UNIVERSITY OF CALIFORNIA

Los Angeles

Ecogeomorphic interactions in drylands: Aeolian processes

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in Geography

by

Michael Raymond Fischella

2024

ABSTRACT OF THE DISSERTATION

Ecogeomorphic interactions in drylands: Aeolian processes

by

Michael Raymond Fischella
Doctor of Philosophy in Geography
University of California, Los Angeles, 2024
Professor Gregory Stewart Okin, Chair

Dryland environments are experiencing shifting ecogeomorphic patterns due to climatic changes and anthropogenic activities, resulting in a shift from grasslands to shrub-dominated landscapes. This dissertation investigates the effects from increasingly variable monsoonal precipitation and ecogeomorphic connectivity on perennial grass growth, litter distribution, and soil organic matter in drylands, with a focus on grass-shrub ecotones. Field experiments were conducted in the Chihuahuan Desert at the Jornada Basin Long-Term Ecological Research (LTER) site using a precipitation manipulation system and connectivity modifiers (ConMods) to assess their effects on plant productivity, recruitment, and soil nutrient distribution. Results show that reducing connectivity, combined with increased monsoonal precipitation, can enhance perennial grass productivity and recruitment, and affect the distribution of soil organic matter and non-photosynthetic vegetation. These findings contribute to our understanding of how aeolian processes and shifting precipitation regimes will shape vegetation patterns and soil properties in dryland environments under future climate scenarios. This research provides insights into potential mitigation strategies for combating shrub encroachment and promoting the sustainability of dryland ecosystems.

The dissertation of Michael Raymond Fischella is approved.

Yongkang Xue
Kyle C. Cavanaugh
Osvaldo Sala
Gregory Stewart Okin, Committee Chair

University of California, Los Angeles,
2024

Dedications

To my friends and family, whose unwavering support and encouragement carried me through this challenging and incredible journey. I extend my deepest gratitude to my advisor, Greg. Your constant encouragement, invaluable guidance, and endless patience have shaped not only this dissertation, but also my growth as a scientist. I cannot thank you enough for advising me throughout my dissertation! Finally, a special thanks to my friends from the Jornada. You turned the hardest days of fieldwork into exciting projects. Your company and time grilling were a much-needed reprieve that made my time there some of the best during my dissertation.

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Table of Acronyms

ANPP - Aboveground Net Primary Productivity

ANCOVA – Analysis of Covariance

ARMS – Automatic Rainfall Manipulation System

BNPP - Belowground Net Primary Productivity

C - Carbon

ConMod – Connectivity Modifier

LTER – Long Term Ecological Research Site

MMRM – Linear Mixed Model for Repeated Measures

N - Nitrogen

NAMS – North American Monsoon Season

NPP – Net Primary Productivity

NPV – Non-Photosynthetic Vegetation

PAWC – Plant Available Water Capacity

PV – Photosynthetic Vegetation

SIC – Soil Inorganic Carbon

SOC – Soil Organic Carbon

SOM – Soil Organic Matter

Vita

Education

University of California, Los Angeles	C.Phil. (Physical Geography)	2022
University of California, Los Angeles	M.A. (Geography)	2017
University of California, Los Angeles	B.A. (Geography)	2024

Research Interests

I am an interdisciplinary eco-geomorphologist whose research aims to understand the role that aeolian processes have in influencing dryland environments. Although most of my research focuses on eco-geomorphology, my research also strives to improve our understanding of the anthropogenic causes and consequences of aeolian processes. Additionally, I am interested in the interactions between fluvial and aeolian processes, how they impact ecosystem composition, and how a changing climate will influence these processes. Questions that I think are interesting, focus on the effects that anthropogenic-driven climate has on the hydrological cycle, how these changes influence ecosystems and local communities through extreme events such as droughts, floods, and haboobs. The primary goal of my research is to improve our understanding of these processes in meaningful ways that can benefit decision and policy makers, that are also interesting to the general public and scientific community.

Research Skills

Ecological fieldwork; computer programming (R, LabVIEW, IDL); geographic information system (GIS) and remote sensing data creation and analysis (QGIS, ENVI, and Arc GIS); designing and operating 3D printers; the construction and design of an autonomous portable wind tunnel; analyzing and collecting remotely sensed datasets; constructing and maintaining an automatic rainfall manipulation system (ARMS); the operation and maintenance of UAV's for fieldwork; geocoding (GIS) analysis; teaching; LaTeX.

Teaching Assistantships

Winter 2024: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 127L. *Soil and Environment Field Laboratory* (Professor Greg Okin).

Winter 2024: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 127. *Soil and Environment Field* (Professor Greg Okin).

Winter 2023: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 127L. *Soil and Environment Field Laboratory* (Professor Greg Okin).

Winter 2023: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 127. *Soil and Environment Field* (Professor Greg Okin).

Winter 2020: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 127L. *Soil and Environment Field Laboratory* (Dr. Lillia Illes).

Winter 2020: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 127. *Soil and Environment* (Dr. Lillia Illes).

Spring 2019: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 7. *Introduction to GIS* (Dr. Sierra Burkhart).

Spring 2018: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 2, *Biodiversity in Changing World* (Professor Daniela Cusack). **Winter 2018**: Teaching Assistant. Department of Geography, University of California, Los Angeles. Geography 113, *Humid Tropics* (Professor Thomas Gillespie).

Summer 2017: Course Reader. Department of Geography, University of California, Los Angeles. Geography 168, *Intermediate GIS* (Dr. Katherine Willis).

Summer 2017: Course Reader. Department of Geography, University of California, Los Angeles. Geography 7, *Introduction to GIS* (Dr. Katherine Willis).

Peer-Reviewed Publications *** Advised Undergraduate**

1. Niu F., Pierce, N., Okin G., Archer S., **Fischella, M. R.**, Nadoum, S. 2023. Sandblasting promotes shrub encroachment in arid grasslands. *New Phytologist.* https://doi.org/10.1111/nph.19238
2. *Payne, Sarah A. R., Okin, Gregory S., Bhattachan, Abinash, and **Fischella, M. R.** 2023. The Two Faces of Janus: Processes Can Be Both Exogenous Forcings and Endogenous Feedbacks with Wind as a Case Study. *Ecology* 104(4): e3998. https://doi.org/10.1002/ecy.3998
3. Huang H., **Fischella M. R.**, Liu Y., Ban Z., Fayne J V, Li D, Cavanaugh K, Lettenmaier D. 2022. Changes in Mechanisms and Characteristics of Western U.S. Floods Over the Last Sixty years. *Geophysical Research Letters*. https://doi.org/10.1029/2021GL097022

Introduction

In the face of climate change, understanding how the earth's various environmental processes will respond is of critical importance (Bestelmeyer et al., 2015; Knapp et al., 2008). In particular, dryland environments are an essential landscape, as it accounts for over 40% of the Earth's terrestrial surface area (Maestre et al., 2021; Van Auken, 2009), and near 40% of global net primary productivity (Wang et al., 2023; Yao et al., 2020). Drylands are home to more than 2.5 billion people, the majority of which reside in the global south (Aliber and Hart, 2009; Armah et al., 2011). These environments have become increasingly strained as a result of climatic changes that are driving extreme shifts in abiotic processes (such as precipitation, temperature, and the carbon cycle) (Asner et al., 2003; Caracciolo et al., 2016; Dintwe and Okin, 2018; Gherardi and Sala, 2015). There has also been an increase in anthropogenic activity (such as livestock and agriculture), which is also contributing to the degradation of these environments globally (Browning et al., 2014a; Burrell et al., 2020; Cipriotti and Aguiar, 2012; Prăvălie, 2016). Drylands are typically defined as regions where the annual rate of potential evapotranspiration significantly exceeds the amount of annual precipitation. In particular, regions are classified as drylands when the aridity index (Precipitation/Potential Evapotranspiration) is less than 0.65 (Bestelmeyer et al., 2015; Maestre et al., 2015). This is due to drylands experiencing limited precipitation for most of the year and receiving most of the annual precipitation during the wet season, which typically only lasts a few months (Gherardi and Sala, 2015; Havstad et al., 2018; Pascale et al., 2017; Thomey et al., 2014). Additionally, precipitation events are highly stochastic, both inter and intra-annually in drylands. However, the potential evapotranspiration rate remains relatively high throughout the year, and is expected to increase under future climate scenarios (Huang et al., 2017; Ji et al., 2015; Wang et al., 2012).

Precipitation is generally the primary factor limiting vegetative growth in dryland environments (Archer et al., 2017; Currier and Sala, 2022; Gherardi and Sala, 2015; Sala et al., 2012). Globally, drylands have been experiencing an ecological transition over the last century, which has resulted in a shift to an alternate ecological state (Archer, 2010; Browning et al., 2014b; Caracciolo et al., 2016; Pierce et al., 2019). This is primarily the result of unsustainable anthropogenic activities in an increasingly stochastic climate (Burrell et al., 2020; Dintwe and Okin, 2018; Okin et al., 2015; Wilcox et al., 2011). Traditionally perennial grasslands (C_4) have been transitioning to shrub dune-lands (C_3), resulting in the degradation of these critical environments (Browning et al., 2014a; Pierce et al., 2019). However, the effects that future climate scenarios will have on precipitation in dryland environments remains somewhat uncertain (Sherwood and Fu, 2014; Zhao and Dai, 2015). Therefore, it is of critical importance to improve upon our current understanding of dryland vegetation (particularly, perennial grasses) and how it will be affected by changes in annual precipitation and plant available water capacity (PAWC) (Guswa et al., 2004; Peters et al., 2015). However, precipitation is not the only abiotic process that has a profound influence in shaping the ecogeomorphology dryland environments (Hand et al., 2017; Okin et al., 2018, 2009; Ravi et al., 2010).

Aeolian processes are an important but often overlooked driver of environmental changes in dryland environments (Okin et al., 2006; Ravi et al., 2011). Soil erosion and sediment transport via wind is one of the primary mechanisms through which aeolian process alter dryland environments, resulting in decreased soil nutrients (Gonzales et al., 2018; Li et al., 2007), plant productivity (Duniway et al., 2019; Niu et al., 2023; Schlesinger et al., 1990), and effect the terrestrial carbon cycle (Brazier et al., 2014; Fu et al., 2021; Throop et al., 2020). This redistribution of soil nutrients is often irreversible and significantly increases perennial grass mortality, while also decreasing the likelihood of perennial grass establishment or re-establishment from these sediment sources (Browning et al., 2014; Peters et al., 2020; Rachal et al., 2015). Another important consequence from sediment transportation via wind is changes to the distribution of soil organic matter (SOM) in drylands (Achakulwisut et al., 2017; Bergametti and Gillette, 2010; Bullard and Baddock, 2019; Okin et al., 2015). Since the distribution of SOM is linked to aeolian processes and monsoonal precipitation (Throop and Belnap, 2019). Thus, it is of critical importance to better understand the physical relationship of aeolian sediment transportation, and how it will help shape ecogeomorphic processes in dryland environments in the 21st century.

The objective of this dissertation is an attempt to explain several important dynamics in dryland environments. The first chapter investigated (1) the influence that variations in connectivity and monsoonal precipitation have on perennial grass growth and establishment in drylands, with a particular focus on perennial grasses present in a grass-shrub-duneland ecotone. Then in chapter two we will improve upon the current understanding of (2) how the spatial distribution of litter in drylands is impacted by changes in monsoonal precipitation and connectivity. Finally, the third contribution from this dissertation will be characterizing the distribution of soil organic matter in drylands, and how it is influenced by monsoonal precipitation and connectivity. In order to complete this dissertation, we developed a mixed-methods approach. This incorporated long-term in-situ field experiments, and analytical laboratory methods; with a focus on dryland environments in the southwestern United States. This dissertation will contribute to and expand upon our current understanding of dryland ecogeomorphology and the role of aeolian processes in shaping dryland environments globally.

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Chapter 1 Precipitation and Connectivity: Primary Drivers of Perennial Grass Growth and Establishment in Drylands

Abstract

Dryland environments are becoming increasingly degraded due to climate change and human activities, leading to a shift from grasslands to shrub-dominated landscapes. Previous studies have tested how precipitation and connectivity independently influenced these landscapes. This study, conducted at the Jornada Basin Long-Term Ecological Research (LTER) site in the Chihuahuan Desert, investigates both the impact of monsoonal precipitation variability and landscape connectivity on perennial grass aboveground net primary productivity (ANPP) and seedling establishment. These findings suggest that reducing connectivity coupled with increased monsoonal precipitation can enhance local conditions - providing favorable conditions for perennial grass growth and recruitment - and potentially mitigating some of the environmental effects of shrub encroachment. This research contributes to understanding how changes in environmental factors may shape vegetation in dryland environments under future climate scenarios.

Introduction

Globally, over half of the Earth's terrestrial surface consists of drylands, which are predicted to increase in area globally as a result of climate change (Huang et al., 2017; Tariq et al., 2024). Drylands are a critical source of sustenance for over one-third of the planet's population, but are becoming increasingly degraded as a result of shifting climatic trends and increasing anthropogenic activity (Altman et al., 2009; Van Auken, 2009; Varela Pérez et al., 2022). This has resulted in the vegetative composition of drylands undergoing a shift from grasslands to shrub-dunelands, since the beginning of the 20th century (Maestre et al., 2021; Pierce et al., 2019; Turnbull and Wainwright, 2019). The transition of dryland vegetation that has been occurring over the last century is projected to accelerate in the 21st century, as future climate scenarios are predicted to result in increasingly stochastic precipitation in dryland environments (Ault et al., 2016; Liang and Zhang, 2022). This is expected to result in an increase in perennial grass mortality and promote shrub recruitment in dryland environments globally (Gherardi and Sala, 2019; Peters et al., 2008; Ravi et al., 2010).

There are a variety of interacting environmental mechanisms and feedbacks that stimulate shifting vegetation patterns in dryland environments (Bestelmeyer et al., 2015). One of the principal mechanisms influencing vegetative growth is precipitation, which in dryland environments is typically characterized by infrequent events annually that are spatially and temporally variable (Higgins et al., 1997; Scholes and Archer, 1997). Drylands experience seasonal precipitation patterns, which are often the result of convective storms, low pressure systems, or monsoonal depressions (Cooke et al., 1993). Most of the annual precipitation occurs during the North American monsoon system (NAMS), from June through September, usually over the course of several extremely large events (D'Odorico et al., 2009; Havstad et al., 2006). Therefore, the soil has a persistent deficit in plant available water capacity (PAWC) throughout most of the year, inhibiting vegetative growth (Guswa et al., 2004; Peters et al., 2015), since it is often the most limiting resource for vegetation in dryland environments (Rodriguez-Iturbe, 2000).

Although precipitation is the primary factor influencing dryland vegetative patterns, there are additional abiotic mechanisms; such as aeolian processes, geomorphology, and climate that also influence the distribution of vegetation (Li et al., 2008; Okin et al., 2018). The 21st century has seen an increasing body of work (Okin et al., 2015; Ravi et al., 2007; Shao, 2008; Wu et al., 2018) investigating the role that aeolian processes have both directly and indirectly in influencing dryland vegetative patterns. In particular, aeolian processes have an important role in regards to the distribution of soil nutrients in dryland environments (Li et al., 2007; Schlesinger et al., 1995). When landscapes (such as a shrub encroached dryland) experience an increase in vegetative heterogeneity, there is also an increase in the amount of bare soil exposed (Okin et al., 2009b). This increase in bare soil intensifies the susceptibly of bare soil to aeolian and fluvial erosion, since these patches of bare soil begin to coalesce and create pathways that promote the redistribution of nutrient rich soil particles (Belnap et al., 2011; Li et al., 2007). Once these particles are entrained, they tend to naturally accumulate within shrub canopies, which results in an accumulation of sediment around the base of shrubs and the formation of "fertile islands" (Schlesinger et al., 1995). This redistribution of nutrient rich sediment is problematic as it is often irreversible, and prevents the establishment or recruitment of perennial grasses within these inter-plant regions of bare soil (Okin et al., 2015; Peters et al., 2020; Schlesinger et al., 1990).

This has contributed to the recent development and implementation of connectivity within an ecological framework to better explain how plant and transport processes influence the vegetative composition of dryland environments (Okin et al., 2009). In order to better understand the role of connectivity in dryland environments and disentangle the spatial and temporal aspects (Turnbull et al., 2008), connectivity is divided into *structural* and *functional* components (Bracken et al., 2013; Okin et al., 2009). *Structural connectivity* is described as the extent over which spatial units of bare soil are linked together physically, and account for the transportation of materials in areas that experience a decrease in vegetative cover (Mayor et al., 2019; Tischendorf and Fahrig, 2000). The term *functional connectivity* refers to the spatial connections arising as a result of specific transportation events (Uezu et al., 2005; With et al., 1997). Previous studies (Okin et al., 2015; Peters et al., 2020; Turnbull and Wainwright, 2019) have shown the critical role that connectivity has in shaping the vegetative composition in drylands.

In an increasingly connected environment, the overall increase in connectivity promotes a an increase in shrub growth and recruitment, which in turn increases the environment's overall connectivity (Peters et al., 2008). The connectivity of the landscape also has the potential to directly impact dryland vegetation. Niu et al. (2023) shows that as the connectivity increases in drylands, perennial grass growth and recruitment decreases. This is primarily due to the fact that physiologically, perennial grasses are significantly more susceptible to damage via aeolian sediment transport than the encroaching shrub species (Niu et al., 2023). This results in a positive feedback loop that discourages perennial grass growth both directly and indirectly in dryland environments.

In this study, we aim to assess the effects that changes in monsoonal precipitation and connectivity will have on perennial grass growth and recruitment in a grass-shrub dune-land ecotone. We hypothesize that (1) ConMods will be most effective at promoting perennial grass ANPP and recruitment when inter-monsoonal precipitation is above-ambient of the study site. When monsoonal precipitation is ambient or below, it will minimize the efficacy of ConMods, since the PAWC will be too low to promote perennial grass ANPP and recruitment. We also hypothesize (2) that reducing the connectivity will increase the deposition of organic matter and sediment locally, creating ideal micro-climates for perennial grass recruitment within the inter-plant region. Decreasing the local connectivity may have a cascading effect on perennial grass recruitment and promote the re-establishment of perennial grasses in a grass-shrub dune-land ecotone.

Methods

Study Area

This experiment was conducted within the Chihuahuan Desert at the Jornada Basin Long-Term Ecological Research (LTER) site (32.5°N, 106.8°W, and 1,188 m above sea level), which is located in southern New Mexico, United States. The long-term mean annual precipitation at Jornada is 247 mm, while the long-term mean monsoonal (growing season) precipitation is 176 mm (Gherardi and Sala, 2015). The average monthly temperatures range from 6 °C in January to 26 °C in June. Current grazing intensities are maintained at low levels throughout the 200,000-ha research site. Locations sampled for perennial grass cover have not been grazed by livestock since the late 20th century. This study takes place on a grass-shrubland that is dominated by *Bouteloua eriopoda*, *Sporobolus flexuosus*, and *Aristida purpurea* perennial grasses (C_4), that are encountering shrub encroachment from *Prosopis glandulosa* (C_3) expansion.

Experimental Design

The experiment was established in May of 2020, consists of 56 plots that are 2.5 m wide and 5 m long, and spread across an area that is approximately 13 hectares. All these plots are located perpendicular to the prevailing wind in a sandy, mesquite-dominated grass-shrub dune-land ecotone. At the time of plot selection, there were no shrubs present within any of the plots. In the initial plot selection phase, 90 plots were selected, and line-intercept (LI) transects were conducted to determine the preliminary vegetation cover. These results were used to identify the interquartile range and remove the 30 least similar plots from the study. The remaining 60 plots were randomly assigned one of five precipitation regiments: -80%, -50%, +0%, +50%, or +80%. During our analysis we also identified two pairs of irrigated (+80%) and drought plots (-80%)

with vegetative patters that were outliers in comparison to the remaining 56 plots, and as a result they were omitted from this study.

To modify the precipitation regimes at the plot level, automated rainfall manipulation systems (ARMS) were deployed (Gherardi and Sala, 2013; Reichmann et al., 2013). Precipitation is captured with a rainout structure, which consists of shingles that are spaced at varying intervals to intercept incoming precipitation (reducing precipitation by 50% or 80%). The shingles consist of acrylic (Piedmont Plastics, LaMirada, California) that is heated with a ceramic heater and bent at a 120° angle, which is transparent to minimize any influence it may have on temperature or incoming solar radiation (Gherardi and Sala, 2013). Once the precipitation is intercepted, a drainage system redirects the precipitation in real-time to a 27-gallon plastic storage tank (EDGE Plastics, Mansfield, Ohio). Once the water reaches the storage tank, there is a float switch (Atwood Marine Automatic, Lowell, Michigan) that will turn on a water pump (TruePower 12 V DC Marine Utility Pump, Simi Valley, California) when the water level is increased. The water is then sent to the corresponding irrigation plot through 12.7 mm (1/2") PVC pipes. The ARMS design (Gherardi and Sala, 2013) allows irrigated plots to receive precipitation levels that are 50% and 80% above the ambient monsoonal precipitation with six sprinkler heads (Rain Bird 4-Van Sprinkler Spray Nozzle, Azusa, California), which were placed evenly around the perimeter of the plots (3 on each side). This resulted in a precipitation gradient with four treatments that spanned between -80% and +80% (-80%, -50% , +50%, and +80%) (Fig. 1). ARMS were not installed on the plots that received ambient (0%) monsoonal precipitation. The experimental setup ensures that only the magnitude of precipitation events is manipulated, and not the frequency of precipitation events.

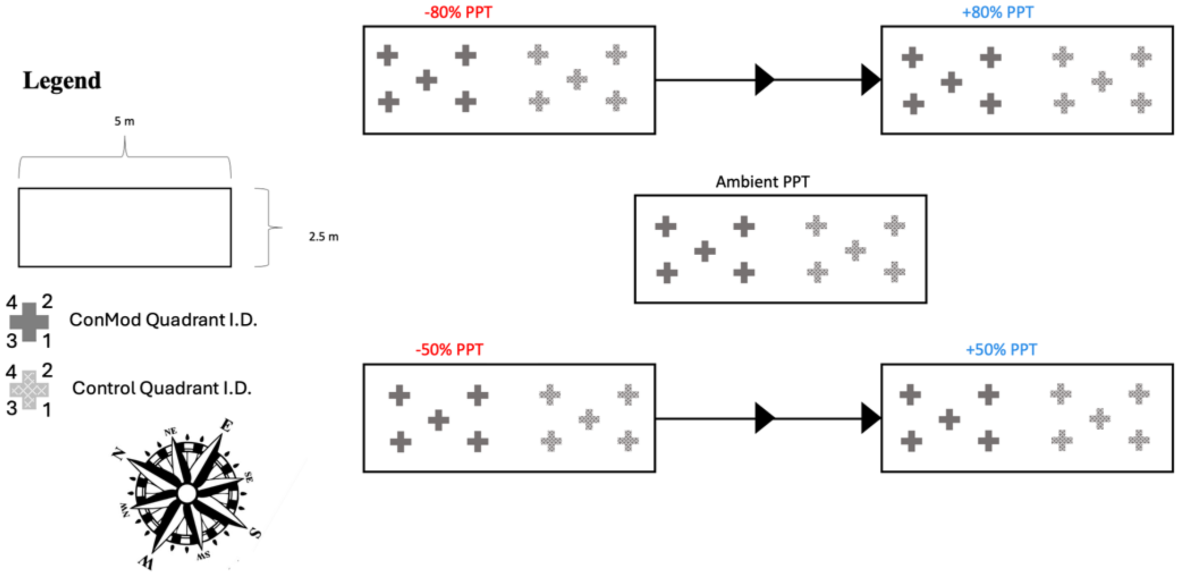

Figure 1. The experimental design and layout of the precipitation (-80%, -50%, 0%, +50%, +80%) and connectivity (ConMod and Control) treatments for this study.

The individual ARMS systems are inspected and calibrated before each monsoon season begins to ensure there are no leaks and the water is evenly applied or diverted consistently within each plot. Once the ARMS have been deployed for the monsoon season, they are maintained and regularly checked to ensure they are functioning correctly. The experiment is maintained throughout the monsoon season until late October, since freezing temperatures will prevent the experiment from functioning. The overwintering process consist of draining the irrigation system at least 3 m from any plots to ensure there was no artificial influence on the drought or irrigation treatments, while the drought shelters remained in place throughout winter.

One of the primary objectives of this study was to alter the connectivity of the landscape with respect to aeolian and fluvial transport (Rachal et al., 2015). Previous work has shown that ConMods are able to effectively promote the germination and establishment of native vegetation in drylands (Fick et al., 2016). Peters et al. (2020) also showed that ConMods promote perennial grass establishment under ambient precipitation in dryland environments. Therefore, we decided that installing ConMods would be the most effective method of reducing the local connectivity.

The 56 plots were divided in half (2.5 m x 2.5 m) and one side was randomly assigned the ConMod treatment, while the other side received the control treatment. A ConMod consists of 0.63 (1/4") mm galvanized hardware cloth that is connected to five 0.63 mm (1/4") diameter reinforced steel stakes. Once the ConMods are installed they are 20 cm tall and 55 cm in both width and length. ConMod placement consists of one stake that is placed in the center while the four remaining stakes are placed equal distances from the center stake, the resulting structure takes the shape of the symbol for addition (+). The control (without ConMod) treatments consist of one 0.63 mm (1/4") diameter reinforced steel stake that is installed and mirrors the location of the center stake in the ConMod. Additionally, both the ConMod and control treatments were installed in a figure five formation (Fig. 1), which were centered within each 2.5 m x 2.5 m sub-plot (Fig. 1).

Data Collection and Measurements

We installed four 250-cm transects (located 110, 220, 330, and 440 cm from the edge of the plots) parallel to the prevailing wind such that there were two transects that spanned each of the connectivity treatments (ConMod & control) (Fig. 1). The transects were used as a non-destructive method (LI) to measure multi-year plant species cover as an alternative to collecting the data via destructive harvesting of vegetation. The vegetation cover was recorded at the end of the monsoon season (mid-September), when vegetation in the Chihuahuan Desert typically reaches peak vegetative biomass (Havstad et al., 2006; Xia et al., 2010). Vegetation along each transect is identified to species and the distance it spans the transect is recorded at 1-cm resolution. In order to quantify the annual net primary productivity (ANPP) (g m^{-2} yr^{-1}), we used a series of allometric equations developed by Flombaum and Sala (2007) calibrated for our study site (Gherardi and Sala, 2015; Reichmann et al., 2013).

To measure vegetation cover along the transects, we recoded the species and distance it spanned along the transect when a plant was green. If the plant was senesced or dead, we did not identify the species and only recorded it as non-photosynthetic vegetation (NPV). We also recorded the distance that bare soil, organic matter (litter), or dead vegetation spanned along each transect at 1-cm intervals. However, we only recorded the amount of bare soil and litter along spans of the transect without any vegetation present. The methods that we deployed for our data collection are modeled on similar methods developed in previous studies at the Jornada LTER (Gherardi and Sala, 2015; Reichmann et al., 2013; Sala et al., 2012). The data was also collected over the course of two days, to minimize any shifting vegetative physiological patterns from influencing perennial grass cover.

In addition to measuring vegetation cover, we also recorded perennial grass germination and establishment throughout the monsoon seasons in 2021 and 2022. To quantify grass germination and establishment, we used the four quadrants of the ConMods and created quadrats to use on the control treatments. We recorded every grass seedling that appeared at the end of the monsoon when peak biomass occurred (09/10/2021 & 09/06/2022). We also recorded perennial grass seedlings, perennial grass stolons, perennial grass tillers, and shrub seedlings within each quadrant.

The demographic data were collected by two teams, each team consisted of one person collecting the data and the second person recording it. These teams were trained together over the course of a week to ensure consistency in plant identification and physiology. Then, we performed vegetative and physiological calibrations together to minimize any potential human error during data collection.

Precipitation data was obtained from the closest meteorological station (< 1 mile), which uses an automatic tipping bucket rain gauge and is maintained by the Jornada LTER. In order to calculate the monsoonal precipitation at each treatment, we followed the methods that Huang et al. (2022) applied in their analysis of monsoonal precipitation throughout the southwestern U.S. We demarcate the onset of the North American monsoon season (NAMS) as the first three consecutive days of precipitation that exceeded 0.5 mm day^{-1} after July 1st, and is based on the framework developed in Higgins et al. (1999). The cutoff for the NAMS was September 30th, since climatic conditions in October inhibit vegetative growth regardless of precipitation.

Statistical Analyses

In this study we used a linear mixed model for repeated measures (MMRM) to assess the effects of connectivity and precipitation on perennial grass production. To control for pre-existing conditions, we included perennial grass ANPP in 2020 as a linear covariate. We specified connectivity treatment (two levels), precipitation treatment (5 levels), year (3 levels: 2021, 2022, and 2023) and their 2-way and 3-way interactions as fixed effects. To account for correlation in time, we used an unstructured temporal covariance. We also included a random effect for ConMod-Control pairs to account for the design feature of each pair being adjacently located under the same independently-applied precipitation treatment.

We also used linear mixed models to test the treatment effects on four grass demography responses (counts of grass seedlings, grass stolons, shrub seedlings, and grass tillers), which were assessed in 2021 and 2022. We characterized each response as a gain score (2021 observed count subtracted from 2022 observed count) to simplify the modeling process. Fixed effects were connectivity treatment (two levels), precipitation treatment (5 levels), quadrant (4 levels) and their 2-way and 3-way interactions. We also included a random effect for ConMod-Control pairs. Although we used R version 4.3.2 (R Core Team 2023) for data manipulation and figure generation (Wickham et al., 2019), we fit mixed models with the MIXED procedure (SAS V9.4; SAS Institute, Cary, NC, USA) and used the Kenward-Roger method to compute denominator degrees of freedom for fixed effects. For all analyses we used a significance level of 0.05

Results

Overview

This experiment simulated an array of precipitation regimes, providing an opportunity to better understand how changes in connectivity and precipitation influence perennial grasses in dryland environments. The long-term average monsoonal precipitation at our study site is approximately 176 mm (Currier and Sala, 2022; Throop et al., 2012). However, throughout the duration of the study period (2020 – 2024) monsoonal precipitation was both above and below the long term average. There were dry conditions in both 2020 and 2023, which resulted in monsoonal precipitation amounts that were 53% (83.31 mm) and 74% (63.51 mm) less than the long-term average, respectively. In contrast, 2021 and 2022 monsoonal precipitation was 44% (253.23 mm) and 3% (180.86 mm) greater than the long-term

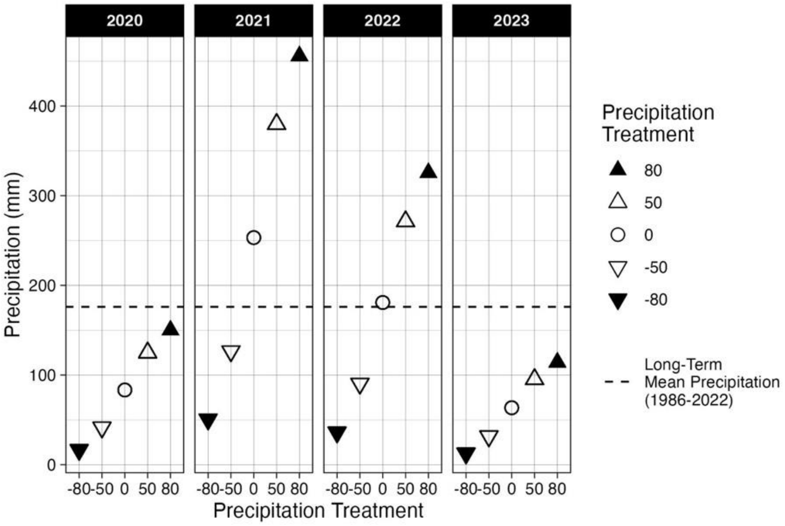

Figure 2. Monsoonal precipitation patterns over the duration of the experiment (2020 – 2024), and across the various (-80%, -50%, 0%, +50%, & +80%) precipitation treatments

average, respectively (Fig. 2). The lack of monsoonal precipitation in 2020 and 2023 resulted in minimal differences (<130 mm) between the drought (-80%) and irrigation (+80%) treatments in 2020 and 2023, relative to the differences (> 290 mm) between precipitation treatments in 2021 and 2022.

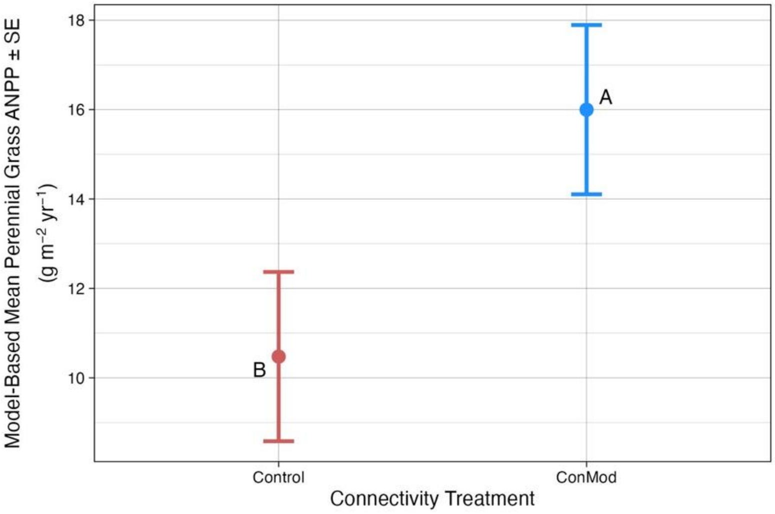

Figure 3. The effect of modifying connectivity on mean (± SEM) perennial grass ANPP (g m^{-2} $year^{-1}$) from 2021 – 2023. Different letters indicate significant differences between treatments based on a repeated measures analysis of covariance (ANCOVA) with an $\alpha = 0.05$

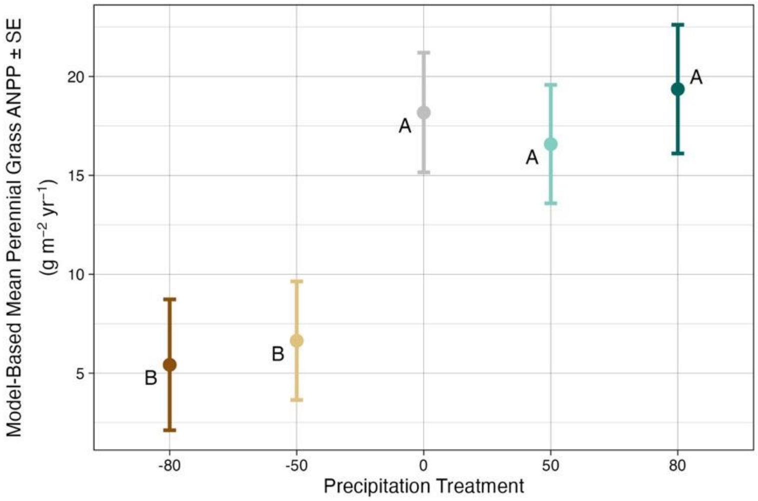

Figure 4. The effect of modifying precipitation on mean (± SEM) perennial grass ANPP (g m-2 year-1) from 2021 – 2023. Different letters indicate significant differences between treatments based on a repeated measures analysis of covariance (ANCOVA) with an $\alpha = 0$.

Perennial Grass Growth

In our repeated measures analysis of covariance (ANCOVA), connectivity treatment (ConMods), initial perennial grass ANPP, precipitation treatment (e.g., -80% - +80%), and year had significant influences on perennial grass ANPP (Table 1). The results from this experiment showed an approximate 50% increase in perennial grass annual net primary productivity (ANPP) (g m^{-2} yr^{-1}) ($P < 0.05$) at the plot level where ConMod treatments were installed (Fig. 3). Precipitation also had a significant ($P < 0.05$) influence on perennial grass ANPP. Plots on average experienced a 100% or greater increase in perennial grass cover when they received ambient or greater amounts of monsoonal precipitation (Fig. 4). Therefore, plots that received above ambient precipitation in conjunction with the ConMod treatment experienced the greatest overall mean increase (~400%) in perennial grass ANPP over the course of this study (2021 – 2023) (Fig. 5).

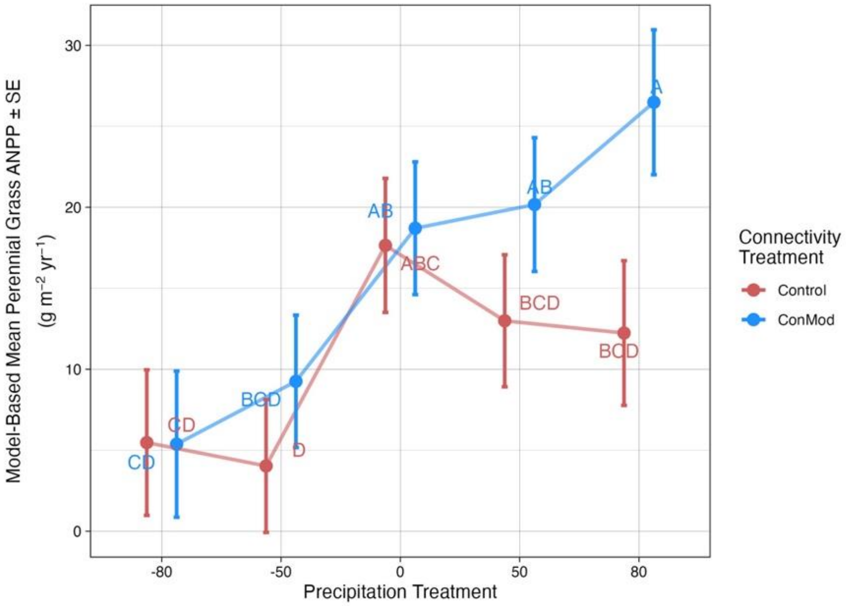

Figure 5. The effects of monsoonal precipitation and modifying the landscapes connectivity the mean (± SEM) perennial grass ANPP (g m^{-2} $year^{-1}$) from 2021 – 2023. Different letters indicate significant differences between treatments based on a repeated measures analysis of Covariance (ANCOVA) with an $\alpha = 0.05$.

After one year (in 2021) the difference in perennial grass ANPP between the ConMod and control plots was minimal, but after the second year (2022) we began to observe a divergence in perennial grass ANPP (Fig. 6A). However, perennial grass ANPP was noticeably subdued in 2023, which was the driest year throughout our study period. We also looked at the effect from connectivity on overall perennial grass ANPP annually. These results show that 2023 perennial grass ANPP was 112% greater than perennial grass ANPP in 2020 despite an approximate 25% decrease in monsoonal precipitation (Fig. 7).

To parse out the impact from the ConMod treatments on perennial grass ANPP, we looked at the difference in perennial grass ANPP between plots with ConMods and the controls (gain score). The results indicate that ConMods, regardless of the precipitation treatment or regime, resulted in an overall increase in perennial grass ANPP (Fig. 8A). In 2022, perennial grasses experienced the greatest difference between connectivity treatments against initial perennial grass ANPP (2020). Although ConMods do not appear to be as effective in 2021 (greatest monsoonal precipitation) or 2023 (lowest monsoonal precipitation), the results show generally that as the amount of initial perennial grass ANPP (2020) increases, so does the effectiveness of ConMods on perennial grass ANPP.

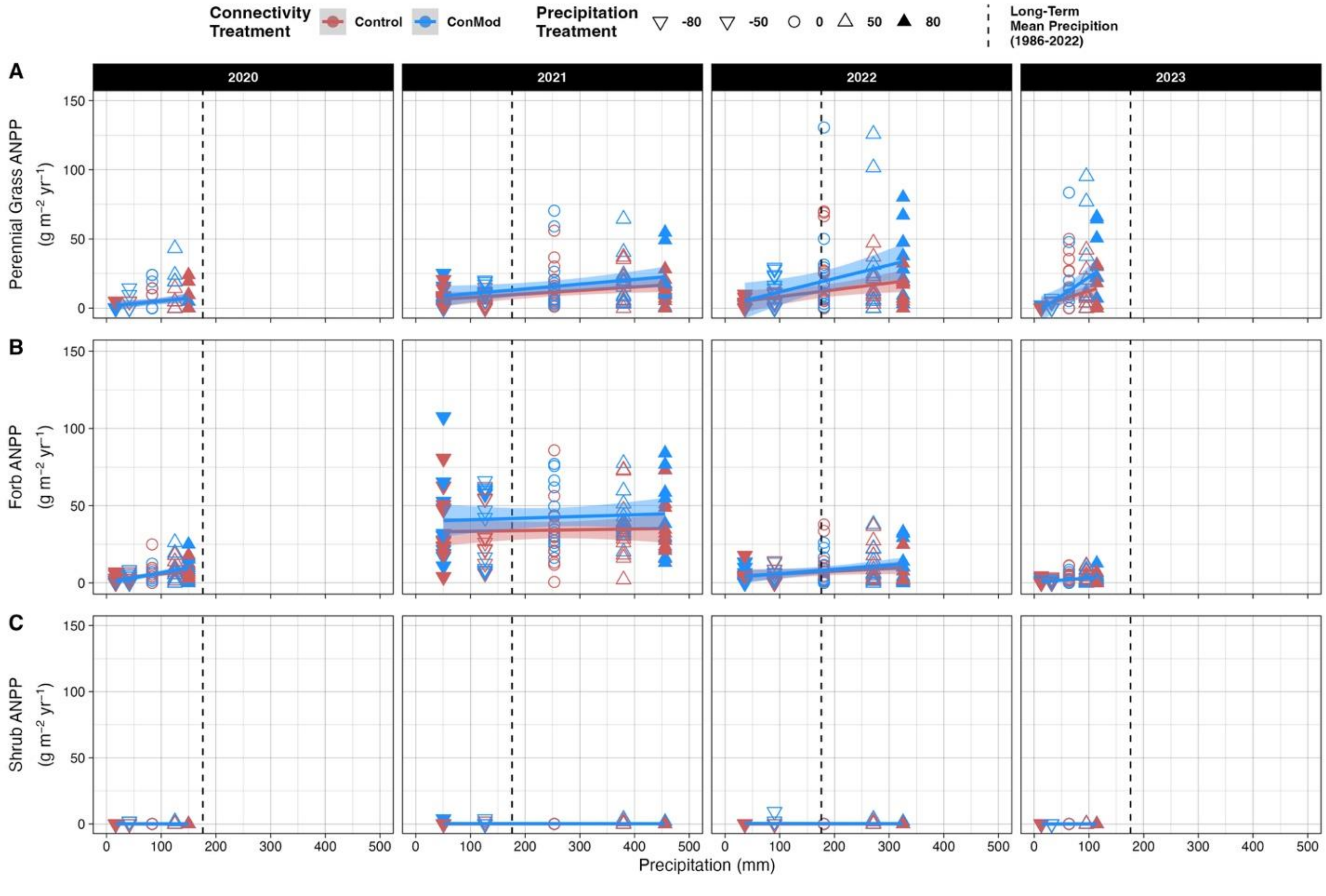

Figure 6. The plot-level effects of monsoonal precipitation and modifying the landscapes connectivity on (A) perennial grass, (B) Forb, and (C) Shrub ANPP (g m^{-2} yr^{-1}) over the course of the experiment.

Independent Variable	Num D.F.	Den D.F.	F Value	P-Value
Initial Perennial Grass ANPP 2020	1	100	18.29	**< 0.0001**
Precipitation Treatment (-80%...+80%)	4	71	4.25	**0.0039**
Connectivity Treatment (ConMod)	1	62.7	4.45	**0.0389**
*Precipitation*Connectivity Treatment*	4	63.2	0.94	0.4461
Year	2	101	14.96	**< 0.0001**
*Precipitation*Year*	8	141	1.17	0.3225
*Connectivity Treatment*Year*	2	101	0.76	0.4715
*Precipitation*Connectivity Treatment*Year*	8	141	0.95	0.4751

Table 1. The repeated measures analysis of covariance (ANCOVA) results for the independent variables: connectivity treatment, initial perennial grass cover (2020), precipitation, year, and the interactions between them. Bold values are significant with an $\alpha = 0.05$.

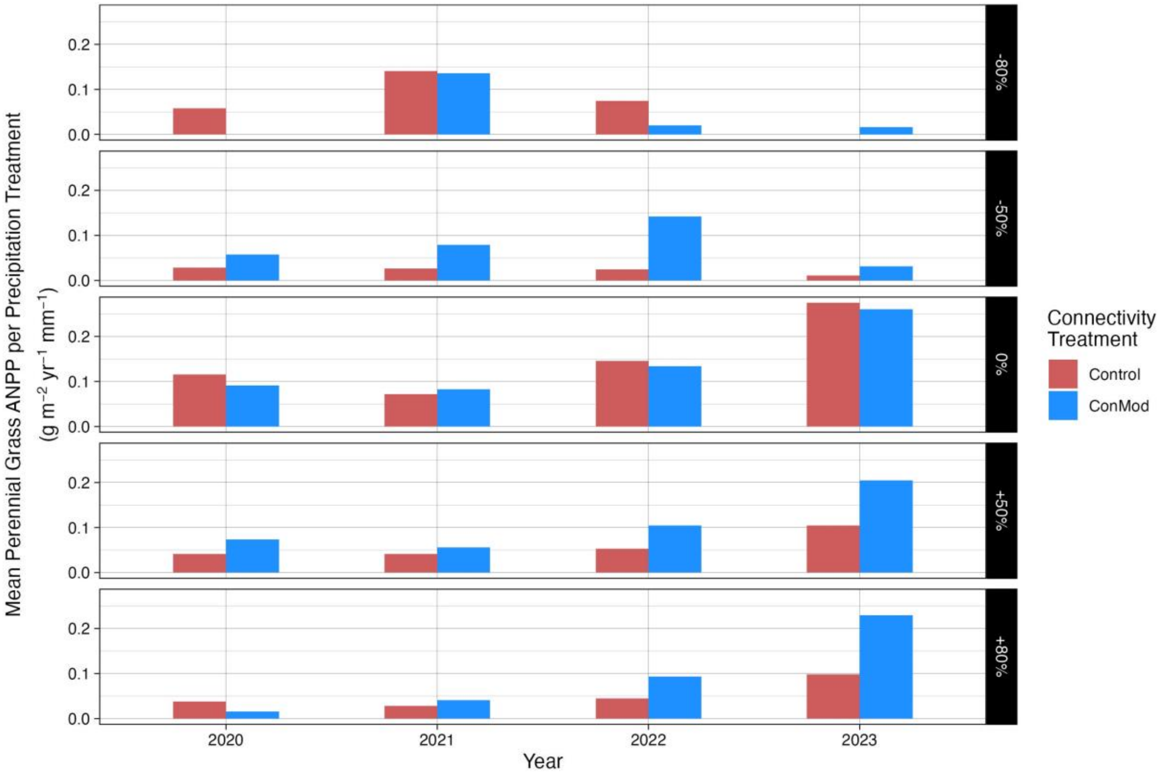

Figure 7. The annual effect of monsoonal precipitation and modifying the connectivity on overall perennial grass ANPP (g m^{-2} yr^{-1}). Each bar is the perennial grass ANPP (g m^{-2} yr^{-1}) from plots with ConMod (red) and without ConMods (blue), and the right (light grey) is precipitation treatments levels.

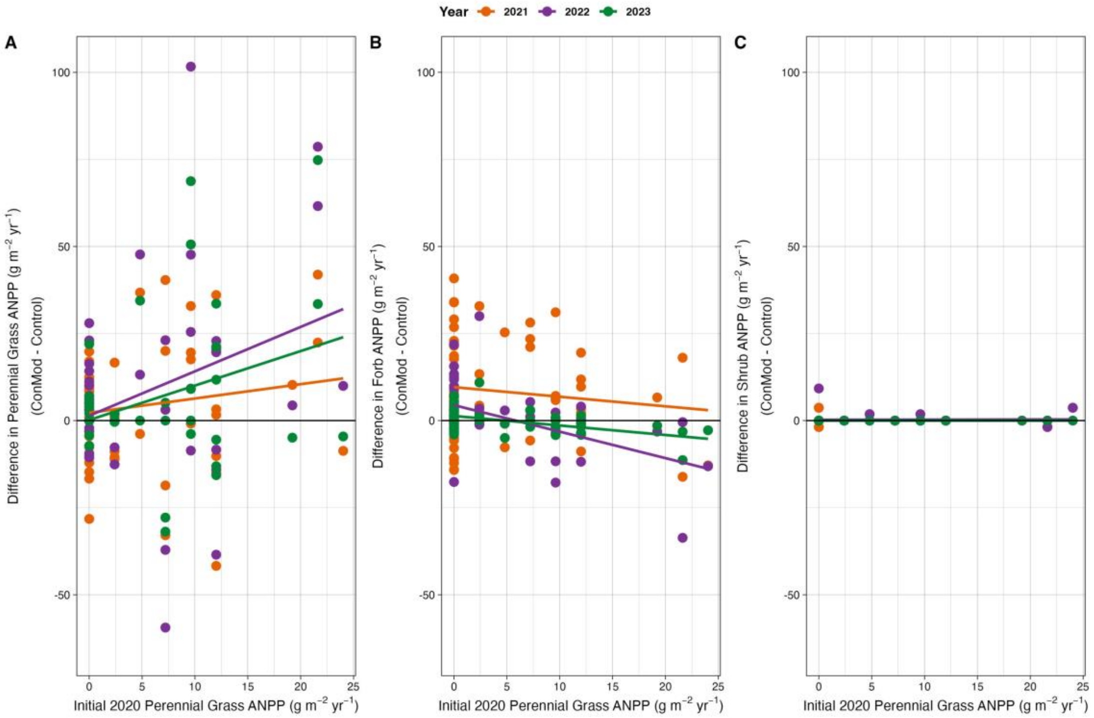

Figure 8. The annual difference (ConMod – Control) in (A) perennial grass, (B) forb, and (C) shrub ANPP (g m^{-2} yr^{-1}) compared to the initial perennial grass ANPP (g m^{-2} yr^{-1}) (2020).

Perennial Grass Establishment

This study also investigated the effects of precipitation and connectivity on perennial grass seedling germination and establishment in 2021 and 2022. We used the year-to-year changes (2022 Seedlings $_{Plot\ i}$ – 2021 Seedlings $_{Plot\ i}$) in perennial grass seedling germination to determine the rate of establishment. The results (Supp. Fig. 1) indicate that perennial grass seedlings germinated in all plots regardless of the precipitation or connectivity treatments. In our ANOVA, connectivity treatment (ConMods), and the interaction between connectivity and precipitation treatment had significant influences on perennial grass recruitment (Table 2). There were significantly ($P > 0.05$) greater germination rates observed within the ConMod plots across all precipitation treatments (Fig. 9A). Among the precipitation treatments, we observed a significant ($P < 0.05$) difference between the above- (+80%) and below-ambient (-50%, -80%) plots (Fig. 9B), regardless of the connectivity treatment. These findings indicate there is a significantly higher establishment rate in ConMod plots subjected to ambient and above precipitation (Fig. 9C). Conversely, a net decrease in seedling establishment was evident in plots receiving below-ambient precipitation with the ConMod treatment. This disparity in grass seedling establishment remains statistically significant ($p < 0.05$) when examining the impacts of structural connectivity in isolation, as well as its interaction with monsoonal precipitation. Additionally, regardless of precipitation and connectivity treatments, grass seedlings were significantly different in the quadrants, and displayed a higher likelihood of establishing in the downwind quadrant (quadrant 4) of individual ConMods or control (Fig. 9D).

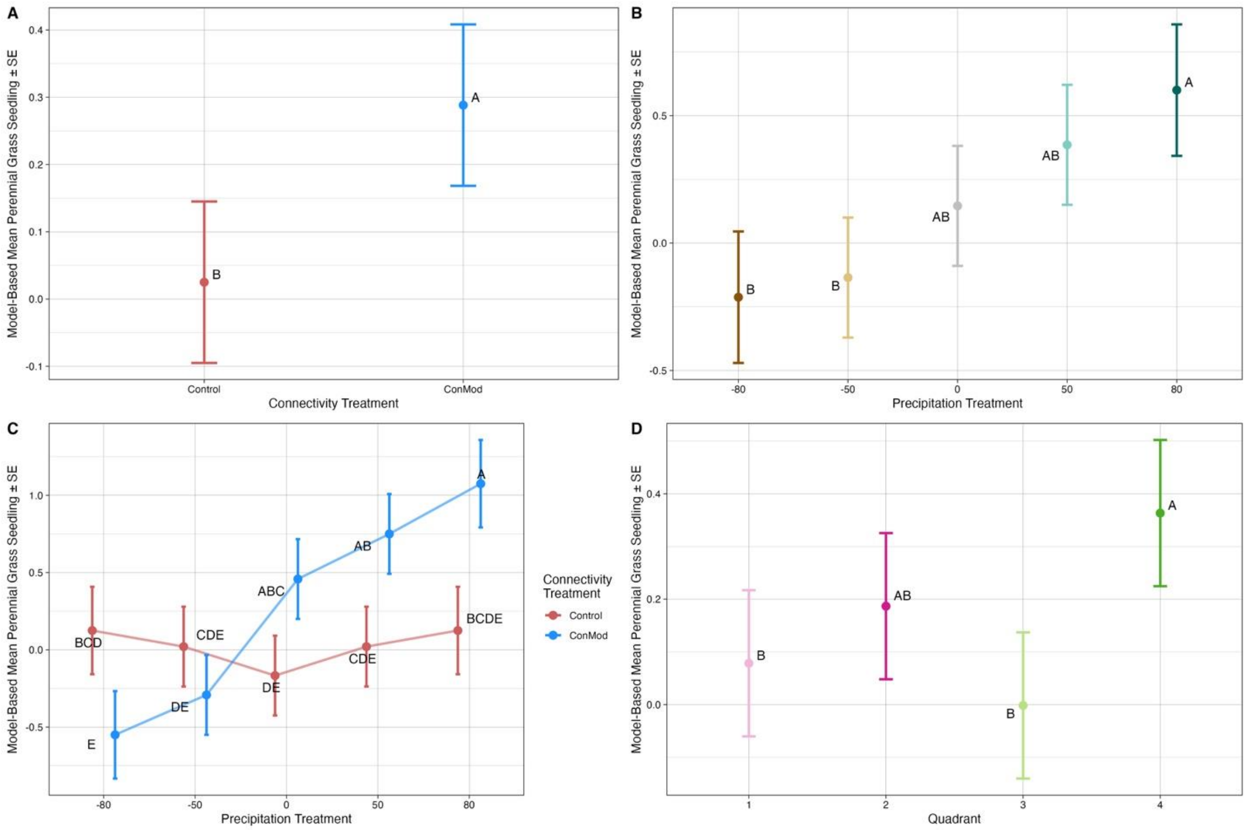

Figure 9. (A) The effects from modifying the landscapes connectivity on mean (± SEM) perennial grass recruitment (2022 – 2021). **(B)** The effect of modifying precipitation on mean (± SEM) perennial grass recruitment. **(C)** The interaction between modifying precipitation and connectivity on mean (± SEM) perennial grass recruitment. **(D)** Perennial grass recruitment within the individual Connectivity treatments (ConMods & Control) quadrants. Different letters indicate significant differences between treatments based on an analysis of covariance (ANOVA) with an $\alpha = 0.05$.

Independent Variable	Num D.F.	Den D.F.	F Value	P-Value
Connectivity Treatment (ConMod)	1	357	7.17	**0.0078**
Precipitation Treatment (-80%...+80%)	4	51	1.87	0.1296
*Precipitation*Connectivity Treatment*	4	357	10.08	**< 0.0001**
Quadrant	3	357	2.58	*0.0535*
*Connectivity Treatment*Quadrant*	3	357	2.07	0.1036
*Precipitation Treatment*Quadrant*	12	357	0.84	0.6039
*Precipitation*Connectivity Treatment*Quadrant*	12	357	1.33	0.2005

Table 2. The repeated measures analysis of covariance (ANCOVA) perennial grass seedling model results for the independent variables: connectivity treatment, precipitation, ConMod quadrant, and the interactions between them. Bold values are significant with an $\alpha = 0.05$ and italic values are with an $\alpha = 0.1$.

Independent Variable	Num D.F.	Den D.F.	F Value	P-Value
Connectivity Treatment (ConMod)	1	357	1.12	0.291
Precipitation Treatment (-80%...+80%)	4	51	1.12	0.3566
*Precipitation*Connectivity Treatment*	4	357	7.17	**< 0.0001**
Quadrant	3	357	2.13	*0.0959*
*Connectivity Treatment*Quadrant*	3	357	0.39	0.7628
*Precipitation Treatment*Quadrant*	12	357	0.97	0.48
*Precipitation*Connectivity Treatment*Quadrant*	12	357	0.53	0.8917

Table 3. The repeated measures analysis of covariance (ANCOVA) perennial grass stolon model results for the independent variables: connectivity treatment, precipitation, ConMod quadrant, and the interactions between them. Bold values are significant with an $\alpha = 0.05$ and italic values are with an $\alpha = 0.1$.

We also analyzed perennial grass stolon density in this study, and how it was affected by changes in monsoonal precipation and connectivity. The results indicate that the interaction between the connecitivity and monsoonal precipitation treatments resulted in a significant ($P < 0.05$) differene in stolon density in this study (Table 3). The other signifcant ($P < 0.1$) effect on perennial grass stolon density was from the ConMod/control quadrant they were located in. Additionally, we analyzed how perennial grass tiller density responded during this study. Our results indicate the interaction between monsoonal precipitation treatment and quadrant was the only variable to have a signifcant influence ($P < 0.1$) on perennial grass tiller density (Supp. Table 1).

Shrubs and Forbs

The plots were selected to exclude any shrubs, so the only shrubs observed during the experiment were the result of local germination within the plots. Throughout the study period, shrub (*Pr. glandulosa*) recruitment was observed, but overall establishment was limited (Fig. 6C; Fig. 8C). We also observed shrub seedling germination during the establishment study, but they were not in great enough numbers to conduct a statistical analysis (< 20 cumulatively) on the dataset. Forb data was collected down to species during peak biomass measurements in September of each year. Although we preliminarily investigated this dataset, there were so many different species with diverse physiological and establishment traits that we were unable to identify any significant trends. Forbs were observed germinating across all precipitation and connectivity treatments, and we observed slightly greater forb ANPP within plots with ConMods (Fig. 6B), but it was not statistically significant. We also observed a consistent negative relationship within the forb data; as initial perennial grass ANPP increased, forb ANPP decreased in the control plots (Fig. 8B). However, the diversity in forb species and their varying responses to environmental factors complicated our ability to draw concrete conclusions. There were also several individual forb species that we were interested in potentially investigating, but they did not appear in great enough frequency to conduct a robust statistical analysis.

Discussion

Overview

This study provided an opportunity to investigate how precipitation and connectivity influence perennial grass growth and establishment in dryland environments. The frequency and intensity of monsoonal precipitation is predicted to become increasingly variable throughout the southwestern U.S. and in drylands globally under future climate scenarios (Ault et al., 2016; Huang et al., 2022; Liang and Zhang, 2022). Thus, identifying how perennial grasses in drylands will respond to shifting climatic patterns remains a pressing global issue ecologically (Throop et al., 2012; Winkler et al., 2019) and economically (Moore et al., 2021; Munson et al., 2020; Varela Pérez et al., 2022). Our study found that perennial grass growth in the Chihuahuan Desert is influenced by both monsoonal precipitation and connectivity at the local plant-soil scale. The results from this study are consistent with previous experiments (Gherardi and Sala, 2019; Okin et al., 2018; Peters et al., 2020; Warter et al., 2023) that have investigated the influence of aeolian or hydrological changes on perennial grasses in drylands. However, this is the first study to investigate the effects from both monsoonal precipitation and connectivity on dryland perennial grasses. Throughout the study period, aeolian events were consistent with historical patterns (Bergametti and Gillette, 2010; Floyd and Gill, 2011), which allowed us to parse out the effectiveness of ConMods in promoting perennial grass growth and recruitment under varying amounts of monsoonal precipitation.

Perennial Grass Growth

In our study, monsoonal precipitation displayed a high degree of stochasticity throughout the duration of the experiment (63 mm – 253 mm; Fig. 2). This provided us a unique opportunity to investigate the ecophysiological responses of perennial grasses to extreme shifts in interannual monsoonal precipitation. The initial year of the experiment (2020) was one of the driest monsoon seasons of the last six years (2018 – 2023; Supp. Fig. 2), resulting in low perennial grass growth across all precipitation and connectivity treatments at the beginning of our study period. The low monsoonal precipitation in 2020 confirms that limited soil PAWC deters perennial grass ANPP and increases mortality, both of which contribute to an overall reduction in perennial grass growth (Duniway et al., 2010; Gherardi and Sala, 2015).

However, in the first year of the study (2021) monsoonal precipitation rebounded and resulted in the greatest amount of monsoonal precipitation (231.23 mm) throughout the duration of the experiment. This increase in monsoonal precipitation corresponded with an overall increase in perennial grass ANPP, even though previous research has shown that the response of perennial grasses to increases in monsoonal precipitation can be muted if the preceding years' monsoonal precipitation is below the long-term mean (Bunting et al., 2017). In 2022, monsoonal precipitation was close to the long-term mean for our study site (Fig. 2). Interestingly, we observed a sustained increase in overall perennial grass ANPP in 2022, relative to 2021 (Fig. 8A). This indicates that the subsequent years perennial grass ANPP is augmented by the above-average monsoonal precipitation legacy from the preceding year. The results (Fig. 8A) also infer that ConMods had the greatest effect on perennial grass ANPP during the 2022 NAMS when monsoonal precipitation (183.23 mm) approached the long-term mean (176 mm). In 2023, there was a precipitous decline in monsoonal precipitation, which ended up being the least amount of monsoonal precipitation over the last six years (2018 – 2023; Supp. Fig; 2). Although, we did not observe a corresponding decline in perennial grass ANPP, there was an overall decrease in perennial grass ANPP. This extreme variability in monsoonal precipitation throughout the study period (2020 – 2023) provided an ideal opportunity to investigate the response of perennial grasses in drylands to varying future climate scenarios.

Our results also demonstrate that reducing the local connectivity of resources by aeolian or hydrlogical transport via ConMods can enhance perennial grass growth in dryland environments. In particular, ConMods appear to be most effective in promoting perennial grass ANPP during years when monsoonal precipitation is comparable to (or exceeds) the region's long-term mean (Peters and Savoy, 2023). This is due in part to the local geomorphology, as Peters et al. (2020) identified ConMods as being most effective in sandy soils where aeolian processes are the predominant mode of transport. ConMods also do not appear to be as effective in promoting perennial grass growth during prolonged periods of below-ambient monsoonal precipitation (Fig. 5), but effectively prevent the erosion and redistribution of soil nutrients during periods of limited vegetative growth (Okin et al., 2018; Rachal et al., 2015). This is critical, since ConMods will help preserve a relatively homogenous distribution of soil nutrients necessary for future perennial grass growth during mesic monsoonal conditions (Fick et al., 2016; Gregory S. Okin et al., 2015). The increase in organic matter on the soil surface will enhance the soil's PAWC by reducing rate of evaporation, while reducing the soil's susceptibility to erosion as well (Peters et al., 2020). This accumulation of organic matter within ConMods helps to support increase perennial grass ANPP and the soil's PAWC within patches of established perennial grass in drylands (Bestelmeyer et al., 2018; Fick et al., 2016; Niu et al., 2021). The study found that ConMods increased perennial grass ANPP; however, the timeframe was not long enough to determine if this outcome will lead to a successful long-term reversal of state. These results affirm the effectiveness of ConMods in reducing the local connectivity and promoting perennial grass ANPP under increasingly stochastic monsoonal precipitation regiments.

The results from this study are consistent with previous research, confirming there is a positive relationship in dryland environments between perennial grass ANPP and monsoonal precipitation that is enhanced with ConMods (Currier and Sala, 2022; Gherardi and Sala, 2015; Okin et al., 2018; Rachal et al., 2015). Notably, in our study, the greatest increase in perennial grass ANPP occurred in plots with ConMods that received above-ambient monsoonal precipitation (Fig. 5). While plots exposed to below-ambient monsoonal precipitation experienced a significant reduction in perennial grass growth relative to the ambient or greater monsoonal precipitation treatments, regardless of the local connectivity (ConMod or control). However, ConMods appeared to be most effective under monsoonal precipitation near the long-term mean, since that is when they will have the greatest effect on the soil's PAWC.

This suggests that during periods of below-ambient monsoonal precipitation, ConMods are not effective in promoting perennial grass growth, due to the soils diminished plant available water capacity (PAWC) limiting vegetative growth in drylands (Butterfield et al., 2023; Sala et al., 2012; Throop et al., 2012). This supports our initial hypothesis that modifying local connectivity is most effective in promoting perennial grass growth under monsoonal precipitation regimes that mimic the long-term mean of the study site. Since during periods of above-ambient monsoonal precipitation, ConMods increase PAWC promoting perennial grass growth. Eventually, the soil's PAWC is near field capacity, so ConMods will have a limited ability to increase the local PAWC further. However, ConMods will help retain the soil's PAWC over a longer period, providing vegetation more time to be photosynthetically active. While inversely, during periods of below-average monsoonal precipitation, the PAWC is approaching or below the wilting point of the soil. Thus, the effect from ConMods on PAWC is subdued, since the soil's PAWC will remain around or below the wilting point. These results infer that ConMods provide an additive effect to monsoonal precipitation, for they promote perennial grass ANPP, but do not amplify each other's effects. This would explain why during our statistical analysis, the interaction between monsoonal precipitation and ConMods was not significant.

This suggests that ConMods enhance the resilience and are effective at buffering perennial grasses to brief inter-annual deviations from the long-term mean monsoonal precipitation (Fig. 7). This is primarily due to the ability of ConMods to maintain a relatively homogenous distribution of necessary soil nutrients and their accumulation of organic matter, which contributes to increasing the soil's PAWC spatially and temporally (Fick et al., 2016; Okin et al., 2018; Peters and Savoy, 2023). Peters et al. (2020) has indicated that given enough time (6 + years) ConMods promote plant-soil feedbacks that become the predominant factor in determining perennial grass ANPP. In addition, other factors, such as improved soil conditions and a decrease in the local sediment flux (g m^{-2} day^{-1}) also play a role in supporting perennial grass growth and recovery in drylands (Gregory S. Okin et al., 2015; Rachal et al., 2015; Throop and Archer, 2007).

This study also provided an opportunity to examine how varying (drying and wetting) precipitation legacies influence perennial grass ANPP in drylands. In the experiment's first two years (2020 – 2021), the study site experienced a shift from below- to above-average monsoonal precipitation, which allowed us to examine the response of perennial grass ANPP to a wetting legacy effect. In 2021, we observed an increase in perennial grass ANPP across all treatments, which is most likely due to the increase in monsoonal precipitation enhancing the soil's PAWC. The diminished monsoonal precipitation during the initial year of our study also confirms that limited PAWC deters perennial grass ANPP and increases mortality, both of which contribute to an overall reduction in perennial grasses in drylands (Bunting et al., 2017; Gherardi and Sala, 2015). Then in 2022, the study site received approximately 30% less monsoonal precipitation (72.37 mm) than in 2021, and was 3% more than the long-term mean (180.86 mm) for the study site. However, perennial grass ANPP experienced an overall increase of 20% in 2022 relative to 2021 despite the decrease in monsoonal precipitation (Fig. 7).

These results show that following an extended period of below-average monsoonal precipitation, concurrent years of average or greater monsoonal precipitation are necessary to initiate perennial grass growth recovery (Peters et al., 2020; Sala et al., 2012). They also suggest that average (or greater) monsoonal precipitation can amplify perennial grass ANPP in the proceeding years (Fig. 7) even if monsoonal precipitation is below the long-term mean. Previous studies have shown similar findings regarding the effects that wetting monsoonal precipitation legacies have on perennial grasses in drylands (Hoover et al., 2021; Reichmann et al., 2013; Sala et al., 2012). In particular, that wetting legacies will help provide a buffer to perennial grass growth during inter-annual periods of below-ambient monsoonal precipitation (Broderick et al., 2022). There were not enough consecutive years of average or greater monsoonal precipitation during our study to further investigate the time necessary for successful perennial grass recovery in response to a wetting (dry – wet) legacy. These findings are consistent with previous work that has investigated the legacy effect of sustained wetting on perennial grasses in drylands (Broderick et al., 2022; Peters and Savoy, 2023). In the final year of this study (2023), our field site experienced the lowest amount of ambient monsoonal precipitation throughout the study period (63 mm; Fig. 2). However, despite experiencing 20% less monsoonal precipitation than in 2020, overall perennial grass ANPP was over 100% greater in 2023 compared to 2020 (Fig. 7).

This provided an opportunity to investigate perennial grasses' response to a drying (wet – dry) legacy, and its ability to cope with brief intervals of below-average monsoonal precipitation.

These patterns indicate that monsoonal precipitation has a cascading effect on perennial grass growth, in both the current and subsequent years in drylands (Reichmann et al., 2013). The results also highlight the overall resilience of perennial grasses in drylands, and their ability to recover from inter-annual fluctuations in monsoonal precipitation when there is average or above-average precipitation in the proceeding years (Butterfield et al., 2023; Peters and Savoy, 2023). The significant increase in perennial grass ANPP in 2023, despite lower precipitation, is consistent with previous work that has investigated how wetting legacies effect perennial grasses in drylands (Bunting et al., 2017; Monger et al., 2015). These results suggest that if fluctuations in inter-annual monsoonal precipitation are relatively brief it is possible through promoting perennial grass growth and recovery to revert the ecological state back to a perennial grassland. If there are extended inter-annual fluctuations in monsoonal precipitation, which are anticipated to become increasingly frequent under future climate scenarios, perennial grass recovery will diminish (Currier and Sala, 2022; Gherardi and Sala, 2019). This will likely impede perennial grass recovery in drylands globally and make it difficult to reverse the ecological state from a shrub-duneland back to a perennial grassland.

Perennial Grass Establishment

Improving our understanding of perennial grass seedling vulnerability to precipitation-induced mortality is a pressing ecological issue globally in dryland environments (Moreno-de Las Heras et al., 2016; Pekas and Schupp, 2013; Wang et al., 2013). In this study, we quantified the effects from precipitation and connectivity on perennial grass germination and physiology over the course of two monsoon seasons (2021 – 2022). In addition, we also wanted to investigate perennial grass recruitment, so we modified previously established methods based on Fenner and Thompson (2005) to quantify the year-year change (Seedlings $_{2022}$ – Seedlings $_{2021}$) in seedlings as a metric for perennial grass seedling recruitment. The results from this study might in part be influenced by the timeframe that we collected perennial grass recruitment data, since 2021 and 2022 were the only years that the study site experienced monsoonal precipitation that was consistent or exceeded the local long-term mean (Fig. 2).

Examining perennial grass recruitment allowed us to parse out the effects that connectivity, initial perennial grass cover, and precipitation have on perennial grass recruitment. We identified a significant ($P < 0.05$) difference in perennial grass recruitment between plots that received below-ambient precipitation and plots that received ambient or greater monsoonal precipitation (Fig. 9B). The suppressed recruitment rate indicates that the long-term mean monsoonal precipitation is a potential threshold, below which the capacity for perennial grass recruitment is significantly reduced. These results suggest that as drylands experience increasingly stochastic monsoonal precipitation in the 21st century, perennial grass recruitment will likely experience a significant decline. The results also infer that perennial grass recruitment decreases during extended inter-annual periods of below-average precipitation (Bunting et al., 2017; Williams et al., 2010). This further supports the perspective that perennial grasses in drylands will experience an increase in seedling mortality, and a decrease in recruitment in the coming decades. In drylands, this is a pressing problem, since successful recruitment is necessary for the long-term survival and re-establishment of perennial grasses in drylands (Peters et al., 2014; Zimmermann et al., 2008). Previous studies (Loydi and Collins, 2021; Winkler et al., 2019) have shown that shrub recruitment in drylands is generally more resistant to inter-annual variations in monsoonal precipitation, and is expected to be more successful under future climate scenarios. This is a critical issue in drylands as it will accelerate the transition from a grass- to shrub-dominated environment. The ecophysiological feedbacks re-enforce a shrub-dominated environment, and makes reversing the change in state under future climate scenarios very difficult without exogenous conservation efforts (Berdugo et al., 2022; Peters et al., 2020).

Perennial grass recruitment was significantly greater in plots with ConMods ($p < 0.05$; Fig. 9A. The increased rate of perennial grass recruitment in plots that have ConMods can be explained in part by an increase in the local seed bank, which is due to the reduction in connectivity resulting in an accumulation of organic material and seeds (Turk et al., 2024). The physical abrasion these seeds experience during transport and prior to entrainment could contribute to the increase in perennial grass germination within ConMods as well (Jarrar et al., 2023; Niu et al., 2021; Rachal et al., 2015). Interestingly, connectivity and precipitation had a significant impact on perennial grass seedling recruitment (Fig. 9C; Table 2), but the interaction between the two variables did not have a significant effect on perennial grass recruitment (Table 2). This implies that both ConMods and monsoonal precipitation enhance perennial grass seedling germination and recruitment but are independent mechanisms that do not appear to influence each other and magnify their effects. Furthermore, these results underscore the potential of ConMods as a tool to help mitigate the adverse effects of future climate scenarios on perennial grass seedling germination and recruitment. In particular, ConMods increase the local seed bank richness and PAWC, while providing ideal microhabitats for perennial grass seedling entrainment and germination (Butterfield et al., 2010).

We analyzed the physiological dataset across the precipitation and connectivity treatments for both years as well. (Table 3; Supp. Table 1). These results indicate that the physiological development of perennial grasses is more resilient to inter-annual variation in monsoonal precipitation than perennial grass recruitment. This is likely due primarily to the short timeframe (two years) of the recruitment study, which appears to lack the temporal resolution necessary to capture the physiological response of perennial grasses to changes in monsoonal precipitation. However, the interaction between connectivity and monsoonal precipitation treatments resulted in a significant effect on perennial grass stolon density (Table 3) and tillers (Supp. Table 1). These insights contribute to better our understanding of perennial grass growth and establishment in drylands, since *Bouteloua eriopoda* is one of the foundation perennial grass species in the Chihuahuan Desert, and the only species that reproduces primarily via stoloniferous growth (Reichmann and Sala, 2014; Svejcar et al., 2015; Whitney et al., 2019). These findings indicate that reducing the local structural connectivity enhances both the vegetative growth and reproductive abilities of *Bouteloua eriopoda*. The results also suggest that the difference in perennial grass tiller density between quadrants increases as monsoonal precipitation deviates further from the ambient amount. This may also help explain why *Bouteloua eriopoda* populations tend to experience an overall decrease in shrublands, since shrub encroachment increases the structural connectivity of the landscape (Okin et al., 2015; Peters et al., 2020; Turnbull and Wainwright, 2019). Furthermore, this suggests that under future climate scenarios *Bouteloua eriopoda* will likely struggle with establishment and vegetative growth (Bosco et al., 2018; Gherardi and Sala, 2015; Hanslin et al., 2019; Niu et al., 2023). Previous studies on perennial grass physiology (Collins and Xia, 2015; Peters et al., 2014; Thomey et al., 2014) have shown that there is typically a two to four-year lag in the physiological response of perennial grasses to fluctuations in monsoonal precipitations. Therefore, it is likely that there will be a similar general lag in the physiological response of perennial grasses to changes in the local connectivity (ConMods) and monsoonal precipitation as well. These findings indicate that extending the duration of data collection in future studies might provide more insightful results regarding the physiological response of perennial grasses to changes in monsoonal precipitation and connectivity. Additionally, incorporating longer-term (6 + years) datasets could help with identifying trends that are not apparent in shorter studies, such as this one.

Shrubs and Forbs

In this study, we analyzed the shrub data, but were unable to identify any significant trends or patterns regarding germination or growth during the study period (2021 – 2023). There are two primary shrubs present at the study site (*Prosopis glandulosa* and *Atriplex canescens*). However, we only observed *Pr. glandulosa* germination during our study, and not in a high enough quantity to conduct a statistical analysis. This could be due in part to the limited presence of shrub seeds within the seed-bank, since previous studies have shown the inter-plant and perennial grass patch level seed-banks consist primarily of perennial grasses and forbs (Moreno-de Las Heras et al., 2016). We suspect that a longer study period might improve our understanding of shrub germination and establishment within the inter-plant and perennial grass patch regions. Additionally, further investigation into shrub germination at the study site could provide insights into any existing thresholds for shrub germination, and whether these thresholds are affected by changes in precipitation and connectivity.

Further investigation into shrub germination at the study site could provide insights into whether there are any thresholds regarding shrub germination and if these thresholds are affected by changes in precipitation and connectivity

In our analysis of forb growth, forb ANPP was positively correlated to monsoonal precipitation, but there was not a significant effect from ConMods on forb ANPP. This is likely due to the variety of forb species, which have different germinating and flowering periods throughout the year. In almost all forb species we identified, there was not a large enough sample size of the species to conduct a statistical analysis. The large degree of forb diversity in the dataset is in part due to the local heterogeneity within the seed bank of each plot (Pekas and Schupp, 2013). It also appears that precipitation has an influence on forb ANPP, but not on forb diversity, which is consistent with previous research (Loydi and Collins, 2021). The results also indicate there is negative correlation between the initial perennial grass and forb ANPP, which previous work has shown to limit seedling germination in drylands. ConMods reduce the local connectivity within the plot and create a significant accumulation of organic matter, but there is likely a time-lag on the effect they have on forb ANPP and diversity (Peters et al., 2020). Extending the study period and incorporating more frequent sampling intervals would help to reveal the trends that were not apparent under the current timeframe. Moreover, examining the role of microclimatic variations in different plots could provide a better understanding of the mechanisms that influence forb growth and diversity under various future climate scenarios.

Conclusions

This study shows for the first time how connectivity, initial perennial grass cover, and monsoonal precipitation, has each been shown to independently influence perennial grass growth and recruitment in drylands. Monsoonal precipitation has a substantial influence on the various stages of perennial grass growth and recruitment in drylands. Our findings also show that disrupting the local connectivity can help mitigate the adverse effects that fluctuations in monsoonal precipitation have on perennial grasses, as well as promoting perennial grass recruitment within the inter-plant region in dryland environments (Okin et al., 2015; Peters et al., 2020; Rachal et al., 2015). Additionally, the ability of perennial grasses to recover following periods of below-average precipitation during a period of average or greater monsoonal precipitation underscores their resilience to brief inter-annual variations of monsoonal precipitation (Hoover et al., 2021; Winkler et al., 2019). These results, along with previous studies (Okin et al., 2018; Peters and Savoy, 2023; Zimmermann et al., 2008), demonstrate the benefits of anthropogenic and ecological interventions. Promoting locally targeted conservation and restoration efforts is critical to preventing and potentially reversing vegetative state changes in drylands.

Moreover, the study highlighted the importance in improving upon our current understanding of legacy effects, and how their interactions with abiotic mechanisms influence perennial grasses ecophysiologically in dryland environments (Hoover et al., 2021; Li et al., 2017; Turnbull et al., 2010). Perennial grass recruitment across various monsoonal precipitation regimes shows that when monsoonal precipitation approaches (or exceeds) the long-term mean, it is sufficient for successful perennial grass recruitment in drylands. This study also highlights the effectiveness of modifying local connectivity through ConMods under favorable monsoonal precipitation, which promotes perennial grass growth by creating ideal microhabitats for germination and recruitment (Berdugo et al., 2022; D'Odorico et al., 2010; He et al., 2015; Mureva and Ward, 2017). Although the shrub and forb data did not reveal significant trends, the results suggest that a longer observation period and a higher sampling resolution could provide novel insights to better understanding the multifaceted dynamics that influence dryland vegetation dynamics. This research underscores the critical role of adaptive management strategies in maintaining the productivity and sustainability of grasslands in dryland environments in the face of increasing climatic variability. These results also provide a foundation for future studies to explore the complex interactions between grass, shrub, and forb species under future climate scenarios.

Current climate model predictions indicate that drylands will experience rising temperatures and increasingly stochastic monsoonal precipitation, which will adversely affect perennial grass growth in drylands in the 21st century (Bestelmeyer et al., 2018; Currier and Sala, 2022; Williams et al., 2022). Decreasing monsoonal precipitation is expected to lead to reduced perennial grass growth and establishment (Gherardi and Sala, 2015), resulting in an increasingly connective landscape over time (Okin et al., 2018; Rachal et al., 2015). The resulting feedback loop—where decreased perennial grass cover increases local connectivity, further inhibiting grass growth and establishment—poses significant environmental challenges globally (O'Connor, 1995; Skaggs et al., 2011; Tariq et al., 2024; Wilcox et al., 2011). The use of ConMods to decrease local connectivity can have a cascading effect on perennial grasses, with regional and global implications for the cultural and ecological services provided by drylands (Dintwe and Okin, 2018; Dudley et al., 2014; Peters et al., 2008). Expanding the implementation of connectivity modifications (like ConMods) globally would be a cost-effective tool to inhibit perennial grass mortality and mitigate some adverse environmental consequences in drylands due to climate change (Gregory S. Okin et al., 2015; Peters et al., 2020).

Drylands are the principle source of dust emission globally (Duniway et al., 2019; Middleton, 2017). Dust reduces the air quality, impairs respiratory health, and transports pathogens across large distances, which exacerbates public health concerns (Bhattachan et al., 2019; Sprigg et al., 2014; Tong et al., 2017). One of the primary consequences from a decrease in perennial grass cover and increase in drylands spatially is a significant increase in dust emissions (Bullard and Baddock, 2019; Field et al., 2010; Green et al., 2020); a result of higher landscape connectivity, which pose severe risks to human health (Achakulwisut et al., 2019; Armah et al., 2011) and ecological stability in drylands (Edwards et al., 2019; Ravi et al., 2010). Perennial grass loss and the resulting soil erosion lead to the depletion of essential nutrients (Li et al., 2008, 2007), compromising the long-term viability of dryland ecosystems that sustain more than one-third of the global population. Over half of the Earth's terrestrial surface consists of drylands currently, but are predicted to increase in surface area by as much as 80% depending on which RPC scenario is used to forecast climate change (Huang et al., 2017; Tariq et al., 2024). Moreover, dryland expansion will primarily occur in the global south where it presents a poignant threat to procuring sustenance, particularly at the local scale (Altman et al., 2009; Lucatello et al., 2020). This innovative method is applicable to drylands worldwide and other ecosystems where local connectivity adjustments are likely to influence plant recovery and drive state change reversals, especially in areas affected by aeolian processes.

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Chapter 2 Precipitation and Connectivity Effect the Distribution of Dryland Litter

Abstract

This study explores the dynamics of organic matter decomposition in a dryland ecosystem, focusing on how structural connectivity and monsoonal precipitation influence the distribution and decomposition of litter and non-photosynthetic vegetation (organic matter). By conducting field experiments across a monsoonal precipitation gradient, we analyzed the ecogeomorphic mechanisms driving the spatial and temporal variability in the distribution and decomposition of organic matter. Our findings reveal that increased monsoonal precipitation accelerates decomposition, particularly when the structural connectivity was reduced, facilitating a more homogenous distribution of organic matter. This research underscores the importance of considering both aeolian and hydrological mechanisms as well as their interactions to better understand litter dynamics in drylands, with implications for predicting how future climate scenarios will alter dryland litter dynamics and the terrestrial carbon cycle.

Introduction

Climate, microbial community, and composition are the primary determinants of organic matter and litter decomposition in terrestrial systems (Cleveland et al., 2014; Song et al., 2013). The decomposition of organic material and litter is a critical component of terrestrial biogeochemical cycles, particularly in regard to the carbon (C) and nitrogen (N) cycle (Throop and Belnap, 2019). Despite litter making up a limited segment of the overall C and N stored in terrestrial environments, it has a disproportionate effect on these biogeochemical cycles due to its relatively rapid rate of decomposition and the functional linkage it makes between C and N (Laskowski and Berg, 2006). Terrestrial environments have the potential to act as either C sinks or sources under futures climate scenarios (Adair et al., 2008; Weltzin et al., 2003). However, this is dependent on the effects that climatic changes will have on overall net primary productivity (NPP) and litter decomposition (Barnes et al., 2015; Chuckran et al., 2020; Laskowski and Berg, 2006) because the amount of standing litter is the product of both. It remains unclear how future climate scenarios will alter dryland biogeochemical cycles globally (Maestre et al., 2012; Ranucci et al., 2022). In particular, there remain many uncertainties within dryland environments, which make up over 40% of Earth's terrestrial surface and account for approximately 32% of terrestrial C storage (Dintwe and Okin, 2018; D'Odorico and Bhattachan, 2012; Van Auken, 2009).

Dryland environments are typically characterized by the soil moisture deficit they experience (Duniway et al., 2010; Gherardi and Sala, 2015), as well as an aridity index (the ratio of precipitation to potential evapotranspiration) of less than 0.65 throughout most of the year (Bestelmeyer et al., 2015; D'Odorico et al., 2019). Under future climate scenarios, it is predicted that drylands could experience an increase in area by as much as 23% globally (Huang et al., 2016). Furthermore, dryland environments have been undergoing a shift in vegetation over the last century (e.g., shrub encroachment), that has been accelerated due to an increasingly stochastic climate (Duniway et al., 2010; Gherardi and Sala, 2019) and unsustainable anthropogenic activities (Fu et al., 2021; Wilcox et al., 2011). This transition in vegetation, from traditional perennial grasslands (C_4) to shrublands (C_3), reduces the overall vegetative cover of the environment (de Graaff et al., 2014; D'Odorico et al., 2012). Since vegetation is the primary source of litter, the composition, as well as spatial and temporal distribution of litter in drylands, is predicted to continue changing in the coming decades (Chuckran et al., 2020; Ranucci et al., 2022). Therefore, it is of critical importance to better understand how future climate scenarios will influence the C and N cycle in drylands by altering the composition and distribution of litter in drylands.

The relatively limited vegetation and large areas of bare soil in dryland environments results in ideal conditions for the transport, and mixing of litter and soil (bioturbation) via aeolian or fluvial processes (Breshears et al., 2003; Hewins et al., 2013; Okin et al., 2015). Bioturbation provides an abiotic input for litter to enter the C and N cycle in drylands (Joly et al., 2017; Throop and Archer, 2007). Additionally, it has a profound influence on the spatial distribution of litter in dryland environments (Rachal et al., 2015; Throop and Belnap, 2019). Aeolian-driven mixing is often observed occurring within patches of vegetation, since the microtopography facilitates the deposition of entrained litter and sediment particles (D'Odorico et al., 2012; Peters et al., 2020; Ravi et al., 2007). Previous studies (Barnes et al., 2015; Evans et al., 2020; Gliksman et al., 2017) have shown the rate of decomposition for litter integrated into the soil matrix is accelerated compared to litter present on the surface (Hewins et al., 2013). There are several drivers (microbial community, soil moisture content, and temperature) that intensify decomposition rates once litter enters the soil matrix (Joly et al., 2017; Yang et al., 2024).

The breakdown and decomposition of litter is one of the primary routes through which litter enters the C and N cycle in terrestrial environments (Adair et al., 2008; Chuckran et al., 2020; Laskowski and Berg, 2006). However, in drylands, the abiotic drivers of litter decomposition differ in comparison to more mesic environments (Barnes et al., 2015; King et al., 2012). Since drylands generally have limited vegetative cover, sunlight is not a limiting factor and results in photodegradation having a significant effect on decomposition rates (Adair et al., 2017; Evans et al., 2020; Lin et al., 2018). This is due to the litter being exposed to ultraviolet (UV) and photosynthetically active radiation (PAR), which accelerates decomposition by breaking down the chemical (photo-oxidation) and organic (photolysis) compounds within litter (Berenstecher et al., 2020; Chen et al., 2016; Day et al., 2019). Photolysis has been found to degrade the protective cuticle (film on vegetation preventing water loss vis transpiration (Peguero-Pina et al., 2020)) on litter, increasing its ability to retain moisture and accelerate microbial processes that contribute to litter decomposition (Logan et al., 2022; Yang et al., 2024). Furthermore, photodegradation breaks down lignin, which is resistant to biotic decomposition and influences the abiotic and biotic decomposition rates (Gliksman et al., 2017; Liu et al., 2015; Wang et al., 2015). However, when litter enters the soil matrix via aeolian-driven mixing, there is a decrease in the rate photodegradation and microbial decomposition increases significantly (Barnes et al., 2015, 2012; Liu et al., 2015). This is likely due to the soil buffering the microbial organisms from direct sunlight and extreme temperatures (Barnes et al., 2015; Hewins and Throop, 2016). The limited understanding of the complexities of litter decomposition in drylands is evident in current models, which tend to underpredict dryland litter decomposition (Hewins and Throop, 2016; Ranucci et al., 2022).

Conventional litter decomposition models are capable of accurately estimating litter production and decomposition rates in mesic environments (such as deciduous forests and boreal forests), but have failed to accurately predict litter decomposition in drylands (Laskowski and Berg, 2006; Throop and Archer, 2009). The traditional models generally underestimate litter decomposition rates (i.e. not taking into account of photodegradation), and overestimating the amount of N that is immobilized via microbial activity (Adair et al., 2008; Parton et al., 2007). This disconnect, regarding litter decomposition in drylands, has spurred various studies (Cleveland et al., 2014; Delgado-Baquerizo et al., 2015; Song et al., 2013) with the objective of identifying and quantifying the primary mechanisms driving dryland litter decomposition.

Although progress has been made in identifying the primary drivers of litter decomposition in drylands, there persists a lack of in-situ experiments quantifying changes in litter under varying amounts of precipitation. Additionally, only a handful of studies (Mayor et al., 2019; Okin et al., 2015a; Throop and Belnap, 2019) have investigated the role that aeolian processes play in the distribution and decomposition of litter in dryland environments.

Precipitation is the primary factor that determines vegetative patterns in drylands; however, there are additional abiotic mechanisms that effect dryland vegetation (such as aeolian, edaphic, and geomorphic processes) (Li et al., 2008; Monger et al., 2015; Okin et al., 2018). There is an increasing body of work in the 21st century (Okin et al., 2015; Ravi et al., 2007; Shao, 2008; Wu et al., 2018) investigating the direct and indirect role that aeolian processes have influencing vegetative patterns dryland environments. In particular, aeolian processes play an integral role in regards to the distribution of litter and nutrients across dryland environments (Li et al., 2007; Schlesinger et al., 1995; Throop and Belnap, 2019). Once vegetatively homogenous landscapes (such as perennial grasslands) begin experiencing an increase in the spatial heterogeneity of vegetation (shrub encroachment), there is an ensuing increase in the amount of bare soil exposed (Caracciolo et al., 2016; D’Odorico et al., 2012; Okin et al., 2009). This increase in bare soil intensifies the susceptibly of the soil surface to both aeolian and fluvial erosion, since these patches of bare soil begin to coalesce and create pathways that promote the redistribution of the litter and soil nutrients present on the soil surface (Belnap et al., 2011; Li et al., 2007; Ludwig et al., 2006, 2005, 2002). Once the litter and soil particles become entrained, they tend to naturally collect within shrub canopies, which results in an accumulation of nutrients and litter around the base of shrubs (Schlesinger et al., 1995). This redistribution of litter and sediment is problematic, as it is often irreversible and inhibits the establishment of vegetation within these inter-plant regions of bare soil (D'Odorico et al., 2012; Eldridge et al., 2011). Furthermore, this results in a change to the composition and distribution of local litter; which will alter the breakdown of litter in the soil, as well as the ability of drylands to continue sequestering atmospheric C (Delgado-Baquerizo et al., 2015; Fu et al., 2021; Ranucci et al., 2022). The result of which could contribute to an overall reduction and disruption to the C and N cycle in drylands under future climate scenarios (Okin et al., 2015; Peters et al., 2020; Schlesinger et al., 1990).

Quantifying how variations in monsoonal precipitation and connectivity influence litter distribution within a grass-shrub dune-land ecotone is the primary focus of this experiment. This study will also provide an opportunity to examine how different (drying and wetting) precipitation legacies influence the distribution of dryland litter (Peters and Savoy, 2023). We hypothesize that (1) the integration of litter into the soil matrix will be amplified by reducing local connectivity, as this promotes the accumulation of litter. Moreover, (2) litter accumulation will be significantly enhanced when prior year's monsoonal precipitation exceeds the annual mean, coupled with reduced local connectivity.

Methods

Study Area

This experiment was conducted within the Chihuahuan Desert at the Jornada Basin Long-Term Ecological Research (LTER) site (32.5°N, 106.8°W, and 1,188 m above sea level), which is located in southern New Mexico, United States. The long-term mean annual precipitation at Jornada is 247 mm, while the long-term mean monsoonal (growing season) precipitation is 176 mm (Gherardi and Sala, 2015). The average monthly temperatures range from 6 °C in January to 26 °C in June. Current grazing intensities are maintained at low levels throughout the 200,000-ha research site, and the study site has been excluded from any livestock grazing since 2014. This study takes place on a grass-shrubland that is dominated by *Bouteloua eriopoda*, *Sporobolus flexuosus*, and *Aristida purpurea* perennial grasses (C_4), that are encountering shrub encroachment from *Prosopis glandulosa* (C_3) expansion.

Experimental Design

The experiment was established in May of 2020, consists of 56 plots that are 2.5 m wide and 5 m long, and spread across an area that is approximately 13 hectares. All plots are located perpendicular to the prevailing wind (Fig. 10) in a sandy, mesquite-dominated shrubland with variable grass cover. No shrubs were present within any of the plots at the time of plot selection. In the initial plot selection phase, 90 plots were selected, and line-intercept (LI) transects were conducted to determine the preliminary vegetation cover. These results were used to identify the interquartile range and remove the 30 least similar plots from the study. The remaining 60 plots were randomly assigned one of five precipitation regiments: -80%, -50%, 0%, +50%, or +80%. During our analysis, we also identified two pairs of irrigated (+80%) and drought plots (-80%) with vegetative patterns that were outliers in comparison to the remaining 56 plots; and as a result, they were omitted from this study.

To modify the precipitation regimes at the plot level, automated rainfall manipulation system (ARMS) were deployed (Gherardi and Sala, 2013; Reichmann et al., 2013). Precipitation is captured with a rainout structure, which consists of shingles that are spaced at varying intervals to intercept incoming precipitation (reducing precipitation by 50% or 80%). The shingles consist of acrylic (Piedmont Plastics, LaMirada, California) that is heated with a ceramic heater and bent at a 120° angle. The material is transparent to minimize any influence it may have on temperature or incoming solar radiation (Gherardi and Sala, 2013). Once the precipitation is intercepted, a drainage system redirects the precipitation in real-time to a 27-gallon plastic storage tank (EDGE Plastics, Mansfield, Ohio). Once the water reaches the storage tank, there is a float switch (Atwood Marine Automatic, Lowell, Michigan) that turns on a water pump (TruePower 12 V DC Marine Utility Pump, Simi Valley, California) when the water level increases. The water is then sent to the corresponding irrigation plot through 12.7 mm (1/2”) PVC pipes. The ARMS design (Gherardi and Sala, 2013) allows irrigated plots to receive precipitation levels that are 50% and 80% above the ambient monsoonal precipitation with six sprinkler heads (Rain Bird 4-Van Sprinkler Spray Nozzle, Azusa, California), which were placed evenly around the perimeter of the plots (3 on each side). This resulted in a precipitation gradient with four treatments: -80%, -50%, +50%, and +80%. (Fig. 10). ARMS were not installed on the plots that received ambient (±0%) monsoonal precipitation. The experimental setup ensures that only the magnitude of precipitation events is manipulated, and not the frequency of precipitation events.

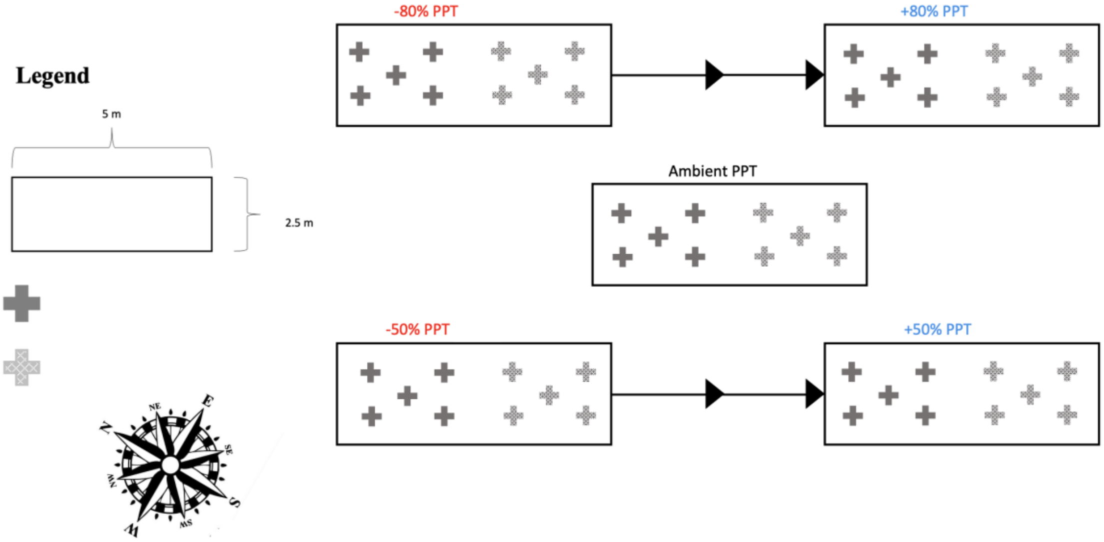

Figure 10. The experimental design and layout of the precipitation (-80%, -50%, 0%, +50%, +80%) and connectivity (ConMod and Control) treatments for this study.

Each individual ARMS was inspected and calibrated before each monsoon season began to ensure there were no leaks, and that the water is evenly applied or diverted consistently within each plot. Once the ARMS had been deployed for the monsoon season, they were maintained and regularly checked to ensure they are functioning correctly. The experiment was maintained throughout the monsoon season until late October, because freezing will damage the equipment. The overwintering process consisted of draining the irrigation system at least 3 m from any plots to ensure the deposited water could have no influence on the drought or irrigation treatments. The drought shelters remained in place throughout winter.

One of the primary objectives of this study is to alter the connectivity of the landscape with respect to aeolian and fluvial transport (Rachal et al., 2015). Previous work has shown that ConMods are able to effectively promote the germination and establishment of native vegetation in drylands (Fick et al., 2016). Peters et al. (2020) also showed that ConMods promote perennial grass establishment under ambient precipitation in dryland environments. Therefore, we decided that installing ConMods would be the most effective method of reducing the local connectivity.

Each of the 56 2.5 m x 5 m plots was divided in half (2.5 m x 2.5 m) and one side was randomly assigned to the ConMod treatment, while the other side received the control treatment. A ConMod consists of 0.63 (1/4”)-cm galvanized hardware cloth that is connected to five 0.63 cm (1/4”)-diameter reinforced steel stakes. Once the ConMods are installed they are 20 cm tall and 55 cm in both width and length. ConMod placement consists of one stake that is placed in the center while the four remaining stakes are placed equal distances from the center stake, the resulting structure takes the shape of the symbol for addition (+). The control (without ConMod) treatments consist of one 0.63 cm (1/4”)-diameter reinforced steel stake that is installed and mirrors the location of the center stake in the ConMod. Additionally, both the ConMod and control treatments were installed in a staggered formation (Fig. 1), which were centered within each 2.5 m x 2.5 m sub-plot (Fig. 10).

Data Collection and Measurements

The primary datasets used in this analysis were peak biomass coverline data (2020 – 2023), and local precipitation (2020 – 2023). For the coverlines we installed four 250-cm transects (located 110, 220, 330, and 440 cm from the edge of the plots) parallel to the prevailing wind such that two transects spanned each of the connectivity treatments (ConMod & control) (Fig. 10). The transects were used as a non-destructive method to measure multi-year vegetation, litter, and NPV cover; as an alternative to collecting the data via destructive harvesting of vegetation. The LPI transects were recorded at the end of the monsoon season (mid-September), when vegetation in the Chihuahuan Desert typically reaches peak vegetative biomass (Havstad et al., 2006; Xia et al., 2010). Vegetation along each transect is recorded at 1-cm resolution. In order to quantify the annual net primary productivity (ANPP) (g m^{-2} yr^{-1}), we used a series of allometric equations developed by (Flombaum and Sala, 2007) and calibrated for our study site (Gherardi and Sala, 2015; Reichmann et al., 2013).

To measure vegetation cover along the transects we used the line-intercept method, which recorded the distance spanned along the transect when a plant was photosynthetically (PV) active and identified the species (e.g. *Bouteloua eriopoda* 34 – 42 cm). If the plant was senesced or dead, we recorded it as NPV, while omitting what was on the soil surface beneath it. We only recorded the amount of bare soil and litter along spans of the transect when there was no vegetation present, also using 1-cm intervals. The methods that we deployed for our data collection are modeled on similar methods developed in previous studies at the Jornada LTER (Gherardi and Sala, 2015; Reichmann et al., 2013; Sala et al., 2012a). The data were collected over the course of two days, to prevent any shifting vegetative physiological patterns from influencing vegetation, litter, and NPV cover.

Precipitation data was obtained from the closest meteorological station (< 1 mile), which using an automatic tipping bucket rain gauge and is maintained by the Jornada LTER. In order to calculate the monsoonal precipitation at each treatment, we followed the methods that Huang et al. (2022) applied in their analysis of monsoonal precipitation throughout the southwestern U.S. We demarcate the onset of the North American monsoon season (NAMS) as the first three consecutive days of precipitation that exceeded 0.5 mm day^{-1} after July 1st, and is based on the framework developed in Higgins et al. (1999). The cutoff for the NAMS was September 30th, since climatic conditions in October inhibit vegetative growth regardless of precipitation.

Statistical Analyses

We used a linear mixed model for repeated measures (MMRM) with our LPI data, as it allowed us to parse out the influence that monsoonal precipitation (-80%, -50%, 0%, +50%, +80%) and connectivity (ConMod or control) have over time (2021 - 2023) on the distribution of litter, NPV, and bare. For an ANCOVA test structure, 2020's litter, NPV, and bare cover was used as a linear covariate for the corresponding dependent variable. The Kenward-Roger method was used to compute the denominator degrees of freedom for our fixed effects (connectivity treatment, precipitation treatment, and year). A random effect of ConMod-control pairs was included to account for the design feature of each pair being adjacently located under the same independently applied precipitation treatment. All statistical analyses were conducted on SAS V9.4 (SAS Institute, Cary, NC USA) with the MIXED procedure. Figures were generated with R version 4.3.2 (R Core Team 2023).

Results

Overview

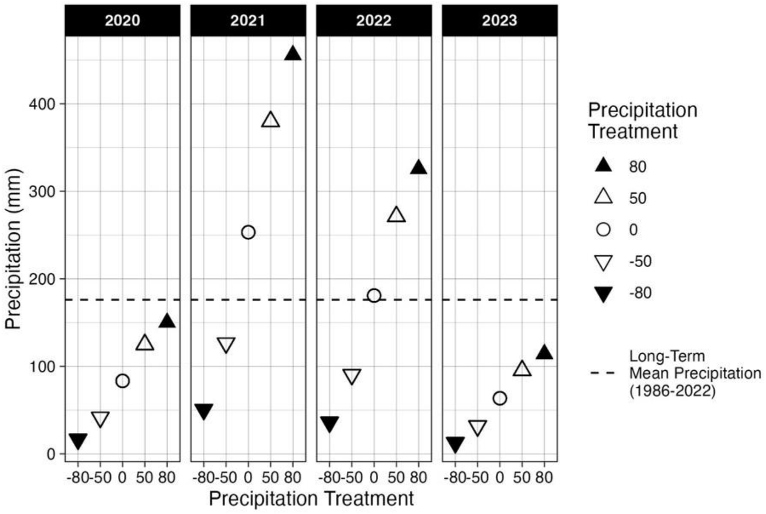

Figure 11.Monsoonal precipitation patterns over the duration of the experiment (2020 – 2024), and across the various (-80%, -50%, 0%, +50%, & +80%) precipitation treatments.

Throughout this experiment, there were large inter-annual variation in monsoonal precipitation, resulting in both above and below average years (Fig. 11). This, in conjunction with the monsoonal precipitation manipulation, allowed us to investigate how shifts in monsoonal precipitation and reductions in structural connectivity influence the distribution and decomposition of litter, NPV, and bare soil in drylands. The long-term average monsoonal precipitation at our study site is approximately 176 mm (Currier and Sala, 2022; Throop et al., 2012). However, there were dry conditions in 2023, which resulted in monsoonal precipitation amounts that were 74% (63.51 mm) less than the long-term average, respectively. In contrast, 2021 and 2022 monsoonal precipitation was 44% (253.23 mm) and 3% (180.86 mm) greater than the long-term average, respectively (Fig. 11). Furthermore, the lack of monsoonal precipitation in 2023 resulted in minimal differences (< 130 mm) between the drought (-80%) and irrigation (+80%) treatments, relative to the differences (> 290 mm) between precipitation treatments in 2021 and 2022.

Litter

The results from our analysis (Table 4) highlight the significant role that variations in monsoonal precipitation and modified structural connectivity have on the distribution of litter in drylands. Manipulating monsoonal precipitation had a significant ($P < 0.05$) influence on the

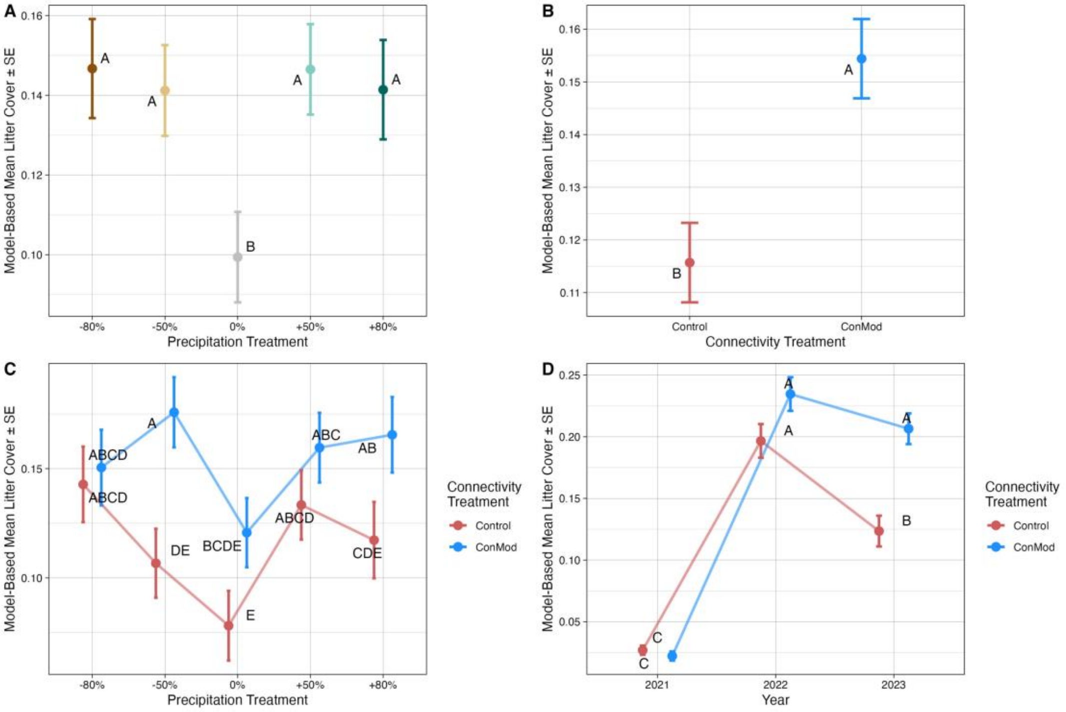

Figure 12. Main effect of modifying precipitation (A) and structural connectivity (B) on mean (± SEM) litter cover (2021 – 2023). The interaction (C) between structural connectivity and monsoonal precipitation on the mean (± SEM) litter cover. (D) The effects from modifying structural connectivity through time (2021 – 2023) on the mean (± SEM) litter cover. Different letters indicate significant differences between treatments based on a repeated measures analysis of covariance (ANCOVA) model with an α = 0.05.

Independent Variable	Num D.F.	F Value	P-Value
Initial Litter Cover 2020	1	62.35	**< 0.0001**
Precipitation Treatment (-80%...+80%)	4	3.08	**0.0196**
Connectivity Treatment (ConMod)	1	12.92	**0.0005**
*Precipitation*Connectivity Treatment*	4	1.03	0.3951
Year	2	227.61	**< 0.0001**
*Precipitation*Year*	8	0.96	0.4698
*Connectivity Treatment*Year*	2	11.37	**<0.0001**
*Precipitation*Connectivity Treatment*Year*	8	1.08	0.3798

Table 2. The repeated measures analysis of covariance (ANCOVA) litter model results for the independent variables: connectivity treatment, precipitation, ConMod, and the interactions between them. Bold values are significant with an α = 0.05.

amount of litter present. Intra-annual precipitation didn't result in a significant difference in the amount of litter present in plots that received above or below-ambient monsoonal precipitation (Fig. 12A). However, plots that received ambient (0%) monsoonal precipitation had atypically low levels of litter relative to the other monsoonal precipitation treatments. Additionally, over the course of this study, we observed that plots with ConMods experienced a significant ($P < 0.05$) overall increase of 33% in the amount of litter present relative to the control plots (Fig. 12B). Although, the interaction between precipitation treatment and connectivity was not significant, ConMods consistently had a greater amount of litter than controls across precipitation treatments (Fig. 12C).

We also observed a significant ($P < 0.05$) temporal difference (inter-annual) in the distribution of litter during this study. In 2021, which received the greatest amount of monsoonal precipitation, there was the least amount of litter (Fig. 12D). There was a large increase (~877%) in the overall amount of litter present in 2022, when monsoonal precipitation approached the long-term mean of the study site. Then, in 2023, the amount of litter present experienced a general decline (~24%), while experiencing the least amount of overall monsoonal precipitation throughout the study period.

The interaction between ConMods and year was significant ($P < 0.05$) as well, which suggests that ConMods had a multiplicative effect on the difference in litter over time (Fig. 12D). Connectivity did not result in a significant difference in the overall amount of litter present in 2021 and 2022. However, we did observe a significant difference in the study's final year (2023), in that, plots with ConMods installed had on average 326% more litter than control plots. Furthermore, we parsed out the impact of each plot's connectivity treatment on litter cover ($\text{Litter}_{\text{ConMod}}$ - $\text{Litter}_{\text{control}}$). These results indicate that the initial amount of litter present also

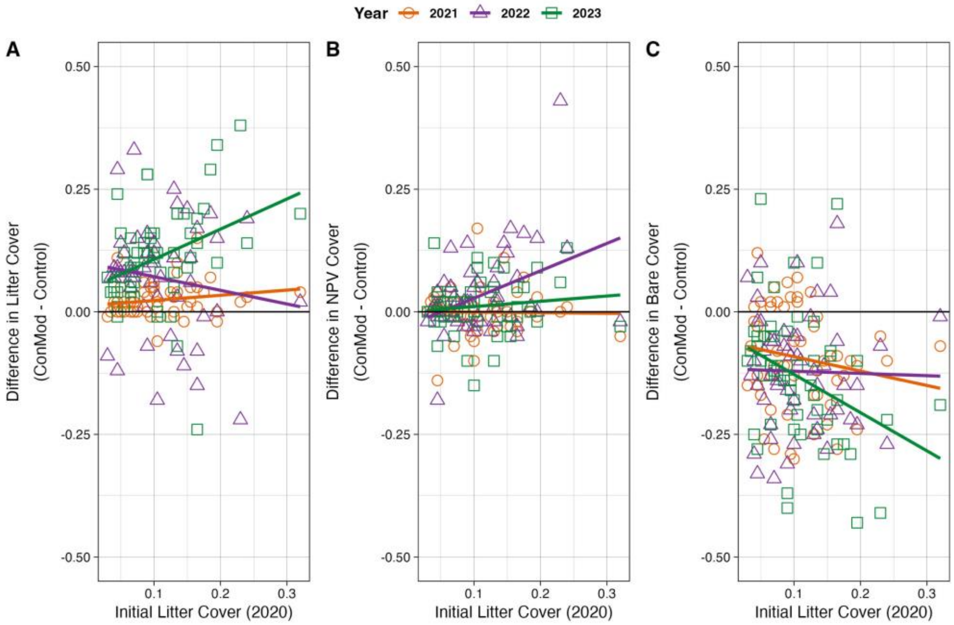

Figure 13. The annual difference (ConMod – Control) in **(A)** litter, **(B)** NPV, and **(C)** bare soil compared to the initial litter cover (2020).

influenced the amount of future litter present between ConMod and control plots (Fig. 13A). When monsoonal precipitation is above or below the long-term mean (2021 and 2023), initial litter cover had positive effect on the amount of litter present, with most of the addition occurring in plots with ConMods installed. However, when monsoonal precipitation approached the long-term mean (2022), we observed a negative relationship between the initial litter present and future litter amounts. Such that, as the amount of initial litter increased, there was an overall decrease in the difference in litter between connectivity treatments.

Non-Photosynthetic Vegetation (NPV)

In this study, we also investigated the effects that connectivity and monsoonal precipitation have on NPV in this study (Table 5). These results indicate the NPV has a different response to environmental manipulations when compared to litter. However, the main effect of connectivity and its interaction with year was significant with an $\alpha = 0.1$, instead of an $\alpha = 0.05$.

The covariate, NPV cover (2020), had a significant influence on future NPV cover (2021 - 2023), and was the most impactful in explaining the future distribution of NPV (Table 5).

Manipulating monsoonal precipitation had a significant influence ($P > 0.05$) on the amount of NPV present. The main effect from the monsoonal precipitation treatments showed a generally negative relationship. As monsoonal precipitation increased, there was a decrease in NPV (Fig. 14A). Similar to the distribution of litter (Fig. 12A), there was a decrease in NPV within plots that received ambient (0%) monsoonal precipitation. Furthermore, the results from this study highlight the significant role that connectivity had on the distribution of NPV in drylands. Plots with ConMods installed experienced a significant ($P < 0.1$), albeit relatively modest, increase in NPV (~16%) in comparison to the control plots (Fig. 14B). The interaction

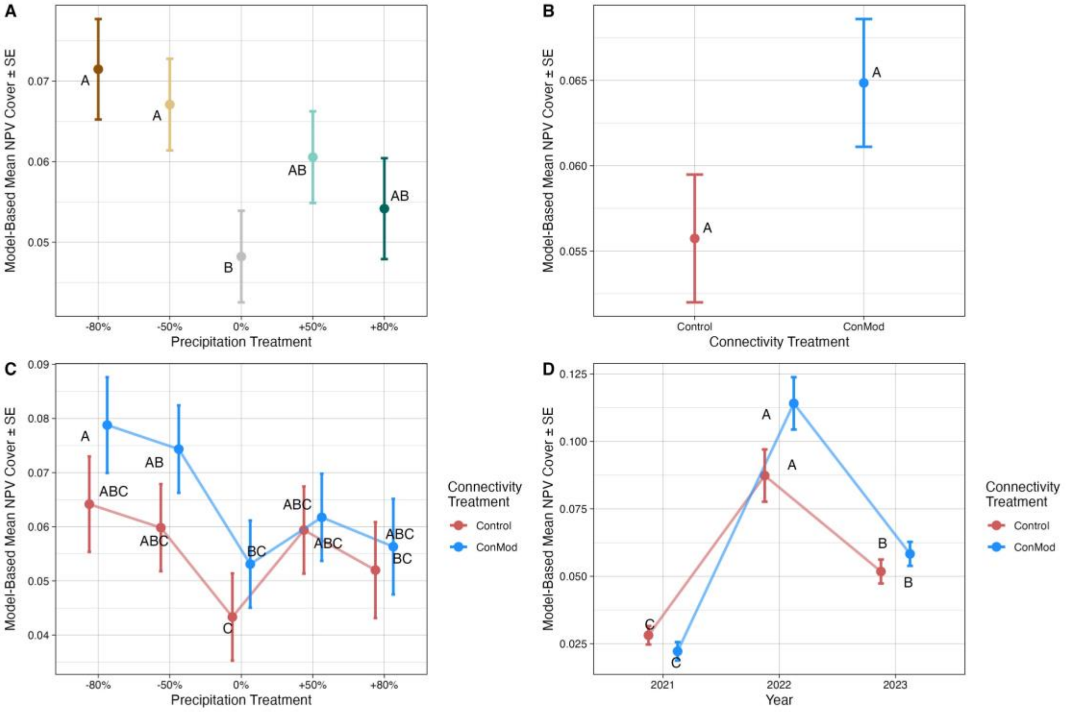

Figure 14. Main effect of modifying precipitation **(A)** and structural connectivity **(B)** on mean (± SEM) NPV cover (2021 – 2023). The interaction **(C)** between structural connectivity and monsoonal precipitation on the mean (± SEM) NPV cover. **(D)** The effects from modifying structural connectivity through time (2021 – 2023) on the mean (± SEM) NPV cover. Different letters indicate significant differences between treatments based on a repeated measures analysis of covariance (ANCOVA) model with an $\alpha = 0.05$.

Independent Variable	Num D.F.	F Value	P-Value
Initial NPV Cover 2020	1	282.53	**< 0.0001**
Precipitation Treatment (-80%...+80%)	4	2.52	**0.0463**
Connectivity Treatment (ConMod)	1	2.96	*0.0887*
*Precipitation*Connectivity Treatment*	4	0.23	*0.921*
Year	2	55.15	**< 0.0001**
*Precipitation*Year*	8	1.27	0.263
*Connectivity Treatment*Year*	2	2.54	*0.0842*
*Precipitation*Connectivity Treatment*Year*	8	0.15	0.9963

Table 3. The repeated measures analysis of covariance (ANCOVA) NPV model results for the independent variables: initial connectivity treatment, precipitation, and the interactions between them. Bold values are significant with an $\alpha = 0.05$ and italic values are significant with an $\alpha = 0.1$.

between precipitation treatment and connectivity was not significant. ConMods had a greater amount of NPV than controls across the precipitation treatments (Fig. 14C). However, above-ambient precipitation treatments had the smallest difference between connectivity treatments compared to ambient and below-ambient precipitation treatments.

We observed that time (year) had a significant influence on the amount of NPV present (Fig. 14D), and displayed similar patterns to those we observed in the distribution of litter present (Fig. 12D). In 2021, the experiment experienced the least amount of overall NPV, when the greatest amount of monsoonal precipitation occurred. When monsoonal precipitation approached the long-term mean of the study site in 2022, there was a significant increase (~400%) in the overall amount of NPV. This was proceeded by a significant decline (~45%) in the amount of NPV present in 2023, when the experiment received the least amount of overall monsoonal precipitation.

We also noticed significant ($P < 0.1$) interannual differences in the amount of NPV present between connectivity treatments (Table 5). The effect from connectivity and year resulted in the greatest difference in 2022. In 2021 and 2023, there was a negligible difference between connectivity treatments (Fig. 14D). Furthermore, we parsed out the impact from the connectivity treatments on NPV cover (NPV_{ConMod} - $NPV_{control}$) (Fig. 13B). In 2021, when monsoonal precipitation exceeded the long-term mean, initial litter cover had no effect on the difference in NPV between connectivity treatments. However, when monsoonal precipitation was less than or approached the long-term mean (2022 and 2023), we observed a positive relationship between the initial litter present and NPV. As initial litter increase, there was an increase in the amount of NPV in ConMods.

Bare Soil

Finally, we analyze the temporal effects that changes in monsoonal precipitation and structural connectivity have on the amount of bare soil present. In our analysis, the initial amount

Independent Variable	Num D.F.	F Value	P-Value
Initial Bare Soil Cover 2020	1	82.48	**< 0.0001**
Precipitation Treatment (-80%...+80%)	4	1.37	0.2615
Connectivity Treatment (ConMod)	1	2.94	*0.0925*
*Precipitation*Connectivity Treatment*	4	2.18	*0.0944*
Year	2	146.88	**< 0.0001**
*Precipitation*Year*	8	0.82	0.5897
*Connectivity Treatment*Year*	2	1.46	0.2377
*Precipitation*Connectivity Treatment*Year*	8	0.59	0.7844

Table 4. The repeated measures analysis of covariance (ANCOVA) bare soil model results for the independent variables: connectivity treatment, precipitation, ConMod quadrant, and the interactions between them. Bold values are significant with an $\alpha = 0.05$ and italic values are significant with an $\alpha = 0.1$.

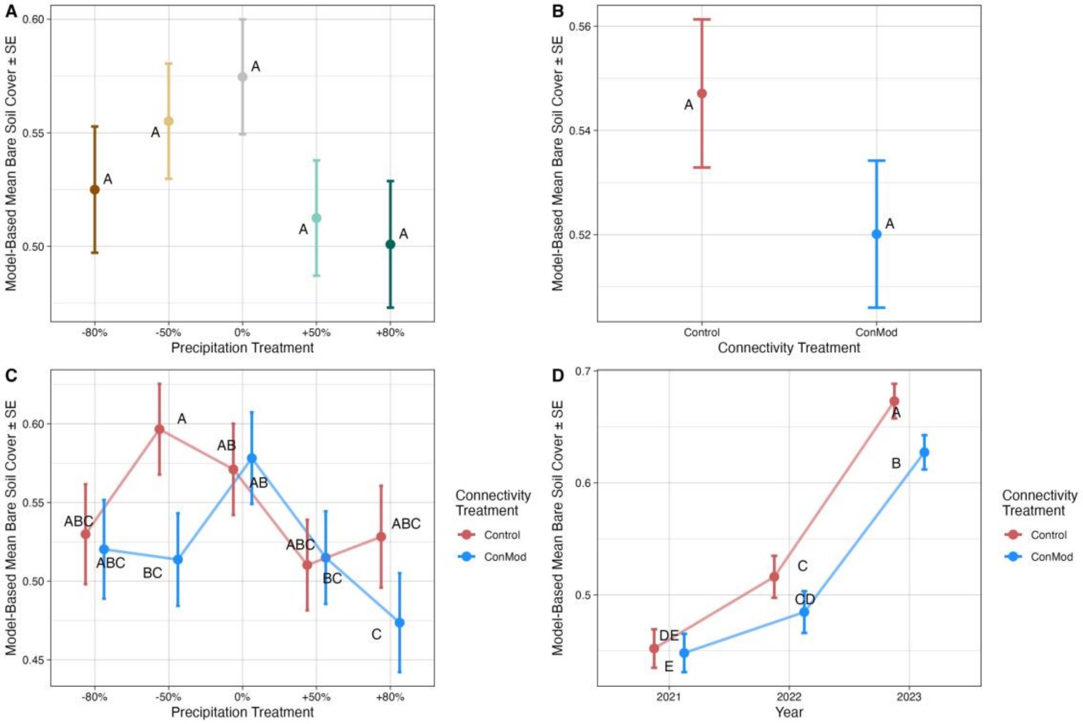

Figure 15. The effect of modifying **(A)** precipitation and structural connectivity **(B)** on the mean (± SEM) amount of bare soil (2021 – 2023). **(C)** The interaction between modulations in structural connectivity and monsoonal precipitation on mean (± SEM) bare soil cover (2021 – 2023). **(D)** The effects from modifying structural connectivity over time on the mean (± SEM) amount of bare soil present (2021 – 2023). Different letters indicate significant differences between treatments based on a repeated measures analysis of covariance (ANCOVA) model with an $\alpha = 0.05$.

of bare soil (2020), connectivity treatment, year, and the interaction between connectivity treatment and monsoonal precipitation treatments had significant influences on the amount of bare soil (Table 6). Furthermore, the effect from connectivity treatment, and it's interaction with monsoonal precipitation treatments are significant when using an $\alpha = 0.1$. Our covariate, the initial amount of bare soil (2020), had a significant ($P < 0.05$) influence on the distribution of future amounts of bare soil. It is the second most impactful effect in explaining the future distribution of NPV.

The results from this study highlight the impact that changes in monsoonal precipitation and connectivity have on the overall amount of bare soil present. Interestingly, manipulating monsoonal precipitation did not have a significant influence ($P > 0.05$) on the amount of bare soil

(Table 6; Fig. 15A), but did have a significant influence on the overall amount of litter (Table 3) and NPV (Table 5). Moreover, plots with ConMods installed experienced a significant ($P<0.1$), albeit modest, reduction in the amount of bare soil of 5% when compared to the control plots (Fig.15B). However, we observed a significant ($P < 0.1$) difference in the amount of bare soil present within the interaction between ConMods and monsoonal precipitation (Table 6). Plots that received -50% and +80% monsoonal precipitation treatment had a significant difference between connectivity treatments, but not in the remaining precipitation treatments (Fig. 15C).

The field site experienced large inter-annual variations in monsoonal precipitation during the study period. This provided years when monsoonal precipitation was either above or below the long-term mean. The overall amount of monsoonal precipitation annually appears to have a significant influence on the amount of bare soil present (Fig. 15D). The wettest year of the study (2021) corresponded with the least amount of overall bare soil during this study. In 2022, when monsoonal precipitation approached the long-term mean of the study site, there was a modest increase (~11%) in the overall amount of bare soil. Then, in 2023 (the driest year of the experiment), the overall amount of bare soil present experienced a significant increase (~30%).

The interaction between year (interannual variation) and connectivity was not significant in the amount of bare soil present, but there seems to be a small multiplicative effect. In the first two years of the study, the difference in bare soil between ConMod and control were relatively similar. However, ConMods resulted in a significant difference in the amount of bare soil during the final year of our study (2023) (Fig. 15D). Furthermore, we parsed out the impact from the connectivity treatment on the amount of bare soil ($\text{Bare}_{\text{ConMod}}$ - $\text{Bare}_{\text{control}}$). The results show that the amount of initial litter cover influences the amount of bare soil present between ConMod and control plots. When monsoonal precipitation exceeds or is less than the long-term mean, there is a stronger negative relationship between the initial amount of litter and bare soil present (Fig. 13C). This suggests that as initial litter cover increases there is also an increase in bare soil within control plots. However, when monsoonal precipitation approaches the long-term mean, the effect from litter on bare soil appears to be modulated (Fig. 13C).

Discussion

Litter

This experiment provided an opportunity to investigate how monsoonal precipitation and connectivity influence the distribution and decomposition of litter in dryland environments longitudinally (3 years). Increasingly variable monsoonal precipitation (Ault et al., 2016; Huang et al., 2022; Liang and Zhang, 2022), and how it will influence litter remains a pressing global issue in dryland ecology (Laskowski and Berg, 2006; Throop and Belnap, 2019). Our study found that litter in drylands is influenced by structural connectivity, and both intra- and inter-annual changes in monsoonal precipitation at the local plant-soil scale. The results from this study are somewhat consistent with previous experiments (Cleveland et al., 2014; Hewins and Throop, 2016a; Rachal et al., 2015) that have investigated the influence that aeolian or hydrological changes have on litter decomposition and distribution in drylands. Although, this is the first study to investigate the effects from both monsoonal precipitation and connectivity on the distribution and decomposition of litter. Throughout the study period, aeolian events were consistent with historical patterns for the study site (Bergametti and Gillette, 2010; Floyd and Gill, 2011), which allowed us to parse out the effectiveness of ConMods in modulating litter decomposition and distribution under varying amounts of monsoonal precipitation.

The intra-annual variability amongst the monsoonal precipitation treatments (-80%, …, +80%) in this study provided an ideal opportunity to investigate how the distribution and decomposition of litter in drylands responds to changes in monsoonal precipitation. Interestingly, our results indicate that manipulating monsoonal precipitation had a negligible effect on the overall amount of litter present (Fig. 12A). We observed consistent litter cover across most of the monsoonal precipitation treatments. However, ambient (0%) plots experienced significantly less litter than any other intra-annual monsoonal precipitation treatment. These results contrast with previous studies (Mayor et al., 2019; Rachal et al., 2015; Throop and Belnap, 2019) that have observed a relatively linear relationship between monsoonal precipitation and litter cover. We suspect this could be a result of monsoonal precipitation indirectly modifying the structural connectivity and litter decomposition rates (Barnes et al., 2012; Mureva and Ward, 2017). When monsoonal precipitation is above-ambient, increased PAWC promotes vegetative growth, which reduces the structural connectivity and inhibits the transport of litter. The increase in monsoonal precipitation also accelerates the decomposition rate of litter (Chuckran et al., 2020; Laskowski and Berg, 2006). Conversely, below-ambient monsoonal precipitation limits vegetative growth via diminished PAWC, increasing the structural connectivity and amplifying aeolian-driven transport. Furthermore, reducing PAWC inhibits vegetative growth and increases mortality, which promotes an increase in litter cover, while decreasing the rate of decomposition. These interactions could potentially explain the confounding effects intra-annual changes in monsoonal precipitation have on litter dynamics in drylands. Ambient monsoonal precipitation had significantly lower litter, which could be due to insufficient PAWC to support a sustained increase in vegetation and structural connectivity increasing enough to modulate litter dynamics. Thus, the distribution and decomposition of litter is critical for predicting how the C and N cycle in drylands will be affected by changes in monsoonal precipitation in the coming decades (Adair et al., 2017; Asner et al., 2003; Brazier et al., 2014; Dintwe and Okin, 2018).

Structural connectivity plays a critical role in shaping litter accumulation and transport patterns spatially (Keesstra et al., 2018; Rachal et al., 2015). The results from this study indicate that reducing the structural connectivity via ConMods is an effective tool capable of altering litter dynamics at the plant-interspace scale (Fig. 12B; Fig. 12C; Table 4). Reducing the local structural connectivity increases the soil surface stability due to increased litter accumulation, which decreases the susceptibility of top soil to aeolian-driven erosion and transport (Hewins et al., 2013; Throop and Archer, 2007). These processes create a positive feedback loop, where litter accumulation shields the surface soil from erosion, thereby reducing local connectivity, and further enhancing litter accumulation (Martınez-Yrızar et al., 1999; Throop and Belnap, 2019). This facilitates an increasingly homogenous distribution of litter, which is necessary for maintaining the soil nutrients in dryland environments (Collins, 2018; Luo et al., 2021; Throop and Belnap, 2019). The results support our initial hypothesis that reducing the structural connectivity will promote the accumulation and integration of litter into the soil matrix. These results affirm that the transport and accumulation of litter is not spatially static, and that structural connectivity has a significant effect on litter dynamics in drylands.

Monsoonal precipitation exhibited significant variability, ranging from 63 mm to 253 mm (Fig. 11). This variability offered a unique opportunity to explore how extreme inter-annual fluctuations in monsoonal precipitation influence litter dynamics. The initial year of the experiment (2021) recorded the highest monsoonal precipitation (231.23 mm) over the past six years (2018-2023; Supp. Fig. 10) and had the least amount of litter present. In 2022, monsoonal precipitation experienced an overall decrease (180.9 mm), but approached the long-term mean for our study site (176 mm). The overall litter in 2022 increased compared to 2021 (Fig. 12D). These results suggest that the above-average monsoonal precipitation and vegetative legacies from 2021, had a marked influenced on litter dynamics in 2022. In 2023, monsoonal precipitation decreased further, resulting in the least amount of monsoonal precipitation in six years (Supp. Fig. 2). The amount of litter in 2023 appeared to be buffered by the prior year's precipitation, as there was only a minor decrease in litter overall. This suggests that litter dynamics in drylands are impacted by the legacy effects of monsoonal precipitation (Bunting et al., 2017; Martinez-Vilalta and Pockman, 2002; Monger et al., 2015). Thus, providing critical insights into how litter dynamics will respond under future climate scenarios to increasingly stochastic monsoonal precipitation patterns.

This experiment also provided novel insights regarding the temporal effects from reducing the structural connectivity on litter distribution and decomposition in drylands. We observed minimal changes in the amount of litter present between structural connectivity treatments in 2021 and suspect this is a result of the above-average amount of monsoonal precipitation (Fig. 11; 12D). The overall amount of litter present was minimal and ConMods did not appear to be very effective. This is most likely due to an overall increase in PAWC increasing vegetative cover, which in turn reduces the structural connectivity, and inhibits litter transport and accumulation. However, in the proceeding years (2022 and 2023), plots with ConMods installed consistently experienced greater amounts of litter when compared to control. The difference in litter between connectivity treatments started to diverge in 2022, and experienced the largest difference in litter during the final year of the study. We suspect that this is due to ConMods being most effective at reducing the structural connectivity and modulating dryland litter dynamics when monsoonal precipitation approaches or is less than the long-term mean. The below-average monsoonal precipitation in 2023 reduced the PAWC, inhibiting vegetative growth, and increased mortality (Currier and Sala, 2022; Gherardi and Sala, 2015; Sala et al., 2012). This, in turn, led to an increase in structural connectivity and potential litter transport collecting in ConMods (Okin et al., 2015; Rachal et al., 2015; Throop and Belnap, 2019). Additionally, reducing the structural connectivity can inhibit the physiological breakdown of litter via aeolian driven transport (Barnes et al., 2012; Logan et al., 2022; Niu et al., 2023). This could result in litter experiencing decreased rates of physiological decomposition and abrasion, which could also explain the difference in litter we observed between structural connectivity treatments. Furthermore, reducing the structural connectivity appears to significantly enhance the effects from monsoonal precipitation legacies on litter accumulation. These findings support our second hypothesis that decreasing structural connectivity enhances litter accumulation and integration into the soil matrix when there is a drying legacy in the inter-annual monsoonal precipitation. Thus, underscoring the effectiveness and versatility provided by ConMods in modulating litter dynamics and distributions in dryland environments under increasingly variable climatic conditions (Collins, 2018; Mayor et al., 2019).

Intra-annual vegetative growth patterns in drylands are also likely to contribute to an increase in litter-soil mixing when ConMods are installed. Aboveground biomass generally increases throughout the monsoon season (June – Sept) before senescing in the fall (Oct – Dec); which is then followed by the spring (Feb – May) windy season. This vegetative growing cycle promotes an enhanced rate of soil-litter mixing over time within ConMods via aeolian-driven mixing (Peters et al., 2020; Wainwright et al., 2011a). This further supports our second hypothesis that reducing the structural connectivity during a drying legacy will amplify the integration of litter into the soil matrix from aeolian-driven mixing with previous year’s vegetation. Soil-litter mixing is one of the primary mechanisms through which we can manage C and N dynamics, nutrient cycling, and reduces the risk of soil erosion in dryland environments

(Chuckran et al., 2020; Delgado-Baquerizo et al., 2015; McBride et al., 2023). These novel insights are of critical importance in maintaining ecological resilience and ecosystem functions.

Microbial processes are one of the primary drivers of litter decomposition and plays a critical role in dryland litter dynamics (King et al., 2012; Liu et al., 2015; Throop and Belnap, 2019). Previous studies (Evans et al., 2020; Hewins and Throop, 2016) have identified PAWC as a primary driver of litter decomposition since increasing PAWC enhances microbial activity, which in turn accelerates the decomposition rate of litter in drylands (Lin et al., 2018; Qu et al., 2024). When monsoonal precipitation is below or approaching the long-term mean, microbial decomposition becomes inhibited due to the limited PAWC. However, ConMods enhance the accumulation of litter while minimizing the redistribution of litter and local soil nutrients. Thus, creating ideal micro-habitats that heighten the local PAWC and support enhanced microbial activity (Chuckran et al., 2020; Cleveland et al., 2014; Wang et al., 2015). Thus, the litter within ConMods is likely to experience an accelerated rate of decomposition compared to control plots due to the reduction in litter transport (Barnes et al., 2012; Gliksman et al., 2017; King et al., 2012). Increasing litter cover has been shown to enhance the PAWC locally, which is critical in facilitating litter decomposition, as PAWC is generally a limiting factor in drylands (Evans et al., 2020; Throop and Belnap, 2019). Additionally, the increase in litter cover helps reduce microbial organisms exposure to UV radiation, further enhancing decomposition rates by preserving these organisms and promoting sustained rates of decomposition (Barnes et al., 2015; Logan et al., 2022; Wang et al., 2015). This is a crucial benefit to reducing the structural connectivity via ConMods, as litter decomposition is a critical element of the C and N cycles in dryland environments (Chuckran et al., 2020; Hoyle et al., 2016; Plaza et al., 2018; Rachal et al., 2015). Furthermore, the sustained efficacy of ConMods in promoting the accumulation of litter over time will further enhance local soil-litter mixing, which is a critical source of soil nutrients in drylands (Joly et al., 2017; Yang et al., 2024).

Non-Photosynthetic Vegetation

We also explored how monsoonal precipitation and connectivity influence the distribution and decomposition of NPV in dryland environments. NPV dynamics are important environmental indicators in drylands of C storage (Hoyle et al., 2016; Lal, 2019), ecosystem function (Hill and Guerschman, 2022; Jackson and Prince, 2016), and potential fire regimes (Hély et al., 2019; Muñoz-Rojas et al., 2016). Our results indicate that NPV at the local plant-soil scale in drylands is influenced by connectivity, intra- and inter-annual changes in monsoonal precipitation, and the interaction between these processes (Table 5). The results from this experiment are consistent with previous studies (Cleveland et al., 2014; Hewins and Throop, 2016a; Rachal et al., 2015) that have investigated the influence that aeolian or hydrological changes have on the distribution of NPV in drylands. This study provides novel insights, as this is the first experiments to quantify the effects from both monsoonal precipitation and connectivity on the distribution of NPV in dryland environments. Thus, providing important insights regarding NPV's role in the C cycle and how it will respond under future climate scenarios.

Manipulating intra-annual monsoonal precipitation (-80%, …, +80%) allowed us to better understand how dryland vegetation dynamics might change under future climate scenarios. This study affirms that as intra-annual monsoonal precipitation increases there is a significant decrease in NPV regardless of the structural connectivity (Fig. 14A). These findings are consistent with previous studies that have investigated how dryland vegetation responds to changes in monsoonal precipitation, and identified a negative relationship between NPV and monsoonal precipitation (Currier and Sala, 2022; Gherardi and Sala, 2019; Zimmermann et al., 2008). This is likely due to an increase in PAWC when monsoonal precipitation is above-ambient, resulting in an overall increase in photosynthetic vegetation (PV), and corresponding decrease in NPV (Gherardi and Sala, 2019, 2015; Peters et al., 2020). The distribution and decomposition of NPV is critical for predicting how the C cycle will be modified in drylands, especially with increasingly stochastic monsoonal precipitation in the coming decades (Adair et al., 2017; Asner et al., 2003; Brazier et al., 2014; Dintwe and Okin, 2018).

We also observed that local reductions in structural connectivity resulted in an increase in the amount of NPV present (Fig. 14B; 14C) This affirms that ConMods facilitate a reduction in structural connectivity, which results in an overall increase in NPV. We suspect that this is a result of the ConMods protecting the NPV from abiotic mechanisms (e.g., aeolian processes and solar decomposition) that accelerate decomposition (King et al., 2012; Liu et al., 2015; Niu et al., 2023). Furthermore, it is likely that NPV itself contributed to a further reduction in structural connectivity and enhance soil stability, preventing the redistribution of nutrient rich topsoil and organic matter via aeolian or hydrological processes (Peters et al., 2020; Turnbull and Wainwright, 2019). Additionally, NPV plays an important role in dryland litter dynamics, in particular, decomposition (Barnes et al., 2015; Chuckran et al., 2020). Previous studies (Yang et al., 2024) have shown that NPV generally degrades quicker than surface litter, which can contribute to diminished C storage in drylands. Reductions in structural connectivity (ConMods) could help inhibit the decomposition of NPV, which may reduce the amount of C emitted during decomposition (Laskowski and Berg, 2006; McBride et al., 2023). Thus, ConMods may be an effective strategy to manage the C cycle in drylands under future climate scenarios.

These results also provide novel insights regarding the effects from inter-annual changes in monsoonal precipitation. The inter-annual patterns we observed during this study period with respect to NPV followed a similar pattern to litter; in that, it responded to preceding year's monsoonal precipitation and vegetation legacy (Fig. 14D). We also investigated how modifying structural connectivity interacted with inter-annual fluctuations in monsoonal precipitation influenced the distribution of NPV. When monsoonal precipitation exceeded the long-term mean (2021), we observed no real difference in NPV based on structural connectivity treatments due to the overall increase in vegetative growth (Fig. 14D). In 2022, monsoonal precipitation approached the long-term mean, and ConMods were the most effective at sustaining NPV. Vegetative growth is constrained by the limited PAWC, contributing to an increase in the overall structural connectivity of the landscape; and in turn, an increase in mortality from aeolian processes. Additionally, NPV is susceptible to abrasion via aeolian-driven sediment transport, that accelerates the physiological breakdown of NPV (Barnes et al., 2012; Logan et al., 2022; Niu et al., 2023). Thus, reducing structural connectivity through ConMods can help preserve NPV, and prevent further mortality in vegetative cover. This would also help counteract the positive feedback loop that results from reduced NPV increasing structural connectivity, and in turn the amount of bare soil; which exacerbate ecological shifts in drylands environments (Mayor et al., 2019; Turnbull and Wainwright, 2019). The least overall monsoonal precipitation during our study (2023) resulted in a significant decrease in NPV, as there were low vegetative growth and high structural connectivity. These results further bolster our second hypothesis, that a drying legacy will significantly enhance litter accumulation in drylands. Thus, improving our understanding regarding how future climate scenarios may affect dryland NPV and the terrestrial C cycle is of critical importance.

Bare Soil

This study also allowed us to quantify the effects of how changes in both monsoonal precipitation and connectivity alter the amount of bare soil present over time. Shifting vegetative patterns and increasingly stochastic monsoonal precipitation is predicted to result in an increase in bare soil throughout drylands globally (Bestelmeyer et al., 2018; Liang and Zhang, 2022; Okin et al., 2015). Our results found that connectivity, time (year), and the interaction between connectivity and monsoonal precipitation have a significant effect on the amount of bare soil present (Table 6). These findings are somewhat consistent with previous studies that have investigated the effect from changes in structural connectivity (Rachal et al., 2015; Throop and Belnap, 2019) and monsoonal precipitation (Gherardi and Sala, 2019, 2015; Throop et al., 2012).

There was not a significant difference in the amount of bare soil between the different monsoonal precipitation treatments (Fig. 15A). Previous studies have shown that monsoonal precipitation is one of the primary mechanisms responsible for modulating the amount of bare soil present (Feng and Fu, 2013; Liang and Zhang, 2022; Sala et al., 2012; Yakir and Morin, 2011). Our results suggest intra-annual precipitation doesn’t have a significant effect, but inter-annual precipitation (year) did have a significant effect modulating bare soil (Table 6). The results from this experiment also indicate that structural connectivity has a significant effect on the amount of bare soil present (Fig. 15B). We found that decreasing structural connectivity, decreased the amount of bare soil present compared to controls plots. Reaffirming the efficacy of ConMods in reducing the structural connectivity at the plant-interspace scale, which results in a decrease in bare soil via increased amounts of litter (Fig. 12B), NPV (Fig. 14B), and photosynthetic vegetation (Fig. 6A; Fig. 6B; Fig 6C). Reducing the amount of bare soil in drylands is of critical importance to minimize diminishing ecosystem function under future climate scenarios.

Our results also indicate that structural connectivity and monsoonal precipitation have a significant interaction. The difference between connectivity treatments in -50% and +80% were significantly greater than the other monsoonal precipitation treatments. Within plots that received -50% precipitation, it appears that the amount of bare soil is influenced by the amount of litter present; as we observed an inverse relationship between bare soil (Fig. 15C) and litter (Fig. 12C) cover based on connectivity treatments. When litter increased within the -50% plots with ConMods installed, we observed a corresponding decrease in the amount bare soil. In control plots receiving -50% precipitation, litter decreased and bare soil increased extensively. Since there was less litter, the effects of aeolian process was compounded, exposing the amount of bare soil momentously. Furthermore, plots with ConMods installed that received ambient or greater monsoonal precipitation had a consistent negative relationship between monsoonal precipitation and the amount of bare soil present (Fig. 15C). The patterns we observe within control plots that received ambient monsoonal precipitation or more are not as linear as the results within plots with ConMods, particularly at the +80% monsoonal precipitation treatment. This could be due to ecohydrological effects moving the litter and breaking down NPV, exposing the bare soil. These findings are supported by previous research (Mayor et al., 2019; Okin et al., 2015; Rachal et al., 2015) that has investigated the effects that changes in structural connectivity and ecohydrological mechanisms have on litter distribution and dynamics in drylands. The results affirm the effectiveness of ConMods in modulating the structural connectivity, lessening the ecohydrological effects, and contributing to a decrease in the overall amount of bare soil present. This study provides novel insights as to how manipulating structural connectivity in drylands can help inhibit an increase in bare soil, regardless of how monsoonal precipitation is altered under future climate scenarios.

Monsoonal precipitation experienced significant inter-annual variations allowing us to investigate how bare cover responds to significant shifts in overall monsoonal precipitation. Our findings are consistent with previous studies (Feng and Fu, 2013; Throop and Belnap, 2019; Yakir and Morin, 2011), that have identified a negative relationship between monsoonal precipitation and the amount of bare soil. This experiment also provided an opportunity to investigate the effects from modifying the structural connectivity, in conjunction with inter-annual variations, in the amount of bare soil (Fig. 15D). Our results show that when monsoonal precipitation exceeds the long-term mean, ConMods are not as effective in reducing bare soil; which is likely due to the overall increase in PAWC and vegetative cover. The increase in vegetative cover reduces the structural connectivity beyond the threshold at which ConMods are able to effectively reduce it. As a result, there was no significant difference between the amount of bare soil present based on connectivity treatments in 2021. When monsoonal precipitation approached or fell below the long-term mean, ConMods became an effective tool to further reduce the overall amount of bare cover in drylands. We suspect that this is due to insufficient PAWC, which cannot sustain enough vegetation to negate the effect from ConMods on bare soil. These results infer that if monsoonal precipitation decreases under future climate scenarios, ConMods would be an effective method to dampen the amount of exposed bare soil; while preventing the redistribution of soil nutrients, enhancing vegetative cover, and ecosystem productivity (Collins, 2018; Throop and Belnap, 2019). Understanding how changes in structural connectivity influence the amount of bare soil when there is below average precipitation (drought conditions) is of critical importance for conservation efforts, since climatic changes may alter the amount of bare soil and inevitably the C and N cycles in drylands (Fu et al., 2021; Lal, 2019; Luo et al., 2021).

Conclusions

This multi-year study highlights the complex interplay between monsoonal precipitation and structural connectivity in dryland environments, particularly regarding the distribution and decomposition of organic matter. Our findings reveal that structural connectivity and both intra- and inter-annual variations in monsoonal precipitation significantly influence litter dynamics and NPV. Reducing the structural connectivity of the landscape via ConMods proved effective in increasing litter and NPV accumulation, affirming their effectiveness at enhancing organic matter retention and accelerating litter decomposition in dryland environments (Collins, 2018; Okin et al., 2015; Wainwright et al., 2011). The effectiveness of ConMods became more pronounced over time in regards to litter, indicating their potential long-term benefits in maintaining soil stability and ecosystem function in drylands. This also indicates that artificial reductions in structural connectivity could help mitigate some of the effects that shifting vegetative patterns and climatic changes will have on dryland litter, and in turn terrestrial C cycles. Inter-annual variations in monsoonal precipitation had a more pronounced effect on the distribution and decomposition of litter and NPV relative to manipulating intra-annual monsoonal precipitation. Specifically, years when monsoonal precipitation exceeded or approached the long-term mean corresponded with reduced bare soil due to increased vegetative cover reducing the structural connectivity and enhancing the rate of organic matter decomposition. Conversely, years when monsoonal precipitation was below the long-term mean, bare soil exposure was exacerbated, which further enhanced aeolian-driven litter transport as a result of the general increase in structural connectivity (Peters et al., 2020). We also found that precipitation legacies, particularly drying legacies, resulted in a significant increase in the overall amount of litter present when the structural connectivity was reduced via ConMods.

These results provide a modest contribution to our understanding of the litter cycle, and highlights the importance of structural connectivity in establishing effective and sustainable dryland conservation or restoration projects. When we interpret our findings within the current literature (Chuckran et al., 2020; Day et al., 2019; Throop and Belnap, 2019), this study builds upon our understanding of these ecogeomorphic mechanisms modulating the distribution and decomposition of dryland organic matter. Particularly, our results quantify how aeolian-hydrological interactions modify the distribution of NPV and litter under shifting monsoonal precipitation patterns. These findings support our hypotheses that 1) decreasing structural connectivity enhances litter accumulation and integration into the soil matrix via aeolian-driven mixing, 2) especially when inter-annual changes in monsoonal precipitation results with the landscape experiencing a drying legacy.

Traditional litter decomposition and distribution models have underestimated both decomposition and accumulation rates, and fail to accurately capture the C and litter cycles in drylands (Dintwe and Okin, 2018; D’Odorico and Bhattachan, 2012; Van Auken, 2009). Thus, incorporating and understanding these dynamics is critical as drylands are projected to expand under future climate scenarios, potentially altering the important role they play in the terrestrial C and N cycles (de Graaff et al., 2014; Li et al., 2019). The insights from this study underscore the necessity of incorporating the unique mechanisms (structural connectivity and aeolian-driven mixing) in dryland environments into conventional litter decomposition and distribution models. Future research should continue exploring the ecological implications from these interactions over larger spatial and temporal scales in order to develop a more comprehensive and nuanced understanding of how these ecogeomorphic mechanisms will change under future climate scenarios.

Drylands are facing ecological challenges due to increasingly stochastic monsoonal precipitation, which exacerbate soil moisture deficits by modulating the structural connectivity (Collins, 2018; Okin et al., 2015; Rachal et al., 2015), and accelerate a shift in vegetative patterns (Duniway et al., 2010; Gherardi and Sala, 2015). The transition from grasslands to shrublands is exacerbated by climatic changes and anthropogenic activity, altering the litter cycle in drylands (Bestelmeyer et al., 2018; Caracciolo et al., 2016; Cleveland et al., 2014; Liu et al., 2015; Throop and Archer, 2009). Furthermore, drylands cover over 40% of Earth's surface and hold approximately 32% terrestrial carbon (Dintwe and Okin, 2018; Throop and Belnap, 2019), and are expected to expand by up to 23% globally under future climate scenarios (Feng and Fu, 2013; Huang et al., 2016). Thus, it is critical to understand how these changes will affect litter dynamics and, consequently, the broader C and N cycles over the coming decades in dryland environments.

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Chapter 3 Connectivity and Precipitation’s Influence on Dryland Soil Organic Matter

Abstract

In dryland ecosystems, the distribution and decomposition of organic matter are intricately linked to structural connectivity and monsoonal precipitation patterns. This study investigates the spatial distribution of organic matter and its decomposition rates across a gradient of monsoonal precipitation and modulations in structural connectivity in drylands. We employed a combination of field experiments and laboratory analyses to assess organic matter dynamics and their responses to aeolian and hydrological processes. Our results reveal that both connectivity and monsoonal precipitation significantly influence the spatial heterogeneity of organic matter distribution, with areas of low connectivity and moderate precipitation showing the greatest accumulation of soil organic matter. These findings underscore the importance of considering both climatic factors and landscape connectivity in understanding organic matter dynamics in drylands. This research provides critical insights for predicting how future climate scenarios will affect dryland ecosystems.

Introduction

Globally, dryland environments make up approximately 41% of the terrestrial surface area and are a critical component of the carbon cycle (Lal, 2019). Dryland environments are characterized by a soil moisture deficit (Duniway et al., 2010; Gherardi and Sala, 2015) and having an aridity index (the ratio of precipitation to potential evapotranspiration) less than 0.65 throughout most of the year (Bestelmeyer et al., 2015; D’Odorico et al., 2019). Historically, many of these environments have consisted primarily of perennial grasslands that have acted as a carbon (C) sink sequestering atmospheric carbon dioxide (CO_2). It is estimated that dryland environments contain more than 241 Pg (1 Pg = 10^{15} g) of soil organic carbon (SOC) (Lal, 2019) and accounts for almost one-third of global terrestrial SOC (Hanan et al., 2021). In addition, dryland environments contain more than 95% of the planet's soil inorganic carbon (SIC) via the formation of calcic horizons, that eventually develop into hardened layers of calcium carbonate (caliche) (Lal, 2019; Naorem et al., 2022). However, climatic changes and increasing anthropogenic activity over the last century have resulted in shifting vegetative patterns (shrub encroachment) across drylands globally (Cipriotti and Aguiar, 2012; D'Odorico et al., 2012; Eldridge et al., 2011). The transition from grasslands (C_4) to shrub duneland (C_3) reduces the overall vegetative cover, which modifies the ability of drylands to sequester atmospheric CO_2 (de Graaff et al., 2014). This has resulted in a large degree of uncertainty regarding future climate scenarios and their impact on C stocks in dryland environments (Throop et al., 2020). Therefore, it is necessary to improve upon our current understanding of how shifting vegetative patterns will influence SOM under future climate scenarios.

Shrub encroachment in drylands results in a heterogenous distribution of vegetation (Caracciolo et al., 2016a; D'Odorico et al., 2012). This vegetative shift alters litter production, local hydrology, vegetative architecture, as well as spatial and temporal vegetative patterns (Throop and Archer, 2007). It also changes the plant available water capacity (PAWC) of the soil, for there is a strong feedback between the vegetation composition and the hydrologic cycle in drylands (D'Odorico et al., 2007; Mayor et al., 2019). Additionally, shrub dunelands promote disparate abiotic processes in inter- and under-canopy regions, likely altering the distribution and stock of SOM (Hamerlynck et al., 2011; Throop and Archer, 2008). Shrub encroachment's impact on the distribution of SOM distribution under future climate scenarios remains unclear, since previous studies provide conflicting results (Throop et al., 2020). This is due to the contrasting effects and interactions that future climate scenarios will have on abiotic processes and vegetative growth in drylands (for example, decreasing precipitation reduces overall PAWC, hindering vegetative growth; while increasing atmospheric CO_2 will increase vegetative growth) (de Graaff et al., 2014; Tietjen et al., 2010).

In terrestrial environments, the C stock is primarily made up of SOC (Fu et al., 2021). The SOC stock in drylands is the balance between organic matter inputs (primarily through aeolian-driven mixing and belowground biomass (roots)) and losses (mainly due to the decomposition of organic matter, microbial respiration, and sediment transport (Brazier et al., 2014; Schulze and Freibauer, 2005)). These mechanisms regulate the soil organic matter (SOM), and in turn the SOC content in drylands; since they influence the quantity and quality of belowground biomass produced and determine its rate of decomposition in the soil (Plaza et al., 2018). The vegetative composition of the landscape also plays a significant role influencing the SOM in drylands (Mayor et al., 2019; Okin et al., 2015). Vegetative growth in drylands is limited by the high temperatures and lack of precipitation, which limits SOM production and increases the rate of decomposition (Martinez-Vilalta and Pockman, 2002; Wheeler et al., 2007). Despite relatively limited vegetative productivity in drylands, dryland vegetation has developed various traits (such as an increased root to shoot ratio and poor quality litter) that promote SOM in dryland environments (De Deyn et al., 2008; Qi et al., 2019). Since vegetation in drylands is characteristically limited in growth and cover, it is particularly susceptible to climatic changes and ecological disturbances (Bestelmeyer et al., 2015; Reynolds et al., 2007).

Precipitation is the primary factor influencing dryland vegetation, but there are additional abiotic mechanisms; such as fluvial, aeolian, edaphic, and geomorphic processes that also influence the distribution of vegetation (Li et al., 2008; Okin et al., 2018). There is an increasing body of work in the 21st century (Okin et al., 2015; Ravi et al., 2007; Shao, 2008; Wu et al.,

2018) investigating the direct and indirect role that aeolian processes have influencing vegetative patterns dryland environments. Aeolian-driven transport is an important force responsible for influencing vegetative patterns and SOM in drylands (Duniway et al., 2019; Fick et al., 2016; Throop and Belnap, 2019). This has supported integrating the concept of connectivity within an ecological framework to better explain how aeolian and hydrological transport influence the vegetative composition of dryland environments (Okin et al., 2009; Turnbull et al., 2008). Connectivity can be divided into *structural* and *functional* components to better understand its effect on dryland. *Structural connectivity* refers to the physical linkage of bare soil patches, facilitating material transport in areas with reduced vegetative cover (Mayor et al., 2019); while *functional connectivity* pertains to spatial connections arising from specific transport events (Uezu et al., 2005; With et al., 1997). Studies have highlighted the critical role of connectivity in shaping vegetative composition in drylands (Okin et al., 2015; Peters et al., 2020). As connectivity increases, it promotes shrub growth and recruitment, further enhancing the landscape's overall connectivity (Turnbull and Wainwright, 2019).

Aeolian-driven transport of organic matter occurs over short distances via surface creep and saltation (ballistic impacts across the soil surface), or longer distances if it becomes suspended in the air (Bullard and Baddock, 2019; Pähtz et al., 2020). However, the bulk of aeolian-driven transport is likely from surface creep, because of the necessary force required to entrain organic matter (Belnap et al., 2011). This results in aeolian processes playing an integral role in regards to the distribution of nutrients and SOM across dryland environments (Li et al., 2007; Schlesinger et al., 1995). When landscapes (such as perennial grasslands) experience an increase in vegetative heterogeneity (shrub encroachment), there is an increase in the amount of bare soil exposed (Gillette and Pitchford, 2004; Okin et al., 2009). This increase in bare soil intensifies the susceptibly of the soil surface to both aeolian and hydrological erosion, since these patches of bare soil begin to coalesce and create pathways that promote the redistribution of both SOM and SOC that is present in the top soil (Belnap et al., 2011; Hewins and Throop, 2016; Li et al., 2007). Once these particles become entrained, they tend to collect within shrub canopies, which results in an accumulation of sediment around the base of shrubs (Schlesinger et al., 1995). This redistribution of sediment, or the creation of "fertile islands", is problematic, as it is often irreversible and inhibits the establishment of vegetation within these inter-plant regions of bare soil (D'Odorico et al., 2012; Eldridge et al., 2011). The feedback loop can negatively impact SOM, as it can result in an increasingly heterogenous distribution of organic matter while increasing the overall amount of bare soil (Okin et al., 2015; Peters et al., 2020; Schlesinger et al., 1990). This can further inhibit the sequestration of SOM via aeolian-driven mixing while reinforcing a shift in the composition of dryland vegetation.

Previous studies that have investigated the effect of changing vegetative patterns on SOM in drylands have primary consisted of in situ experiments spanning either precipitation or vegetation gradients (Hoyle et al., 2016; Li et al., 2019, 2016; Throop et al., 2020; Throop and Archer, 2007). However, these studies focus on larger scales spatially (from landscape to regional levels) and have relatively limited temporal resolution. Furthermore, prior studies have focused on quantifying the change in SOM from grasslands to shrub-dunelands (Li et al., 2019; Throop et al., 2020; Throop and Archer, 2007), or agricultural crops (Plaza-Bonilla et al., 2015; Wang et al., 2023; Zhuo et al., 2022). This has resulted in a relatively limited understanding of how SOM changes at the inter-plant scale and within grass-shrub-duneland ecotones. There remains a gap in the current literature regarding the effects that changes in monsoonal precipitation will have on SOM in the southwestern U.S.; as well as quantifying the influence from local changes in structural connectivity on SOM, which will further clarify vegetation-soil feedbacks in drylands and their role in the terrestrial C cycle.

In this study, we aim to assess the effects that changes in connectivity and monsoonal precipitation will have on SOM in shrub dominated dryland environments. We hypothesize that (1) reducing the connectivity will increase the deposition of organic matter and sediment locally, creating ideal micro-climates within bare inter-plant regions where microbial decomposition can increase overall SOM. Moreover, (2) reducing structural connectivity will be most effective at increasing SOM locally as monsoonal precipitation increases. Finally, (3) multi-year periods of below-ambient monsoonal precipitation will reduce SOM via diminished belowground primary productivity and microbial activity due to the limited PAWC. Our novel approach to examining the interaction of perennial grass cover, connectivity, and monsoonal precipitation will help address current inconsistencies and improve predictions of SOM dynamics in dryland ecosystems under future climate scenarios.

Methods

Study Area

This experiment was conducted within the Chihuahuan Desert at the Jornada Basin Long-Term Ecological Research (LTER) site (32.5°N, 106.8°W, and 1,188 m above sea level), which is located in southern New Mexico, United States. The long-term mean annual precipitation at the Jornada LTER is 247 mm, while the long-term mean monsoonal (growing season) precipitation is 176 mm (Gherardi and Sala, 2015). The average monthly temperatures range from 6 °C in January to 26 °C in June. Current grazing intensities are maintained at low levels throughout the 200,000-ha research site. Locations selected for soil sample collection have not been grazed by livestock since the late 20th century. This study takes place across a vegetation gradient, spanning playa grasslands to shrub-dunelands. These environments are dominated primarily by *Bouteloua eriopoda*, *Sporobolus flexuosus*, and *Aristida purpurea* perennial grasses (C_4), that are experiencing encroachment from an expansion of the perennial shrub *Prosopis glandulosa* (C_3).

Experimental Design

The experiment was established in May of 2020, consists of 56 plots that are 2.5 m wide and 5 m long and spread across an area that is approximately 13 hectares. All the plots in this experiment were located perpendicular to the prevailing wind (Fig. 1) in a sandy, mesquite-dominated shrubland with varying levels of perennial grass cover. No shrubs were present within any of the plots, at the time of plot selection and when the experiment began. In the initial plot selection phase, 90 plots were selected, and line-intercept (LI) measurements were conducted within each plot to determine the preliminary vegetation cover. These results were used to identify the interquartile range and the 30 least similar plots from the study were removed. The remaining 60 plots were randomly assigned one of five precipitation regiments: -80%, -50%, 0%,

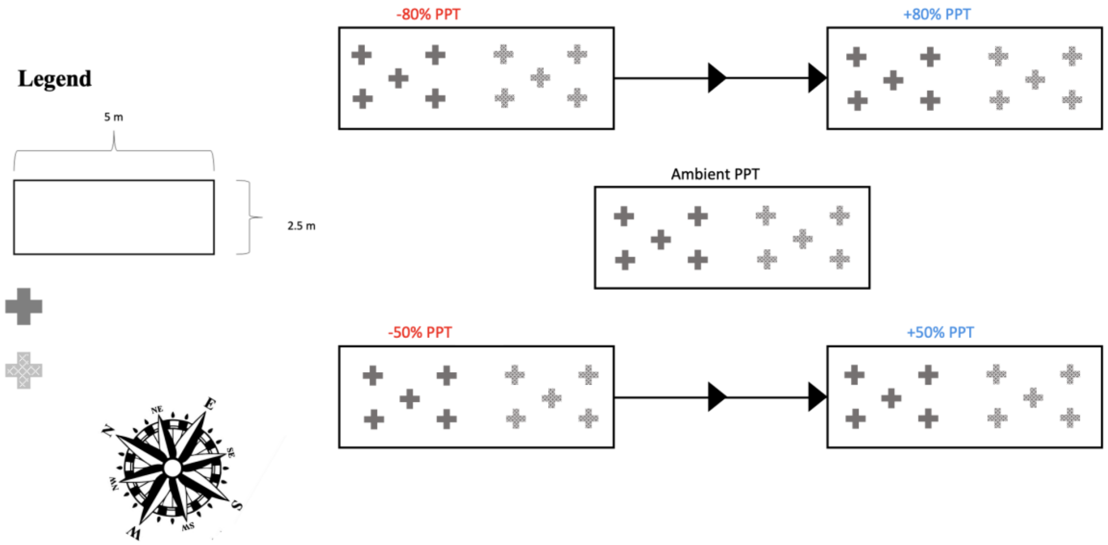

Figure 16. The experimental design and layout of the precipitation (-80%, -50%, 0%, +50%, +80%) and connectivity (ConMod and Control) treatments for this study.

+50%, or +80%. During our analysis we also identified two pairs of irrigated (+80%) and drought plots (-80%) with vegetative patters that were outliers in comparison to the remaining 56 plots, and as a result they were omitted from this study.

To modify the precipitation regimes at the plot level, automated rainfall manipulation systems (ARMS) were deployed (Gherardi and Sala, 2013; Reichmann et al., 2013). This provides an opportunity to investigate the influence that varying levels of monsoonal precipitation could have on SOM. Precipitation is captured with a rainout structure, which consists of shingles that are spaced at varying intervals to intercept incoming precipitation (reducing precipitation by 50% or 80%). The shingles consist of acrylic (Piedmont Plastics, LaMirada, California) that is heated with a ceramic heater and bent at a 120° angle. The material is transparent to minimize any influence it may have on temperature or incoming solar radiation (Gherardi and Sala, 2013). Once the precipitation is intercepted, a drainage system redirects the precipitation in real-time to a 27-gallon plastic storage tank (EDGE Plastics, Mansfield, Ohio). Once the water reaches the storage tank, there is a float switch (Atwood Marine Automatic, Lowell, Michigan) that turns on a water pump (TruePower 12 V DC Marine Utility Pump, Simi Valley, California) when the water level increases. The water is then sent out to the corresponding irrigation plot through 12.7 mm (1/2”) PVC pipes. The ARMS design (Gherardi and Sala, 2013) allows irrigated plots to receive precipitation levels that are 50% and 80% above the ambient monsoonal precipitation with six sprinkler heads (Rain Bird 4-Van Sprinkler Spray Nozzle, Azusa, California), which were placed evenly around the perimeter of the plots (3 on each side). This resulted in a precipitation gradient with four treatments: -80%, -50%, +50%, and +80%. (Fig. 16). ARMS were not installed on plots that received ambient (±0%) monsoonal precipitation. The experimental setup ensures that only the magnitude of precipitation events is manipulated, and not the frequency of precipitation events.

Each individual ARMS system was inspected and calibrated before each monsoon season begins to ensure there are no leaks, and that the water is evenly applied or diverted consistently within each plot. Once the ARMS have been deployed for the monsoon season, they were maintained and regularly checked to ensure they are functioning correctly. The experiment was maintained throughout the monsoon season until late October, because freezing temperatures will damage the equipment. The overwintering process consisted of draining the irrigation system at least 3 m from any plots to ensure the deposited water could have no effect on the drought or irrigation treatments. The drought shelters remained in place throughout winter.

One of the primary objectives of this study was to alter the connectivity of the landscape with respect to aeolian and hydrological transport (Okin et al., 2018). Rachal et al. (2015) showed that ConMods are effective at decreasing the local connectivity and increasing the rate of organic matter deposition within the ConMod structure. Fick et al. (2016) and Peters et al. (2020) have shown this accumulation of organic material promotes the germination and establishment of native vegetation in drylands via the creation of ideal microhabitats. Vegetative recruitment will contribute to an increase in above ground biomass and litter production, while also increasing the SOM through increased belowground biomass (González-Megías and Menéndez, 2012; Hanan et al., 2021). Therefore, we decided that installing ConMods would be the most effective method of reducing the structural connectivity locally and collecting organic matter/seeds that promote the accumulation and sequestration of SOM.

Each of the 56 plots was divided in half (2.5 m x 2.5 m) and one side was randomly assigned to the ConMod treatment, while the other side receives the control treatment. A

ConMod consists of 0.63 (1/4”) mm galvanized hardware cloth that is connected to five 0.63 mm (1/4”) diameter reinforced steel stakes. Once the ConMods are installed, they are 20 cm tall and 55 cm in both width and length. ConMod placement consists of one stake that is placed in the center, while the four remaining stakes are placed equal distances from the center stake. The resulting structure takes the shape of the symbol for addition (+). The control (without ConMod) treatments consist of one 0.63 mm (1/4”) diameter reinforced steel stake that is installed and mirrors the location of the center stake in the ConMod. Additionally, both the ConMod and control treatments were installed in a staggered formation, which were centered within each 2.5 m x 2.5 m sub-plot (Fig. 16).

Data Collection and Measurements

The primary datasets used in this analysis were peak biomass coverline data (2020 – 2023), local precipitation (2020 – 2023), and SOM content. The coverlines we installed consisted of four 250-cm transects (located 110, 220, 330, and 440 cm from the edge of the plots) parallel to the prevailing wind such that two transects spanned each of the connectivity treatments (ConMod & control) (Fig. 16). The transects were used as a non-destructive method to measure annual vegetation cover; as an alternative to collecting the data via destructive harvesting of vegetation. The line-intercept transects were recorded at the end of the monsoon season (mid-September), when vegetation in the Chihuahuan Desert typically reaches peak vegetative biomass (Havstad et al., 2006; Xia et al., 2010). Vegetation along each transect is recorded at 1-cm resolution. In order to quantify the annual net primary productivity (ANPP) (g m^{-2} yr^{-1}), we used a series of allometric equations developed by (Flombaum and Sala, 2007)) and calibrated for our study site (Gherardi and Sala, 2015; Reichmann et al., 2013).

To measure vegetation cover along the transects we used the line-intercept method, which recorded the distance spanned along the transect when a plant was photosynthetically (PV) active and identified the species (e.g. *Bouteloua eriopoda* 34 – 42 cm). The methods that we deployed for our data collection are modeled on similar methods developed in previous studies at the Jornada LTER (Gherardi and Sala, 2015; Reichmann et al., 2013; Sala et al., 2012). The data were collected over the course of two days, to prevent any shifting vegetative physiological patterns from influencing vegetation, litter, and NPV cover.

Precipitation data was obtained from the closest meteorological station (< 1 mile), which uses an automatic tipping bucket rain gauge and is maintained by the Jornada LTER. In order to calculate the monsoonal precipitation at each treatment, we followed the methods that Huang et al. (2022) applied in their analysis of monsoonal precipitation throughout the southwestern U.S. We demarcate the onset of the North American monsoon season (NAMS) as the first three consecutive days of precipitation that exceeded 0.5 mm day^{-1} after July 1st, and is based on the framework developed in Higgins et al. (1999). The cutoff for the NAMS was September 30th, since climatic conditions in October inhibit vegetative growth regardless of precipitation.

We collected soil surface (depth: 1-4 mm) samples (~15 - 30 g) from each ConMod or control structure within each plot at the end of the monsoon season in 2019 (when the ConMods were installed) and 2023. The samples were collected from the central rebar within the ConMods and control rebars, when the soil was dry. If photosynthetically active vegetation was in the center of the ConMod, we collected the soil surface sample as close to the central rebar as possible without disturbing the vegetation. The samples were stored in a cool temperature-controlled environment until they were transported and processed in a soil lab. The methods that we used in this analysis to quantify the temporal changes in SOM are based on the previously developed methods of Zhang and Wang (2014). This method was developed in southeastern Texas and quantifies the SOM content of a soil sample via oxidation, which converts organic matter to CO_2 when placed in a furnace at an elevated temperature (360° C).

First, we weighed the empty crucibles and recorded their weight. Next, we split the soil sample collected from each ConMod/control center rebar into a one-gram sub-sample using a Jones Micro-Splitter (Los Angeles, CA). This ensured that each sub-sample was unbiased and representative of the overall soil sample. We then composited the five sub-samples from each plots' connectivity treatments (ConMod or control) to investigate the changes in organic matter at the plot level. Once the samples were composited, they were placed in a crucible of known weight and placed in a drying oven (Fischer Scientific, Waltham MA) at 105° C for 150 minutes to remove any remaining hygroscopic water. The crucibles were then removed from the drying oven, and the weight was recorded. Then, they were placed in a Thermolyne™ benchtop muffle furnace (Fischer Scientific, Waltham MA) at 360° C for another 150 minutes. Crucibles were then transferred to a desiccator until cool enough to weigh after loss on ignition. SOM content of the soil was obtained using:

$$Eq.1 \qquad OM\% = \frac{Crucible \,\&\, Soil (Pre.Combustion) - Crucible \,\&\, Soil\ (Post.Combustion)}{Crucible \,\&\, Soil (Pre.Combustion) - Crucible\ (Empty)} \times 100$$

that will quantify the percent of organic matter in the soil. In this analysis, we use an analytical balance (Fischer Scientific, Waltham MA) with a resolution of 1 mg, which results in a sample sensitivity of 0.02% to changes in SOM.

Results

Abiotic Mechanisms

The long-term average monsoonal precipitation at our study site is approximately 176 mm (Currier and Sala, 2022; Throop et al., 2012). However, throughout the duration of the study period (2020 – 2023), annual monsoonal precipitation was both above and below average. There were dry conditions in 2020 and 2023, which resulted in monsoonal precipitation amounts that were 53% (83.31 mm) and 74% (63.51 mm) lower than the long-term average, respectively. In contrast, 2021 and 2022 monsoonal precipitation was 44% (253.23 mm) and 3% (180.86 mm) greater than the long-term average, respectively (Fig. 17). The lack of monsoonal precipitation in 2020 and 2023 resulted in minimal differences (<130 mm) between the drought (-80%) and irrigation (+80%) treatments in 2020 and 2023, relative to the differences (> 290 mm) between precipitation treatments in 2021 and 2022. We found no statistical difference (P<0.05) in SOM content between the connectivity treatments in 2019. We used an analysis of variance (ANOVA) model (Table 7) to assess the effects of connectivity and precipitation on the change in SOM ($\text{SOM}_{2023} – \text{SOM}_{2019}$). We observed a statistically significant (at 95%) increase from 2019 to 2023 of approximately 75% in SOM in plots that had ConMods installed. In contrast, plots that had control points installed experienced a net decrease of almost 25% in SOM (Fig. 18A). The precipitation manipulation treatments did not have a

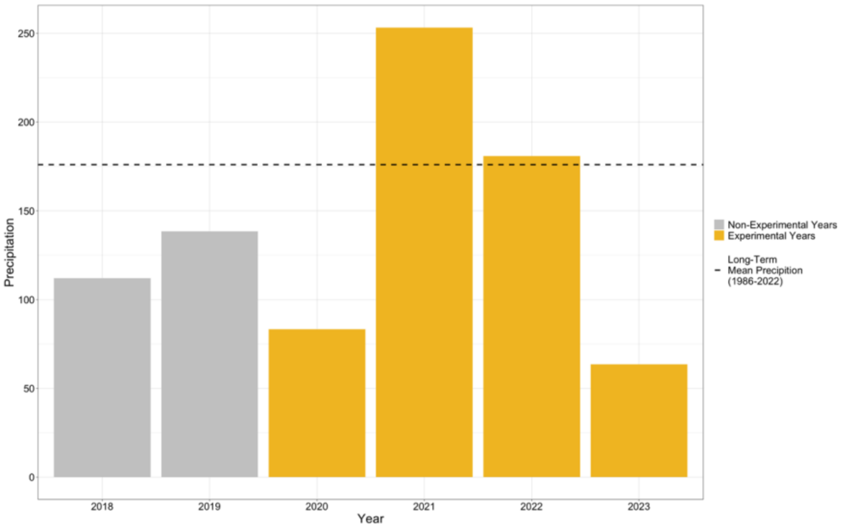

Figure 17. Monsoonal precipitation (mm) patterns at our study over the last five years (2018 – 2023). The grey bars are years prior to the deployment of the experiment, and the gold bars indicate the years that the experiment was operational. The long-term mean (1915 – 2022) monsoonal precipitation (176 mm) of the study site is included as a dashed line.

SOM (2023 – 2019) ANOVA

Independent Variables	Num D.F.	Dem D.F.	F Value	P-Value
Precipitation Treatment (-80%...+80%)	4	51	1.04	0.395
Connectivity Treatment (ConMod)	1	51	14.39	**0.0004**
*Precipitation*Connectivity Treatment*	4	51	1.86	0.1325

Table 5. The repeated measures analysis of variance (ANOVA) SOM model results for the independent variables: connectivity treatment, precipitation, and the interactions between them. Bold values are significant with an $\alpha = 0.05$.

SOM (2023 – 2019) T-Test

Independent Variables	Estimate	Std. Er.	DF	t-value	p-value
ConMod	0.218	0.054	101	4.05	**0.0001**
Control	-0.057	0.054	101	-1.06	0.290
-80%	-0.013	0.094	51	-0.13	0.893
-50%	0.050	0.086	51	0.58	0.565
0%	0.046	0.086	51	0.54	0.595
+50%	0.225	0.086	51	2.64	**0.011**
+80%	0.093	0.094	51	0.99	0.326
ConMod-80%*	0.020	0.127	101	0.16	0.876
ConMod-50%*	0.120	0.116	101	0.95	0.345
*ConMod*0%*	0.166	0.116	101	1.43	0.155
ConMod+50%*	0.533	0.116	101	4.61	**<0.0001**
ConMod+80%*	0.260	0.127	101	2.05	**0.043**
Control-80%*	-0.045	0.127	101	-0.36	0.723
Control-50%*	-0.011	0.116	101	-0.09	0.927
*Control*0%*	-0.074	0.116	101	-0.64	0.522
Control+50%*	-0.082	0.116	101	-0.71	0.479
Control+80%*	0.074	0.127	101	-0.58	0.561

Table 6. Two degrees of freedom test using a t-statistic to test if the least squares mean is significantly different ($\alpha = 0.05$) from zero, results for the independent variables: connectivity, precipitation, and the interactions between them.

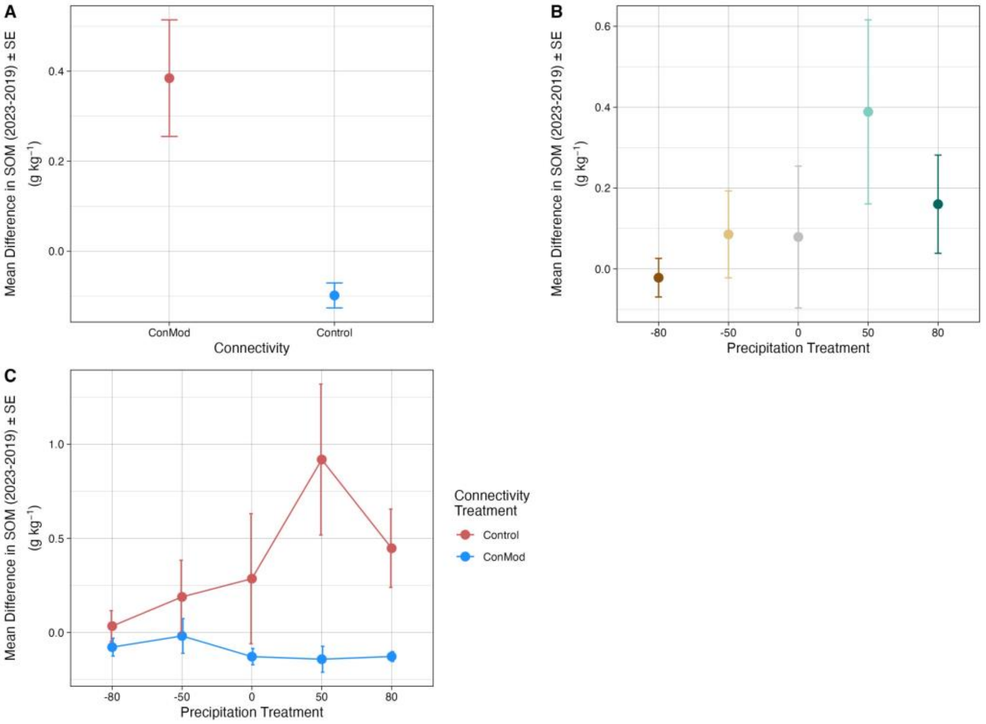

Figure 18. Main effect of modifying precipitation **(A)** and structural connectivity **(B)** on the mean (± SEM) difference (2023 – 2019) in SOM. The interaction **(C)** between structural connectivity and monsoonal precipitation on the mean (± SEM) difference (2023 – 2019) in SOM. Different letters indicate significant differences between treatments based on a repeated measures analysis of covariance (ANCOVA) model with an α = 0.05.

significant influence on SOM but do appear to have an indirect influence (Fig. 18B). Although, the interaction between connectivity and precipitation treatment wasn't statistically significant, we performed a t-test since the interaction p-value was approaching significance (~0.1). We identified structural connectivity had a significant effect on the SOM content within plots that received above-ambient precipitation and a reduction in structural connectivity via ConMods (Table 8). Plots experiencing a reduction in structural connectivity along with above-ambient monsoonal precipitation on average experienced a net increase in SOM of at least 50%, with some plots experiencing an increase of more than 100% (Fig. 18C). Thus, plots that received above-ambient precipitation and had ConMods installed resulted in the greatest overall increase in SOM during this experiment (2019 – 2023). During the study period, we also collected imagery during peak biomass in early September to qualitatively assess the efficacy modifying connectivity has on the distribution and accumulation of litter (Fig. 19). The imagery makes it evident, that plots with ConMods installed experienced different litter-soil dynamics when compared to control plots. There was a greater accumulation and more homogenous distribution of litter within plots that had ConMods installed. Contrastingly, the plots with control treatments had larger amounts of bare soil present, that were also more connected. We also observed an increase in overall vegetation in plots with ConMods, which helps to further reduce the local connectivity.

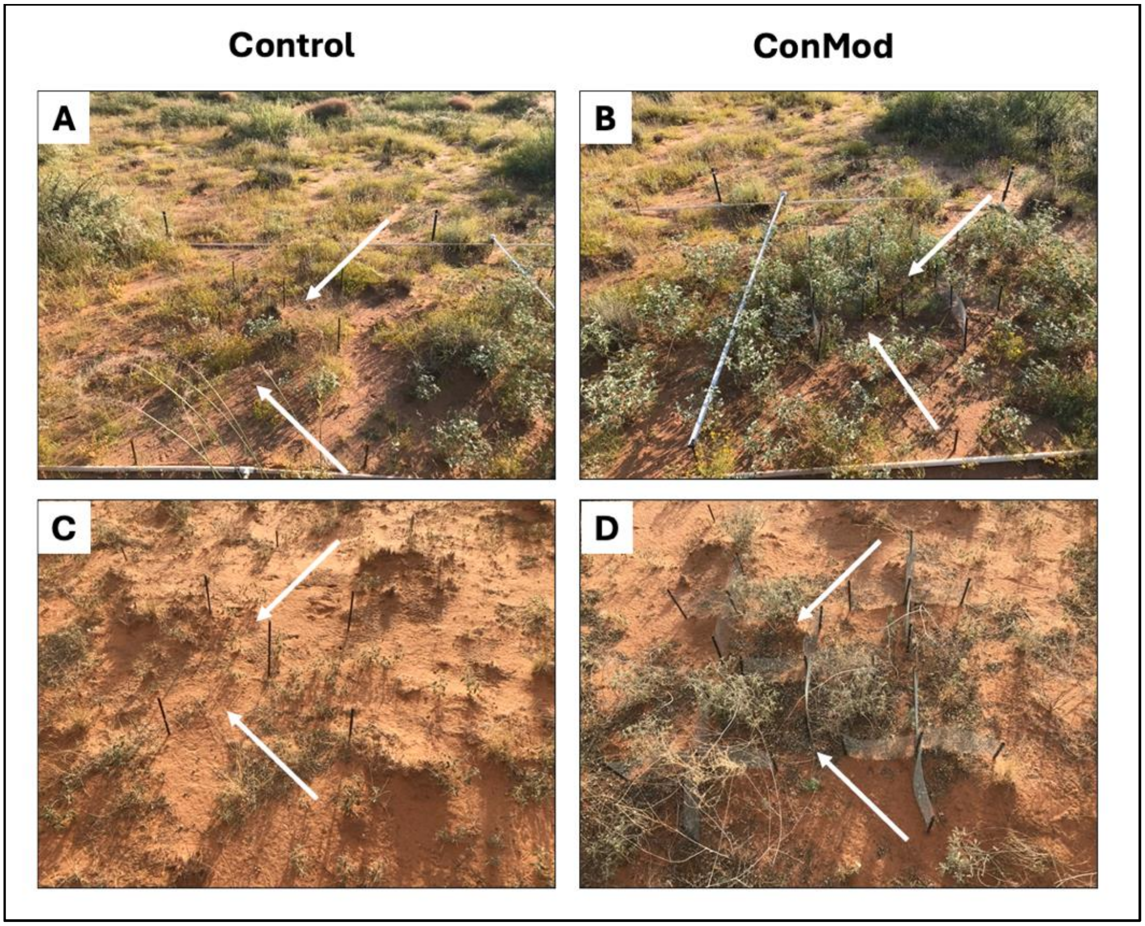

Figure 19. Impact from modifying the local connectivity on litter accumulation and distribution (arrows) grass-shrub duneland (Chihuahuan Desert, JLTER; Fig.1 contains configuration details). Litter distribution in an above-ambient monsoonal precipitation (+80%) plot's control **(A)** and ConMod **(B)** treatments. The effect of control **(C)** and ConMod **(D)** connectivity treatments in a plot receiving below-ambient monsoonal precipitation (-80%). Note: ¼" rebar for scale (Photos: M.R. Fischella).

Biotic Mechanisms

In addition, this study provided an opportunity to investigate the influence that vegetative change, coupled with connectivity and precipitation, has on SOM content. In our linear mixed model, we used the change in vegetative ANPP ($ANPP_{2023}$ - $ANPP_{2020}$) at the functional group levels (grass, forb, and shrub). The results show there is not a strong correlation between changes in perennial grass ANPP and SOM throughout the connectivity and precipitation treatments (Fig. 20A). Generally, we observed the greatest increase in SOM occurring in plots that experienced the least amount of change in perennial grass ANPP (negative relationship). The connectivity pattern is similar to the overall trend we observed in SOM, especially in ambient and above precipitation treatments. The results for the change in forb ANPP also showed that there was not

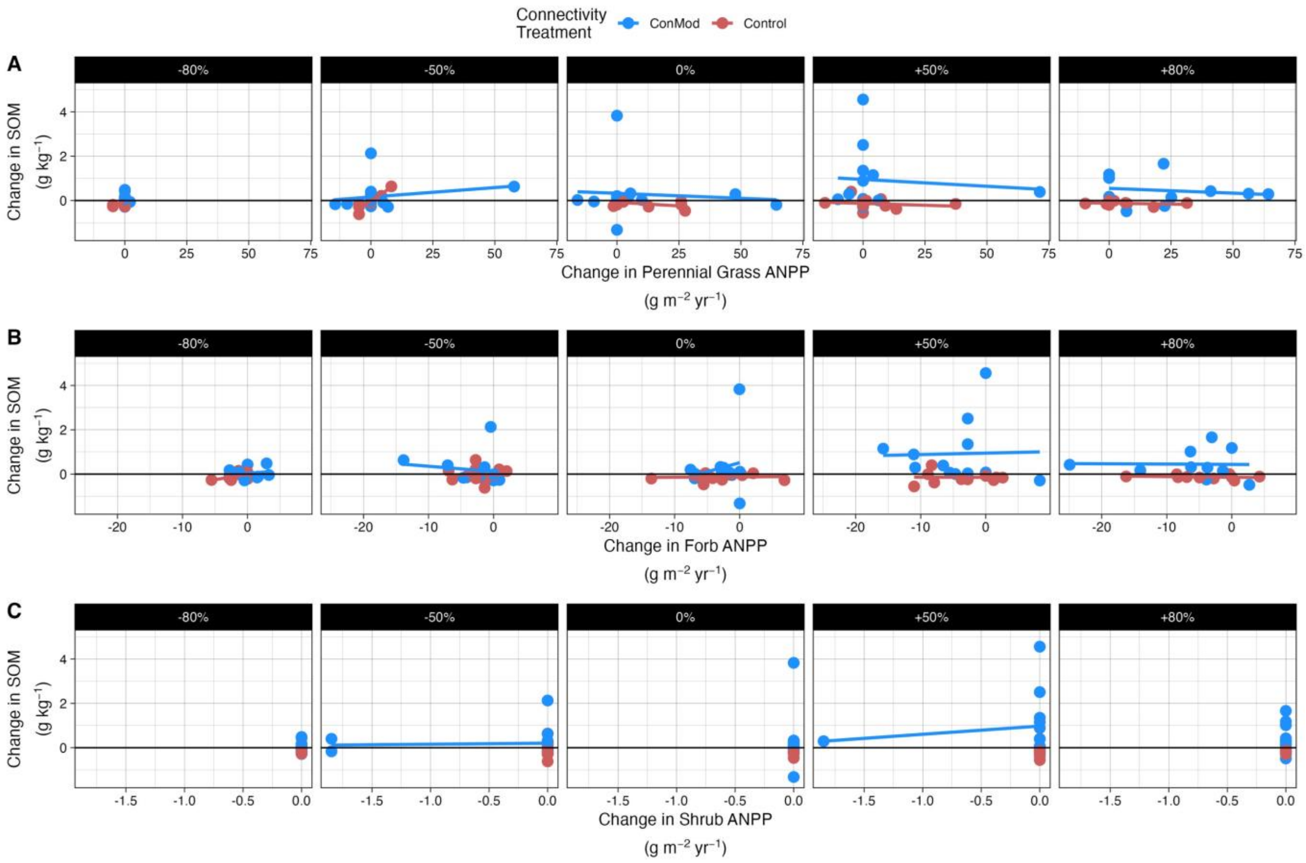

Figure 20. The effects of modifying connectivity, precipitation treatments, and the mean (± SEM) change in vegetative ANPP on mean (± SEM) SOM ($g\ m^{-2}\ year^{-1}$). Vegetation classes are based on the following plant functional types **(A)** perennial grass, **(B)** forbs, and **(C)** shrubs.

a significant relationship with SOM throughout the connectivity and precipitation treatments. However, we do see that there is an overall weak positive relationship between increasing forb ANPP and increased SOM. Our results also indicate that change in forb ANPP was greatest in plots with ConMods installed. We also analyzed the effect that change in shrub ANPP had on SOM across the treatments, but the results were difficult to interpret; primarily due to the limited amount of shrub data. Although, the results are not statistically significant ($P > 0.05$), we do see a very weak positive relationship exists between change in shrub ANPP and SOM in ConMods. Interestingly, the change in shrub ANPP did not result in a net increase in SOM, but rather prevented it from being depleted any further. The lack of an observed effect from the change in shrub ANPP on SOM for the precipitation treatments (-80%, 0%, and +80%) and control plots is potentially a result of the limited sample size of shrubs for this analysis.

Discussion

Abiotic Mechanisms

The results of this experiment demonstrate the critical role that connectivity has in influencing SOM dynamics in dryland environments. The findings from previous research (Okin et al., 2015; Rachal et al., 2015) quantifying the effect from connectivity on the distribution and accumulation of litter and sediment are consistent with the results of this experiment. This study also indicates, that under future climate scenarios, connectivity has the potential to increase or decrease the overall rate of dryland SOM sequestration. The significant ($P<0.005$) increase (~ 75%) of SOM in plots with ConMods installed and net decrease (~ 25%) in control plots, resulted in a net change of approximately 100% in SOM over the course of this experiment. Although Rachal et al. (2015) nor Okin et al. (2015) quantified changes in SOM, their results affirm the effectiveness of ConMods in reducing the local connectivity, but underscores its potential role regarding SOM in dryland environments. Furthermore, connectivity in drylands is projected to increase under future climate scenarios (Duniway et al., 2019; Gherardi and Sala, 2015; Li et al., 2016), and will likely promote an overall decrease in SOM sequestration in drylands.

This study provided an opportunity to investigate the effect that variations in monsoonal precipitation had on SOM as well. Throughout the study period, monsoonal precipitation displayed a high degree of stochasticity during the duration of the experiment (63 mm – 253 mm; Fig. 17). Our results indicate that monsoonal precipitation did not independently have a significant influence on SOM (Fig. 18B); which was surprising, as previous studies (Hewins and Throop, 2016; Throop and Archer, 2007) have identified precipitation as one of the key drivers of SOM in dryland environments. This could be due to the relatively limited temporal resolution (2020 and 2024), and stochastic monsoonal precipitation patterns over the course of the study (Fig. 17).

This is also the first study to investigate how the interaction between connectivity and monsoonal precipitation influences SOM. The results show that connectivity and monsoonal precipitation have an influence on SOM. We observed an increase in SOM across all the monsoonal precipitation treatments that had ConMods installed (Fig. 18C). Plots with control treatments experienced a decrease in SOM throughout all the monsoonal precipitation treatments. In our ANOVA analysis, we were unable to identify a significant influence from the interaction between connectivity and monsoonal precipitation (Table 7; Fig. 18C). However, we also applied an t-test to determine whether the various connectivity and precipitation interactions resulted in a significant change from zero in SOM (Table 8). The results indicated that there was a significant increase in SOM within plots that had ConMods and received above-ambient monsoonal precipitation (+50% and +80%). However, it remains somewhat unclear as to why there was such a significant increase in SOM in plots with ConMods that received +50% precipitation relative to plots with ConMods that received +80% of monsoonal precipitation.

One potential explanation for this discrepancy in SOM, is a potential increase in microbial activity. It has been shown that increasing monsoonal precipitation in drylands corresponds to an increases in microbial activity, which could in turn accelerate the decomposition of litter and increase the overall amount of microbial respiration (Barnes et al., 2012; Cleveland et al., 2014; Maestre et al., 2015). Thus, plots that received +80% monsoonal precipitation might have experienced a greater loss on SOM via microbial respiration, relative to plots receiving +50% monsoonal precipitation. This could explain in part the rather limited increase in SOM observed between plots that received +50% and +80% monsoonal precipitation. Furthermore, the additional monsoonal precipitation in +80% treatments could result in the soil exceeding its field capacity and accelerating fluvial erosion, which has also been shown to accelerate the loss of SOM (Brazier et al., 2014). Overall, the results of this analysis are in general agreement with previous studies (Boeken and Orenstein, 2001; Luo et al., 2021; Zhuo et al., 2022) that have investigated the effects abiotic mechanisms have on litter decomposition and SOM in drylands.

Biotic Mechanisms

The experimental design of this study also provided an opportunity to examine the influence that biotic mechanisms have on SOM in drylands. We investigated the influence that vegetative (grass, forb, and shrub) ANPP, connectivity, and precipitation treatments had on SOM. The influence of vegetation on SOM appears somewhat obfuscated and lacking any significant trends (Fig. 20A; 20B; 20C). When we look at the effect of perennial grass ANPP on SOM, the regression lines are parallel, regardless of the connectivity treatment. The y-intercept for the

ConMod treatment was consistently greater in comparison with the control treatment, which indicates that there was a net increase in SOM within plots with ConMods compared to the control plots (where there was a slight net decrease in SOM). The results also suggest that as perennial grass ANPP increases, there is not a corresponding increase (negative relationship) in SOM in ambient and above precipitation treatments for both ConMods and control. We suspect this could be in part explained by the distribution and physiology of perennial grasses, as well as vegetative competition for available soil resources. Established perennial grasses are less likely to experience significant competition or encroachment from neighboring vegetation during the study period, due to the absence of shrubs within these plots (Pierce et al., 2019). The lack of competition allows established perennial grasses to focus on allocating C on belowground biomass, rather than aboveground biomass (McGlone et al., 2012). This enhances their ability to uptake soil nutrients and access the soil's overall PAWC (Holguin et al., 2022). Furthermore, during periods of below-ambient monsoonal precipitation, perennial grasses focus on reallocating the available C from aboveground to belowground biomass. That way, they can increase the likelihood of surviving extended periods of below-ambient monsoonal precipitation (droughts) (Meng et al., 2022; Poorter et al., 2012).

New perennial grass recruits, in general, need to allocate a greater proportion of available C towards aboveground biomass; so they can maintain photosynthetically active and compete with neighboring vegetative seedlings (Holdaway et al., 2014; Pierce et al., 2019). Furthermore, perennial grass recruits are less effective at reducing the local connectivity than established perennial grasses. This increases their vulnerability to physiological damage from aeolian sediment transport; and in turn, limits the local accumulation of litter and microbial activity (Barnes et al., 2012; Niu et al., 2023; Peters et al., 2020). This could also explain why we observed a minimal increase in SOM within plots that experienced the greatest overall increase in perennial grass ANPP. It also suggests that the ability of perennial grasses to increase SOM depends on their current demographic stage, as well-established patches of perennial grass are more likely to contribute to SOM than perennial grass recruits (Bosco et al., 2018; Zuo et al., 2018). These results further emphasize the importance in preserving established perennial grasses, since they have a disproportionate impact on the C cycle; as perennial grass recruits experience a temporal lag before contributing to SOM in drylands.

Additionally, we explored the effect that forb ANPP, connectivity, and monsoonal precipitation have on SOM (Fig. 20B). The results presented similar connectivity patterns to perennial grass ANPP; for the regression lines of ConMod and control were relatively parallel, with the y-intercept for the ConMod treatment being greater than the control treatment. Intriguingly, we observed a general positive relationship; such that, when forb ANPP increases, there is also an increase in SOM. It also appears that the relationship between forb ANPP and SOM best reflects the distribution of SOM across the precipitation and connectivity treatments in this study (greatest gain in SOM in ConMods with above-ambient precipitation). Despite a relatively limited amount of literature investigating the influence that forb ANPP has on SOM in drylands, previous research has shown increasing vegetative cover and decreasing bare soil, promote an increase of SOM (Blanco-Canqui et al., 2013; Simon et al., 2022). Unlike perennial grasses, forbs are predominantly annual species that are able to respond quickly to environmental changes (Butterfield et al., 2023; Fan et al., 2024). This may explain why our SOM study with connectivity and precipitation aligns so well with forb ANPP, as these species are able to swiftly adapt to dynamic changes in climate. Furthermore, Fan et al. (2024) determined that CO_2 drawdown from forbs increases with PAWC, which supports our findings regarding the impact of forb ANPP on SOM. However, under future climate scenarios, forb ANPP is predicted to decrease in drylands (Gherardi and Sala, 2019; Palmquist et al., 2021), and may contribute to a net decrease in overall C sequestration. Therefore, it is of critical importance to better understand the role that forbs have on the C cycle in dryland environments.

This study also investigated the effect that shrub ANPP had on SOM. However, since there were no shrubs present in any of the plots, we were only able to focus on the impact from shrub recruitment had on SOM. We observed the greatest overall amount of shrub recruits in plots with ConMods that also received ambient or greater monsoonal precipitation (Fig. 20C). Although, these results are not significant, they do infer that shrub recruits allocate a greater amount of C towards belowground biomass compared to perennial grasses; which is supported by previous studies that have investigated the influence increases in shrub ANPP has on SOM in drylands (Brazier et al., 2014; Throop et al., 2020). The allocation of C in shrub recruits has also been shown to be relatively unaffected by environmental changes (Kleczewski et al., 2010; Meng et al., 2022). However, our results imply that a decrease in connectivity and increase in monsoonal precipitation does in fact promote shrub recruitment in drylands. Thus, under future climate scenarios, shrubs may become a principal source of SOM in dryland environments (Hoyle et al., 2016; Li et al., 2016).

Conclusions

This study investigated the impact that changes in monsoonal precipitation and structural connectivity have on the distribution and decomposition of SOM in dryland ecosystems, specifically within the southwestern U.S. Intra-annual variations in monsoonal precipitation didn’t have a significant effect on SOM, but there was a modest positive relationship between monsoonal precipitation and SOM accumulation due to enhanced vegetative productivity

(Gherardi and Sala, 2019) and microbial processes (Maestre et al., 2015). Modulating the structural connectivity at the inter-plant scale also played a critical role in altering the overall distribution of SOM. ConMods were shown to significantly increase SOM by reducing the movement of organic matter and soil particles across the landscape, supporting our initial hypothesis that reducing structural connectivity will increase the SOM content. Reducing the structural connectivity also helped mitigate some of the negative effects that below-ambient monsoonal precipitation had on SOM. However, ConMods proved to be most effective at increasing SOM in plots receiving above-ambient monsoonal precipitation, which supports our second hypothesis that reducing the structural connectivity will be most effective under above-ambient monsoonal precipitation. Overall, these results underscore the important role both monsoonal precipitation and structural connectivity have in regulating dryland SOM dynamics, and the potential implications for the C cycle in drylands under future climate scenarios.

Previous research has primarily focused on the role that shifting monsoonal precipitation or vegetation gradients have on dryland SOM (Hoyle et al., 2016; Li et al., 2019; Throop et al., 2020; Throop and Archer, 2007). This study helps address a current gap in the literature by quantifying the effects that changes in both monsoonal precipitation and structural connectivity have on dryland SOM at the inter-plant scale. These results re-affirm the important role that aeolian processes have in modifying the distribution of SOM and nutrients in dryland environments (Duniway et al., 2019; Li et al., 2008; Ravi et al., 2007). Particularly, as shrub encroachment results in an increasingly heterogenous distribution of dryland vegetation, which increases the amount of bare soil and amplifies the influence of aeolian processes (Bestelmeyer et al., 2018; Fick et al., 2016; Okin et al., 2018). However, these results imply that ConMods are an effective tool that can help mitigate the redistribution and accumulation of nutrient rich sediment and organic matter around the base of shrubs (Rachal et al., 2015; Schlesinger et al., 1995). This is of critical importance since the creation of these “fertile islands” is often irreversible and inhibits vegetative establishment within the inter-plant region, which results in an increase in the overall amount of bare soil (D’Odorico et al., 2012; Eldridge et al., 2011). Thus, inhibiting the accumulation and sequestration of SOM and reducing the landscape’s overall amount of SOC (Okin et al., 2015; Peters et al., 2020; Schlesinger et al., 1990). This study shows that ConMods are an effective tool that can decrease the structural connectivity at the local scale, which can help prevent the redistribution of SOM and the formation of fertile-islands slowing the transition to a shrubland. Although, ConMods have been applied predominantly in the southwestern U.S., these results and previous studies indicate that reducing the structural connectivity is a cost-effective method to mitigating some of the ecological consequences of shrub encroachment in dryland environments under future climate scenarios (Li et al., 2016; Throop and Archer, 2007).

Dryland environments are responsible for storing approximately 1/3 of the planets terrestrial SOC (Hanan et al., 2021). Increasing anthropogenic activity in conjunction with future climate scenarios will alter the dryland C cycle and in turn SOC storage (Hoyle et al., 2016; Lal, 2019). However, this study improves upon our current understanding regarding the effects that abiotic mechanisms such as aeolian processes and monsoonal precipitation have on SOM in dryland environments (Duniway et al., 2019; Throop and Archer, 2009; Throop and Belnap, 2019). Thus, providing novel insights into how the SOM and the C cycle in drylands may respond to future climate scenarios (Hoyle et al., 2016; Plaza et al., 2018). This remains a pressing issue in the conservation and management of dryland environments, since the redistribution of organic matter and soil nutrients may compromise the long-term stability and productivity of these landscapes (Li et al., 2016; Plaza et al., 2018; Wang et al., 2023). Furthermore, dryland environments are predicted to experience an increase in surface area globally, with some estimates as high as 80% depending on the future climate scenario (Huang et al., 2017; Tariq et al., 2024).

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Conclusions

This dissertation underscores the critical interplay that exists between aeolian processes and monsoonal precipitation in shaping the ecogeomorphic dynamics in dryland environments. The findings presented across these chapters highlight that monsoonal precipitation has a significant influence on the structural connectivity of the landscape by influencing vegetative growth. These results also highlight the critical role that aeolian processes, and in particular, structural connectivity have in dryland environments via modulating the distribution of both organic matter and perennial grasses. Changes in structural connectivity and monsoonal precipitation not only influences the establishment and growth of dryland vegetation (Gherardi and Sala, 2015; Peters et al., 2020; Rachal et al., 2015), but also impacts biogeochemical cycles by facilitating the redistribution of soil nutrients and organic matter (Dintwe et al., 2015; Fu et al., 2021; Throop and Archer, 2009; Throop and Belnap, 2019).

In the preceding chapters, aeolian processes emerged as a powerful agent of change in this dissertation, particularly in its ability to mobilize and redistribute organic matter. Coupling structural connectivity with monsoonal precipitation provided an opportunity to investigate how these processes interact, and how this interaction effects ecogeomorphic feedbacks. For instance, the first chapter highlights that when monsoonal precipitation approaches a region's long-term mean, structural connectivity has the greatest influence in promoting perennial grass growth and establishment. The second and third chapters investigated how the interaction between structural connectivity and monsoonal precipitation modified the distribution of litter and soil organic matter.

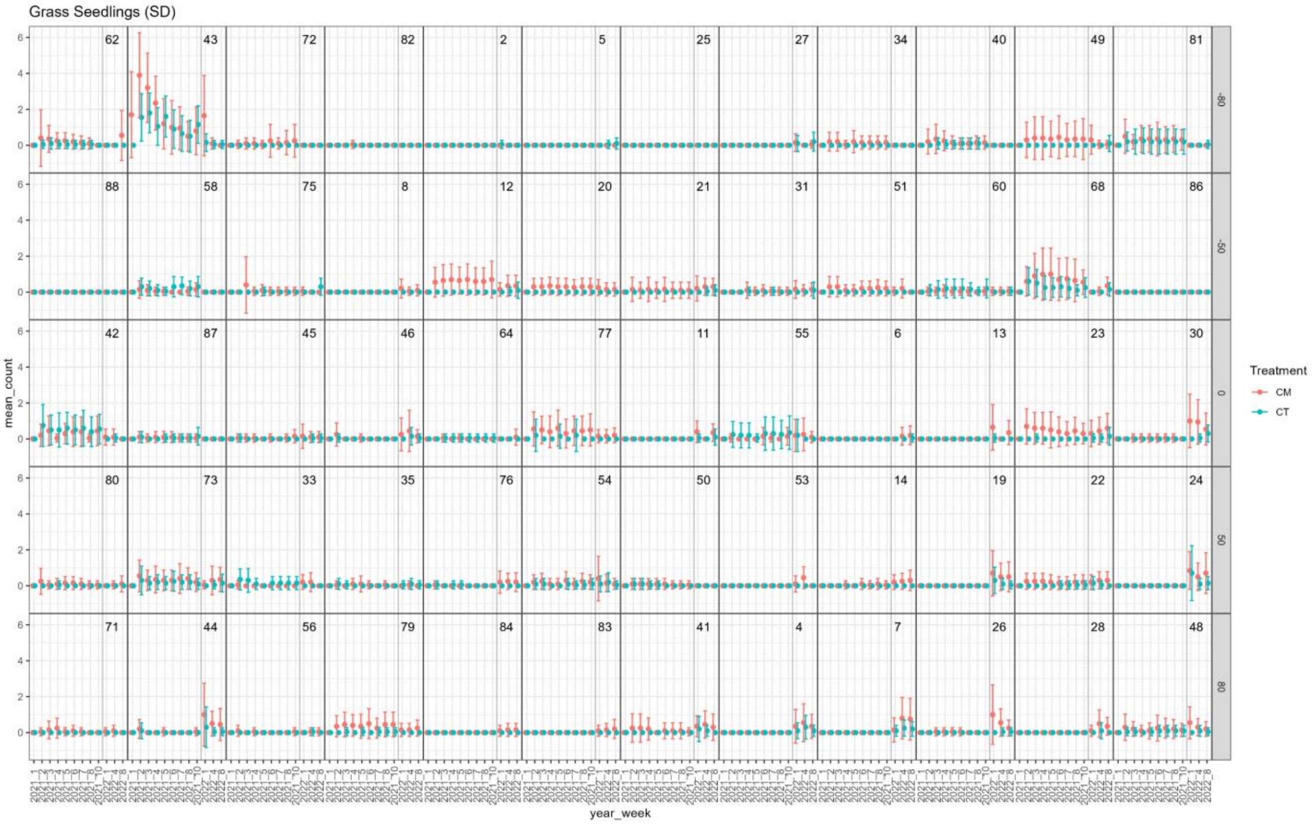
In the second chapter, monsoonal precipitation and monsoonal precipitation did have an influence on litter. However, reducing the structural connectivity in conjunction with increasing monsoonal precipitation promoted an increasingly homogenous distribution of litter and reduced the overall amount of bare soil. This further reduces the landscape's connectivity and prevents the formation of fertile-islands, which enhances soil-litter mixing and perennial grass recruitment. The third chapter focused on the effects that monsoonal precipitation and structural connectivity had on the distribution of soil organic matter (SOM) in a dryland environment. These findings indicated that above-ambient monsoonal precipitation and reduced structural connectivity resulted in the greatest increase in SOM. Increasing monsoonal precipitation expands the amount of organic matter present. However, the subsequent drying and exposure on the soil surface makes litter vulnerable to aeolian transport, but reducing the structural connectivity minimizes the loss of soil nutrients and reduces the amount of bare soil present (Keesstra et al., 2018; Mayor et al., 2019; Rachal et al., 2015). This cycle of deposition and erosion, driven by the alternating influence of precipitation and wind, has profound implications in dryland environments, particularly under future climate scenarios.

Thus, this dissertation provides a comprehensive exploration of how the interaction between aeolian processes and monsoonal precipitation drives key changes in dryland environments. This is of critical importance as drylands make up over 40% of Earth's terrestrial surface, accounts for nearly 40% of global net primary productivity, and is home to more than 2 billion people (Gherardi and Sala, 2019; Van Auken, 2009; Wilcox et al., 2011). However, as climatic changes intensify, and monsoonal precipitation becomes increasingly stochastic, understanding the interactions between aeolian and monsoonal precipitation is likely to become even more critical. These processes are further complicated by anthropogenic activities (Burrell et al., 2020; Dintwe and Okin, 2018), which can disrupt ecogeomorphic dynamics and exacerbate the ecological strain in dryland environments. Therefore, preserving these environments hinges on understanding these complex interactions and developing strategies to account for the influence from both wind and water. This is necessary to help mitigate and improve current predictions regarding the impact that climatic changes will have on dryland environments globally.

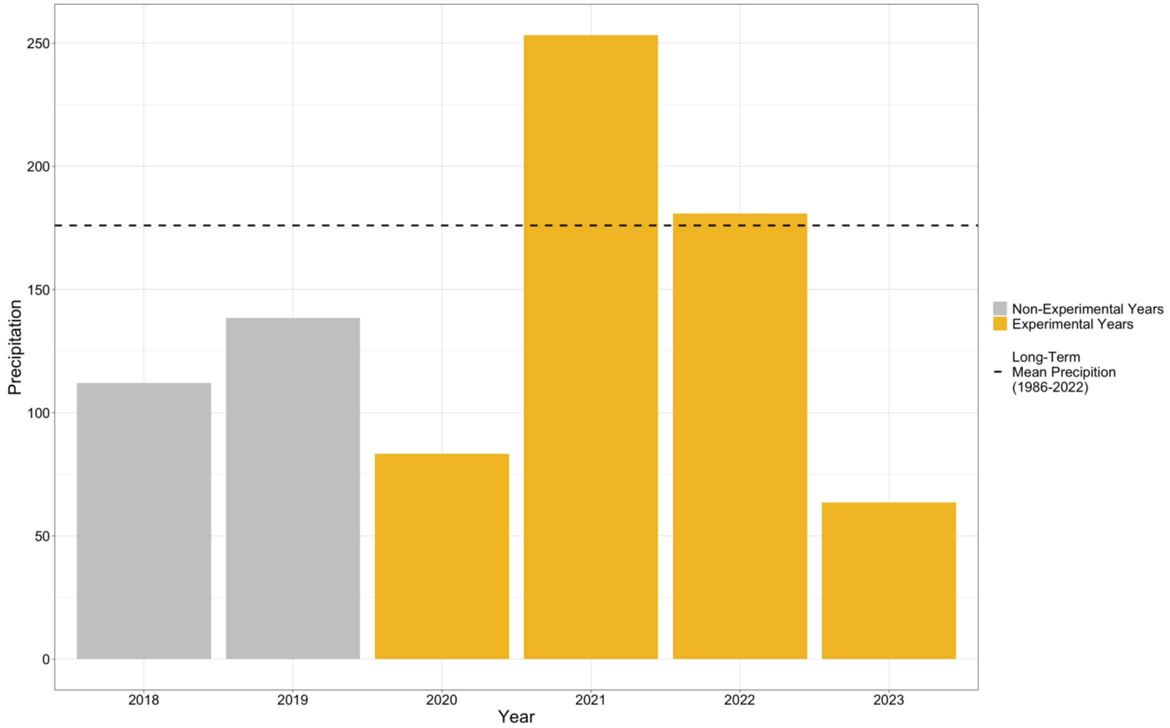
Acknowledgements

We would like to thank the following people: S. Lin, S. Payne, J. Yanowitz, K. Hettinger, M. Roth, C. O’Connor, L. Weber-Grullon, L. Gherardi, S. Doucette-Riise, B. Sutter, C. Vito, K. Andreoni, B. Brown, Bandit, J. Murray, F. Ochoa, S. Jordan, C. Currier, M. Sauceda, S. Smith, G. Baur, S. Jung, and B. Damiata for their help and support throughout the deployment and maintenance of these experiments. Additionally, this experiment would not have been possible without the help of the following Jornada LTER personnel: D. James, J. Anderson, B. Bestlemeyer, H. Campos, C. Gamboa, S. Hall, N. Hanan, C. Nelson, B. Thatcher, D. Thatcher, R. Dunlap, and J. Ramirez. This work was supported by funding from the National Science Foundation Jornada Basin Long-Term Ecological Research Grant (DEB 2025166), National Science Foundation Graduate Research Fellowship under Grant No. (2034835).

Supplementary Materials



Supplementary Figure 1. Perennial grass seedling germination results for each plot (organized by precipitation treatment) in the study based on connective ty treatment, blue points represent ConMod treatments and red points denote Control plots.



Supplementary Figure 2. Monsoonal precipitation patterns at our study over the last five years (2018 – 2023). The grey bars are years prior to the deployment of the experiment, and the gold bars indicate the years that the experiment was operational. The long-term mean (1915 – 2022) monsoonal precipitation (176 mm) of the study site is included as a dashed line.

Independent Variable	Num D.F.	Den D.F.	F Value	P-Value
Connectivity Treatment (ConMod)	1	357	1.56	0.2127
Precipitation Treatment (-80%...+80%)	4	51	0.98	0.4245
*Precipitation*Connectivity Treatment*	4	357	0.92	0.4498
Quadrant	3	357	0.22	0.885
*Connectivity Treatment*Quadrant*	3	357	1.02	0.3821
*Precipitation Treatment*Quadrant*	12	357	1.68	*0.0702*
*Precipitation*Connectivity Treatment*Quadrant*	12	357	0.5	0.9153

Supplementary Table 1. The repeated measures analysis of covariance (ANCOVA) total perennial grass tiller model results for the independent variables: connectivity treatment, precipitation, ConMod quadrant, and the interactions between them. Italic values are significant with an α = 0.1.

Independent Variable	**Num D.F.**	**Den D.F.**	**F Value**	**P-Value**
Connectivity Treatment (ConMod)	1	357	1.56	0.2127

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