.6	0.490
2024	66	12	35.0	0.292	87.6	0.381

Plant Community Responses to Resource Addition

Native grasses (*Bouteloua eriopoda, Bouteloua aristidoides, Aristida purpurea*) and forbs (mainly *Amaranthus palmeri* and *Solanum elaeagnifolium*) were dominant in the study site, accounting for over 50-75% and 25-40% of total plant cover, respectively, throughout the experiment (Figure 4.1). Plant cover was highest in the first year and decreased in each year of the experiment as conditions became drier (Figure 4.1a, Figure S4.1). Water addition increased native grass cover in all three years of the experiment, decreased forb cover in the first year only, and had little effect on the introduced Lehmann lovegrass (Figure 4.1a, Table 4.2, Table S4.1). Nutrient additions of either N or P did not significantly affect plant cover of any functional group (Figure 4.1a, Table 4.2, Table S4.1).

Table 4.2. Multi-way ANOVA results for plant community characteristics and plant tissue nutrient concentrations with Year, Functional Group, and dummy variables for N, P, and water (see Methods) as main effects. Significant results (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) are displayed in blue, and marginal trends ($0.05 < p < 0.10$) are displayed in light orange. Functional Group was not included in the analyses for Shannon Diversity, Species Richness, or Species Evenness, so those boxes are filled grey.

	Plant Community Metrics				Plant Tissue Concentrations		
ANOVA Effects	Shannon	Richness	Evenness	Plant Cover	Plant C	Plant N	Plant P
Year	***	***	***	***	***	***	***
FxGroup				***	***	***	**
Year*FxGroup				***	***	**	.
N			*				
Year*N	.		*				
FxGroup*N					*		
Year*FxGroup*N							
P	**	**	*				
Year*P							
FxGroup*P							
Year*FxGroup*P					*		
N*P							
Year*N*P							
FxGroup*N*P							
Year*FxGroup*N*P							
Water	.	***	*	***			**
Year*Water	***		*		.		
FxGroup*Water				***			
Year*FxGroup*Water				***			
N*Water							
Year*N*Water							
FxGroup*Water							
Year*FxGroup*Water							
P*Water			.				
Year*P*Water							
FxGroup*P*Water				.			
Year*FxGroup*P*Water							
N*P*Water							
Year*N*P*Water							
FxGroup*N*P*Water							
Year*FxGroup*N*P*Water							

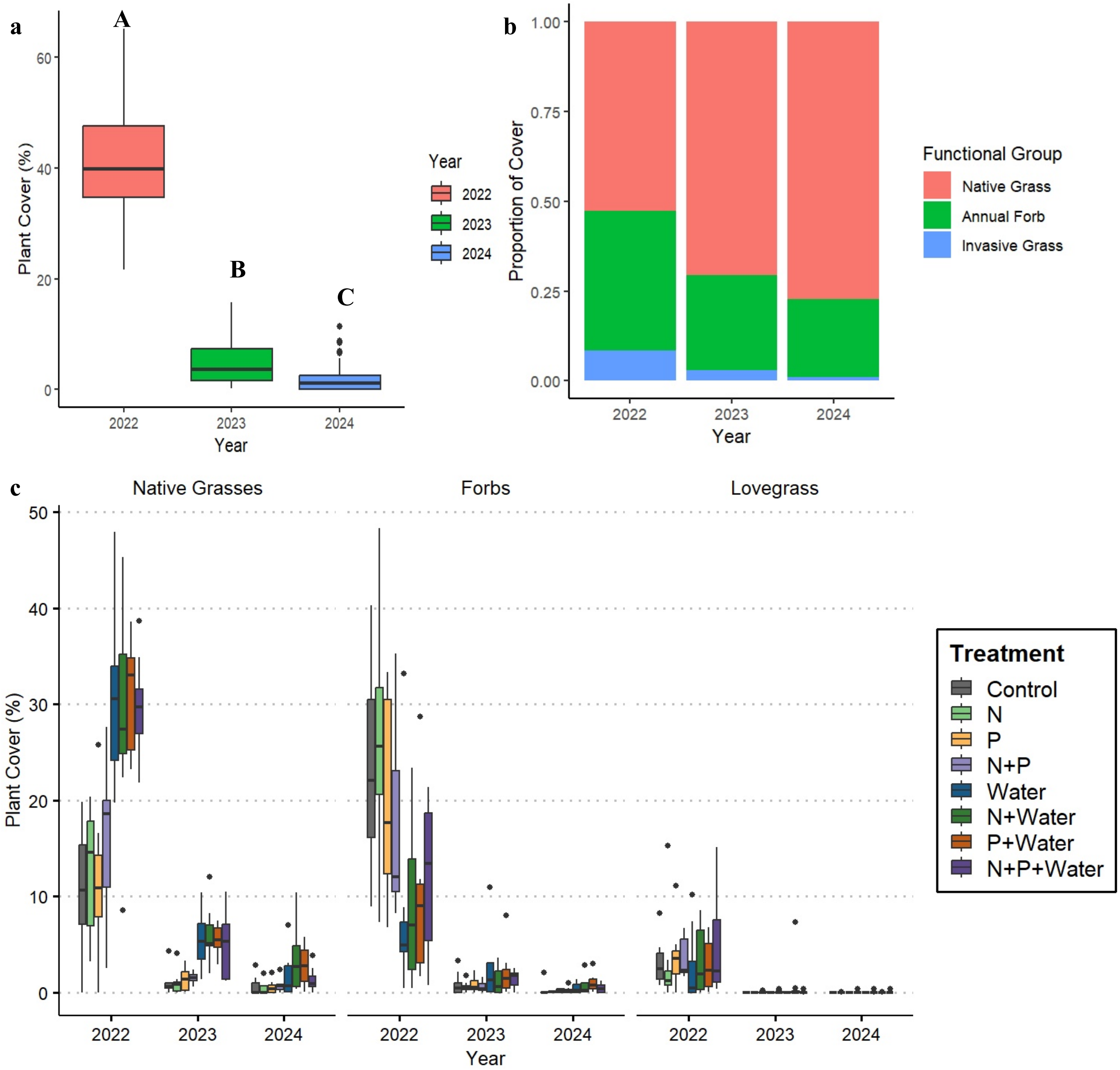
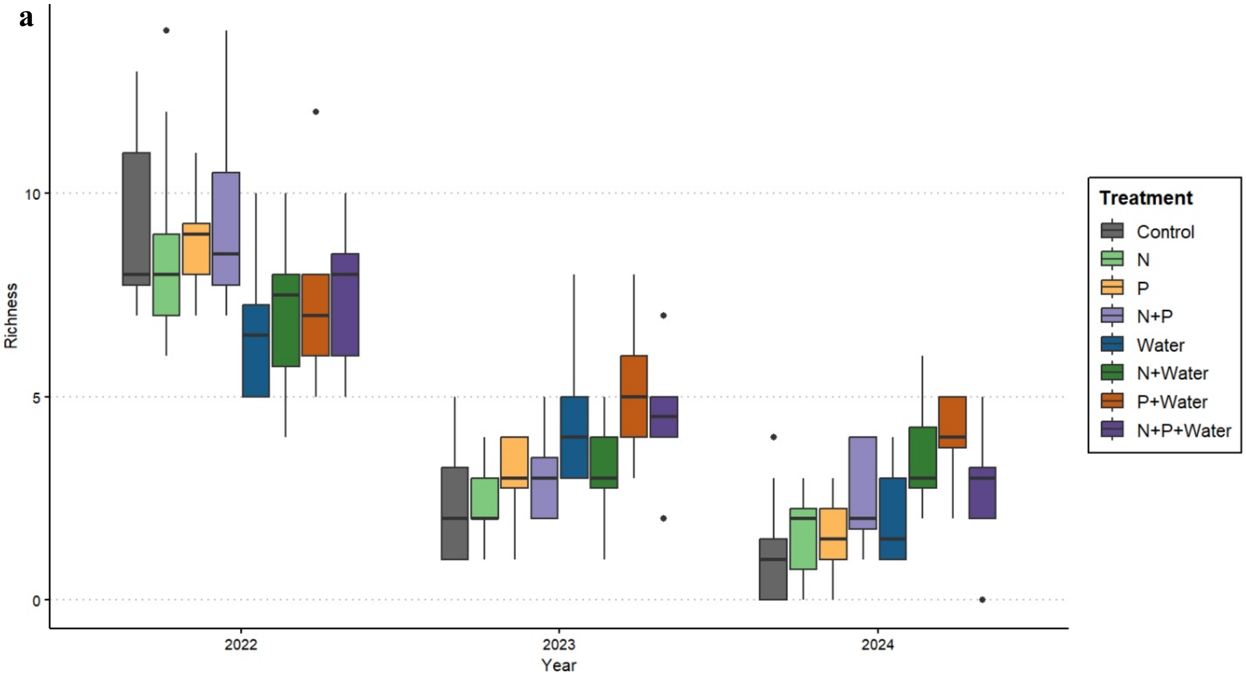


Figure 4.1. Changes in plant cover throughout the experiment. 2022 experience average rainfall and temperatures while 2023 and 2024 experienced hot and dry monsoon seasons (Table 4.1). a) Boxplots showing changes in total plant cover in each year of the experiment. Letters denote significant differences in plant cover at $p < 0.05$). b) Relative plant cover of the three plant functional groups analyzed. c) Boxplots showing changes in cover for each plant functional group in response to resource addition in each year of the experiment. For significant ANOVA effects, refer to Table 4.2.

Species richness and Shannon diversity were higher in 2022 than 2023 and 2024, while species evenness became more variable and at times higher in 2023 and 2024 compared to 2022 (Figure 4.2, Table 4.2, Table S4.2). Species richness and Shannon diversity both decreased in response to the watering treatment in 2022 then increased in response to independent water and P additions in 2023 and 2024 (Figure 4.2a-b, Table 4.2, Table S4.2). N addition increased species evenness in 2023 and 2024, while water addition increased evenness in 2024 and P addition increased evenness throughout the experiment (Figure 4.2c, Table 4.2, Table S4.2).



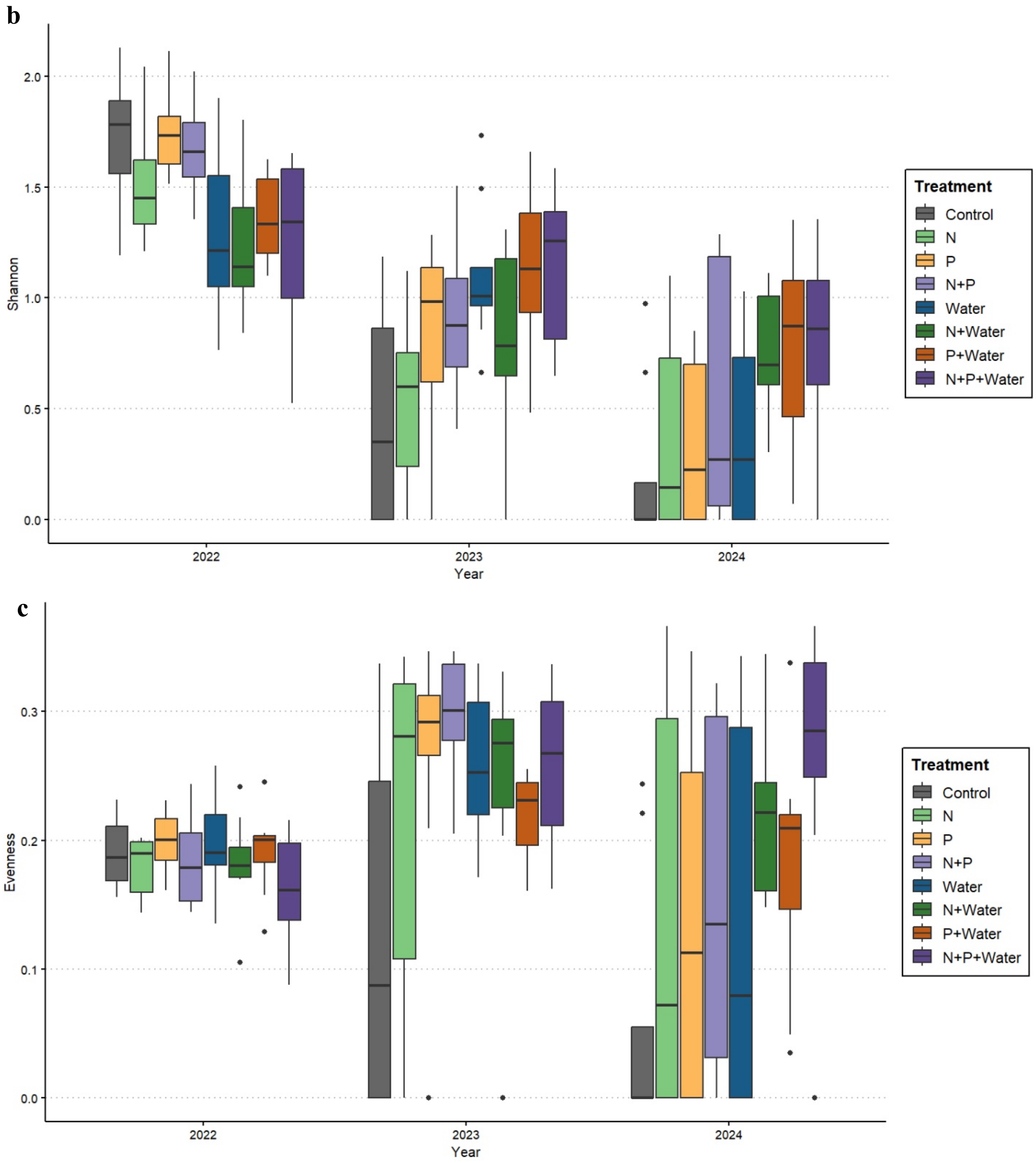
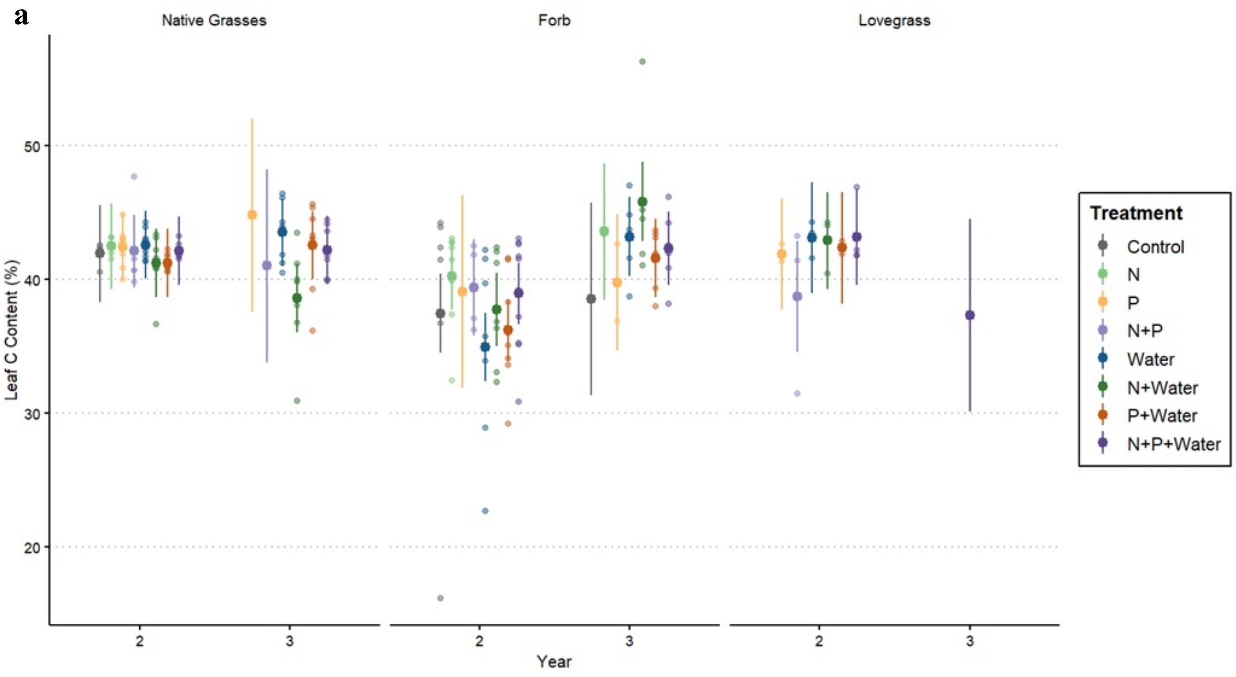


Figure 4.2. Changes in plant community composition in response to resource addition treatments throughout the experiment. a) Shifts in Species Richness (S); b) shifts in the Shannon Diversity Index (H); c) shifts in Species Evenness, calculated as H divided by the natural log of S (H/ln(s)). For significant ANOVA effects, refer to Table 4.2.

Plant Leaf Nutrient Concentrations

Generally, leaf C content was significantly affected separately by N and P additions and marginally affected by water – the N and P treatment effects were inconsistent across functional groups, and the P effect also changed across years (Table 4.2, Table S4.1). N addition caused a small but significant decrease in leaf C in native grasses only, and P additions decreased leaf C in *E. lehmanniana* (Figure 4.3a, Table S4.1). Watering significantly affected leaf P content, appearing to decrease total leaf P, though the data were too limited to draw contrasts between functional groups or years (Figure 4.3c, Table S4.1). Leaf C:N and C:P ratios were typically higher in 2024 than 2023 stemming from lower N and P contents, with the strongest effect coming from P additions and watering; N:P ratios did not have a clear trend (Table S4.3).



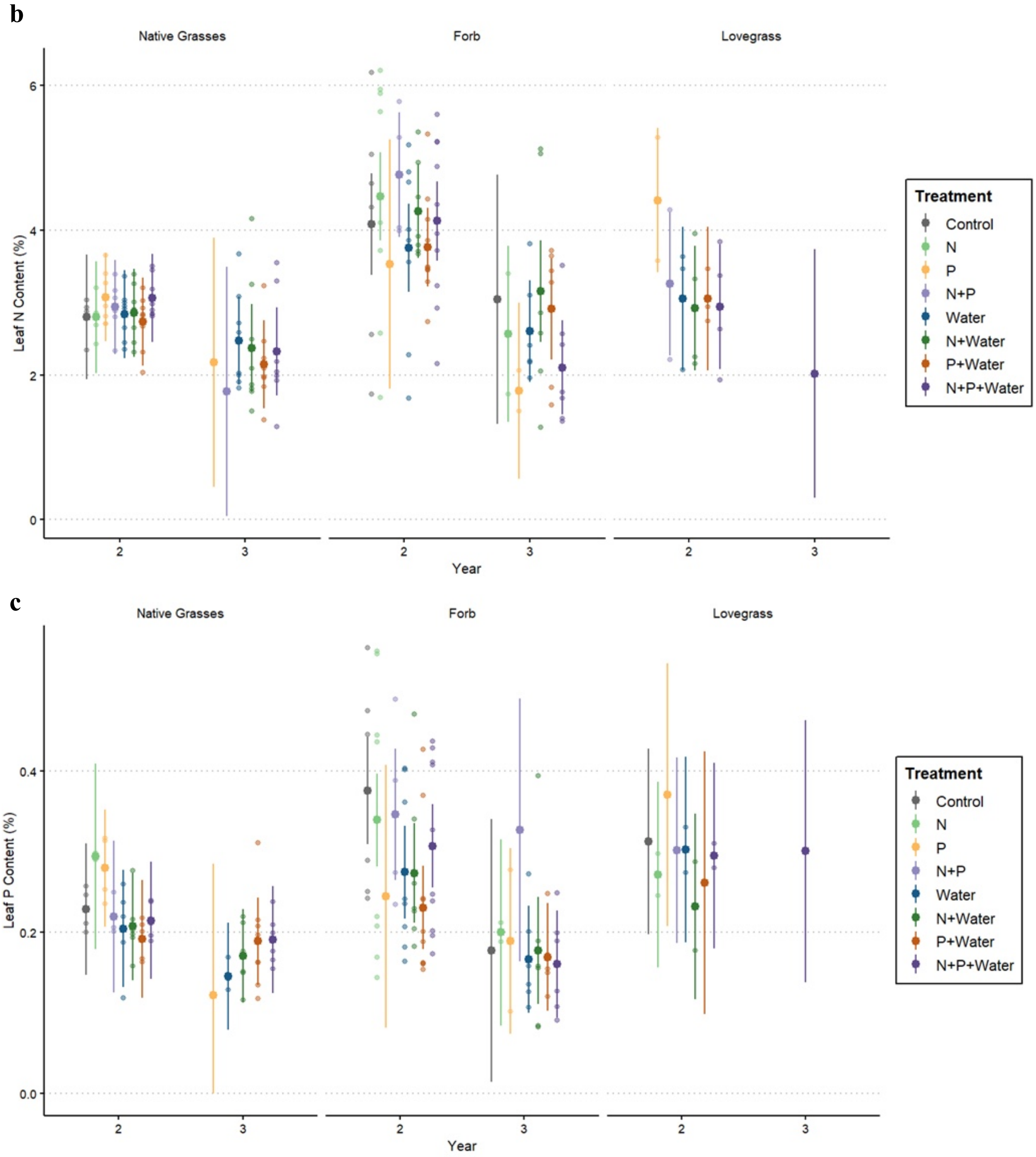


Figure 4.3. 95% confidence intervals for foliar (a) C, (b) N, and (c) P concentration in each plant functional group in response to resource additions treatments throughout the experiment. Due to limited plant growth, plant tissue samples could not be collected for every treatment in each year of sample collection. Figures present data for the samples we were able to collect (see Methods).

DISCUSSION

We conducted a factorial N, P, and water addition in the Chihuahuan Desert to determine how dryland plant communities will respond to predicted future shifts in resource availability. A severe drought during two of the three years of the experiment presented the opportunity to compare treatment effects and plant community composition between a year with typical rainfall and temperatures with years that were substantially hotter and drier. Generally, we found that water was the sole resource limiting plant cover in both dry years and years with typical rainfall, although native grasses were the primary group benefitted by additional watering (Figure 4.1a; Table 4.2). Nutrient (N and P) additions did not alter total plant cover but did influence the plant community composition, typically increasing diversity (P only) and species evenness (N and P) in the hot and dry years.

Water limitation outweighs nutrient addition's effects on the plant community

Water was the primary factor limiting plant cover during our study. Water additions dramatically increased native grass cover and decreased annual forb cover in year 1, with average ambient rainfall, then significantly increased cover in both native grasses and annual forbs in the hotter and drier years 2 and 3, while having little effect on invasive grasses (Figure 4.1a). The importance of water – and drought – to grassland productivity is globally consistent (Bondaruk et al. 2025; DeMalach et al. 2017), and the observed loss of species diversity after watering in the year with typical climate conditions is expected of an arid grassland released from water limitation (Harpole and Suding 2011; Hutchinson 1957). In the typical year, the supplemental water allowed native grasses to outperform annual forbs and invasive grasses (Figure 4.1), resulting in an increase in native grass cover. However, the subsequent hot and dry years saw an opposite response, where both native grasses and forbs – and species diversity – increased with watering, further demonstrating the importance of water limitation in determining productivity and community composition in this grassland.

The lack of nutrient addition effects on plant cover also aligns with past research showing minimal signs of nutrient limitation on grasses in the Chihuahuan Desert (Chapin et al. 1986; Holguin et al. 2025; Stephens and Whitford 1993). Although nutrient addition increases productivity in most types of grasslands (Bondaruk et al. 2025; DeMalach et al. 2017), this grassland system is primarily water limited (Buerdsell et al. 2022; Stephens and Whitford 1993; Yahdjian et al. 2011). While its dependence on water may supersede nutrient requirements and reveal nutrient limitation when water availability is high (Harpole et al. 2011), our results show no effect of nutrient additions on plant growth even when water was added alongside nutrients (Figure 4.1a; Table 4.2).

However, nutrient limitation in plants can also be detected through shifts in internal nutrient concentrations (Koerselman and Meuleman 1996). N and P additions at times decreased leaf C content in native and invasive grasses, respectively (Figure 4.3a), but these effects were not paired with increases in N or P content (Figure 4.3b-c), leading to an overall decrease in the C:N and C:P. Increased soil N or P availability should increase plant N or P content (Koerselman and Meuleman 1996), so it is possible that the plants responded by increasing N and P in tissues other than leaves (e.g. stems, roots). Alternatively, the lack of significant summer precipitation in the years when samples were collected (Table 4.1) may have limited nutrient uptake, preventing any significant response in internal nutrient concentrations. Foliar P concentrations did at times decrease in response to watering (Figure 4.3c), but this effect was inconsistent across functional groups and years. It is possible that the dry conditions decreased plant P uptake, and the rapid growth following watering diluted the P already in the leaves without increasing P uptake (Jarrell and Beverly 1981; Kandhol et al. 2024; Sardans and Peñuelas 2007). Koerselman and Meuleman (1996) found that N:P ratios of < 14 or > 16 can indicate N or P limitation, respectively, at a community level. The leaf N:P ratios from our study site suggest the presence of weak nutrient limitation by N or P, varying across functional groups, treatments, and years (Table S4.3); however, the lack of significant nutrient effects on cover or internal N and P concentrations underscore the greater importance of water limitation compared to nutrient limitation in this plant community.

Under the niche dimension hypothesis, species diversity should increase with the number of limiting resources, as each species can inhabit a specialized niche, promoting greater coexistence (Harpole and Suding 2011; Hutchinson 1957). Consequently, adding limiting resources (e.g. water and nutrients) is expected to decrease plant diversity by decreasing the niche space available, providing key insights about the factors limiting plant growth at the community level. Contrary to this hypothesis, we found that only water consistently influenced the plant community, with only minimal increases in diversity after P additions in the hot and dry years (Figure 4.2a-b). While N, P, and water additions separately increased species evenness in 2023 and 2024 but not 2022 (Figure 4.2c), this was more likely caused by the lack of significant plant growth due to the severe drought, as most study plots were bare. Because the severe drought experienced in these years greatly limited all plant growth, adding any amount of the most limiting resource (i.e. water) may have promoted growth across all functional groups while plant cover remained too low for competitive exclusion to occur.

Water was the primary factor limiting productivity in this ecosystem during our study period, consistent with other grasslands (Bredenkamp et al. 2002). Aside from minimal responses to nutrient addition, including shifts in plant leaf C content and community composition, the plant community only responded to water addition. While the increased growth in the dominant functional group (native grasses) after water addition aligns with expectations, the lack of nutrient treatment effects and the community-level responses to watering suggest that this plant community may need to receive very large amounts of supplemental water before the plants can exhibit signs of nutrient limitation.

Drought presents an opportunity for B. eriopoda restoration

Our results suggest that while native grasses can persist in drought years, the invasive *E. lehmanniana* had virtually no aboveground growth after two years of consecutive drought (Figure 4.1a). Although our experiment ended after three years, the following year (2025) received above-average rainfall, leading to a significant recovery in *B. eriopoda* but not *E. lehmanniana* in the study area (Valdovinos, Pers. Comm.). This pattern may be explained in part by differences in soil texture and topography, as *E. lehmanniana* was able to recover at sites further downslope from the mountain and its rain shadow and differ greatly in soil texture. Additionally, *E. lehmanniana* germination from the seed bank may have been reduced in this year, as seeds may have been buried or moved by this year's intense windstorms (National Weather Service 2025), which produced high levels of aeolian sediments partly because drought increases dust (Achakulwisut et al. 2019). We suggest that drought may be an unexpected ally to future efforts to restore *B. eriopoda* and control *E. lehmanniana*, though future research needs to track the plant community through drought and the subsequent post-drought recovery to provide a full picture of native and invasive grass responses to changing temperatures and precipitation patterns.

Our results show a sharp decline in aboveground growth in both *B. eriopoda* and *E. lehmanniana* during severe droughts*,* with *B. eriopoda* growing in small amounts while *E. lehmanniana* stopped nearly all aboveground growth (Figure 4.1), consistent with past studies

(Buerdsell et al. 2022; Fernández et al. 2002; Holguin et al. 2025; Luo et al. 2025). Buerdsell et al. (2022) found that during the summer monsoon, *B. eriopoda* requires slightly less rainfall than *E. lehmanniana* to increase its aboveground growth, possibly explaining why the native *B. eriopoda* continues to grow in dry conditions while *E. lehmanniana* does not. In a system with scarce and heterogeneous precipitation (Collins et al. 2008; Noy-Meir 1973), even a slight difference in the amount of precipitation required for growth may be large enough to provide a small competitive advantage for the native species.

However, key similarities and differences between the two species require further consideration. Perennial grasses can allocate more resources to root growth in dry seasons and can remain dormant to survive droughts (Sprague 1933; Coupland and Johnson 1965; Buerdsell et al. 2022), but *E. lehmanniana* also maintains a highly viable seedbank that can persist in the soil for years (Voigt et al. 2004; Anable et al. 1992). At the edge of its geographic range *E. lehmanniana* can behave as an annual or transient grass on account of its robust seedbank (Crimmins and McPherson 2008). *E. lehmanniana* may reappear when moisture conditions are sufficient, either through vegetative growth or germination from the seed bank while *B. eriopoda* primarily spreads vegetatively and rarely propagates by seed (Moreno-de las Heras et al. 2016; Crimmins and McPherson 2008). The strong positive effect of supplemental watering on native grasses but not *E. lehmanniana* (Figure 4.1a) indicates that drought may favor native grasses, which maintain a dormant root system, potentially allowing them to quickly utilize soil moisture as it becomes available rather than relying on germination from the seed bank like *E. lehmanniana* (Crimmins and McPherson 2008; Moreno-de las Heras et al. 2016; Buerdsell and Lehnhoff 2023).

One last consideration for grass restoration is grazing, which can alter the plant community and compound with other stresses like drought to impact productivity (Allington and Valone 2014;

Bai et al. 2001; Heitschmidt et al. 2005; Koerner and Collins 2014; Scasta et al. 2016). While cattle grazing has been excluded from this site since before 1936 (Rango et al. 2002), grazing by javelina and oryx was common in the study site, impacting the plant community by clipping grasses nearly to the ground (Stover, Pers. Obs.; Anderson, Pers. Obs.). This study did not focus on grazing, so we assume that grazing pressure was equal across all study plots. Persistent removals of *E. lehmanniana* by herbivores can greatly decrease aboveground growth and deplete the seedbank (Crimmins and McPherson 2008) – cattle have been shown to prefer *E. lehmanniana* over *B. eriopoda* when summed across a full year (Reese 1980), and if wild herbivores have similar preferences, grazing may provide the persistent removals needed to effectively control *E. lehmanniana* recruitment.

Grazing and drought also interact to alter the plant community, and this relationship can differ across species, functional groups, and climate (Loeser et al. 2007; Verwijmeren et al. 2014). Drought and grazing both typically decrease productivity, but moderate grazing tends to increase species diversity, though this effect can be smaller in drought years (Heitschmidt et al. 2005; Koerner and Collins 2014; Loeser et al. 2007). In our experiment, species richness and diversity both decreased dramatically in drought years compared to the wet year (Figure 4.2a-b), suggesting that this plant community responded more to drought than grazing, possibly because forage levels were too low to produce a response to grazing (Heitschmidt et al. 2005). Future work should explore the relationship between grazing intensity and drought severity on plant communities to determine how interactions between these two pressures may alter plant communities in dryland regions.

CONCLUSION

Our results demonstrate the central role of water as a driver of plant cover and composition in dryland ecosystems and the influence that climate (e.g. temperature, precipitation) has on plant responses to resource additions. Supplemental watering benefitted native grasses but either decreased or did not affect annual forbs and invasive grasses across all years of the study, suggesting that supplemental watering may favor native species regardless of the overarching climate. Nutrient addition did not influence plant growth even when water availability was high, demonstrating the plant community's ability to satisfy nutrient demand despite the characteristic scarcity of drylands. However, both water and nutrient additions increased species diversity in the two drought years, likely because plant growth was so limited that any increase in resource availability was sufficient to stimulate plant growth without facilitating enough growth to create significant competition. Further work should explore whether the relationship between drought and resource addition effects is influenced by other factors like the relative native and invasive grass abundance, physical soil properties, or topographic position to better understand how dryland plant ecosystems will respond to growing global change pressures.

We found that *B. eriopoda* is both more resistant to drought and more responsive to summer watering treatments than *E. lehmanniana*. Although its competitive advantage is slight, drought conditions may favor *B. eriopoda* over *E. lehmanniana*, presenting a possible opportunity for *B. eriopoda* restoration and invasive grass control. The combined stresses of herbivory, drought, and heat no doubt have complex interactive implications for native grasses like *B. eriopoda*. Future work should explore how the productivity and composition of dryland plant communities respond to and recover from the compounded effects of these stressors. Understanding the implications of climate change and other key global change pressures for plant communities in these increasingly vulnerable ecosystems will be essential to future efforts to preserve and restore dryland regions.

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AUTHOR CONTRIBUTION STATEMENT

Dylan J. Stover: Writing – original draft preparation, review and editing, Investigation, Methodology, Visualization, Project Administration, Data Curation. **Elizabeth A. La Rue** - Writing – review and editing. **Jennie R. McLaren:** Conceptualization, Funding Acquistion, Writing – review and editing, Methodology, Project Administration, Data Curation, Supervision.

DATA AVAILABILITY STATEMENT

Data will be made publicly available when the manuscript is published.

Chapter 5: Evidence of microbial phosphorus limitation in the Chihuahuan Desert: An integrative definition of resource limitation reveals previously unseen limitations in dryland microbial communities

ABSTRACT

Resource limitation occurs when scarcity of one or more resources (e.g. water, soil nutrients) constrains biological activity or growth. While the signatures and effects of resource limitation have been thoroughly investigated in plants and plant communities, our understanding of limitation in microbial communities remains lacking despite widespread evidence that microbes experience resource limitation and that global shifts in resource availability will have complex effects on microbial function. To investigate microbial resource limitation and responses to shifting resource availability, we conducted a factorial resource addition experiment and measured a suite of microbial response variables. We found that, while water was the primary factor limiting microbial growth, the microbial community was also experiencing serial limitation by N and P. Additionally, we demonstrated evidence that plant-microbe interactions influence microbial responses to resource addition. By recognizing the importance of both plant-microbe interactions and limitation by both N and P in drylands, we raise new questions about dryland biogeochemistry and how it will respond to global change pressures.

INTRODUCTION

Under its most basic definition, nutrient limitation occurs when supply of an essential nutrient is too low to support organismal growth (Harpole et al. 2011), but nutrient scarcity can also alter biological processes not directly related to growth (Bracken et al. 2015; Saito et al. 2008; Sinsabaugh and Follstad Shah 2012). For example, changes in nitrogen (N) supply can influence soil carbon (C) stocks (Averill et al. 2018; Ramirez et al. 2012; Anjum and Khan 2021) or enhance other soil nutrient pools by increasing potential extracellular enzyme production (Sinsabaugh et al. 2009; Xu et al. 2020). Likewise, increased phosphorus (P) availability can accelerate litter decomposition or increase N mineralization (Bracken et al. 2015; Güsewell et al. 2002) and has been shown to influence biological processes related to N uptake and use (see Chapter 2; (Reed et al. 2007). Accordingly, an improved understanding of nutrient limitation is increasingly critical as human activities and climate change have brought drastic changes to global C, N, and P cycles (Vitousek et al. 1997; Penuelas et al. 2020).

Despite widespread documentation of ecosystem responses to shifting nutrient availability (Ramirez et al. 2012; Sinsabaugh et al. 2015; Du et al. 2020; Clark and Tilman 2008; Goldberg and Miller 1990), our knowledge of nutrient limitation in microbial communities is lacking, both due to the inherent difficulty in detecting microbial nutrient limitation (Cui et al. 2023; Sinsabaugh and Follstad Shah 2012; Hobbie and Hobbie 2013) and because most nutrient limitation studies have focused primarily on plants (Chapin et al. 1986; Miransari 2011; Čapek et al. 2018). While plant limitation can be easily detected from changes in growth or tissue stoichiometry (Du et al. 2020; Koerselman and Meuleman 1996), signatures of microbial limitation can include a broad and variable range of responses including shifts in biomass or respiration (Ramirez et al. 2012), internal stoichiometry (Cleveland and Liptzin 2007), or extracellular enzymatic activity (Cui et al.

2025; Sinsabaugh and Follstad Shah 2012). Nevertheless, microbial N and P limitation and co-limitation have been shown to be globally widespread (Cui et al. 2025). A recent model (Cui et al. 2023) employs the Threshold Elemental Ratio to determine microbial limitation by measuring microbial investments to acquire C, N, and P (e.g. extracellular enzyme activity) under the assumption that enzyme production is costly and microbes will invest the most energy to acquiring resources in limited supply (Allen and Gillooly 2009; Sinsabaugh et al. 2009). This model provides a novel and robust approach to directly detect microbial limitation when traditional approaches are insufficient or implausible (Čapek et al. 2016; Cui et al. 2025; Hobbie and Hobbie 2013). Effectively and directly detecting microbial limitation can help to address fundamental questions about limitation in microbial communities and their potential responses to shifts in global nutrient pools.

The relationship between resource limitation and the processes affected by scarcity is further complicated by the complex interactions that exist between soil resources. For example, N but not P availability is essential to extracellular enzyme production, which can increase C or P supply (Sinsabaugh and Moorhead 1994); however, N uptake is regularly limited by P availability (Bracken et al. 2015; Reed et al. 2007). Additionally, co-limitation by N and P is globally prevalent in both microbial and autotrophic communities (Harpole et al. 2011; Cui et al. 2025; Du et al. 2020), which can simultaneously experience limitation by the same or different resources. Plants and microbial communities can form competitive or mutualistic relationships depending on organismal needs, resource availability, or environmental conditions (Karst et al. 2008; Čapek et al. 2018) necessitating a consideration of how these relationships might influence ecosystem responses to resource limitation and co-limitation. Despite evidence that plant-microbe interactions (both competitive and collaborative) can significantly impact primary productivity and biogeochemistry, most studies of limitation have focused on plants or microbes in isolation (Čapek et al. 2016; Zechmeister-Boltenstern et al. 2015; Zhu et al. 2017), resulting in a gap in our understanding of how interactions between above- and belowground processes alter responses to resource scarcity.

This knowledge gap is especially salient in dryland regions, where inherent resource scarcity (Schlesinger et al. 1990; Jordaan et al. 2022a) and highly variable, primarily pulse-driven, plant growth and microbial activity (Luo et al. 2025; Gherardi and Sala 2019; Noy-Meir 1973; Collins et al. 2008) can help answer questions about the link between resource limitation and plant-microbe interactions. Addressing these questions in drylands is particularly important, as these regions are highly sensitive to global change (Scholes 2020; Huang et al. 2017), play a major in role in global C, N, and P cycling (Ahlström et al. 2015; Weber et al. 2015; Elbert et al. 2012; Belnap 2011) and have unique biogeochemistry compared to mesic systems. For example, oil organic matter, the typical storage and proximate source of organic N and P, is scarce in drylands, potentially rendering living biotic pools such as microbial biomass more important to organic nutrient cycling and storage (Schimel and Bennett 2004; Collins et al. 2014; Rudgers et al. 2018). Co-limitation by water and N is widespread in drylands (Yahdjian et al. 2011; Bondaruk et al. 2025), but – despite evidence of P's importance as a potentially limiting resource in arid regions (Belnap 2011; Cui et al. 2025) – only a few studies have also considered P as a limiting factor with mixed results . Further, because plant growth is largely tied to water availability (Brown et al. 2022; Cleverly et al. 2016; Huxman et al. 2004), the strength of plants' influence on the system may change significantly between wet (strong plant influence) and dry (weak plant influence) periods (i.e. monsoon seasons or drought years) while the microbial community remains active throughout the year.

In this study, we explored how microbial stoichiometry responds to shifts in N, P, and water availability in both seasons with weak and with strong plant influence and whether these responses are reflected in microbial efforts to acquire C, N, and P. First, we asked if microbial stoichiometry shifts in response to resource addition. We hypothesized that, if the system is co-limited by water and either N or P, water addition would increase microbial biomass C (MBC), while N and P additions would only increase MBC with sufficient water. Additionally, N and P additions would increase internal microbial N and P concentrations, respectively, and P addition would also positively affect microbial N as N uptake is biochemically dependent upon P availability (Xia et al. 2023). Second, we asked whether shifts in microbial stoichiometry would coincide with shifts in nutrient demand or acquisition effort in the form of extracellular enzyme activity. We expected N and P additions to decrease the activity of N- and P-acquiring enzymes, respectively, as readily available nutrients would decrease the need for investment in N or P acquisition. We also hypothesized that if the microbial community is limited by N or P, adding N to the system would increase the production of nutrient acquiring enzymes to help acquire limiting nutrients, because enzyme production requires large amounts of N (Sinsabaugh and Moorhead 1994). For example, if P is limiting, elevated N supply would increase P-acquiring enzymes. Meanwhile, if both N and P are limiting factors, concurrent N and P additions may increase microbial effort to acquire C through the production of C-acquiring enzymes (Bracken et al. 2015), generating a corresponding increase in microbial biomass C. Finally, we asked if changes in plant-microbe interactions associated with seasonal changes would influence microbial responses (e.g. internal nutrient content and enzyme production) to resource addition. Plant-microbe competition should decrease when the system transitions from strong to weak plant influence, so it is possible that, once released from this competition, microbes could increase enzyme production after the growing season to process that season's fresh plant litter.

METHODS

Study Site

This study was conducted at the Jornada Experimental Range (JER) in southern New Mexico as part of a factorial nitrogen, phosphorus, and water addition experiment from May 2022 to February 2025 (see Chapter 3, this dissertation, for detailed description of study site and experimental design). In short, the study site was in a semi-arid grassland dominated by black grama (*Bouteloua eriopoda*), a native perennial grass, and Lehmann lovegrass (*Eragrostis lehmanniana*), an introduced annual grass. The study site receives around 247 mm of precipitation annually (Greenland and Anderson 1997). N, P, and water were added individually and in all possible combinations to determine individual and interactive effects of each. Nitrogen was added as 10 g ammonium nitrate (NH_4NO_3) per square meter per year, and phosphorus was added as 5 g calcium dihydrogen phosphate hydrate ($CaH_4O_8P_2$). 8 mm of water were added weekly throughout the 12-week monsoon season (July – September) each year for a total of 96 mm of added water per year.

Sample Collection

We collected soil samples from each plot to a depth of 10 cm in 2022, 2023, and 2024. Each year, samples were collected at three time points throughout the growing season: 1) Peak Season (PS) – mid-August, with high growing activity; 2) Peak Biomass (PB) – early- to mid-November, with low growing activity and biomass just beginning to senesce; 3) Winter (W) – late January to early February, with low plant activity and biomass already senesced.

Because of the spatial heterogeneity within and between plots, soil respiration (CO_2 flux) was collected from the edge of one black grama patch in each plot biweekly throughout each monsoon season using an EGM5 Portable CO_2 Gas Analyzer (PP Systems, Amesbury, MA, USA). When black grama was not present in a plot, respiration samples were collected from beside the largest patch of vegetation within the plot.

Microbial C/N/P Concentrations

We measured microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) using modified chloroform fumigation methods (Brookes et al. 1985). We extracted samples before and after a 24-hour chloroform fumigation then subtracted the pre- and post-fumigation values for each nutrient. In the first year of the experiment, the fumigation used 5 g of soil placed in a 250 mL Erlenmeyer flask with 2 mL of chloroform. In the second and third years, the fumigation used 10 g of soil placed in a 250 mL Erlenmeyer flask with 3 mL of chloroform, and these samples were split into two 5 g subsamples for extractions after fumigation.

In the first year, we extracted pre- and post-fumigation soil samples in 0.5 M potassium sulfate for 2 hours before filtering through glass filter paper to measure MBC, MBN, and MBP. In the second and third years of the experiment, one pre-fumigation sample and one post-fumigation subsample were extracted in 0.5 M potassium sulfate as before to measure MBC and MBN. The remaining pre-fumigation and post-fumigation sub-samples were extracted in 0.5 M sodium bicarbonate (Olsen-P; Olsen 1954) to measure MBP.

MBC and MBN were analyzed using a Shimadzu CN Analyzer (Shimadzu Scientific Instruments, Inc., Columbia, Maryland, USA). MBP was measured using a colorimetric malachite green assay with a BioTEK Synergy HT microplate reader (BioTek Instruments Inc., Winooski, VT, USA). Although MBP was measured with two different extractants (0.5 M potassium sulfate and Olsen-P), alternate values were used regardless of extraction type for statistical analysis.

Potential Exoenzyme Activity

We analyzed soils collected during the peak growing season (mid-August) and winter (late January – early February) only for potential hydrolytic and oxidative enzyme activities using standard high-throughput microplate protocols (Saiya-Cork et al. 2002; McLaren et al. 2017). Samples were stored at -80 ºC until analyzed. We measured hydrolytic extracellular enzyme potential for enzymes associated with carbon cycling – α-1,4-glucosidase (Agluc), 1-4-β-glucosidase (Bgluc), cellobiohydrolase (Cello), and β-1,4-xylosidase (Xylo), nitrogen cycling – leucine aminopeptidase (LAP) and β-1-4-N-acetylglucosaminidase (NAG), and phosphorus cycling – acid phosphatase (Phos) and phosphodiesterase (PhosD). We also measured the oxidative enzymes phenol oxidase (Phenol) and peroxidase (Perox), which help decompose recalcitrant organic matter (Sinsabaugh 2010).

We first blended 1 g of thawed soil with 125 mL of modified universal buffer at a pH ranging from 6.75 to 7.44, according to the average measured soil pH at time of collection. Next, we pipetted the soil slurries into 96-well opaque microplates with eight analytical replicates per sample. Fluorescing, 4-methylumbelliferone (MUB) tagged substrate (4-MUB- α-D-glucoside, 4-MUB-β-D-glucoside, 4-MUB-β -D-cellobioside, 4-MUB- ß-D-xyloside, 4-MUB-N-acetyl-β-D-glucosaminide, 4-MUB-phosphate, bis-(MUB)-phosphate) or 7-amino-4-methylcoumarin (MC) tagged substrate (L-Leucine-7-amido-4-methylcoumarin hydrochloride) were added to each hydrolytic enzyme assay. We incubated the hydrolytic enzyme assays at room temperature (20 °C) for 3 hours, measuring fluorescence every 30 minutes to ensure a linear rate of reaction. Background fluorescence was measured for soil, substrate, and quenching of MUB or MC by soils, and we used MUB/MC standard curves to calculate the rate of substrate hydrolysis. We measured oxidative enzymes using L-3,4 dihydroxyphenylalanine (L-DOPA) and hydrogen peroxide (perox only) as substrate and incubating for 23 - 25 hours. Sample fluorescence of hydrolytic enzymes and oxidative enzyme color absorbance was measured at 360 nm excitation and 460 nm emission, respectively, using a BioTek Synergy HT microplate reader (BioTek Instruments Inc., Winooski, VT, USA).

Statistical Analysis

We tested for differences in treatment effects on exoenzyme activity and microbial C, N, and P across years and seasons using a multi-way analysis of variance (ANOVA) with N, P, water, season, and year as the main factors with effects considered significant at $p < 0.05$ and marginal at $0.05 < p < 0.10$. N, P, and water were treated as binary dummy variables, where Control plots = (0, 0, 0), N addition plots = (1, 0, 0), P addition plots = (0, 1, 0), water addition plots = (0, 0, 1), and mixed treatments plots were the respective combination of these terms. We used Type II ANOVA to account for an unequal number of samples across treatments for the extracellular enzymatic potential activities.

We calculated Pearson's correlation coefficients between extracellular enzymatic potential activities, microbial stoichiometry, and the available nutrient pools measured in chapter 2 of this dissertation. While correlations between enzymatic activity and other variables were limited to only Peak Season and Winter (when exoenzymes were measured), the correlations between microbial stoichiometry and available nutrients used data from every season.

We tested microbial N and P limitation (MNL and MPL, respectively) using an extracellular enzyme stoichiometric model (Cui et al. 2023):

$$\mathrm{MNL} = \ln\left(\frac{1.5 \times \mathrm{n_0}}{\mathrm{EEA_{C:N}}}\right), \tag{5.1}$$

$$\mathrm{MPL} = \ln\left(\frac{1.5 \times \mathrm{p_0}}{\mathrm{EEA_{C:P}}}\right), \tag{5.2}$$

$$\mathrm{EEA_{C:N}} = \left(\frac{\mathrm{C-acquiring\ enzymes}}{\mathrm{N-acquiring\ enzymes}}\right),\ \mathrm{EEA_{C:P}} = \left(\frac{\mathrm{C-acquiring\ enzymes}}{\mathrm{P-acquiring\ enzymes}}\right)$$

where n_0 and p_0 are normalization constants denoting the baseline of microbial investments in enzyme production, or the microbial demand for C by C-acquiring enzymes when N and P are not limiting. Normalization constants are derived from standardized major axis (SMA) regressions of extracellular enzyme activity: $\mathrm{n_0} = \mathrm{e^{intercept}}$ in the regression of ln(BGluc)~ln(NAG+LAP) and $\mathrm{p_0} = \mathrm{e^{intercept}}$ in the regression of ln(BGluc)~ln(Phos) (Figure S5.1; see Cui et al. 2023 for more details). MNL and MPL > 0 show the potential for N and/or P limitation relative to C availability for the microbial community; larger numbers indicate stronger limitation. We tested for microbial limitation averaged across the full dataset, then separated the dataset by season and year to explore intra-annual seasonal trends in limitation.

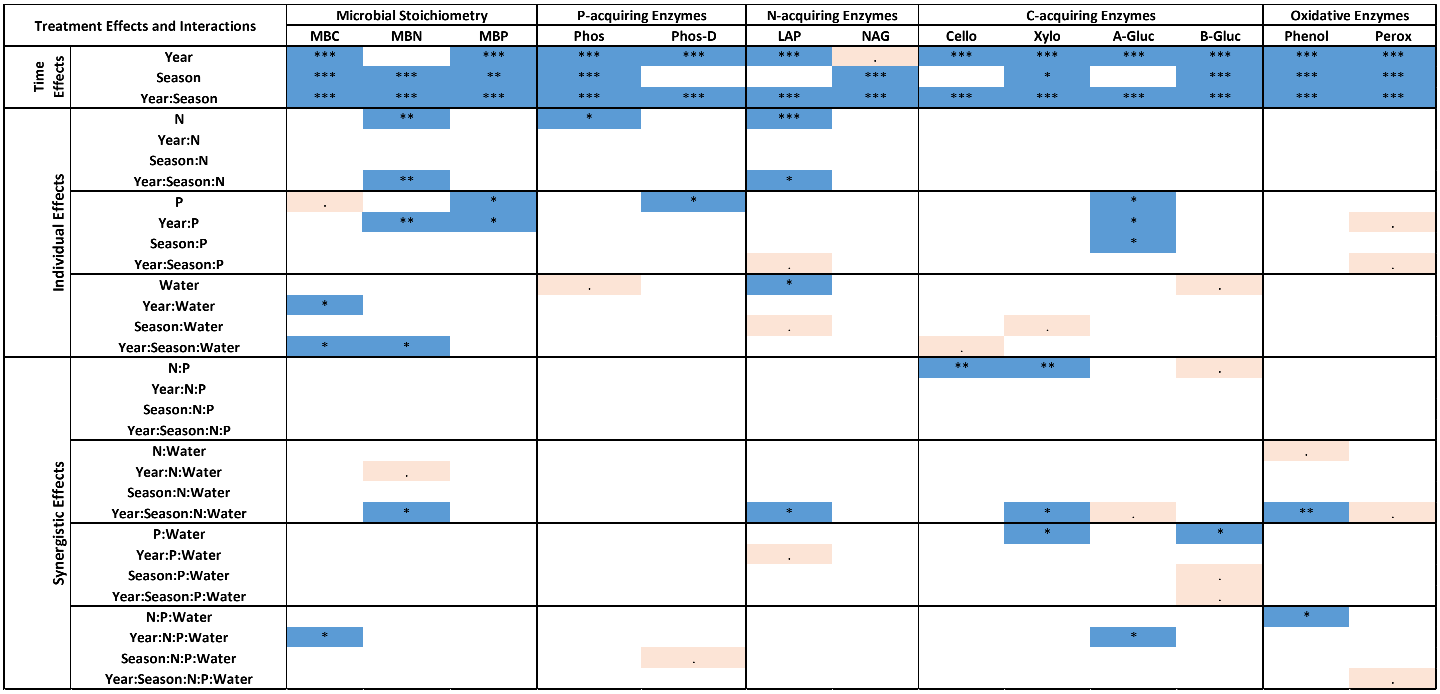
Assumptions of normality were tested using the Shapiro-Wilk Test. When needed, data were log-transformed to meet assumptions of normality. Data were analyzed using the "dplyr," "car," "lmodel2," and "emmeans" packages in R Version 12.1.402 (Lenth 2025; Posit team 2024; Wickham et al. 2018; Fox & Weisberg 2019; Legendre 2025), and plots were made using the "ggplot2," "ggthemes," and "corrgram" R packages (Arnold 2024; Wickham 2016; Wright 2006).

RESULTS

Microbial Responses to Resource Addition in Plant- vs Microbe-Dominated Seasons

There was significant variation across years and seasons for Microbial biomass C, N, and P (Figure 5.1, Table S5.1). MBC consistently decreased between Peak Season (PS) and Peak Biomass (PB) in each year and generally decreased across the three years of the experiment until

Winter of the third year when MBC returned to original levels. (Figure 5.2a). Seasonal patterns in MBC between PB and Winter were less consistent, with little apparent change in some years, and increases in others (Figure 5.2a). In contrast, MBN was relatively consistent across seasons and years, except for increases between PB and winter in the third year of the experiment which paralleled the increase seen in MBC during the same time period (Figure 5.2b). Seasonal variation in MBP differed between years, with little variation in year 1 but variation between seasons in years 2 and 3, with highest MBP in year 2 during PS, but highest MBP in year 3 during PB (Figure 5.2c).



Treatment Effects and Interactions		Microbial Stoichiometry			P-acquiring Enzymes		N-acquiring Enzymes		C-acquiring Enzymes				Oxidative Enzymes	
		MBC	MBN	MBP	Phos	Phos-D	LAP	NAG	Cello	Xylo	A-Gluc	B-Gluc	Phenol	Perox
Time Effects	Year	***		***	***	***	***	.	***	***	***	***	***	***
	Season	***	***	**	***			***		*		***	***	***
	Year:Season	***	***	***	***	***	***	***	***	***	***	***	***	***
Individual Effects	N		**		*		***							
	Year:N													
	Season:N													
	Year:Season:N		**				*							
	P	.		*		*					*			
	Year:P		**	*							*			.
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	Water				.		*					.		
	Year:Water	*												
	Season:Water						.			.				
	Year:Season:Water	*	*						.					
Synergistic Effects	N:P								**	**		.		
	Year:N:P													
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	P:Water									*		*		
	Year:P:Water						.							
	Season:P:Water											.		
	Year:Season:P:Water											.		
	N:P:Water												*	
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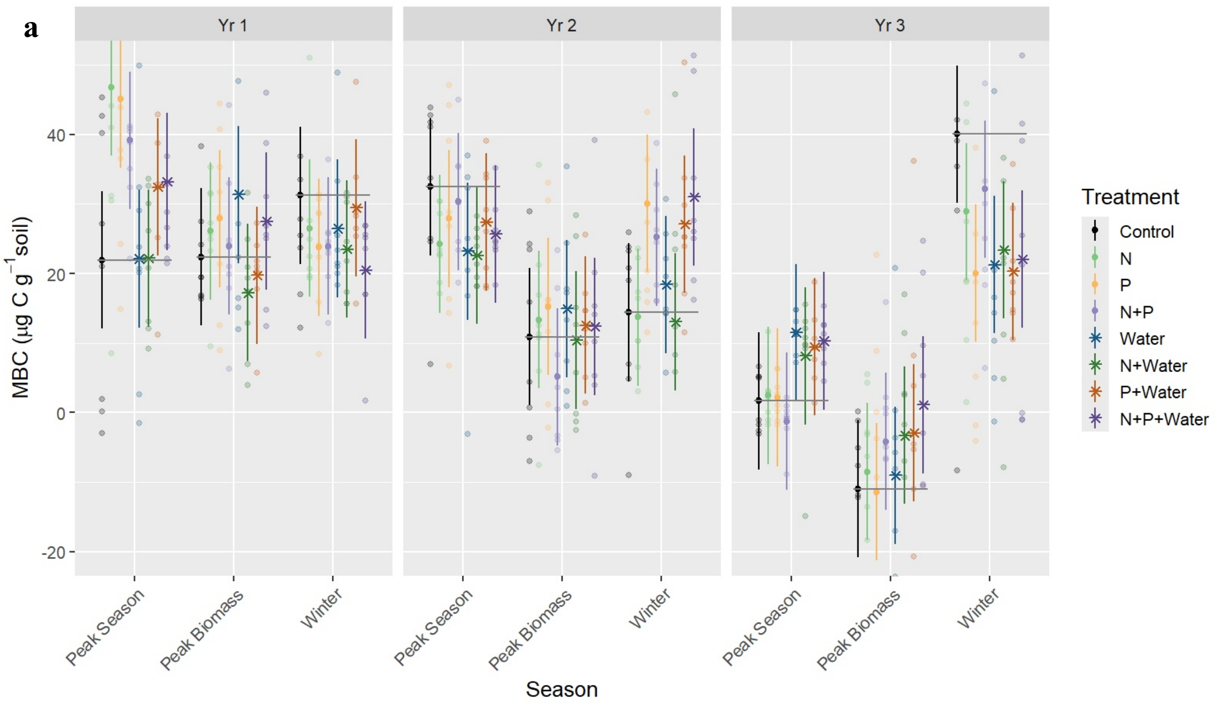
	Year:Season:N:P:Water													.

Figure 5.1. A multiway ANOVA was used to detect significant ($p < 0.05$) differences in microbial function across Years, Seasons, and Treatment Effects (N, P, and Water). Blue boxes denote significant effects, with * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. Pink boxes denote marginal effects ($0.05 < p < 0.10$). See Table S5.1 for summarized ANOVA results.

MBC, MBN and MBP were all affected by resource additions (N, P and water), although these effects varied by season and year (Figure 5.1 & Table S5.1). MBC responded to a significant interaction between N, P, and water, and this effect differed by year (Figure 5.1). In year 1, N and P additions increased MBC both separately and together with no interactive effect, but these N and

P effects were dampened by concurrent water addition (Figure 5.2a). In years 2 and 3, P addition slightly increased or decreased MBC, respectively, while N little effect (Figure 5.2a). In year 3, water significantly increased MBC (Figure 5.2a). MBN was affected by a significant Year*Season*N*Water interaction and a P*Year interaction (Figure 5.1). Generally, N addition decreased MBN with a more consistent decrease when added in combination with water and with stronger effects in PS, though this was not consistent across all years (Figure 5.2b). P addition had an inconsistent effect on MBN, increasing, decreasing, or not changing MBN depending on measurement timing (Figure 5.2b). MBP was increased by P addition, with a much larger increase in Year 3 (Year*P interaction, Figure 5.1; Figure 5.2c).



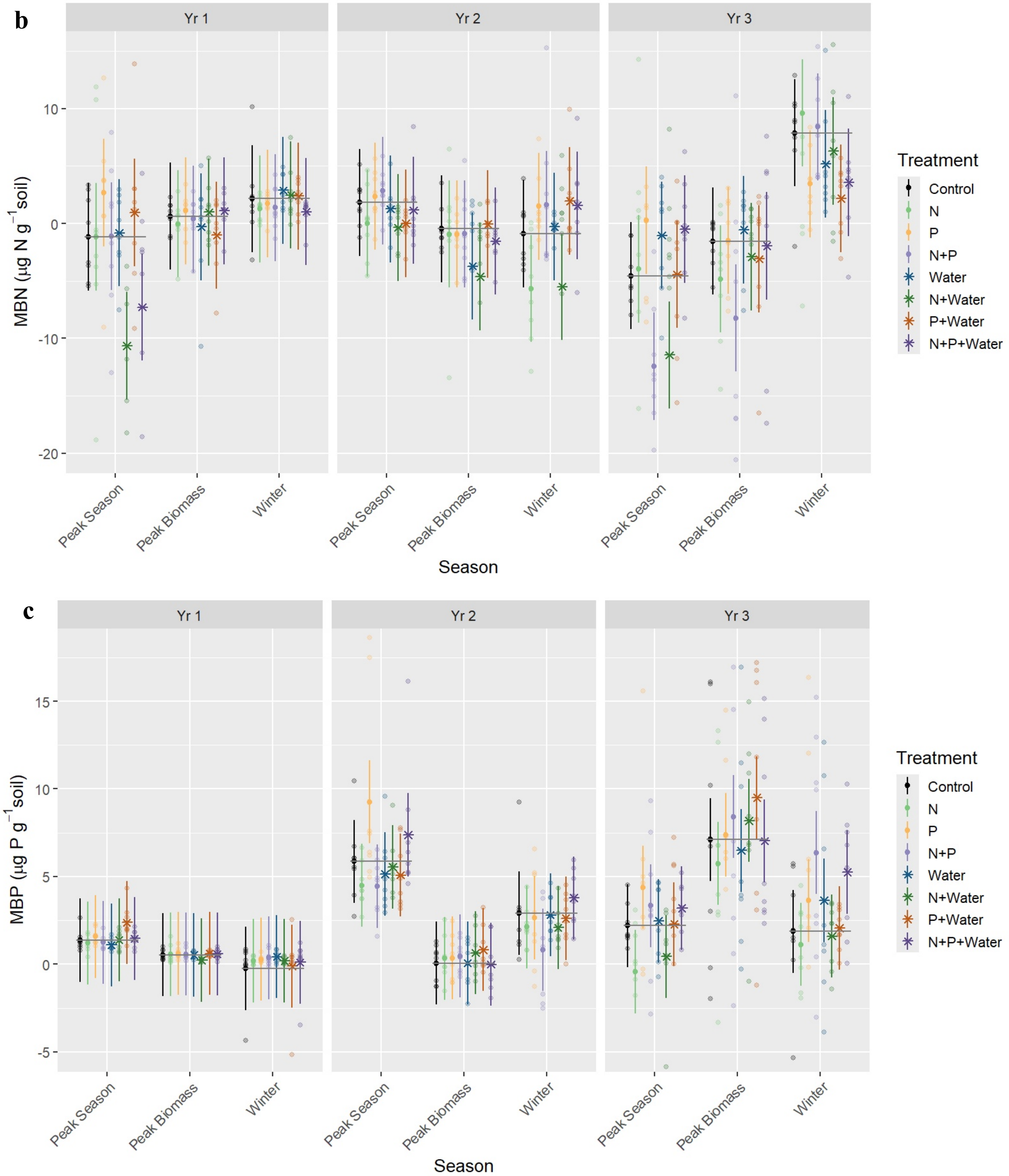


Figure 5.2. 95% Confidence Intervals showing seasonal responses in microbial C, N, and P within each year of the experiment. Horizontal grey lines indicate the mean value of control plots within that season. For significant ANOVA effects, refer to Figure 5.1.

Soil respiration showed no consistent patterns of variation (Figure S5.2). Soil respiration was significantly different between sampling times, and there was a significant interaction between N and P treatments, but CO_2 fluxes did not vary widely between treatments or sampling times (Figure S5.2; Table S5.2).

Responses of Extracellular Enzyme Potential Activity to Resource Addition in Plant- and Microbe-Dominated Seasons

All extracellular enzymes had a significant Year*Season interaction (Figure 4.1). BGluc, Phos, LAP, NAG, Phenol, and Perox are often considered the core soil enzymes (Moorhead et al. 2016; Sinsabaugh et al. 2008; Sinsabaugh and Follstad Shah 2012), and responses in other enzymes largely mirrored responses in this select group. As such, our results focus on these select enzymes (see Figure S5.3 for other enzymes analyzed). BGluc was higher in PS than Winter, with the difference between seasons and the overall BGluc magnitude decreasing across years (Figure 5.3a; Table S5.3). In contrast, Phos was generally higher in PS than Winter, though the seasonal differences in Phos increased over time while the overall magnitude of Phos still decreased between years (Figure 5.3b; Table S5.3). NAG and LAP both had higher activity in PS than Winter in year 3 only, whereas the seasons were similar in other years, or winter activity was higher (LAP year 1 and NAG year 2; Figure 5.3c, d; Table S5.3)).

Activity of multiple enzymes was affected by resource additions, often with interactions between resources or with time (Figure 5.1). Water decreased BGluc activity except when added in combination with P (significant Water*P interaction (Figure 5.1)), where the combination of water and P even slightly increased BGluc activity in PS of year 1 (Figure 5.3a). N addition significantly increased Phos activity, mostly driven by effects in year 1, whereas water had a marginal ($p<0.10$) negative effect (Figure 5.3b). NAG was not significantly affected by any treatments (Figure 5.1; Figure 5.3c) while LAP activity had both a significant Year*Season*N*Water interaction and a marginal Year*P*Water interaction (Figure 5.1). N and water separately decreased LAP in most cases, but in combination increased LAP activity in Winter of year 2 (Figure 5.3d). P addition marginally decreased LAP activity in Winter Year 1 but marginally increased LAP in year 2 (Figure 5.3d).

Phenol activity had significant N*P*Water and Year*Season*N*Water interactions (Figure 5.1; Table S5.4) because in Winter of Year 2 (but not Year 1), N and water together increased Phenol oxidase activity but activity decreased when P was also added (Figure 5.3e). In Winter Year 3, N alone increased Phenol activity but water dampened this effect, and P addition only increased Phenol activity when added with water (Figure 5.3e). Treatment effects on Perox activity were few and complicated, with only a marginal Year*Season*N*P*Water interaction (Figure 5.1; Figure 5.3f; Table S5.4).

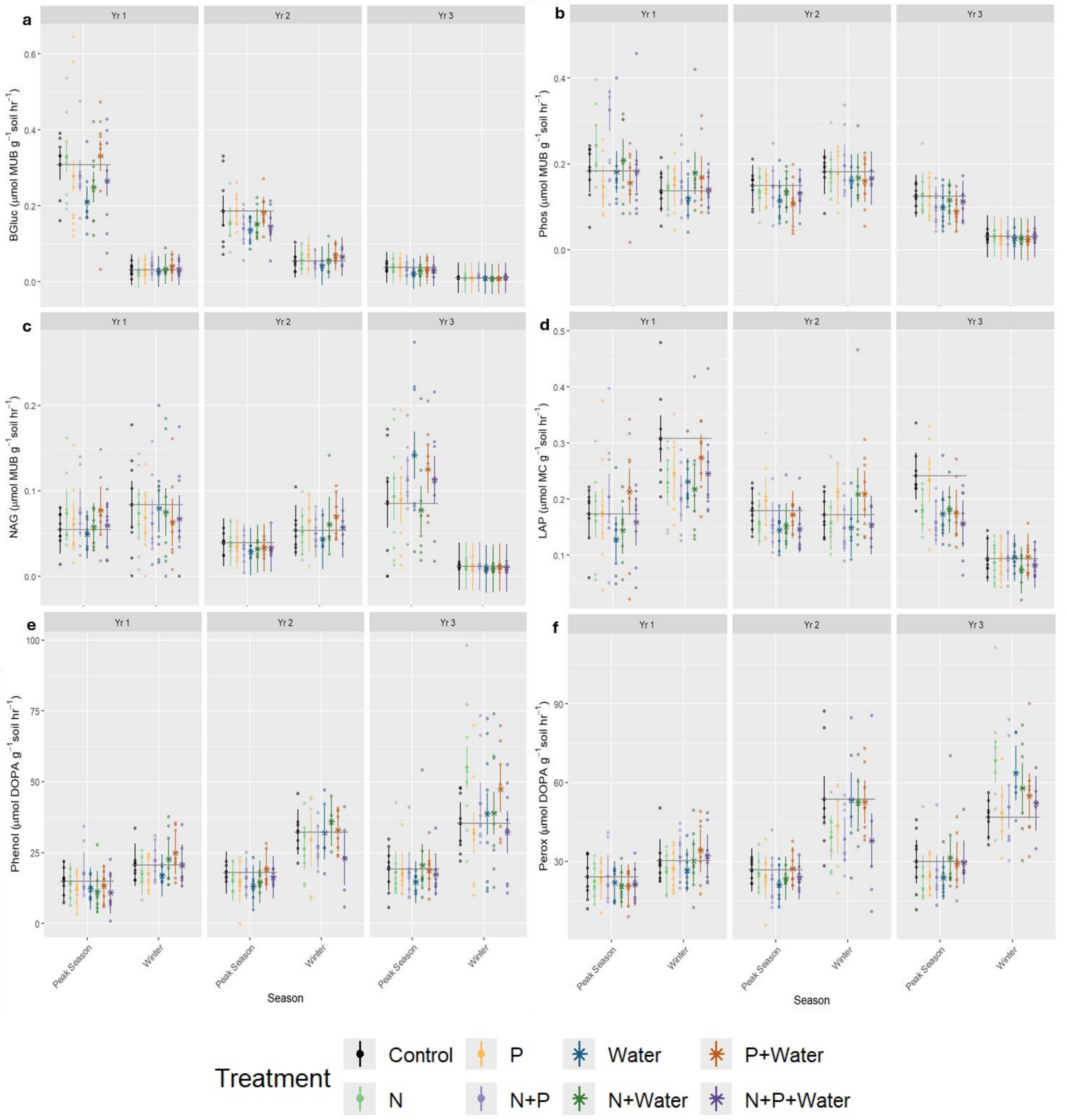


Figure 5.3. 95% Confidence Intervals showing the seasonal and annual trends in potential extracellular enzyme activity for the core hydrolytic enzymes and the oxidative enzymes. Horizontal grey lines within each season indicate the mean value of potential enzymatic activity in control plots for that season only. Refer to Figure 5.1 and Table S5.1 for significant ANOVA effects.

Using the extracellular enzyme stoichiometric model (Cui et al. 2023; 2025; Sinsabaugh et al. 2009) and Standardized Major Axis regressions (Figure S5.1), we found MCL = -3.2, MNL = 1.9, and MPL = 1.3 averaged across all treatments, years, and seasons (Table 5.1). Values > 0 signify potential limitation by that resource (i.e., MNL and MPL), and larger values signify stronger limitation. When analyzing each sampling event individually, we found similar trends where N and P limited microbial activity, and N and P limitation were stronger in the Winter than the Peak Season except in year 2 when N limitation was strongest in Peak Season (Table 5.1).

Table 5.1: Enzyme stoichiometric model results for each sampling point and averaged across all samples. MCL is Microbial Carbon Limitation, MNL is Microbial Nitrogen Limitation, and MPL is Microbial Phosphorus Limitation. PS is Peak Season (samples collected in August) and W is Winter (samples collected in January). Positive values indicate limitation by that resource, with larger positive values corresponding to stronger limitation. Negative values indicate no limitation by that resource.

Season, Year	MCL	MNL	MPL
PS Yr 1	-0.402	0.278	0.124
W Yr 1	-0.996	0.570	0.427
PS Yr 2	-1.550	1.407	0.143
W Yr 2	-1.370	0.730	0.640
PS Yr 3	-1.305	0.698	0.607
W Yr 3	-2.117	1.135	0.982
Average	-3.2	1.9	1.3

Correlative Relationships Between Soil Nutrients and Microbial Activity

MBC and MBN were positively correlated, MBC and MBP were negatively correlated, and MBN and MBP had no significant relationship (Figure 5.4). For correlations between microbial biomass and the soil N and P pools, MBC was only positively correlated with Weakly Bound P, while correlations between both MBC and MBN and other pools were negative. In contrast, MBP was positively correlated with most P pools and ammonium (Figure 5.4). All enzymes except NAG and Perox were positively correlated with MBC, Phos and NAG were positively associated, and the oxidative enzymes negatively correlated. All enzymes except BGluc were negatively correlated with MBP (Figure 5.4). BGluc and Phos activity generally decreased with P availability, though BGluc did increase with the enzyme-P pool (Figure 5.4). NAG and LAP were negatively related to N availability and positively associated with P availability (Figure 5.4). Oxidative enzymes increased with the available P pool but otherwise decreased with increasing P and nitrate availability (Figure 5.4). Correlative relationships between the full suite of analyzed variables followed similar trends (Figure S5.4).

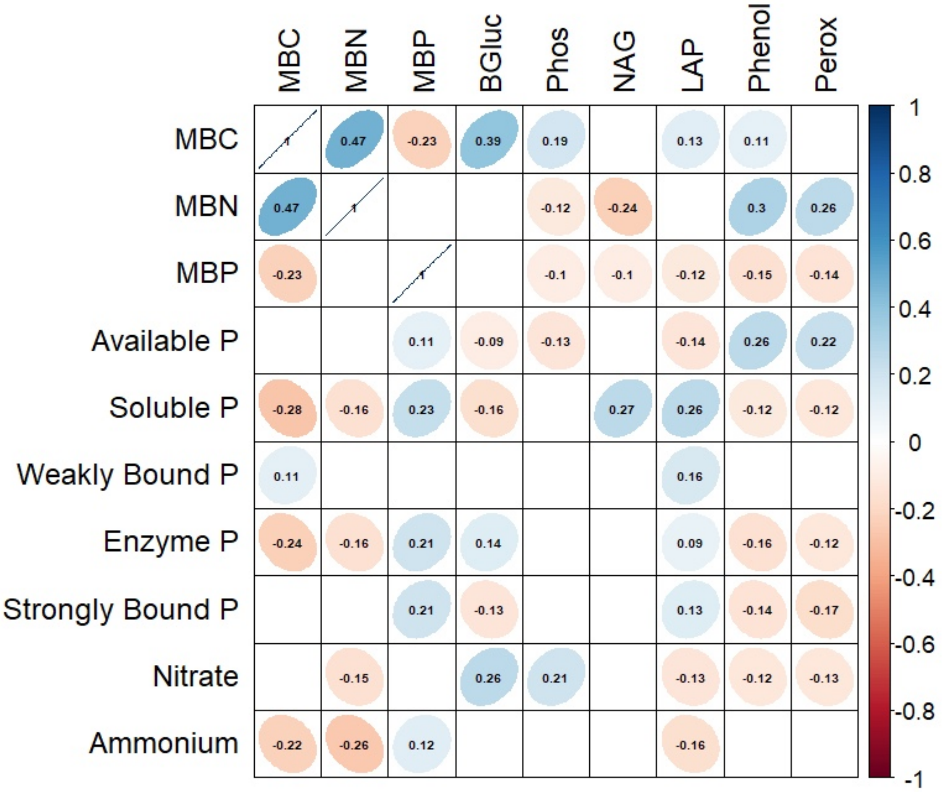


Figure 5.4. Correlogram showing significant ($p < 0.05$) correlative relationships between internal microbial concentrations and nutrient pools (left) and microbial C, N, P content and potential extracellular enzymatic activity (top), with blue and red cells indicating positive and negative correlations, respectively. Darker shades of blue or red and more apparent ellipses within each cell denote stronger relationships between variables. See Figure S5.4 for a correlogram including every analyzed variable.

DISCUSSION

Evidence of Multiple Resource Limitation by N, P, and Water on Microbes in the Chihuahuan Desert

Microbial biomass (MBC) significantly responded positively to N, P, and water addition, indicating that resource scarcity limits microbial communities in drylands under the classical definition of limitation (Liebig 1840; Bracken et al. 2015). Interactive effects of the water and nutrient treatments, as well as variability in treatment effects between seasons and years with differing water availability, also indicate that this soil microbial system is experiencing multiple resource limitation by water, N, and P (Figure 5.1) with water as the primary limiting factor. These effects were not reflected by changes in soil respiration (Figure S5.2), which can be highly temporally variable (Throop et al. 2020; Dacal et al. 2020) and may not be an appropriate signature of microbial resource limitation (Schimel and Weintraub 2003). Our site experienced large swings in temperature and rainfall throughout the experiment, with average rainfall and temperatures in year 1 while years 2 and 3 were abnormally hot and dry (Table S5.5), providing a contrast between treatment effects under drastically different climatic conditions. In the first year, sufficient rainfall appeared to allow the microbial community to overcome water limitation and increase MBC in response to N and P additions, signaling serial limitation of water, N, and P (Harpole et al. 2011). The lack of significant N or P effects in hot and dry conditions and the positive effect of water on MBC in the growing season of year 3 (Figure 5.2a) further supports the possibility of multiple resource limitation or serial limitation with water as the primary – but not sole – limiting factor.

Shifts in internal N and P concentrations (MBN and MBP) after resource additions also suggest a release from resource limitation (Bracken et al. 2015; Harder and Dijkhuizen 1983). Our results show that MBN increased with P addition (Figure 5.2b), suggesting that microbial N uptake is indeed biochemically limited by P availability in this system as in others (Reed et al. 2007; Xia et al. 2023), demonstrating the importance of P as a control of key N cycling processes (Ch2, this dissertation; Cole and Heil 1981)). Regardless of limitation status, increased supply of one nutrient is known to produce corresponding increases in internal concentrations of that nutrient (Bracken et al. 2015), and MBP follows this trend, generally increasing with P availability (Figure 5.2c; Figure 5.4).

However, N additions rarely increased MBN, even decreasing MBN in some cases (Figure 5.2b). While N additions should increase MBN by alleviating N limitation or stimulating luxury consumption (Deinema et al. 1980; Sharma and Steuer 2019; Harder and Dijkhuizen 1983), our results suggest that MBN may not reflect N availability or uptake. Microbial communities use resources more efficiently in times of scarcity and inefficiently in times of abundance (Koch 1985; Mooshammer et al. 2014). Therefore, it is possible that, even if N limited microbial growth, N addition may have promoted N-intensive efforts to acquire other limiting resources (e.g. C and P), leading to a net-zero or at times negative change in MBN despite elevated N supply (Figure 5.2b).

It is important to note that our values for MBC, MBN, and MBP included both negative and positive values (Figure 5.2). Negative values of these three variables should be impossible, as microbial biomass values should have a minimum value of 0, though methodological limitations can produce results similar to those seen here (Martens 1995). One of the most common methods for measuring microbial biomass – and the method we used – chloroform fumigation extraction (CFE), requires analyzing two separate subsamples. The high heterogeneity of dryland soils (Bird et al. 2002; Fransen et al. 2001) likely translates to high spatial heterogeneity in microbial biomass with biomass concentrated in soils with higher nutrient availability and organic matter (Bauke et al. 2025; Kuzyakov and Blagodatskaya 2015), producing highly variable subsamples despite standard homogenization of the soil. Analytical replicates of samples from two separate Shimadzu TOC/ETN analyzers produced similar values, increasing our confidence in our measurements. This result suggests that we are operating near to the practical detection limit for the CFE technique in these soils, and reinforces both the highly heterogeneous distribution of nutrients and microorganisms and the exceptionally restricted nutrient pools characteristic of dryland soils (Jordaan et al. 2022a; Plaza et al. 2018; Osborne, Bestelmeyer, et al. 2022). With negative MBN and MBP values, we were unable to simply compare shifts in N:P ratios to determine microbial limitation, but comparing the raw values nevertheless revealed significant signatures of limitation.

Shifts in Extracellular Enzyme Activity Provide Evidence of Microbial N and P Limitation in Dryland Soils

Extracellular enzyme activity provides further evidence of N and P limitation. Using definitions of limitations provided by the enzyme stoichiometric model (Cui et al. 2023), microbial C limitation was not prevalent while both N and P were potentially limiting resources (MNL and MPL > 0; Table 5.1). As hypothesized, enzyme activity had a clear relationship with soil nutrient availability. N- and P-acquiring enzymes were negatively correlated with N and P availability, respectively, while the activity of C- and P-acquiring enzymes were positively correlated with N availability (Figure 5.4), demonstrating both the importance of soil nutrient supply to enzymatic responses and the N-intensive cost of enzyme production. N addition influenced enzyme activity, increasing Phos (P-acquiring) and Phenol (oxidative) enzyme activities (Figure 5.3a & e), likely by stimulating enzyme production (Sinsabaugh and Moorhead 1994; Xu et al. 2022; Cui et al. 2025), and shifting nutrient demand toward P- and C- acquisition, shown by decreased LAP (N-acquiring) activity. These findings align with the conclusion of multiple resource limitation drawn from the microbial stoichiometry and biomass, emphasizing the value of considering enzyme stoichiometry as a signature of limitation and further reinforcing our evidence of multiple resource limitation by water, N, and P in this study system.

The use of extracellular enzyme activity as a signature of nutrient limitation is especially valuable in drylands, where responses in microbial growth and activity are temporally variable, differing in both when and how quickly they occur (Nannipieri et al. 1983; Brock 1971; Bell et al. 2009; Darrouzet-Nardi et al. 2023). Because of this temporal variability, it may be valuable to measure both terminal steps in responses (e.g. biomass growth, shifting internal stoichiometry) alongside earlier downstream responses (e.g. increased extracellular enzyme production). However, our study also necessitates further development of the extracellular enzyme stoichiometric model, which cannot detect water limitation and thus would prove less useful when detecting or describing multiple resource limitation – especially water-dependent serial limitation – in arid regions.

There is a chance that changes to the analytical method employed contributed to the observed decrease in potential hydrolytic enzyme activity in the Winter of Year 3 and the increased strength of microbial N and P limitation. For this season only, we used a lower-range MUB standard curve to measure fluorescence for the enzymatic activity assay because the higher soil pH (Figure S5.6) caused MUB fluorescence to far exceed that of our samples when using the original standard curve (Profeta et al. 2017). While the overall method remained the same, it is possible that the two standard curves used differed in their accuracy or precision. However, this methodological difference did not affect LAP, Phenol, or Perox, as these assays did not use the MUB curve. LAP exhibited the same pattern as the other hydrolytic enzymes while Phenol and Perox showed a large increase, indicating that environmental conditions likely influenced extracellular enzyme activity and the use of a different MUB standard curve was not the sole reason for our findings.

Seasonal Patterns in Microbial Growth and Activity are Influenced by Plant-Microbe Interactions

Because plant growth and biogeochemical cycling in drylands are largely tied to pulses of precipitation (Noy-Meir 1973; Austin et al. 2004; Huxman et al. 2004), the biotic community undergoes shifts from plant-dominated in the wet season to microbe-dominated in the dryer seasons. If changes in microbial activity were entirely caused by differences in rainfall and temperature, we would expect years with similar climate (e.g. Years 2 and 3; Table S5.5) to be similar. However, differences in the plant community can also alter microbial biomass and community composition (Zhu et al. 2017; Čapek et al. 2018; Aira et al. 2010; Spinella et al. 2024). By contrasting the magnitude of changes in microbial growth and activity between the Summer and Winter across a gradient of years with strong to weak plant influence (i.e. high to low plant cover (Figure S4.5), we can begin to disentangle seasonal effects caused by changing temperature and water availability from those caused by plant-microbe interactions.

The seasonal differences in microbial growth and activity typically grew as the strength of plant influence – measured here as aboveground plant cover (Ch. 4, this dissertation) – became more similar between seasons. MBC and MBN best demonstrate this pattern, where both increased greatly between Peak Season and Winter in the third year (Figure 5.2a-b). There was little to no plant growth in this year (Figure S5.5), producing weak plant influence and thus limited competition from the plant community across all seasons. The low levels of plant influence and low plant-microbe competition may have enabled greater levels of nutrient uptake in the microbial community, resulting in more microbial growth (Moreau et al. 2015; Čapek et al. 2018). However, the drier conditions in this same year may have increased geochemical “competition” for nutrients (mainly phosphorus) by decreasing solubility and increasing mineral sorption (Zhu et al. 2016; Guppy et al. 2005), necessitating further work studying the effects of drought on soil-microbe interactions. While environmental conditions (e.g. temperature, soil moisture) may not have been favorable to microbial growth in either the drought year or the Winter in any year of the study, decreased plant-microbe competition during these times may mitigate the negative seasonal effects by enabling greater nutrient uptake and growth by microbes. Patterns of nutrient availability (Ch. 2, this dissertation) help explain this pattern, as high rates of plant activity in Year 1 depleted soil N and P while nutrient availability was highest in Year 3 when plant uptake was minimal. The larger changes in microbial biomass and activity between Peak Season and Winter in Year 3 compared to other years suggest that minimal plant influence in this year enhanced the nutrient supply available to microbes, benefitting the microbial community despite the adverse environmental conditions.

Our measure of microbial activity – extracellular enzyme potential activity – exhibited a similar pattern where the most dramatic seasonal change was observed in the third year. While the altered MUB standard curve may have contributed to this pattern, the consistency in this pattern observed in microbial biomass and across the full suite of enzymes makes it unlikely that this methodological change alone produced this result. Increased investment in enzyme production may have a negative (Ramin and Allison 2019) or positive (Nannipieri et al. 1983) relationship with microbial growth; our results show that the activity of most enzymes was positively correlated with MBC (Figure 5.4). It is possible that elevated enzyme activity enabled greater acquisition of limiting nutrients, thus increasing microbial growth (Sinsabaugh et al. 2009); alternatively, greater MBC may increase the capacity for enzyme production. However, in the third year, the significant increase in MBC in Winter was contrasted by decreases in enzyme activity, contrary to our hypothesis. Nutrient availability was highest in Year 3 of the experiment (Ch. 2, this dissertation), potentially rendering enzyme production unnecessary (Koch 1985). With the lack of plant litter in the third year and the corresponding decrease in organically bound nutrients that would be targeted by enzymes, the microbial community likely would not have produced more enzymes (Sinsabaugh and Moorhead 1994; Srilakshmi et al. 2012). Instead, decomposition by oxidative enzymes – the only enzymes to increase in the third Winter – and nutrients from previously decomposed litter from Year 2 may have provided sufficient nutrients for microbial activity; alternatively, the increase in oxidative enzymes may have occurred after easily hydrolyzed matter was depleted, necessitating oxidative enzymes for further decomposition. However, oxidative enzyme activity can be driven by abiotic factors other than nutrient availability, including interaction with mineral surfaces, temperature, and soil pH (Sinsabaugh 2010; Darrouzet-Nardi et al. 2023). In either case, hydrolytic enzymes produced during the growing season would likely have degraded by Winter, explaining the observed decrease (Schimel et al. 2017).

CONCLUSION

Our study presents evidence of multiple resource limitation by nitrogen, phosphorus, and water in the microbial community in the Chihuahuan Desert while also presenting plant-microbe interactions as a potential driver of seasonal changes in addition to changes in temperature and precipitation. By considering traditional (biomass and respiration) and novel (extracellular enzymatic stoichiometry) methods of detecting microbial resource limitation, we found that N and P limitation are prevalent in this dryland ecosystem and may become stronger as aridity increases. Despite their low productivity, we suggest that nutrient limitation can significantly constrain dryland microbial communities in some circumstances, possibly because of naturally low supply or increased nutrient loss and mineral occlusion in increasingly arid conditions. Drylands are a dominant part of the global carbon cycle in part due to microbial activities (Ahlström et al. 2015; Poulter et al. 2014; Liu et al. 2018), but these regions are also increasingly sensitive to climate change (Bestelmeyer et al. 2015; Osborne, Bestelmeyer, et al. 2022; Scholes 2020). By recognizing the importance of both plant-microbe interactions and limitation by both N and P in drylands, we raise new questions about dryland biogeochemistry and how it will respond to global change pressures.

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AUTHOR CONTRIBUTION STATEMENT

Dylan J. Stover: Writing – original draft preparation, review and editing, Investigation, Methodology, Visualization, Formal Analysis, Project Administration, Data Curation. **Anthony J. Darrouzet-Nardi** - Writing – review and editing, Funding Acquisition, Conceptualization, Visualization. **Jennie R. McLaren:** Conceptualization, Funding Acquistion, Writing – review and editing, Methodology, Project Administration, Data Curation, Supervision.

DATA AVAILABILITY STATEMENT

Data will be made publicly available when the manuscript is published.

Chapter 6: Conclusions

SUMMARY OF DISSERTATION FINDINGS

In this dissertation, I provided insights into the processes that drive ecological function in dryland ecosystems. Chapter 2 details the importance of spatial scale and geomorphology to soil fertility and biological activity. Chapters 3 through 5 detailed findings about multiple resource limitation and biogeochemical processes from a resource addition experiment conducted in a native grassland in the northern Chihuahuan Desert. Findings from each chapter are summarized below.

In **Chapter 2**, I investigated how the fertile island effect, the ability of biotic structures to enhance soil conditions in their proximity, changes across geomorphic landforms and local patch types (i.e. shrubs, grasses, biocrusts, and bare soil) along a piedmont slope in the Jornada Experimental Range. Here, I measured a suite of physical soil characteristics, nutrient availability, and microbial variables including community structure and potential extracellular enzyme activity then calculated the size of the fertile island effect for each variable. I found that every patch type considered can act as a fertile island, and that patch-level patterns in the fertile island effect are consistent across landforms. Additionally, I found that nutrient availability is most improved by fertile islands in coarse-textured soils while the microbial community is most benefited in fine-textured soils. These findings provide evidence that biocrusts can act as fertile islands, which have historically been defined as only being created by large plants like shrubs. Because fertile islands drive productivity in dryland ecosystems, current models may underestimate dryland productivity and should consider a broader definition of fertile islands, as well as the effect of geomorphic factors, to better predict patterns of productivity and function in drylands.

In **Chapter 3**, I described the effects of water, N, and P addition on soil nutrient pools in a Chihuahuan Desert Grassland. I measured a range of soil nutrient fractions to consider how different biologically accessible nutrient pools vary through time and after application of experimental treatments. All nutrient pools were highly variable across seasons and years, emphasizing the importance of precipitation patterns on biogeochemical cycling. Water was a major – but not lone – factor influencing biogeochemical cycling, as N and P additions also influenced nutrient availability. I also found interactions between resource additions - water significantly altered N availability, but soil P pools were resistant to watering. Additionally, P additions significantly altered soil N pools, suggesting that the importance of P availability to an array of N cycling processes can extend to patterns of soil nutrient availability.

In **Chapter 4**, I detailed the plant community's responses to these resource addition treatments and extended drought conditions. I found that water was the only resource limiting plant growth, and was most beneficial to native grasses, which consistently exhibited the largest positive response to watering, even outcompeting annual forests in the year with average rainfall. Nutrient additions did not impact plant cover, though they did appear to increase species diversity in the hot, dry years of the experiment, suggesting that in stressful conditions, the addition of any supplemental resources can improve conditions and facilitate some growth. Lastly, native grasses persisted throughout drought years and benefitted from the watering treatment while invasive grasses did not, presenting an opportunity to explore drought as a tool for native grass restoration and invasive grass control.

Finally, in **Chapter 5**, I discussed microbial responses to the above resource addition treatments and opportunely compared these responses along a temporal gradient of plant influence. I presented evidence that microbial growth is limited primarily by water and, when water requirements are met, N and P limitation can also arise. Additionally, P addition promoted microbial N uptake while N availability promoted extracellular enzyme production to acquire C and N. Using a model of enzyme stoichiometry provided further evidence of N and P limitation p, also suggesting that N and P limitation are apparent regardless of water availability, even growing stronger as aridity increased. The magnitude of the microbial responses differed through time in part due to the low levels of plant influence in the dry years, which decreased plant-microbe competition. In these years, the microbial community was able to acquire and use more resources and thus exhibited larger differences between the growing season and the winter, suggesting higher levels of microbial growth and activity. These findings present the first evidence of microbial limitation by P in the Chihuahuan Desert while also supporting a growing body of evidence that plant-microbe interactions significantly impact the microbial community.

IMPLICATIONS AND FUTURE RESEARCH NEEDS

Drylands are globally important (Ahlström et al. 2015; Bestelmeyer et al. 2015), and their influence on biogeochemistry and human health will only grow as they continue to expand (Lal 2019; Feng and Fu 2013; Bestelmeyer et al. 2015; Millennium Ecosystem Assessment 2005a). Human activities are dramatically altering global cycling of water, C, and nutrients (Penuelas et al. 2020; Vörösmarty and Sahagian 2000), and dryland systems are particularly vulnerable to these shifts (Scholes 2020; Huang et al. 2017). Advancing our understanding of how dryland biogeochemistry, microbial function, and plant communities will respond to these shifts is vital to predicting how the relationship between drylands and global biogeochemical cycles will change under growing global change pressures.

This dissertation demonstrates the complex biogeochemical and biological interactions that drive ecosystem function in dryland ecosystems and how these interactions are affected by changes in climate and soil conditions (Figure 6.1). These findings provide evidence that broadening our definitions of the processes that control soil fertility and productivity (e.g. fertile islands, resource limitation) will advance our understanding of dryland biogeochemistry and its implications for global biogeochemical cycles.

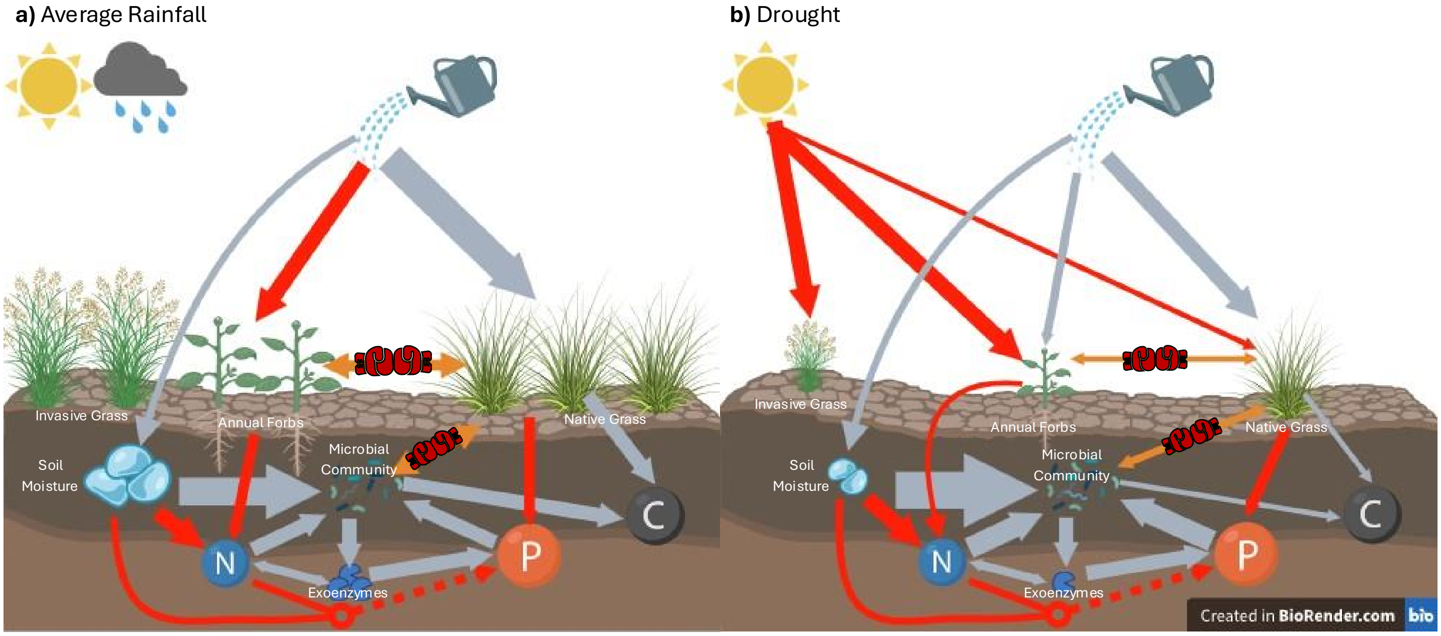

Figure 6.1. Conceptual diagram of the dryland plant-microbe-soil interface in years with (a) average rainfall and (b) drought conditions. Arrow width increases with the strength of the effect. Grey arrows from resources (Water, N, and P) indicate a positive effect of increased resource availability. Red arrows denote a negative effect of increased availability or activity on the availability, activity, or growth of the resources or organisms at the ends of the arrows (i.e. increased plant activity depletes soil nutrient pools). The dashed line connecting soil water and N to soil P indicates that concurrent increases in both N and water are required to elicit the effect on soil P. Orange arrows with boxing gloves signify competition between plants or microbes. Arrows that cross from above to below the soil are assumed to exist for all plant functional groups but are not shown for each group. Created with BioRender.com.

Here, we highlight key results from this body of work and outline future research directions that will provide further insights into dryland ecology and biogeochemistry. I showed that, while water plays a major role in promoting biological activity and biogeochemical cycling in drylands, it is not the sole resource driving either of these processes. In Chapter 3 of this dissertation I show that P availability can influence soil N cycling regardless of water availability, and in Chapter 5 I show that the microbial community can experience both N and P limitation when water requirements are met. Nevertheless, the findings presented in this dissertation underscore the importance of water availability and describe possible ecological and biogeochemical responses that may be observed in dryland regions as precipitation regimes become increasingly variable (Rudgers et al. 2018).

Considering the biogeochemical interactions that exist between key soil resources (water, N, and P) will strengthen our understanding of dryland biogeochemistry and how it might shift under future climate scenarios. There is widespread evidence that N and P cycling interact (Reed et al. 2007; Bauke et al. 2025; Chen et al. 2017; Xu et al. 2022; Cole and Heil 1981), but studies in dryland systems have heavily focused on water and nitrogen (Austin 2011; Yahdjian et al. 2011), resulting in a significant gap in our knowledge of N-P interactions in dry soils. Our results show that P availability plays an important role in N cycling regardless of water availability while N availability only impacts soil P pools with sufficient water. Further work should address questions about N-P interactions and how they will be impacted by projected increases in aridity (Le Houérou 1996), variability of rainfall (Rudgers et al. 2018; Gherardi and Sala 2019), and disruptions to global resource cycles (Penuelas et al. 2020; Vörösmarty and Sahagian 2000).

Drylands are a dominant part of the global carbon cycle (Ahlström et al. 2015; Poulter et al. 2014) and represent a major carbon sink (Lal 2019). Two major findings of this dissertation suggest that carbon cycling in drylands may be underestimated, presenting an opportunity to improve their representation in global models (MacBean et al. 2021). First, Chapter 2 demonstrates that biocrusts and perennial grasses can behave as fertile islands, which drive productivity in dryland ecosystems by improving soil conditions to promote biological activity

(Schlesinger et al. 1990; Aguiar and Sala 1999). A fertile island's effect on its surrounding soil conditions has been shown to increase with plant size (Fitzpatrick et al. 2024); however, this result indicates that biological soil crusts, which regulate nearly all soil inputs and outputs when present (Belnap et al. 2016), can have a fertile island effect comparable to that of shrubs despite their low-lying stature.

Second, Chapter 5 presented the first evidence of microbial limitation by P in the Chihuahuan Desert and reinforced past findings of the prevalence of N limitation in drylands (Yahdjian et al. 2011). Microbial biomass responses were only detected when water availability was sufficient (Figure 5.1), suggesting this system is experiencing serial limitation with water as the primary limiting factor. However, extracellular enzymatic stoichiometry revealed that nutrient limitation may be present even when water availability is low (Table 5.2). Together, these findings demonstrate the urgent need for a renewed focus on soil fertility and resource limitation in drylands. Drylands are underrepresented in global models (MacBean et al. 2021), and this may be in part due to significant gaps in our knowledge of the processes that constrain their ecological function. Because of the historical focus on mesic systems, it is difficult to directly apply many ecological and biogeochemical concepts to drylands. As shown in this dissertation, broadening our definitions of fertile islands and resource limitation can reveal new insights about the processes limiting drylands' ecological function.

Lastly, Chapters 4 and 5 show that, while resource limitation differs between the plant (water only) and microbial (water, N, P serial limitation) communities, plant-microbe interactions play a large role in determining microbial function. In years with low plant-microbe competition, the microbial community was able to acquire and use more soil resources compared to years with high levels of plant-microbe competition, evidenced by the larger differences in microbial biomass and enzyme production between the year's growing season and Winter. Recent studies have found that including plant-microbe competition improves predictions of nutrient effects on primary productivity (Čapek et al. 2018; Zhu et al. 2017; Moreau et al. 2015). By considering plant-microbe interactions and employing a more integrative and dryland-focused definition of limitation, future research can improve our predictions of how and where microbial communities are resource limited and advance our understanding of the prevalence and implications of resource limitation in drylands.

CONCLUSION

This dissertation presents evidence that widely accepted assumptions about dryland systems may need to be adjusted to better explain these unique systems. First, our definition of fertile islands should be expanded to include more than just large plants in order to improve predictions of productivity in drylands. Second, as regions driven primarily by pulses of water availability, it is presumed that nutrient cycles are inherently linked to rainfall. We presented evidence that, while water does influence soil nutrient pools, the relationship between N and P cycling is driven more by P availability than water. To close the gaps in our understanding of dryland biogeochemistry, future work must consider these key resource cycles in concert, exploring how they interact and what implications these interactions may have on resource availability in drylands. Lastly, we showed that plant and microbial communities are differently impacted by resource limitation, and temporal variability in plant-microbe interactions can significantly impact microbial activity. Further research to separately examine resource limitation in plants and microbes while also exploring how plant-microbe interactions (e.g. competition) influence biological activity in drylands will provide critical insights into the factors limiting these systems' ecosystem function. In conclusion, this dissertation demonstrates the urgent need to improve our understanding of the role of drylands in the global C, N, and P cycles by elucidating how their unique biogeochemical characteristics drive soil fertility, resource availability, and ultimately productivity.

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Supplemental Tables

Table S2.1. Summary of 3-way ANOVA of physical soil characteristics with the main factors of landform, patch type, and soil depth. Bold values are significant at $p<0.05$, and italicized values are significant at $0.05<p<0.1$.

		Gravel (%)		Sand (%)		Silt (%)		Clay (%)		Percent Saturation		Soil pH		EC		% Calcite	
	df	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
LF	3	52.045	**<0.001**	27.848	**<0.001**	23.74	**<0.001**	30.071	**<0.001**	66.478	**<0.001**	16.912	**<0.001**	8.694	**<0.001**	33.822	**<0.001**
PT	2	18.321	**<0.001**	10.819	**<0.001**	9.320	**<0.001**	13.087	**<0.001**	19.688	**<0.001**	8.593	**<0.001**	9.076	**<0.001**	2.751	**0.0498**
SD	1	24.635	**<0.001**	88.006	**<0.001**	66.94	**<0.001**	144.860	**<0.001**	14.765	**<0.001**	7.704	**0.0072**	10.334	**0.0020**	30.564	**<0.001**
LF x PT	6	10.145	**<0.001**	6.377	**<0.001**	5.803	**<0.001**	5.717	**<0.001**	2.8610	*0.0067*	1.818	*0.0821*	3.327	**0.0022**	2.548	**0.0144**
LF x SD	3	6.926	**<0.001**	5.613	**0.0018**	4.207	**0.0089**	14.778	**<0.001**	24.896	**<0.001**	1.029	0.3856	1.487	0.2266	3.389	**0.0232**
PT x SD	2	9.781	**<0.001**	4.553	**0.0059**	3.974	**0.0116**	6.365	**<0.001**	15.727	**<0.001**	3.076	**0.0338**	5.075	**0.0032**	1.225	0.3078
LF x PT x SD	6	7.532	**<0.001**	2.765	**0.0085**	2.619	**0.0121**	3.609	**0.0011**	3.336	**0.0020**	0.470	0.8892	3.607	**0.0011**	0.448	0.9035

Table S2.2. Summary of 3-way ANOVA of variables related to microbial community activity with the main factors of landform, patch type, and soil depth. Bold values are significant at $p<0.05$, and italicized values are significant at $0.05<p<0.1$.

		Total Microbial Biomass		Microbial Diversity		C-acquiring enzymes		N-acquiring enzymes		P-acquiring enzymes		Oxidative Enzymes	
	df	F	p	F	p	F	p	F	p	F	p	F	p
LF	3	3.246	**0.0299**	5.174	**0.0035**	10.907	**<0.001**	12.555	**<0.001**	11.465	**<0.001**	6.335	**0.001**
PT	2	0.053	0.9488	0.400	0.6723	3.332	**0.0442**	8.923	**<0.001**	3.866	**0.0278**	0.925	0.4037
SD	1	0.028	0.8669	32.020	**<0.001**	28.52	**<0.001**	26.320	**<0.001**	40.149	**<0.001**	2.113	0.1525
LF x PT	6	0.258	0.9536	0.862	0.5295	0.835	0.5488	0.562	0.7583	0.495	0.8091	0.535	0.7787
LF x SD	3	2.587	*0.0639*	7.042	**<0.001**	0.208	0.8902	3.317	**0.0275**	2.453	*0.0746*	6.947	**<0.001**
PT x SD	2	0.039	0.9614	3.072	*0.0556*	0.735	0.4851	0.030	0.9710	0.278	0.7589	0.282	0.7553
LF x PT x SD	6	0.190	0.9783	0.831	0.5516	0.538	0.7768	1.202	0.3216	0.614	0.7177	0.452	0.8397

Table S2.3. Summary of 3-way ANOVA of variables related to nutrient availability with the main factors of landform, patch type, and soil depth. Bold values are significant at p<0.05, and italicized values are significant at 0.05<p<0.1.

		Organic C		Available Nutrients		Biologically Accessed Nutrients		Occluded P	
	df	F	p	F	p	F	p	F	p
LF	3	0.922	0.4374	0.582	0.6307	1.550	0.2137	2.042	0.1205
PT	2	2.513	*0.0916*	2.930	*0.0630*	1.007	0.3729	1.094	0.3431
SD	1	15.836	**<0.001**	11.430	**0.0014**	1.437	0.2365	9.479	**0.0034**
LF x PT	6	1.678	0.1469	1.913	*0.0979*	0.625	0.7092	0.280	0.9436
LF x SD	3	0.764	0.5197	3.297	**0.0282**	10.171	**<0.001**	9.194	**<0.001**
PT x SD	2	0.059	0.9428	5.833	**0.0054**	2.262	0.1151	1.134	0.3301
LF x PT x SD	6	1.054	0.4032	0.766	0.6005	0.761	0.6038	0.360	0.9007

Table S3.1. **Summary of multi-way ANOVA** for soil nutrient pools with the main factors of Year, Season, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at $p<0.05$, and italicized values in pink cells are marginally significant at $0.05<p<0.1$.

	Treatment Effects and Interactions	df	Inorganic P Fractions										Inorganic N			
			Olsen-P		CaCl2-P		Citrate-P		Enzyme-P		HCl-P		Nitrate		Ammonium	
			F	p	F	p	F	p	F	p	F	p	F	p	F	p
Time Effects	**Year**	2	75.13	**<0.001**	88.84	**<0.001**	0.001	**0.001**	14.20	**<0.001**	15.12	**<0.001**	176.91	**<0.001**	200.57	**<0.001**
	Season	2	8.64	**<0.001**	5.50	**0.004**	0.000	**<0.001**	38.29	**<0.001**	38.09	**<0.001**	120.92	**<0.001**	14.96	**<0.001**
	Year:Season	1	15.80	**<0.001**	44.00	**<0.001**	0.000	**<0.001**	64.98	**<0.001**	43.34	**<0.001**	102.56	**<0.001**	21.23	**<0.001**
Individual Effects	**N**	1	0.39	0.531	0.48	0.488	0.68	0.679	2.82	*0.094*	1.92	0.167	36.12	**<0.001**	311.93	**<0.001**
	Year:N	1	0.06	0.943	0.22	0.807	0.62	0.621	1.76	0.173	0.27	0.767	7.71	**0.001**	11.65	**<0.001**
	Season:N	4	0.33	0.722	0.01	0.993	0.13	0.130	0.40	0.672	1.20	0.302	1.54	0.216	13.61	**<0.001**
	Year:Season:N	2	0.28	0.894	0.54	0.710	0.96	0.963	0.79	0.532	0.31	0.874	2.19	*0.069*	9.37	**<0.001**
	P	2	152.65	**<0.001**	219.09	**<0.001**	0.00	**<0.001**	35.77	**<0.001**	0.01	0.936	0.000	0.985	0.09	0.770
	Year:P	2	19.10	**<0.001**	9.91	**<0.001**	0.04	**0.028**	1.28	0.278	1.48	0.229	3.17	**0.043**	9.08	**<0.001**
	Season:P	2	0.002	0.998	0.84	0.431	0.95	0.945	0.60	0.547	0.08	0.926	3.48	**0.032**	2.40	*0.092*
	Year:Season:P	1	0.22	0.928	0.58	0.681	0.18	0.175	1.62	0.172	0.47	0.761	2.46	**0.044**	2.86	**0.023**
	Water	2	16.80	**<0.001**	1.86	0.173	0.18	0.182	0.06	0.802	3.29	*0.070*	34.06	**<0.001**	246.96	**<0.001**
	Year:Water	2	8.00	**<0.001**	2.51	*0.083*	0.90	0.897	3.19	**0.042**	3.32	**0.037**	13.19	**<0.001**	76.5	**<0.001**
	Season:Water	1	0.23	0.793	1.12	0.328	0.69	0.685	0.13	0.880	2.16	0.116	0.98	0.375	2.451	*0.087*
	Year:Season:Water	1	0.49	0.740	1.50	0.200	0.58	0.583	0.60	0.665	0.69	0.598	8.29	**<0.001**	2.66	**0.032**
Synergistic Effects	**N:P**	4	1.44	0.232	3.89	**0.049**	0.60	0.604	1.19	0.276	0.98	0.324	0.56	0.454	1.66	0.199
	Year:N:P	4	0.55	0.576	0.53	0.587	0.31	0.307	0.16	0.852	0.45	0.640	1.40	0.248	3.95	**0.020**
	Season:N:P	2	0.28	0.756	0.98	0.376	0.71	0.709	0.08	0.924	0.05	0.951	0.09	0.910	1.79	0.169
	Year:Season:N:P	2	0.05	0.995	0.40	0.809	0.40	0.403	0.27	0.897	0.50	0.737	0.83	0.507	1.42	0.225
	N:Water	4	6.91	**0.009**	4.39	**0.037**	0.00	**<0.001**	4.43	**0.036**	0.37	0.544	1.97	0.161	36.74	**<0.001**
	Year:N:Water	2	0.51	0.599	1.36	0.258	0.12	0.124	0.85	0.428	0.86	0.426	4.19	**0.016**	20.01	**<0.001**
	Season:N:Water	2	0.95	0.386	0.52	0.596	0.76	0.763	0.22	0.802	1.29	0.276	0.023	0.977	1.46	0.233
	Year:Season:N:Water	2	0.46	0.768	1.81	0.126	0.42	0.420	0.75	0.561	0.16	0.960	0.78	0.541	1.18	0.320
	P:Water	2	1.05	0.307	0.40	0.530	0.34	0.340	0.10	0.754	0.02	0.903	0.26	0.611	2.22	0.137
	Year:P:Water	1	4.37	**0.013**	0.53	0.590	0.87	0.866	1.77	0.172	1.82	0.163	0.13	0.878	1.86	0.157
	Season:P:Water	4	1.06	0.349	0.20	0.816	0.65	0.652	1.35	0.259	2.56	0.078	1.24	0.291	0.25	0.781
	Year:Season:P:Water	4	0.28	0.891	0.80	0.528	0.97	0.968	0.51	0.727	0.83	0.507	2.51	**0.041**	1.99	0.103
	N:P:Water	4	2.18	0.141	0.51	0.474	0.01	**0.013**	21.99	**<0.001**	13.60	**<0.001**	0.04	0.839	4.28	**0.039**
	Year:N:P:Water	2	0.61	0.545	0.01	0.986	0.47	0.467	0.10	0.907	3.26	**0.039**	1.18	0.307	0.170	0.844
	Season:N:P:Water	2	0.11	0.898	2.47	*0.086*	0.99	0.992	1.16	0.316	0.93	0.395	0.70	0.495	0.47	0.627
	Year:Season:N:P:Water	4	0.51	0.725	0.74	0.566	0.15	0.154	1.14	0.335	0.60	0.660	1.05	0.383	0.65	0.628
	Residuals	504														

Table S3.2. Summary of multi-way ANOVA for Inorganic and Organic C, Total N, and Total P with the main factors of Year, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at p<0.05, and italicized values in pink cells are marginally significant at 0.05<p<0.1.

	Treatment Effects and Interactions	df	Total Elemental Pools							
			Inorganic C		Organic C		Total N		Total P	
			F	p	F	p	F	p	F	p
Time	Year	1	1088.15	**<0.001**	32.87	**0.000**	30.21	**0.000**	17.55	**0.000**
Individual Effects	N	1	1.32	0.254	0.36	0.547	0.01	0.914	1.90	0.171
	Year:N	1	1.75	0.189	0.00	0.997	0.02	0.881	0.04	0.833
	P	1	1.48	0.226	0.13	0.721	1.36	0.246	0.01	0.934
	Year:P	1	1.93	0.167	0.03	0.863	0.45	0.506	1.24	0.269
	Water	1	0.94	0.333	2.03	0.157	3.38	*0.069*	0.57	0.452
	Year:Water	1	0.64	0.427	0.44	0.506	1.21	0.274	0.68	0.413
Synergistic Effects	N:P	1	0.11	0.740	0.33	0.568	0.00	0.991	0.08	0.779
	Year:N:P	1	0.26	0.613	1.57	0.213	0.49	0.486	0.59	0.444
	N:Water	1	0.44	0.509	0.83	0.363	0.80	0.374	0.03	0.861
	Year:N:Water	1	0.70	0.405	0.01	0.942	0.20	0.653	0.88	0.350
	P:Water	1	0.01	0.911	1.98	0.162	0.32	0.570	0.62	0.433
	Year:P:Water	1	0.08	0.775	1.06	0.305	0.23	0.632	0.21	0.646
	N:P:Water	1	0.25	0.621	2.15	0.146	2.87	*0.093*	10.51	**0.002**
	Year:N:P:Water	1	0.45	0.504	0.03	0.863	0.29	0.592	0.16	0.689
	Residuals	112								

Table S3.3. Summary of multi-way ANOVA for soil pH and bulk density with the main factors of Year, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at $p<0.05$, and italicized values in pink cells are marginally significant at $0.05<p<0.1$. Soil pH was measured in a different season each year, so the multi-way ANOVA omitted Season as a factor. Grey boxes indicate factors that were not included in the multi-way ANOVA for Bulk Density, which was measured only once.

Treatment Effects and Interactions		**Physical Soil Properties**					
		df	**Soil pH**		**df**	**Bulk Density**	
			F	**p**		**F**	**p**
Time	**Year**	1	166.20	**<0.001**			
Individual Effects	**N**	1	34.31	**<0.001**	1	0.68	0.413
	Year:N	1	9.01	**0.003**			
	P	1	2.52	0.114	1	0.00	0.987
	Year:P	1	0.05	0.819			
	Water	1	5.89	**0.016**	1	0.04	0.833
	Year:Water	1	1.21	0.273			
Synergistic Effects	**N:P**	1	0.97	0.326	1	0.01	0.905
	Year:N:P	1	0.35	0.552			
	N:Water	1	2.05	0.154	1	0.02	0.876
	Year:N:Water	1	0.37	0.546			
	P:Water	1	5.57	**0.019**	1	0.02	0.900
	Year:P:Water	1	2.20	0.140			
	N:P:Water	1	1.95	0.164	1	4.95	**0.030**
	Year:N:P:Water	1	0.36	0.549			
Residuals		176			56		

Table S3.4: Changes in climate throughout the experiment compared to the thirty-year average maximum temperature (36ºC) and annual and monsoon precipitation (230mm and 119.6mm, respectively). Heat waves are defined as consecutive days during the 90-day monsoon season with a daily maximum temperature greater than the historic maximum of 36ºC.

Year	Days above 36ºC	Longest Heat Wave	Total Monsoon (Jul-Sep) Precipitation (mm)	Monsoon Precipitation / Historical Average (119.6 mm)	Total Annual Precipitation (mm)	Annual Precipitation / Historical Average (230mm)
2022	27	15	123.4	1.032	234.5	1.020
2023	59	41	46.2	0.386	112.6	0.490
2024	45	12	35	0.292	87.6	0.381

Table S4.1. Summary of multi-way ANOVA for total species cover and plant tissue C, N, and P content with Year, Functional Group (Fx Group), and N, P, and Water additions as main factors, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at p<0.05, and italicized values in pink cells are marginally significant at 0.05<p<0.1.

	Treatment Effects and Interactions	**df**	**Total Species Cover**		**df**	**Plant Tissue C, N, and P**					
						Foliar C		**Foliar N**		**Foliar P**	
			F	**p**		**F**	**p**	**F**	**p**	**F**	**p**
Time	**Year**	2	466.61	**<0.001**	1	16.96	**<0.001**	45.56	**<0.001**	26.71	**<0.001**
	Fx Group	2	132.32	**<0.001**	2	10.13	**<0.001**	23.39	**<0.001**	5.41	**0.006**
	Year:Fx Group	4	66.74	**<0.001**	2	11.79	**<0.001**	3.06	**0.049**	2.43	*0.092*
Individual Effects	**N**	1	0.21	0.644	1	0.58	0.446	0.35	0.553	0.74	0.392
	Year:N	2	0.68	0.505	1	1.72	0.191	1.77	0.185	0.17	0.684
	FxGroup:N	2	0.06	0.946	2	3.80	**0.024**	1.32	0.270	0.48	0.620
	Year:FxGroup:N	4	0.03	0.998	1	0.20	0.653	0.52	0.474	0.35	0.558
	P	1	0.01	0.944	1	0.01	0.908	0.36	0.550	0.22	0.640
	Year:P	2	0.01	0.988	1	0.56	0.455	0.90	0.344	0.93	0.338
	FxGroup :P	2	0.89	0.411	2	0.30	0.743	0.15	0.863	0.54	0.586
	Year: FxGroup:P	4	0.99	0.413	1	4.03	**0.046**	0.02	0.900	0.31	0.579
	Water	1	15.15	**<0.001**	1	0.31	0.579	0.65	0.422	10.21	**0.002**
	Year:Water	2	0.89	0.412	1	3.27	*0.072*	1.16	0.284	0.62	0.432
	FxGroup :Water	2	76.98	**<0.001**	2	1.42	0.245	0.74	0.480	0.41	0.663
	Year: FxGroup:Water	4	47.34	**<0.001**	1	0.78	0.378	0.15	0.702	1.16	0.283
Synergistic Effects	**N:P**	1	0.18	0.668	1	0.53	0.469	0.09	0.759	0.52	0.471
	Year:N:P	2	0.03	0.974	1	0.02	0.896	0.87	0.352	1.21	0.273
	FxGroup:N:P	2	0.11	0.900	2	1.23	0.296	0.62	0.541	0.76	0.471
	Year: FxGroup:N:P	4	0.43	0.784	1	0.60	0.440	0.89	0.346	0.17	0.679
	N:Water	1	0.14	0.708	1	0.22	0.640	0.82	0.365	0.00	0.953
	Year:N:Water	2	0.06	0.940	1	0.00	0.945	0.30	0.583	0.65	0.421
	FxGroup:N:Water	2	0.52	0.592	2	0.27	0.766	0.54	0.586	0.02	0.977
	Year: FxGroup:N:Water	4	0.86	0.487	0						
	P:Water	1	0.84	0.359	1	0.00	0.946	0.00	0.982	0.00	0.997
	Year:P:Water	2	1.36	0.259	1	0.15	0.703	0.42	0.520	2.03	0.157
	FxGroup:P:Water	2	2.35	*0.096*	1	0.11	0.739	0.00	0.955	0.18	0.832
	Year: FxGroup:P:Water	4	1.75	0.138	0						
	N:P:Water	1	0.02	0.890	1	0.82	0.366	0.02	0.892	0.10	0.758
	Year:N:P:Water	2	0.69	0.501	0					0.14	0.711
	FxGroup:N:P:Water	2	0.85	0.428	1	0.01	0.906	0.85	0.358	0.88	0.415
	Year: FxGroup:N:P:Water	4	0.36	0.834	0						
	Residuals	504			159						

Table S4.2. Summary of multi-way ANOVA for plant community diversity metrics with Year and N, P, and Water additions as main factors, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at p<0.05, and italicized values in pink cells are marginally significant at 0.05<p<0.1.

Treatment Effects and Interactions		**df**	**Plant Community Diversity**					
			Shannon		**Richness**		**Evenness**	
			F	**p**	**F**	**p**	**F**	**p**
Time	**Year**	2	100.81	**<0.001**	220.68	**<0.001**	9.82	**<0.001**
Individual Effects	**N**	1	0.08	0.771	0.03	0.859	4.33	**0.039**
	Year:N	2	2.59	*0.078*	1.10	0.336	3.13	**0.046**
	P	1	9.86	**0.002**	7.58	**0.007**	4.60	**0.033**
	Year:P	2	1.12	0.327	0.29	0.747	1.36	0.260
	Water	1	2.85	*0.093*	2.02	0.157	4.98	**0.027**
	Year:Water	2	18.74	**<0.001**	22.25	**<0.001**	3.35	**0.037**
Synergistic Effects	**N:P**	1	0.01	0.934	0.07	0.790	0.22	0.639
	Year:N:P	2	0.50	0.610	1.14	0.324	0.19	0.828
	N:Water	1	0.21	0.648	0.79	0.376	0.18	0.675
	Year:N:Water	2	0.61	0.547	0.60	0.550	0.81	0.446
	P:Water	1	0.34	0.560	0.39	0.535	2.74	*0.099*
	Year:P:Water	2	0.45	0.639	0.10	0.903	1.67	0.192
	N:P:Water	1	0.10	0.750	1.77	0.185	1.02	0.314
	Year:N:P:Water	2	0.81	0.448	1.35	0.262	0.47	0.624
	Residuals	168						

Table S4.3. Leaf Stoichiometric Ratios from each functional group in 2023 and 2024 separated by resource addition treatment. N:P ratios of < 14 or > 16 can indicate N or P limitation (Koerselman and Meuleman 1996). Missing values are from functional groups and treatments for which samples could not be collected due to insufficient plant material within the experimental plot in that year.

	Functional Group	C:N		C:P		N:P	
		2023	2024	2023	2024	2023	2024
Control	Native Grass	15.12		183.39		12.23	
	Forb	8.98	12.66	99.55	217.46	10.84	17.17
	Exotic Grass						
N	Native Grass	15.32		144.19		9.49	
	Forb	9.05	18.99	118.55	218.06	13.16	12.84
	Exotic Grass						
P	Native Grass	13.95	20.58	151.81	367.81	10.97	17.87
	Forb	11.08	23.19	159.84	209.85	14.42	9.39
	Exotic Grass	9.72		112.89		11.89	
N+P	Native Grass	14.51	23.16			13.40	
	Forb	8.39		113.66		13.75	
	Exotic Grass	12.35		128.33		10.81	
Water	Native Grass	15.23	18.65	208.17	299.02	13.87	17.00
	Forb	9.88	17.47	127.13	259.33	13.65	15.64
	Exotic Grass	11.57		142.51		10.10	
N+Water	Native Grass	14.66	18.26	198.73	226.15	13.78	13.86
	Forb	8.95	17.97	137.88	258.49	15.57	17.81
	Exotic Grass	16.02		184.76		12.57	
P+Water	Native Grass	15.39	20.95	214.87	225.29	14.23	11.36
	Forb	9.82	16.26	156.86	245.39	16.31	17.20
	Exotic Grass	14.00		161.97		11.67	
N+P+Water	Native Grass	13.87	19.90	196.22	221.35	14.24	12.18
	Forb	9.08	22.38	126.74	263.64	13.42	13.08
	Exotic Grass	12.57	18.49	146.27	124.08	9.96	6.71

Table S5.1. Summary of multi-way ANOVA for microbial C, N, and P content with the main factors of Year, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at p<0.05, and italicized values in pink cells are marginally significant at 0.05<p<0.1.

	Treatment Effects and Interactions	**df**	**Microbial Biomass**					
			MBC		**MBN**		**MBP**	
			F	**p**	**F**	**p**	**F**	**p**
Time Effects	**Year**	1	167.41	**<0.001**	0.12	0.728	88.44	**<0.001**
	Season	2	52.81	**<0.001**	25.49	**<0.001**	6.42	**0.002**
	Year:Season	2	43.80	**<0.001**	12.18	**<0.001**	22.37	**<0.001**
Individual Effects	**N**	1	0.07	0.791	6.89	**0.009**	0.97	0.326
	Year:N	1	0.40	0.528	0.72	0.397	0.04	0.846
	Season:N	2	0.27	0.762	1.85	0.158	0.59	0.553
	Year:Season:N	2	1.88	0.154	3.09	**0.047**	0.35	0.702
	P	1	3.30	*0.070*	0.51	0.474	6.41	**0.012**
	Year:P	1	1.06	0.305	4.01	**0.046**	4.85	**0.028**
	Season:P	2	0.37	0.692	0.05	0.949	0.61	0.542
	Year:Season:P	2	1.64	0.194	0.37	0.692	0.20	0.818
	Water	1	0.68	0.411	0.91	0.340	0.26	0.613
	Year:Water	1	4.34	**0.038**	2.86	*0.091*	0.00	0.964
	Season:Water	2	1.42	0.244	0.20	0.821	0.17	0.840
	Year:Season:Water	2	6.63	**0.001**	6.84	**0.001**	0.23	0.796
Synergistic Effects	**N:P**	1	0.12	0.724	0.15	0.697	0.31	0.576
	Year:N:P	1	1.45	0.229	0.07	0.788	1.88	0.171
	Season:N:P	2	0.91	0.405	0.87	0.421	0.71	0.490
	Year:Season:N:P	2	1.17	0.312	0.41	0.663	1.08	0.340
	N:Water	1	0.17	0.681	0.22	0.636	1.44	0.231
	Year:N:Water	1	0.95	0.329	4.23	**0.040**	0.06	0.804
	Season:N:Water	2	0.09	0.916	0.68	0.508	0.97	0.380
	Year:Season:N:Water	2	0.09	0.916	4.29	**0.014**	0.10	0.902
	P:Water	1	1.02	0.312	0.05	0.816	0.30	0.581
	Year:P:Water	1	0.14	0.711	0.08	0.772	1.08	0.300
	Season:P:Water	2	0.14	0.872	0.25	0.778	0.05	0.947
	Year:Season:P:Water	2	0.11	0.895	0.05	0.954	0.09	0.915
	N:P:Water	1	1.16	0.281	1.92	0.166	0.23	0.628
	Year:N:P:Water	1	4.06	**0.044**	1.21	0.272	0.15	0.698
	Season:N:P:Water	2	1.66	0.191	1.74	0.177	1.57	0.208
	Year:Season:N:P:Water	2	0.32	0.723	0.60	0.548	0.90	0.408
	Residuals	528						

Table S5.2. Summary of multi-way ANOVA for soil respiration measured as CO_2 flux with the main factors of Year, Date, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at $p<0.05$, and italicized values in pink cells are marginally significant at $0.05<p<0.1$.

	Treatment Effects and Interactions	**df**	**Soil Respiration**	
			F	**p**
Time Effects	**Year**	2	1.72	0.180
	Date	14	8.00	**<0.001**
Individual Effects	**N**	1	0.36	0.549
	Year:N	2	0.92	0.399
	Date:N	13	0.33	0.988
	P	1	0.83	0.362
	Year:P	2	0.96	0.384
	Date:P	12	0.34	0.982
	Water	1	0.09	0.759
	Year:Water	2	1.03	0.359
	Date:Water	12	1.11	0.352
Synergistic Effects	**N:P**	1	3.41	*0.065*
	Year:N:P	2	0.04	0.956
	Date:N:P	12	1.09	0.361
	N:Water	1	0.36	0.550
	Year:N:Water	2	1.14	0.319
	Date:N:Water	12	0.68	0.773
	P:Water	1	0.01	0.940
	Year:P:Water	2	2.36	*0.095*
	Date:P:Water	12	1.92	**0.029**
	N:P:Water	1	0.00	0.957
	Year:N:P:Water	2	1.67	0.189
	Date:N:P:Water	12	0.70	0.750
	Residuals	835		

Table S5.3. Summary of multi-way ANOVA for potential activity of hydrolytic extracellular enzymes with the main factors of Year, Date, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at $p<0.05$, and italicized values in pink cells are marginally significant at $0.05<p<0.1$.

Treatment Effects and Interactions	**df**	**P-acquiring**				**N-Acquiring**				**C-Acquiring**							
		Phos		**PhosD**		**LAP**		**NAG**		**Cello**		**Xylo**		**AGluc**		**BGluc**	
		F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Year	1	128.79	**<0.001**	66.86	**<0.001**	86.45	**<0.001**	3.24	**<0.001**	45.15	**<0.001**	97.99	**<0.001**	96.78	**<0.001**	349.21	**<0.001**
Season	1	21.21	**<0.001**	0.86	0.355	0.62	0.433	23.49	**<0.001**	0.03	0.863	6.29	**0.013**	0.14	0.713	437.28	**<0.001**
Year:Season	1	2.46	0.118	24.25	**<0.001**	132.57	**<0.001**	88.01	**<0.001**	28.15	**<0.001**	0.83	0.363	49.97	**<0.001**	240.24	**<0.001**
N	1	6.24	**0.013**	0.03	0.856	12.75	**<0.001**	0.20	0.652	0.38	0.539	0.03	0.858	0.13	0.718	0.62	0.430
Year:N	1	4.13	**0.043**	0.04	0.850	0.00	0.944	0.32	0.573	0.11	0.737	0.11	0.740	1.01	0.316	0.00	0.962
Season:N	1	1.62	0.204	0.21	0.649	0.07	0.798	0.01	0.919	0.49	0.485	0.20	0.657	0.00	0.986	0.60	0.437
Year:Season:N	1	2.52	0.113	0.34	0.562	4.91	**0.027**	0.97	0.324	0.06	0.803	0.41	0.521	0.00	0.955	0.00	0.976
P	1	0.01	0.921	2.05	0.153	0.99	0.320	0.21	0.651	0.10	0.746	0.03	0.859	3.88	**0.050**	1.26	0.262
Year:P	1	0.30	0.587	5.27	**0.022**	1.59	0.208	0.45	0.504	0.34	0.562	0.28	0.597	6.48	**0.011**	0.46	0.498
Season:P	1	0.27	0.606	0.62	0.432	0.36	0.548	0.82	0.367	0.49	0.486	0.00	0.951	4.59	**0.033**	0.02	0.902
Year:Season:P	1	0.00	0.979	1.46	0.228	3.49	*0.063*	0.31	0.576	0.14	0.704	0.17	0.681	0.95	0.329	0.06	0.801
Water	1	5.25	**0.023**	0.28	0.597	3.90	**0.049**	0.13	0.719	2.09	0.149	7.31	**0.007**	0.10	0.752	2.77	*0.097*
Year:Water	1	0.25	0.618	0.26	0.609	0.19	0.667	1.10	0.295	0.15	0.698	0.02	0.900	0.20	0.654	0.64	0.426
Season:Water	1	1.40	0.238	1.49	0.224	3.74	*0.054*	0.11	0.746	1.04	0.308	3.25	*0.072*	1.44	0.231	2.19	0.140
Year:Season:Water	1	0.85	0.358	0.67	0.415	0.13	0.715	1.37	0.243	3.02	*0.083*	0.06	0.812	0.02	0.901	1.07	0.301
N:P	1	0.08	0.777	0.00	0.978	2.45	0.119	0.00	0.970	7.39	**0.007**	8.23	**0.004**	0.44	0.509	3.03	*0.083*
Year:N:P	1	0.08	0.776	1.57	0.211	0.00	0.968	0.99	0.321	0.81	0.370	0.21	0.650	2.03	0.155	0.91	0.340
Season:N:P	1	1.01	0.316	0.67	0.414	0.12	0.725	0.26	0.611	2.91	*0.089*	0.06	0.802	2.03	0.155	1.57	0.211
Year:Season:N:P	1	2.65	0.104	0.89	0.347	0.00	0.987	1.58	0.209	0.11	0.740	0.20	0.656	0.01	0.911	0.68	0.412
N:Water	1	0.31	0.576	0.22	0.641	2.08	0.150	1.47	0.227	0.11	0.737	0.00	0.982	0.49	0.485	0.00	0.960
Year:N:Water	1	2.26	0.134	0.37	0.545	0.35	0.553	0.93	0.337	0.02	0.891	1.33	0.250	0.63	0.429	0.26	0.612
Season:N:Water	1	0.04	0.837	0.42	0.518	0.00	0.997	2.23	0.136	0.86	0.355	0.16	0.686	0.37	0.546	0.03	0.858
Year:Season:N:Water	1	3.04	*0.082*	0.55	0.458	6.67	**0.010**	0.33	0.564	0.19	0.660	4.65	**0.032**	3.54	*0.061*	0.22	0.642
P:Water	1	0.18	0.675	0.47	0.493	2.65	0.105	0.32	0.571	0.23	0.630	5.12	**0.024**	0.05	0.832	5.28	**0.022**
Year:P:Water	1	0.95	0.331	0.46	0.496	3.29	*0.071*	0.09	0.764	0.14	0.709	1.78	0.183	0.41	0.522	2.64	0.105
Season:P:Water	1	0.29	0.588	0.53	0.467	0.33	0.566	0.01	0.922	0.01	0.920	0.13	0.718	0.73	0.395	3.11	*0.079*
Year:Season:P:Water	1	0.34	0.562	2.02	0.156	0.64	0.426	0.09	0.762	1.34	0.248	0.06	0.814	0.15	0.698	3.00	*0.084*
N:P:Water	1	1.84	0.176	1.53	0.218	2.58	0.109	0.00	0.953	1.25	0.265	1.30	0.254	1.26	0.263	1.55	0.214
Year:N:P:Water	1	2.62	0.106	0.09	0.769	1.20	0.273	0.34	0.562	0.00	0.975	0.27	0.605	4.26	**0.040**	0.92	0.338
Season:N:P:Water	1	0.10	0.748	3.07	*0.081*	0.00	0.977	0.13	0.718	1.18	0.279	0.25	0.614	0.05	0.821	0.27	0.602
Year:Season:N:P:Water	1	0.16	0.693	0.52	0.472	0.13	0.721	0.55	0.460	0.02	0.892	0.09	0.768	0.18	0.671	0.19	0.665
Residuals	340																

Table S5.4. Summary of multi-way ANOVA for potential activity of oxidative extracellular enzymes with the main factors of Year, Date, N, P, and Water, where N, P, and Water were treated as binary dummy variables. Bold values in blue cells are significant at $p<0.05$, and italicized values in pink cells are marginally significant at $0.05<p<0.1$.

	Treatment Effects and Interactions	**Oxidative Enzymes**					
		Phenol			**Perox**		
		df	**F**	**p**	**df**	**F**	**p**
Time	**Year**	1	84.43	**<0.001**	1	91.49	**<0.001**
	Season	1	168.05	**<0.001**	1	216.53	**<0.001**
	Year:Season	1	32.26	**<0.001**	1	48.04	**<0.001**
Individual Effects	**N**	1	0.14	0.705	1	0.26	0.611
	Year:N	1	0.54	0.463	1	0.43	0.512
	Season:N	1	0.04	0.840	1	0.10	0.758
	Year:Season:N	1	0.26	0.610	1	0.13	0.721
	P	1	0.24	0.626	1	1.34	0.249
	Year:P	1	1.32	0.252	1	3.48	*0.063*
	Season:P	1	0.85	0.358	1	1.84	0.176
	Year:Season:P	1	0.88	0.350	1	2.94	*0.087*
	Water	1	0.05	0.827	1	1.33	0.249
	Year:Water	1	0.06	0.814	1	1.22	0.271
	Season:Water	1	0.67	0.415	1	2.34	0.127
	Year:Season:Water	1	1.29	0.257	1	0.41	0.523
Synergistic Effects	**N:P**	1	1.63	0.203	1	0.32	0.571
	Year:N:P	1	2.54	0.112	1	1.22	0.269
	Season:N:P	1	1.66	0.199	1	0.22	0.637
	Year:Season:N:P	1	0.27	0.600	1	0.38	0.537
	N:Water	1	2.74	*0.099*	1	0.02	0.876
	Year:N:Water	1	2.18	0.141	1	0.45	0.502
	Season:N:Water	1	2.31	0.129	1	1.83	0.177
	Year:Season:N:Water	1	7.54	**0.006**	1	3.69	*0.056*
	P:Water	1	1.15	0.284	1	0.85	0.357
	Year:P:Water	1	0.62	0.432	1	0.05	0.821
	Season:P:Water	1	0.02	0.902	1	0.09	0.762
	Year:Season:P:Water	1	0.28	0.600	1	0.55	0.460
	N:P:Water	1	6.25	**0.013**	1	1.65	0.199
	Year:N:P:Water	1	0.26	0.607	1	0.74	0.390
	Season:N:P:Water	1	0.38	0.536	1	0.00	0.966
	Year:Season:N:P:Water	1	0.39	0.535	1	3.76	*0.053*
	Residuals	339			327		

Table S5.5. Changes in climate throughout the experiment compared to the thirty-year average maximum temperature (36ºC) and annual and monsoon precipitation (230mm and 119.6mm, respectively). Heat waves are defined as consecutive days during the 90-day monsoon season with a daily maximum temperature greater than the historic maximum of 36ºC.

Year	Days above 36ºC	Longest Heat Wave	Total Monsoon (Jul-Sep) Precipitation (mm)	Monsoon Precipitation / Historical Average (119.6 mm)	Total Annual Precipitation (mm)	Annual Precipitation / Historical Average (230mm)
2022	27	15	123.4	1.032	234.5	1.020
2023	59	41	46.2	0.386	112.6	0.490
2024	45	12	35	0.292	87.6	0.381

Supplemental Figures

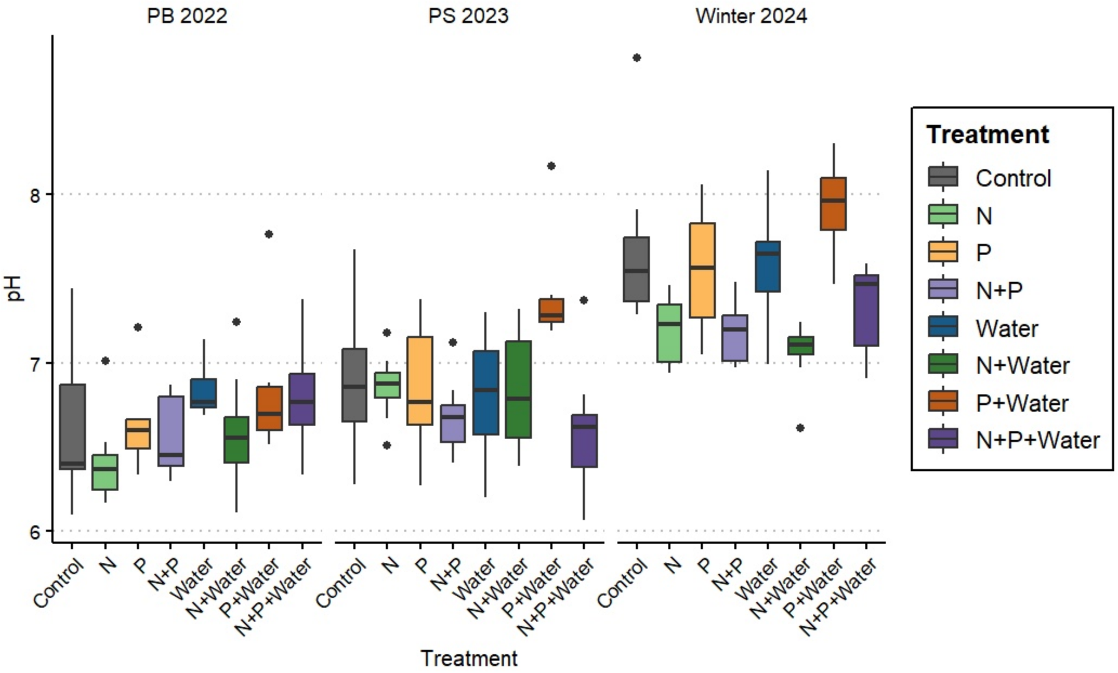


Figure S3.1. Soil pH throughout the experiment. pH was measured for Peak Biomass samples in 2022, Peak Season samples in 2023, and Winter samples in 2024. See Figure 1 for significant ANOVA effects.

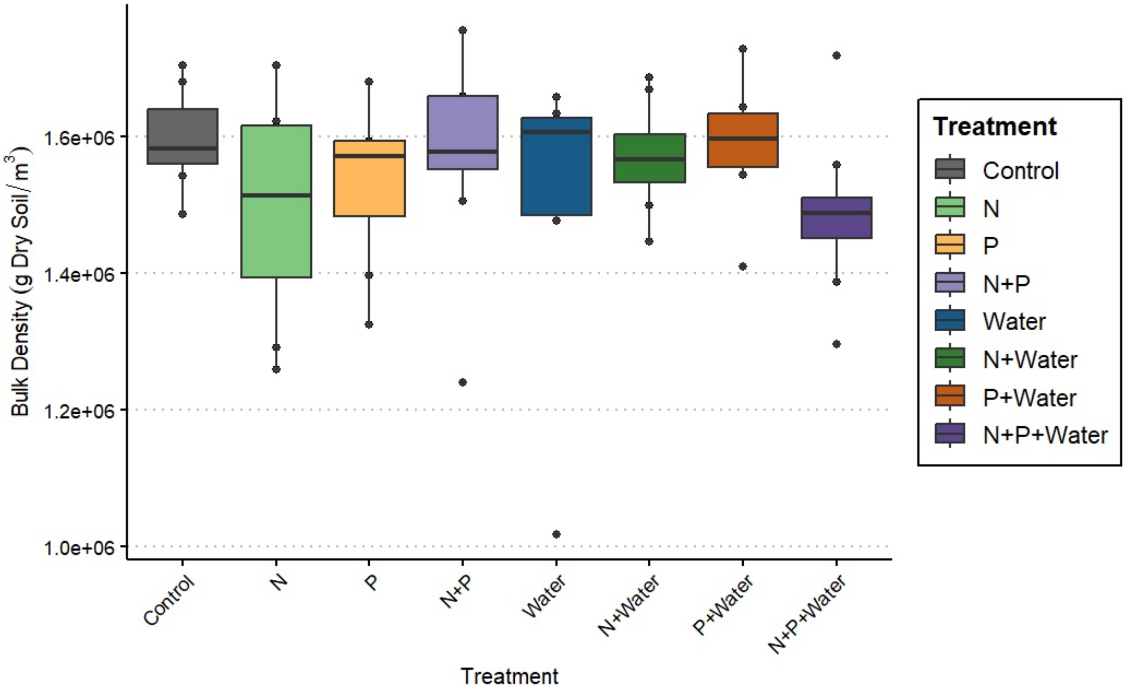


Figure S3.2. Changes in soil bulk density (dry soil mass / soil volume) in response to resource addition treatments. For significant ANOVA effects, see Figure 1.

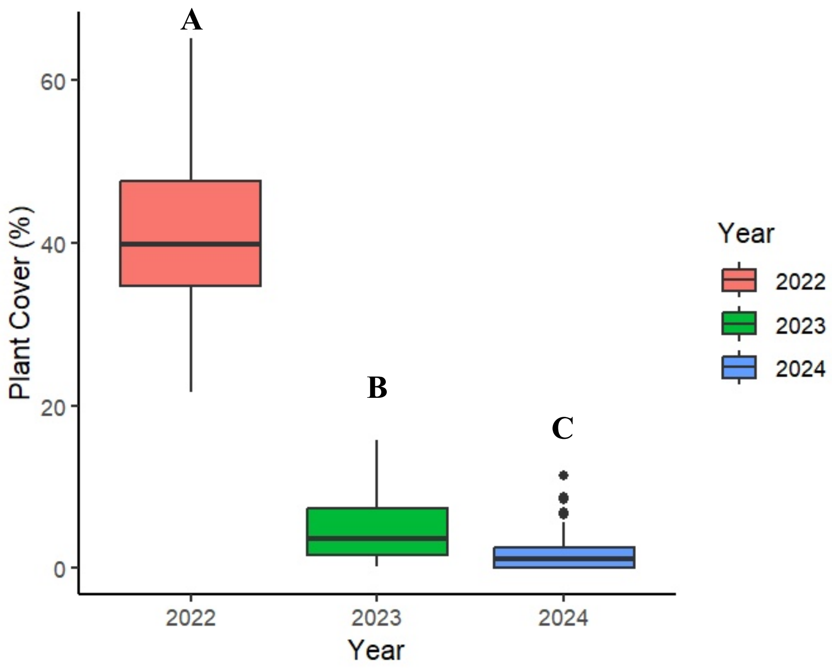


Figure S4.1. Changes in total plant cover between years. Letters denote significant (p<0.05) differences between years.

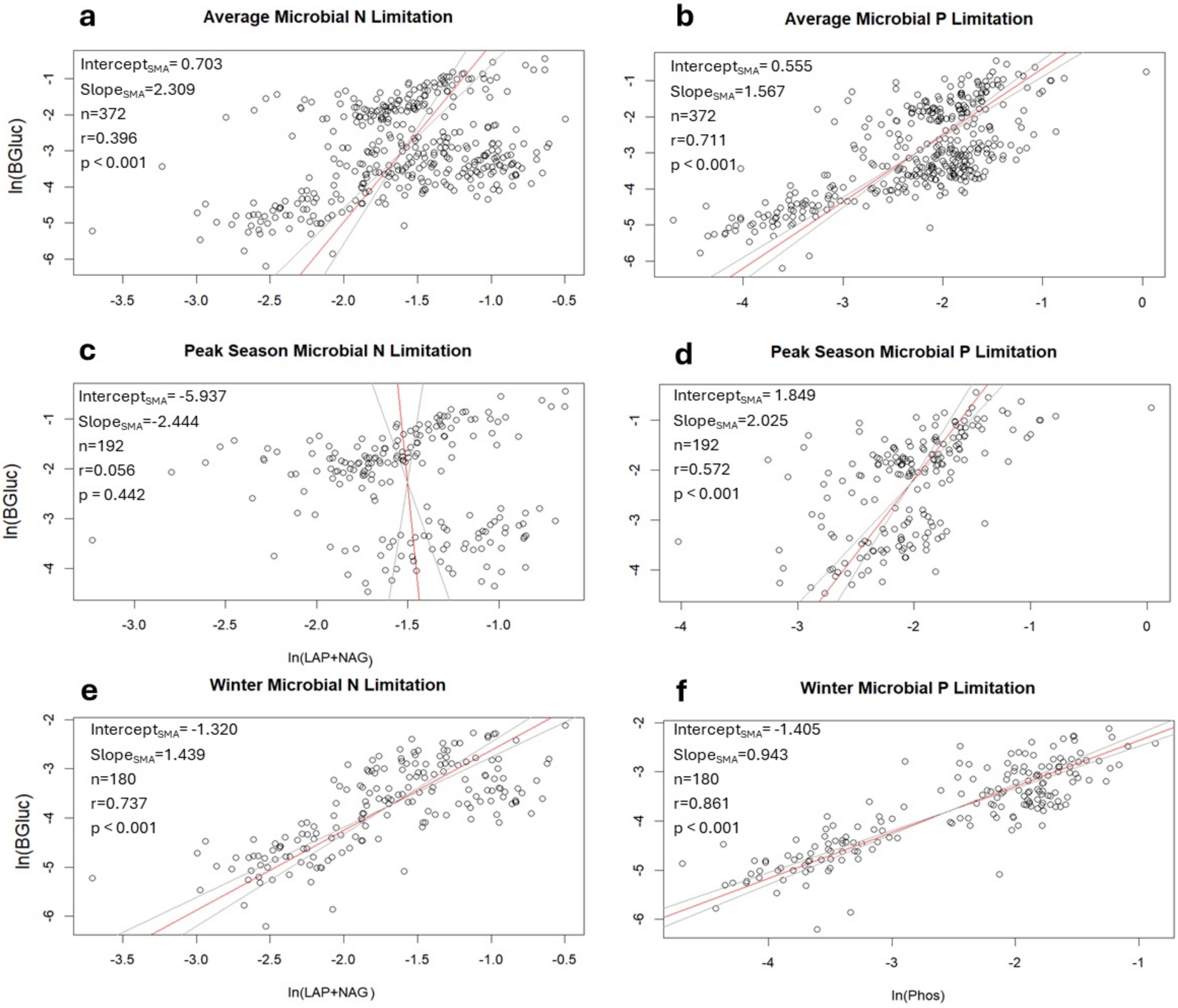


Figure S5.1. Standardized Major Axis (SMA) Regression analysis using extracellular enzymatic activity to produce normalization constants (n_0 and p_0) from data averaged across the full experiment (a & b) and seasons (c – f) for the limitation model formulated by Cui et al. (2023).

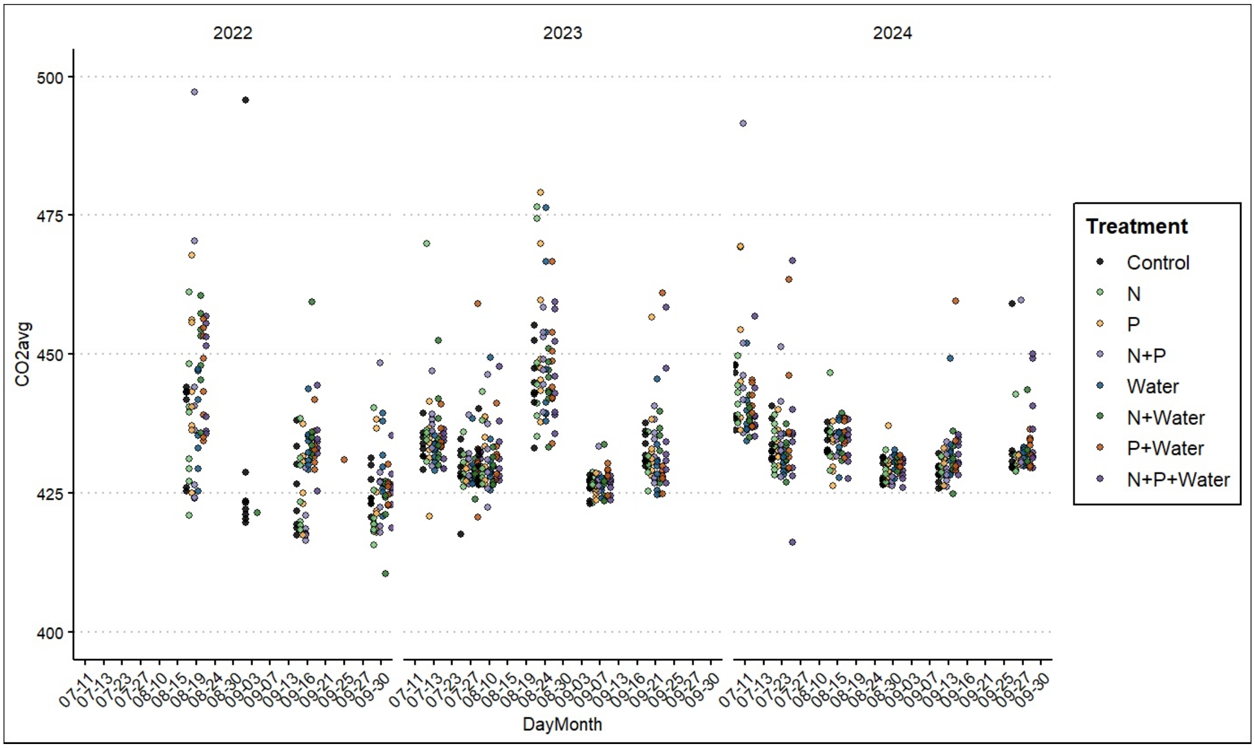


Figure S5.2. Soil Respiration measured as CO_2 flux from the soil surface. Data were collected from within each experimental plot once every two weeks during each monsoon season. Multi-way ANOVA found significant differences within but not between years and a significant P*Water*Date interaction ($p<0.05$).

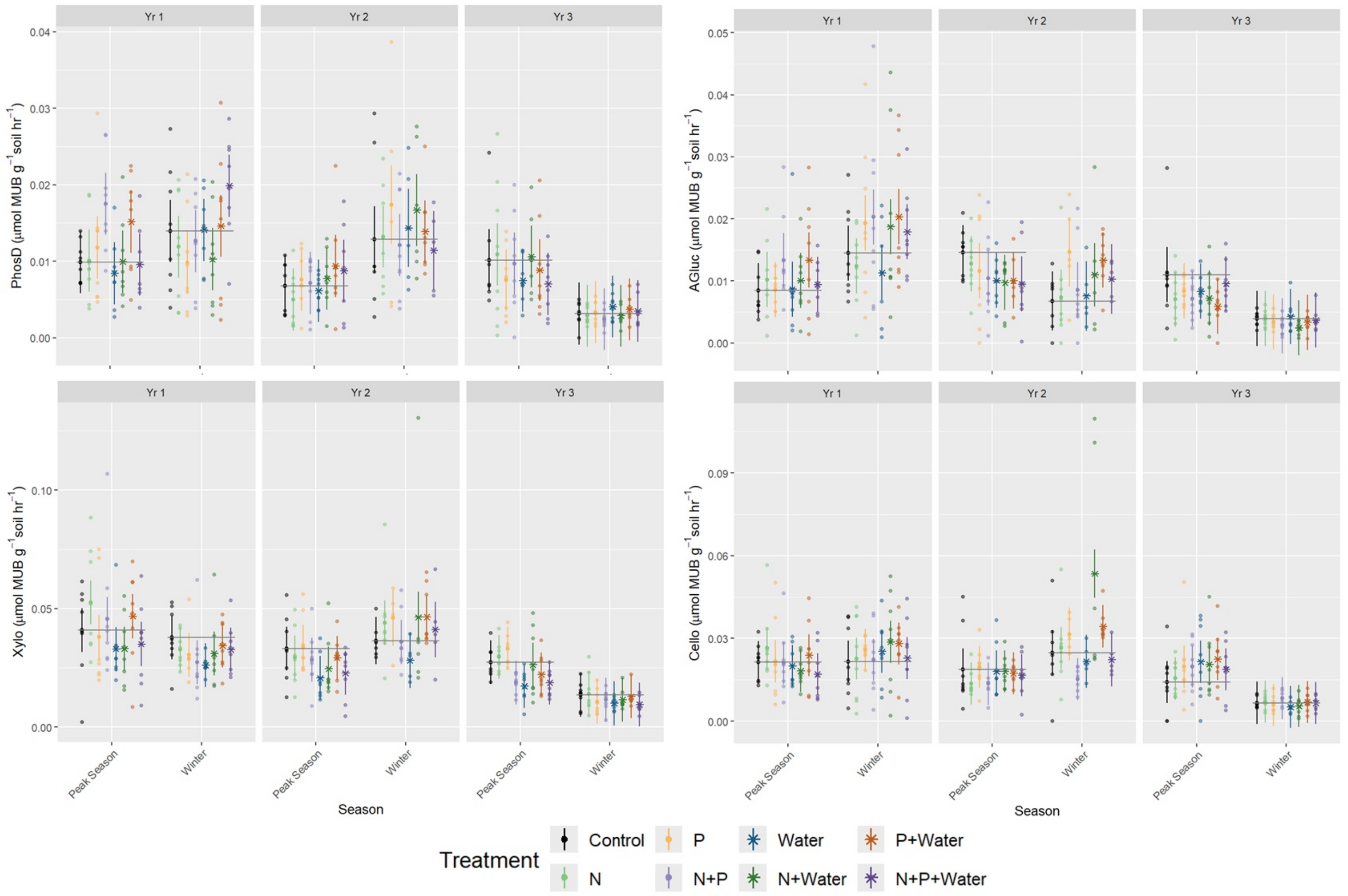
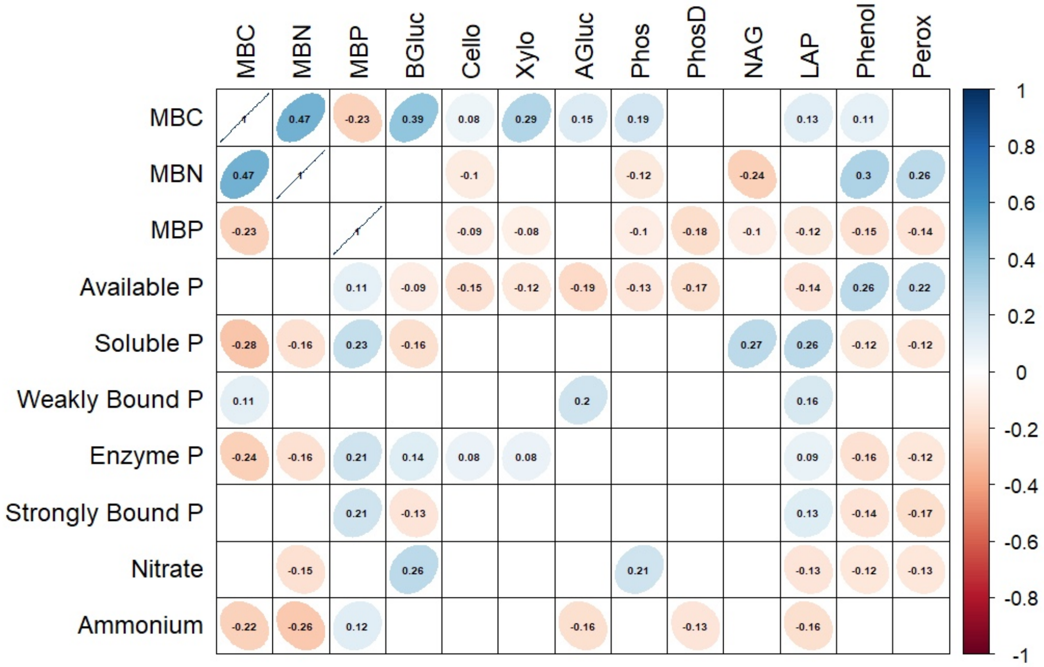


Figure S5.3. 95% Confidence Intervals showing the seasonal and annual trends in potential extracellular enzyme activity for the supplemental hydrolytic enzymes. Horizontal grey lines within each season indicate the mean value of potential enzymatic activity in control plots for that season only. Refer to Figure 4.1 and Table S4.1 for significant ANOVA effects.



	MBC	MBN	MBP	BGluc	Cello	Xylo	AGluc	Phos	PhosD	NAG	LAP	Phenol	Perox
MBC	1	0.47	-0.23	0.39	0.08	0.29	0.15	0.19			0.13	0.11	
MBN	0.47	1			-0.1			-0.12		-0.24		0.3	0.26
MBP	-0.23		1		-0.09	-0.08		-0.1	-0.18	-0.1	-0.12	-0.15	-0.14
Available P			0.11	-0.09	-0.15	-0.12	-0.19	-0.13	-0.17		-0.14	0.26	0.22
Soluble P	-0.28	-0.16	0.23	-0.16						0.27	0.26	-0.12	-0.12
Weakly Bound P	0.11						0.2				0.16		
Enzyme P	-0.24	-0.16	0.21	0.14	0.08	0.08					0.09	-0.16	-0.12
Strongly Bound P			0.21	-0.13							0.13	-0.14	-0.17
Nitrate		-0.15		0.26				0.21			-0.13	-0.12	-0.13
Ammonium	-0.22	-0.26	0.12			-0.16		-0.13			-0.16		

Figure S5.4. Correlogram showing significant ($p < 0.05$) correlative relationships between internal microbial concentrations and nutrient pools (left) and internal microbial concentrations and potential extracellular enzymatic activity (top), with blue and red cells indicating positive and negative correlations, respectively. Darker shades of blue or red and more apparent ellipses within each cell denote stronger relationships between variables.

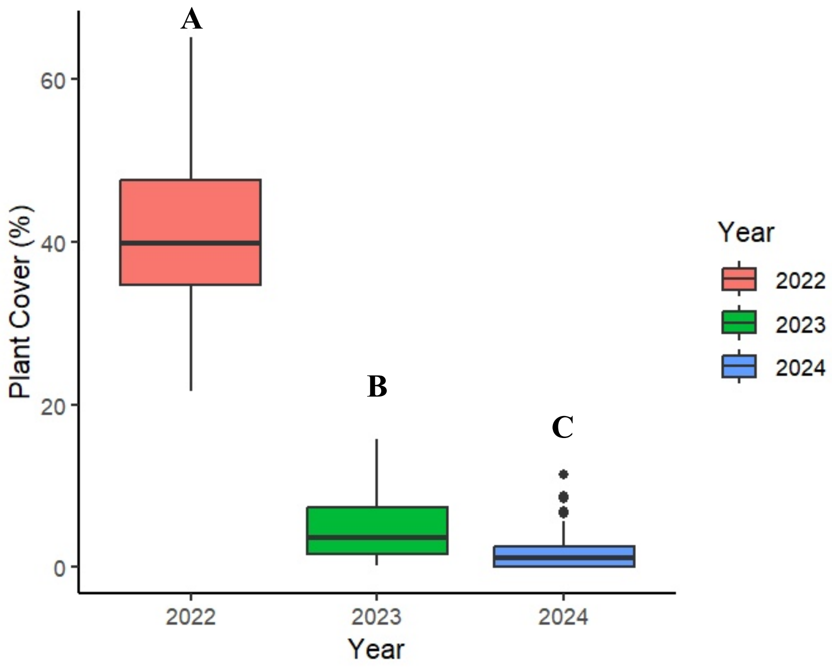


Figure S5.5. Changes in total plant cover between years. Letters denote significant ($p<0.05$) differences between years.

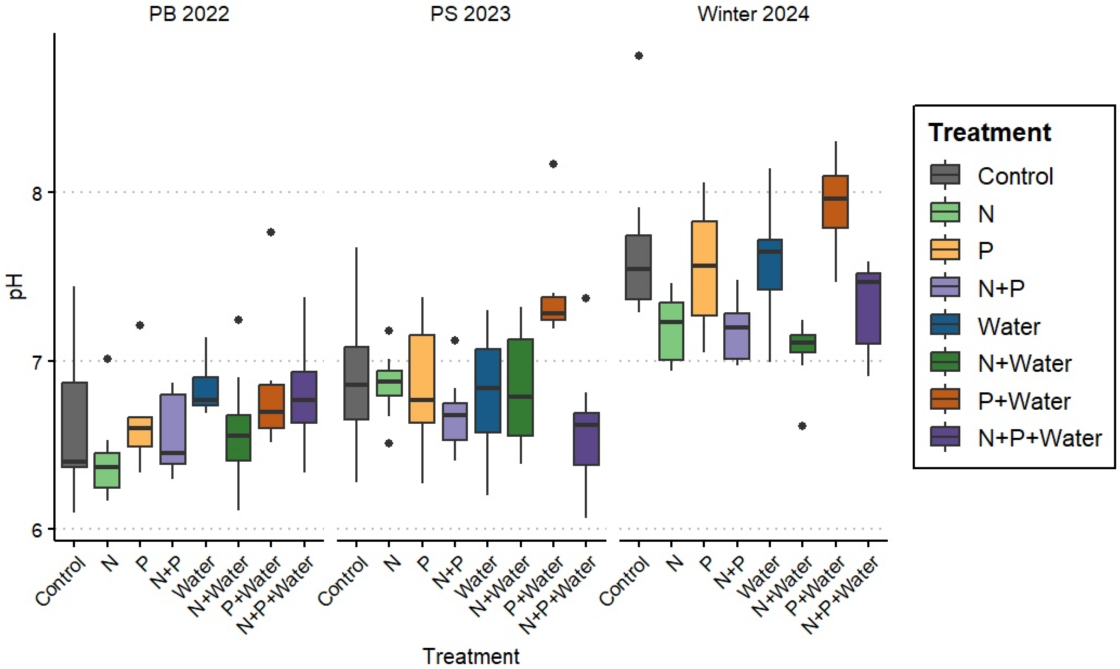


Figure S5.6. Soil pH throughout the experiment. pH was measured for Peak Biomass samples in 2022, Peak Season samples in 2023, and Winter samples in 2024. See Figure 5.1 for significant ANOVA effects.

Vita

Dylan Stover received a B.S. in Molecular Environmental Biology from the University of California, Berkeley in 2019 where he was awarded the UC Berkeley Summer Undergraduate Research Fellowship. At UTEP, Dylan served as a Graduate Research Assistant under Dr. Jennie McLaren and mentored 18 undergraduate, post-baccalaureate, and graduate students conducting field and laboratory research. As a graduate student, Dylan was awarded the Jornada Basin Long Term Ecological Research Program's Graduate Student Fellowship (2023 and 2025), the Ecological Society of America's Emerging Southwestern Ecologist Award (2024), the UTEP Graduate Student Travel Grant (2024), the UTEP Department of Earth, Environmental, and Resource Sciences' White Award (2023), and the UTEP Department of Biological Sciences' Academic and Research Excellence Award (2025). Dylan has been deeply involved in collaborative research, leading a multi-institutional ecological field experiment with Drylands Critical Zone Thematic Cluster, participating in a Synthesis Working Group funded by the National Center for Ecological Analysis and Synthesis, and conducting an experiment with the United States Geological Survey. Dylan has published his research in *Grasslands* and *Cambridge Prisms: Drylands* and presented his research at academic conferences including the *Ecological Society of America*, the *Long Term Ecological Research Network,* the *Soil Ecology Society,* and the *Chihuahuan Desert Education Coalition*. Lastly, Dylan has been committed to service and outreach, partnering with local groups including the Frontera Land Alliance, Insights El Paso, and the Asombro Institute and serving as a Graduate Student Representative on the LTER Network's Graduate Student and Broadening Participation Committees to increase accessibility and equity in the field of Ecology.

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