

EFFECTS OF ALTERED PRECIPITATION REGIMES ON ECOSYSTEM  
PROCESSES AND PLANT COMMUNITIES IN TERRESTRIAL ECOSYSTEMS

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This is dedicated to my son, Declan Ploughe. You are truly a special gift, and I hope my work will encourage you in the future to shoot for your dreams.

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## ABBREVIATIONS

ANPP	Aboveground Net Primary Productivity
CRED	Community Response to Extreme Drought
invD	Inverse Simpson's Diversity index
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
MDT	Mean Daily Temperature
N	Nitrogen
P	Phosphorus
PFT	Plant Functional Type
RCC	Relative Community Change
RGR	Relative Growth Rate
SLA	Specific Leaf Area
SWC	Soil Water Content
VPD	Vapor Pressure Deficit
VWC	Volumetric Water Content
WUE	Water Use Efficiency

## ABSTRACT

Laura Weber Ploughe Ph.D., Purdue University, December 2018. Effects of Altered Precipitation Regimes on Ecosystem Processes and Plant Communities in Terrestrial Ecosystems. Major Professor: Jeffrey S. Dukes.

Since the pre-industrial age, the Earth has been warming at unparalleled rates, and this warming is changing climate and weather, creating a more extreme global hydrological cycle. In this dissertation, I explore how these changes to the hydrological cycle may affect ecosystem and community level responses of terrestrial plants in the Midwestern United States. In this region, it is projected that mean annual precipitation (MAP) will increase, but precipitation will become more variable across and within seasons. Ecosystem structure and function are vulnerable to changes in hydrologic patterns, including changes in biogeochemical cycles, plant productivity, and plant community structure and function. In this dissertation, I explore how changes in precipitation will alter these processes using two field experiments, and I suggest potential hypotheses that could explain drought-induced community change.

In chapter 1, I explore how alterations to seasonal precipitation in the winter and summer affect ecosystem and community processes in a temperate deciduous forest. Biogeochemical processes and plant communities are sensitive to changes in abiotic conditions, and these conditions will alter forest succession, particularly juvenile woody plant species. Using a fully factorial experiment, I manipulated winter snowfall and summer precipitation to create wet, dry, and control (ambient conditions) treatments and investigated how changes in seasonal precipitation would affect mineralization rates, woody plant recruitment, and understory composition. I found that the effects of winter and summer precipitation on these processes acted independently of one another in this system, and the system was resistant to changes

in mineralization rates and understory composition. Woody plant recruitment may be more sensitive to altered precipitation, as recruitment of at least one of the four species planted, *Lindera benzoin*, was impacted by changes in seasonal precipitation. Snow removal treatments reduced germination and increased summer precipitation decreased the relative growth rate of this species. In the short term, slight changes to woody plant recruitment may have little impact on long-term forest succession, but as these changes persist over longer periods of time, they could alter the direction of succession, which could lead to changes in the understory community composition and nutrient cycling.

The second and third chapters explore the effects that drought intensification will have on terrestrial plant communities. Numerous studies have investigated the effects of individual droughts on ecosystem and community responses, but the effects that both the timing and duration of drought have on these responses remain largely unknown. To explore this gap in the literature, I conducted a field experiment using rainout shelters to reduce growing season precipitation, creating dry periods that varied in length and timing. Drought can impact productivity and diversity in this system, and the timing in which the drought occurs influences these effects. Surprisingly, I found that the length of drought did not affect productivity or community composition.

The final chapter introduces the Community Response to Extreme Drought framework (CRED), which addresses the potential temporal progression of mechanisms and plant-plant interactions that may lead to community changes during and after a drought. The mechanisms for the temporal evolution of community-level drought responses are not fully understood, but plant-plant interactions, both competitive (-) and facilitative (+), are increasingly being recognized as important drivers of community compositional changes. The CRED framework provides hypotheses for the roles that plant-plant interactions have on drought-induced community change. CRED addresses how system-specific variables and the intensity of drought may influence the

strength of plant-plant interactions over time, and ultimately the systems resistance and resilience to drought.

The results from this dissertation work have revealed that more research needs to be done to fully understand how changes in precipitation regimes and patterns will affect terrestrial ecosystems and plant communities. A better understanding of how ecosystems and communities respond to drought timing and length can help improve climate models and restoration strategies.

## 1. INTRODUCTION

Anthropogenic activities have increased the temperature of the Earth by approximately  $1.0^{\circ}\text{C}$  since pre-industrial levels [1] . This unprecedented warming is anticipated to reach  $1.5^{\circ}\text{C}$  between 2030-2052, regardless of drastic and immediate mitigation strategies to reduce greenhouse gas emissions. This warming has been attributed to changes in climate and weather, including increases in mean annual temperatures and changes to hydrological processes [1, 2] . The global hydrological cycle is expected to become more extreme in the future, where some regions are expected to experience increases in the frequency or intensity of drought, and other regions are anticipated to experience increases in precipitation variability [1–3]. In the mid-western United States, mean annual precipitation (MAP) is projected to increase, but it is also expected that precipitation patterns are changing within and across seasons [3–5]. Although projections remain relatively uncertain in this region, seasonal precipitation is expected to increase in the winter and spring and decrease in the fall and summer, and within season patterns are expected to be characterized by longer periods between rainfall events and larger precipitation events [4, 5].

Ecosystem structure and function are vulnerable to changes in hydrologic patterns, as these changes can result in more extreme soil moisture dynamics, the direct link between precipitation and ecological processes [3, 6, 7]. Many global processes respond to changes in soil moisture dynamics and effects on terrestrial plants will be seen across ecosystem, community, and population levels [3, 8]. Changes to the hydrological cycle, not only alters the water cycle, but is expected to alter carbon (C) and nitrogen (N) cycles, which can all impact plant community assembly and structure [3, 8, 9]. The aim of my research was to gain insight into the potential consequences of how the redistribution of precipitation will alter mesic, terrestrial ecosystems (Chapters 1 and

2) and to provide potential additional mechanisms that may influence how and why a plant community responds to drought-induced change (Chapter 3).

In chapter 1, I investigate the impacts that changes in seasonal precipitation in the winter and summer had on ecosystem and community level responses in a forest ecosystem. Studies manipulating precipitation in forests are relatively rare, and few studies have been conducted that manipulate seasonal precipitation in any ecosystem [3]. This lack of research limits our understanding of the impact that changes in seasonal precipitation can have on biogeochemistry and successional patterns in forest systems [3,6]. Changes in seasonal precipitation patterns will likely affect the temporal and spatial availability of soil resources with subsequent consequences for vegetative and N cycling [10–12]. Using a field experiment, I explored how changes to winter snowfall and summer precipitation impacted soil moisture and temperature dynamics, and the impacts that these changes had on plant available nitrogen ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ), understory composition, and plant recruitment in a lightly managed temperate deciduous forest.

In chapter 2, I explored how the timing and/or length of growing season drought impacts ecosystem functioning and plant community composition in a tallgrass prairie. Drought intensification and increases in precipitation variability during the growing season could create more frequent dry periods in this region. This type of episodic disturbance is expected to cause more rapid and lasting effects on plant communities than more gradual but chronic changes, such as rises in atmospheric  $\text{CO}_2$  or changes in mean annual precipitation (MAP), particularly in grassland ecosystems [3,9,13,14]. Numerous studies have investigated the effects of individual drought on ecosystem and community responses, but the effects that both the timing and duration of drought have on these responses remains largely unknown [3]. Separate studies manipulating timing or length of drought have found that both can be important for ecosystem productivity [15–17]. However, to the best of my knowledge, research has not been conducted exploring the interactive effects of the timing and length of drought on productivity, or the impacts that the timing and/or length of drought has on com-

munity composition. This chapter explores this gap in the literature using a field experiment in a restored, tallgrass prairie by manipulating the timing and duration of drought during the growing season using rainout shelters.

Research has shown that the ecological impacts of a period of climatic extremity, such as a drought, can be highly variable depending on the system (e.g. [18–20]). Further, not all droughts that fall within a statistically rare climatic period alter ecosystem structure or function, indicating variation in the resistance and resilience of systems, particularly in regard to compositional changes [21]. The mechanisms for the temporal evolution of community drought responses are not fully understood, but plant-plant interactions, competitive (-) and facilitative (+), are increasingly being recognized as important drivers of community compositional changes [22–25]. In chapter 3, I discuss the Community Response to Extreme Drought framework (CRED), which addresses the potential temporal progression of mechanisms and plant-plant interactions that may lead to community changes during and after a drought. I also address how system-specific variables and the intensity of drought may influence the strength of these interactions, and ultimately the systems resistance and resilience to drought conditions.

## 2. UNDERSTORY PLANT COMPOSITION AND NITROGEN TRANSFORMATIONS RESISTANT TO CHANGES IN SEASONAL PRECIPITATION IN A TEMPERATE FOREST

### 2.1 Introduction

Global mean surface temperatures are rising and are directly and indirectly altering the global chemical and physical environment. As a result of this warming, changes to hydrological processes are occurring, altering mean annual precipitation (MAP), increasing precipitation variability, and altering the seasonality of precipitation in some regions [26,27]. Ecosystem structure and function can respond to hydrologic changes, as these changes will alter soil conditions, including water availability, soil temperatures, and soil nutrient content and availability [6,7,28]. Alterations to soil conditions can lead to changes in plant community composition. Several studies have examined how plant communities respond to changes in MAP (e.g. [29–31]) or variable precipitation (e.g. [32–34]), but few have explored how shifts in precipitation across seasons could impact plant communities (e.g. [11,12]). Changes in seasonal precipitation patterns affect the availability of resources in space and time, translating into changes to plant community composition through alterations in plant recruitment, phenology, community composition, and nutrient cycling [3,7,12]. Studies manipulating precipitation in at least two seasons have occurred primarily in grassland or savannah plant communities, likely because of logistical constraints in forest and woodland systems [3]. Studies manipulating precipitation in forests are relatively rare, limiting our understanding of the impact of temporal changes in precipitation on below-ground processes, community composition, and recruitment in these systems [3]. In forest ecosystems, early developmental stages of plants are expected to

be more sensitive than adult stages to changes in abiotic conditions created through climate change, which could translate to strong effects on recruitment [35]. Differential growth and survivorship of seedlings and saplings caused by shifting precipitation regimes could ultimately lead to changes in species composition [7].

While some aspects of projections remain relatively uncertain, particularly for summer and fall precipitation, in the Midwestern United States, it is projected that precipitation in the spring and winter will increase with a decline in winter snowfall, and summer precipitation is expected to decrease [4,26,36]. Changes in precipitation during these seasons would alter soil conditions, with consequences for vegetation and N cycling [3,6]. Many precipitation manipulations have been conducted during the growing season, often during summer months, across a variety of systems. These studies have found that changes in precipitation can alter aboveground net primary productivity (ANPP; e.g. [37,38]), community composition (e.g. [20,34]), plant phenology (e.g. [19,39]), and microbial activity (e.g. [40,41]). Studies conducted in herbaceous systems manipulating both winter and summer precipitation found that increases in snowfall can also have considerable effects on community composition, increase productivity, and increase invasion by exotic species [10–12].

These changes are likely the result of alterations to the timing and variability of available resources, particularly soil water and inorganic nitrogen ( $\text{NH}_4^+/\text{NO}_3^-$ ). Research suggests that plants and microbes are commonly limited by inorganic nitrogen, even on relatively fertile soils [42–44]. Microbial processes responsible for mineralization and nitrification of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  are sensitive to soil moisture and temperature, with temperature sensitivity depending on soil moisture [45–49]. Changes to seasonal precipitation in temperate regions would alter the soil temperature and moisture and result in a change in the timing of inorganic N supply, potentially altering the intensity of nitrogen limitation.

Currently, little is known about the impacts of seasonal shifts of precipitation on mineralization and nitrification rates, but meta-analyses suggest that climate warming could lead to increases in N mineralization and, therefore, inorganic N supply [50,51].

Conversely, research at the Hubbard Brook Experimental Forest (HBEF; New Hampshire, USA) has consistently found cooler soil temperatures and higher soil water availability increase mineralization and nitrification rates at high elevation sites compared to low elevation sites [52, 53]. These studies suggest that warmer temperatures could lead to drier soils through increases in evapotranspiration, which could counteract the potential increases in activity anticipated with higher temperatures [53]. Reductions in snowpack can result in increases in soil temperature variability, freeze/thaw events, and soil frost during the winter, and all of these have been found to reduce extractable inorganic N, rates of N mineralization and nitrification, and increase in N<sub>2</sub>O fluxes to the atmosphere, all of which could decrease in N retention in temperate hardwood forests [53, 54].

In the winter, soil temperatures can fluctuate depending on the amount of snow cover, ambient air conditions, and the number of freeze-thaw events [52, 53, 55]. Winter ecology is an understudied discipline as it is often misclassified as the dormant season, but research suggests that this can be an important time for ecological processes, particularly microbial activity [53, 56]. The mineralization that occurs over winter can impact mineralization rates in subsequent seasons, such as summer, when plants grow fastest in many temperate regions [53, 57]. Summer precipitation also affects N mineralization rates and has a more direct effect on plant productivity and composition [58, 59].

We were interested in understanding how changes in winter and summer precipitation will alter plant available nitrogen, and the impact that changes to the timing and amount of soil water and nutrients will have on forest understory composition and the recruitment of woody plant species. Here, we explore four main questions: (1) Will changes in seasonal precipitation impact inorganic N availability, which could be important for plant recruitment?, (2) Will winter snowfall affect mineralization in other seasons?, (3) Will forest plant recruitment and understory community composition be affected by changes in precipitation and any accompanying changes in nutrient availability?, and (4) Will forest plant communities be more prone to invasion as a

result of these shifts in water and nutrient availability? To address these questions, we established a field experiment that manipulated winter snowfall and summer precipitation in a temperate deciduous forest. We hypothesized that snow cover plays an important role in the insulation of soils, reducing freeze-thaw cycles, and allowing soils to maintain more constant temperatures. We predicted that more constant soil conditions in ambient and wet winter treatments would have positive effects on mineralization and nitrification rates, understory diversity, and woody plant recruitment. We expected that stress from either a lack of or excess of water in summer-dry or summer-wet, respectively, would suppress microbial and plant activity. We anticipated that the combined effect of stressful environmental conditions in both winter and summer (declines in snowpack in winter-dry treatments and unusually wet or dry summer conditions created by summer-wet and summer-dry, respectively) would exacerbate any negative effects on plants and microbes.

## 2.2 Materials and Methods

### 2.2.1 Experimental Site

The study site was located at the Purdue Wildlife Area (PWA) in West Lafayette, Indiana, USA ( $40^{\circ}26'50.1''N$ ,  $87^{\circ}03'13.8''W$ ). The experiment took place in a temperate, deciduous forest stand that was one of the only wooded sections of PWA when Purdue obtained the property in 1958. Prior to Purdues acquisition, it was primarily used for grazing livestock. The largest trees in the stand were *Carya* spp. and *Quercus* spp. Abundant trees in the smaller class sizes included *Prunus serotina* and *Acer saccharum*. The understory vegetation consisted primarily of native species *Actaea racemosa*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, *Persicaria virginiana*, *Circaea lutetiana*, and *Phryma leptostachya*, and invasive species *Lonicera maackii* and *Alliaria petiolata*.

The region has a humid continental climate with cold winters and warm, wet summers. Precipitation data were obtained from weather stations in West Lafayette,

IN at the Purdue Agronomy Center for Research and Education (ACRE), located approximately 8 km from PWA, and air temperature data were collected from the Purdue University Airport, located approximately 11 km from PWA (iclimete.org). MAP over the past 100 years at this site is approximately 960 mm with an average of 295 mm of precipitation during the summer months (Jun-Aug) and 58 mm of precipitation during the winter months (Jan-Mar), including an average of 337 mm of snow. The mean annual temperature (MAT) from 2003-2016 is 11.5°C with mean summer (Jun-Aug) temperatures of 22.7°C and mean winter temperatures (Jan-Mar) of -0.1°C. A climate diagram created using precipitation from the period of 2003-2016 appears to indicate an increase in MAP with an average of 1051 mm (Fig. B1) with similar MAT of 11°C. The soil type is a silt loam with approximately 27.5% clay, 20.8% sand, and 51.7% silt [60].

## **2.2.2 Experimental Treatments**

We established the experiment in November 2014. We applied nine precipitation treatments (three summer by three winter) to the forest understory using rainout shelters and snow shovels. Summer treatments (dry, control (ambient), wet) were applied to whole plots (6.5m x 5.5m) and each of the three winter treatments (dry, control (ambient), wet) were applied to subplots (3m x 2m) within each whole plot (Fig. 2.1). We used a blocked design with three replicates, for a total of 27 subplots nested within 9 plots. Because this study focused on herbaceous understory plants, plots were selected to exclude trees and shrubs. Deer fencing was installed around each block to exclude large mammals.

Summer treatments were applied from June 1 through August 31 of 2015 and 2016. Summer-dry plots were covered with partial rainout shelters designed to remove 50% of throughfall. Shelters consisted of clear, corrugated polycarbonate slats spaced evenly on a sloping support structure approximately 1.8 m above the soil surface. The slats covered 50% of the plot area. Throughfall intercepted by the slats was

diverted from the site using a gutter and pipe system. Similar structures without the polycarbonate sheets were built over control and wet plots to simulate shading from the rainout shelters. Summer-wet plots were manually watered approximately every 2 weeks, beginning June 1st of each year. We applied a volume of water equivalent to the 50% of the ambient rainfall that fell between water additions or the start of the applied treatment (i.e. June 1st). Summer-control plots received ambient throughfall. Precipitation and throughfall were monitored on-site using 8 tipping-bucket rain gauges beginning in October 2015 (Rain collector with flat base for Vantage Pro2; Davis Instruments, Hayward, CA, USA): 4 gauges were placed within the forest to measure throughfall and 4 gauges were placed in an open field near the experimental plots to measure ambient precipitation. Precipitation data from ACRE were used in the summer of 2016. Both summers had precipitation

<b>Treatments</b>	<b>Winter (W)</b>	<b>Summer (S)</b>
<b>Dry (D)</b>	(-100%) Snow removal	(-) 50% throughfall
<b>Control (C)</b>	Ambient snow	Ambient throughfall
<b>Wet (W)</b>	(+100%) Snow addition	(+)50% precipitation

	<b>Dry (WD)</b>	<b>Control(WC)</b>	<b>Wet (WW)</b>
<b>Dry (SD)</b>	WD-SD	WC-SD	WW-SD
<b>Control (SC)</b>	WD-SC	WC-SC	WW-SC
<b>Wet (SW)</b>	WD-SW	WC-SW	WW-SW

Fig. 2.1.: Experimental treatments for winter (W) and summer (S) for each subplot in a block. (Top) Treatment manipulations for winter and summer. (Bottom) Nine treatments applied.

above the 50th percentile for this region (Fig. B2). The summer of 2015 received 469 mm of rain, which is around the 95th percentile, and the summer of 2016 received 386 mm of rain, which is above the 50th percentile. This resulted in summer-wet

treatments well above the 95th percentile, and summer-dry below the 25th percentile for this region in both years. Winter treatments were maintained from January 1 through March 31 of 2015 and 2016 (Fig. 2.1). Snow was removed from winter-dry plots using a shovel and added to winter-wet plots within 1 or 2 days of each snowfall event. Winter-control plots received ambient snow. In the winter of 2015, as much snow as possible was removed from winter-dry plots to maximize snow removal while minimizing disturbance and movement of litter. All subplots were covered with window screening during the winter of 2016 to further decrease any disturbance caused by shoveling. This allowed for nearly 100% snow removal from the winter-dry plots with no movement of litter.

The amount of snowfall was measured by haphazardly sampling the depth of snow to the forest floor in a 500 mm x 500 mm sampling area near each block. The snow from each sampling area was shoveled, allowed to melt, and the volume of the melted snow was measured. Equivalent precipitation was calculated by dividing the average volume of liquid water (mm<sup>3</sup>) from the 3 blocks by the area sampled. The winter of 2015 had a mean minimum temperature (MMT) of -8.8°C, a mean daily temperature (MDT) of -2.8°C, and 535 mm of snow, equivalent to 73 mm of precipitation. This amount of snowfall was above the 90th percentile for snowfall in this region (Fig. B2). The winter of 2016 was warmer and had less snowfall than 2015, with a MMT of -3.37°C, a MDT of 1.75°C, and 322 mm of snow, equivalent to 22 mm of precipitation. This amount of snowfall was greater than the 50th percentile for this region. In both years, snow removal created snow accumulation similar to the 5th percentile for this region, and snow addition resulted in snow accumulation greater than the 95th percentile (Fig. B2).

Each subplot consisted of a 1 m x 2 m sampling area surrounded by a 0.5 m buffer area. Half of the sampling area (1m x 1m) was reserved for measuring N mineralization and nitrification, soil temperature, soil moisture, and understory plant community composition. Seeds of four woody plant species, *L. maackii*, *Lindera benzoin*, *Acer ginnala*, and *A. saccharum*, were planted in the other half of the subplot (1 m x 1 m)

in November 2014. In December 2015, plastic boxes (35.6 cm x 20.3 cm x 12.4 cm) with multiple drainage holes were partially buried in the buffer area of each subplot. Each box was refilled with the soil that was removed during installation. The area of soil at the top of the box was divided into equal halves, and each half was planted with seeds one of the local invasive plants, *L. maackii* and *A. petiolata*.

### 2.2.3 Soil Temperature and Moisture

Soil temperature and moisture were monitored in all subplots in one block, and measurements were taken every 6 hours (CR1000; Campbell Scientific, Logan, UT, USA). Soil temperature was monitored using thermistors that were buried horizontally at 10 cm depth. Soil moisture (as volumetric water content; VWC) was monitored at 10 cm depth (10HS; Decagon Devices, Pullman, WA, USA). Defective sensors resulted in substantial losses of soil moisture data (see below) and equipment failure led to a loss of soil temperature data between March 1- May 5, 2016.

Daily soil temperatures were calculated by averaging soil temperature over each day. Daily soil temperature variability was calculated using the absolute value of the difference of daily temperature between each pair of consecutive days from January 1 to March 31. Yearly soil temperature variability for each subplot was determined by averaging these values, where a higher value indicates greater variability in soil temperature. The number of freeze-thaw events were calculated using 6-hour measurements based on the frequency with which soil temperatures changed from below to above 0°C. We only included an event when the difference in temperature varied by at least 0.1°C. This created a conservative number of freeze-thaw events, masked the slight fluctuations in soil temperatures that may have occurred, and minimized any effects of thermistor measurement error.

Daily soil moisture was obtained by averaging VWC over each day. Our Decagon soil moisture sensors were defective, so only soil moisture data from July 20, 2016 until the end of the experiment were usable. When the equipment failure was recognized

(June 20, 2016), soil moisture data were supplemented with manual measurements twice weekly and before and after watering events using a Theta Probe ML3 (Delta-T Devices, Cambridge, England).

#### **2.2.4 Mineralization and Nitrification Rates**

Intact soil cores were used to estimate plant available N in the form of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  and during the winter, spring, and summer seasons of 2015 and 2016. At the beginning of each season, one initial soil core (5 cm diameter x 10 cm depth) was collected in each subplot and immediately extracted for  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . A smaller soil core (2.54 cm diameter x 10 cm depth) from each subplot was placed in a PVC tube that was capped with one ion-exchange resin bag on the top and two ion-exchange resin bags on the bottom [61,62]. This core was incubated in a vertical PVC sleeve buried in the subplot, with the top of the sleeve even with the soil surface. Resin bags were constructed from sheer fabric and filled with 3g of resin. The top and bottommost ion-exchange resin bags were used to prevent contamination of the sample with external  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . The ion-exchange resin bag on the bottom next to the incubated sample was used to trap any  $\text{NH}_4^+$  and  $\text{NO}_3^-$  that may have leached out of the sample. The incubated samples were removed and extracted approximately every 3 months. After each incubation period, the initial and incubated samples were homogenized (separately) and rocks and roots were removed from each by hand. Soils (10 g) and resin bags were extracted with 50 ml of 2M KCl and extracts were analyzed for  $\text{NH}_4^+$  or  $\text{NO}_3^-$  using an AQ2 discrete analyzer (SEAL Analytical Inc., Mequon, WI, USA).

Net N mineralization rates were estimated by taking the sum of the extracted  $\text{NH}_4^+$  and  $\text{NO}_3^-$  from the incubated soil sample and the top resin bag on the bottom of the soil core and subtracting the amount of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in the initial soil core sample taken before the incubation period. Net nitrification rates were estimated the same way but only extracted  $\text{NO}_3^-$  values were used. Since incubation periods were

not exactly the same amount of days, net N mineralization and nitrification were divided by the number of days per incubation period to determine the net daily N mineralization and nitrification rates. Leaching of nitrate was examined by looking at  $\text{NO}_3^-$  concentrations in the top resin bag on the bottom of the soil core.

### 2.2.5 Plant Recruitment

The woody plant species selected for this experiment were chosen to represent common native and exotic tree and shrub species in the area. *L. benzoin*, a shrub, and *A. saccharum*, a tree, are common native woody plant species found in the forests of northern Indiana. *L. maackii*, a shrub, and *A. ginnala*, a tree, were selected to represent common exotic species found in northern Indiana and are both currently a concern at the experimental site. With the exception of *L. maackii*, seeds were obtained from F.W. Schumacher Tree & Shrub Seeds (Sandwich, MA). Berries for *L. maackii* were collected from PWA in October of 2014 and 2015 and de-pulped in the lab. All seeds were stratified and/or scarified according to planting instructions in the USDA Woody Plant Seed Manual [63].

In the 1m x 1m subplot designed for the woody seedling experiment, we identified 80 locations to receive seeds, and each of the four species was randomly planted in 20 of them. Three seeds of *A. saccharum*, *A. maackii*, or *A. ginnala* were planted in each of the species assigned locations, for a total of 60 seeds per species. We only had enough seed of *L. benzoin* to plant two seeds per location for a total of 40 seeds per subplot. Each seed planting location was spaced 10 cm apart and marked with color-coded plastic markers. From March through September 2015, each location was checked weekly for seedling emergence. If multiple seedlings emerged at a given marker, additional seedlings were randomly pulled to leave one seedling at a marker.

All seedlings that emerged were considered when calculating germination rates, and only seedlings that died naturally were considered for mortality rates. Seedling

height (H) was measured weekly in 2015 and monthly in 2016 and relative growth was calculated using the following equation:

$$RGR = \frac{\ln(H_2H_1)}{(T_2T_1)}$$

RGR was calculated using heights (H) from the time period between September 2015 and 2016 to ensure that RGR was calculated to include all surviving seedlings at the end of the experiment.

In December 2015, soil in the installed plastic boxes (see above) was demarcated into two equal halves, and each half was haphazardly planted with either seeds of *L. maackii* (200) or *A. petiolata* (500). Seeds of *A. petiolata* were collected from a location 25 miles from the experimental site in September 2015. Seedlings were counted weekly beginning in March 2016. Seedlings of *A. petiolata* grew very close together, making it difficult to clearly identify counted, new, or dead seedlings. As a result of this, the weekly count that resulted in the maximum number of seedlings in each subplot was identified and used to estimate germination rate. In June 2016, *A. petiolata* plants were weeded down to 5 individuals of similar size, with a leaf length (from stem to leaf edge) of at least 2 cm and a minimum of 3 leaves. The plants that were removed were dried at 70°C for 72 hours and weighed to determine aboveground productivity.

### 2.2.6 Cover Estimation

Using a 1m x 1m quadrat, the percent cover of each herbaceous, understory species was visually estimated in June and September of each year in each subplot. Cover values could be greater than 100 percent as multiple layers of vegetation were included. Community composition and structure was examined using species and plant functional type (PFT) composition (see Fig. B1), richness, diversity, and evenness. Species composition was analyzed using informative species, which were determined to be species that appeared at least 3 times throughout the entire data set. Rich-

ness (R) was calculated by adding the total number of all species in each subplot. Diversity was calculated using the inverse Simpsons diversity index,

$$invD = \frac{1}{\sum_{i=1}^R p_i^2}$$

where  $p_i$  is the percentage cover of the  $i$ th species in the plot [64].

### 2.2.7 Data Analysis

Data were analyzed using mixed-model analysis of variance with the lmer function in the lme4 package [65] R version 3.3.0 [66], and degrees of freedom were calculated using the Kenward-Roger method. Models were created using all relevant explanatory variables, and model quality was verified using the Akaike information criterion (AIC). Block was used as a random variable in all models except those analyzing continuous measurements of soil moisture and soil temperature. Data for soil temperature and soil moisture were only collected in one block, so in these analyses plot was used as a random variable. Continuous variables were transformed when necessary to meet model assumptions. Freeze-thaw events were analyzed with a generalized linear mixed model (GLMM) using a binomial distribution, and the type II Wald chi-squared test was used to test the null hypothesis [67]. The GLMM was generated using the glmer function in the lme4 package. Tukey HSD post-hoc analyses were performed on all models using the lsmeans package [68].

## 2.3 Results

### 2.3.1 Soil Temperature and Moisture

Daily soil temperatures varied temporally throughout the experiment depending on the month, year, and the interaction between the two (Month:Year,  $F_{2, 1219} = 61.60$ ,  $p < 0.001$ ; Fig. 2.2; Table A1). Daily soil temperature variability from January to March was significantly affected by the interactive effect of winter treatment,

month, and year (Winter treatment:Month:Year,  $F_{4,119} = 2.504$ ,  $p = 0.0413$ ; Table A1). In 2015, the yearly soil temperature variability values for each treatment were: control  $0.43\text{ }^{\circ}\text{C d}^{-1}$ , dry  $0.55\text{ }^{\circ}\text{C d}^{-1}$ , and wet  $0.32\text{ }^{\circ}\text{C d}^{-1}$ . In 2016, soil temperature variability values for control, dry, and wet treatments averaged  $0.33\text{ }^{\circ}\text{C}^{-1}$ ,  $0.18\text{ }^{\circ}\text{C}^{-1}$ , and  $0.36\text{ }^{\circ}\text{C}^{-1}$ , respectively. In the snowier winter of 2015, soil temperatures were more variable in 2015 in winter-dry plots compared to winter-wet and control plots when averaged over month, and in 2016, winter-dry plots were only different from winter-wet plots (Winter treatment:Year,  $p < 0.05$ , Tukey HSD). There were no treatment differences in the number of freeze-thaw events in either year (Fig. 2.2; Table A1). From both the manual and continuous soil moisture measurements (Jun-Sept 2016), we found that summer treatments affected soil moisture during some periods (Summer treatment:Date,  $p < 0.001$ ; Table A2). Manual measurements demonstrate that soil moisture increased following watering events in summer-wet treatments compared to summer-dry treatments. (Summer treatment:Date,  $p < 0.05$ , Tukey HSD; Table A3).

### 2.3.2 Mineralization and Nitrification Rates

Mineralization and nitrification rates were primarily affected by the timing of the incubation period (Fig. 2.3A). Over the course of the experiment, daily mineralization rates varied from  $-4.06 \times 10^{-4}$  to  $1.49 \times 10^{-2}\text{ g N d}^{-1}$  (Table 13). Net mineralization varied by incubation period (IP) (IP,  $F_{2,126.27} = 6.342$ ,  $p = 0.0024$ ), and the incubation period and year had an interactive effect (IP:Year,  $F_{2,109.38} = 13.152$ ,  $p < 0.001$ ; Table A4). Net mineralization rates were greater in the spring incubation period in 2015 compared to the other incubation treatments, and in 2016, the summer incubation period had greater mineralization rates than the other incubation periods (IP:Year,  $p < 0.05$ , Tukey HSD; Fig. 2.3A). Daily mineralization rates were similar during the winter incubation period in both years (IP:Year,  $p < 0.05$ , Tukey HSD; Fig. 2.3A). Winter treatments had marginally significant effects on daily mineraliza-

tion rates (Winter treatment,  $F_{2, 126.08} = 2.732$ ,  $p = 0.0689$ , Table A4), and summer treatments had no significant effect. Daily mineralization rates were higher during the spring 2015 incubation period in winter-wet treatments compared to winter-dry treatments (Winter treatment:IP:Year,  $p < 0.05$ , Tukey HSD), but winter treatments did not have an effect on mineralization in other incubation periods (Fig. 2.3B).

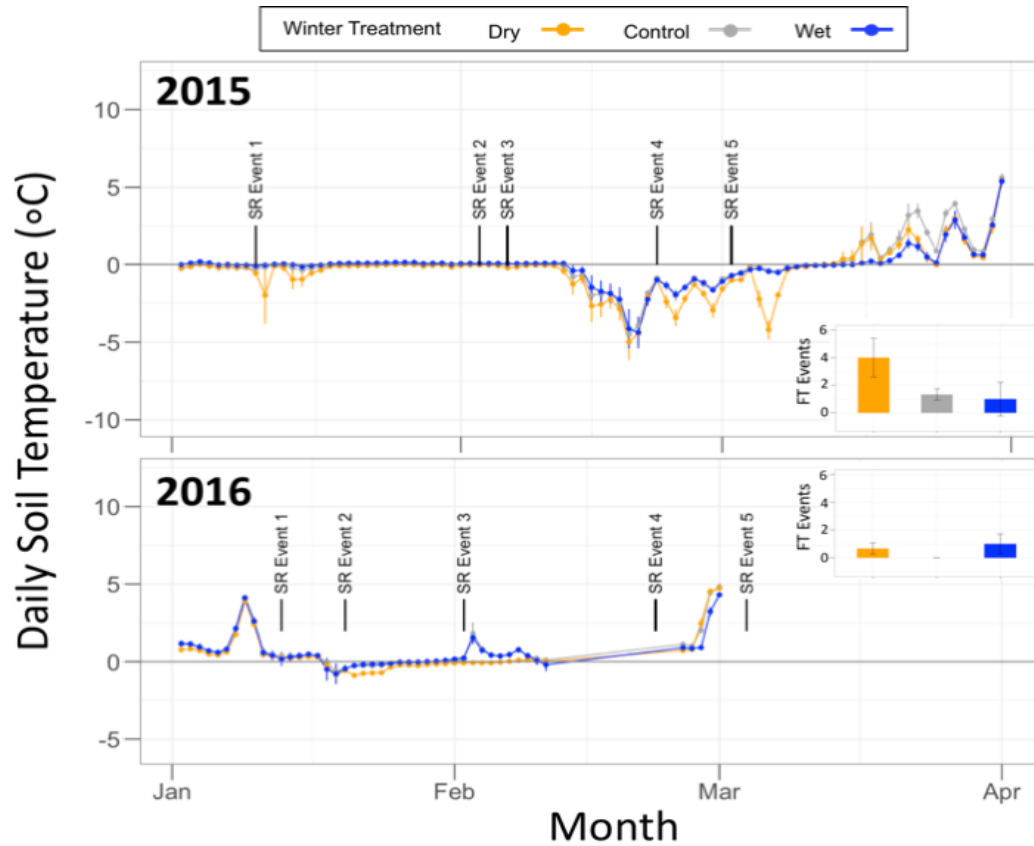


Fig. 2.2.: Daily soil temperature for the winters of 2015 (top) and 2016 (bottom) according to the three winter treatments used in this study. Orange indicates winter-dry conditions, gray indicates winter-control conditions, and blue indicates winter-wet conditions. Snow removal events are indicated by black lines and are labeled SR Event #. The inset panels show the number of freeze-thaw (FT) events by winter treatment for the respective years. Error bars indicate the standard error from the mean. The box in the top graph contains the significant variables from the daily soil temperature statistical model: M = Month and Y = Year.

Daily mineralization rates was found to be quadratically related to average soil temperature (ST) over the incubation period ( $ST + ST^2$ ,  $F_{2, 168.2} = 9.992$ ,  $p < 0.001$ ,

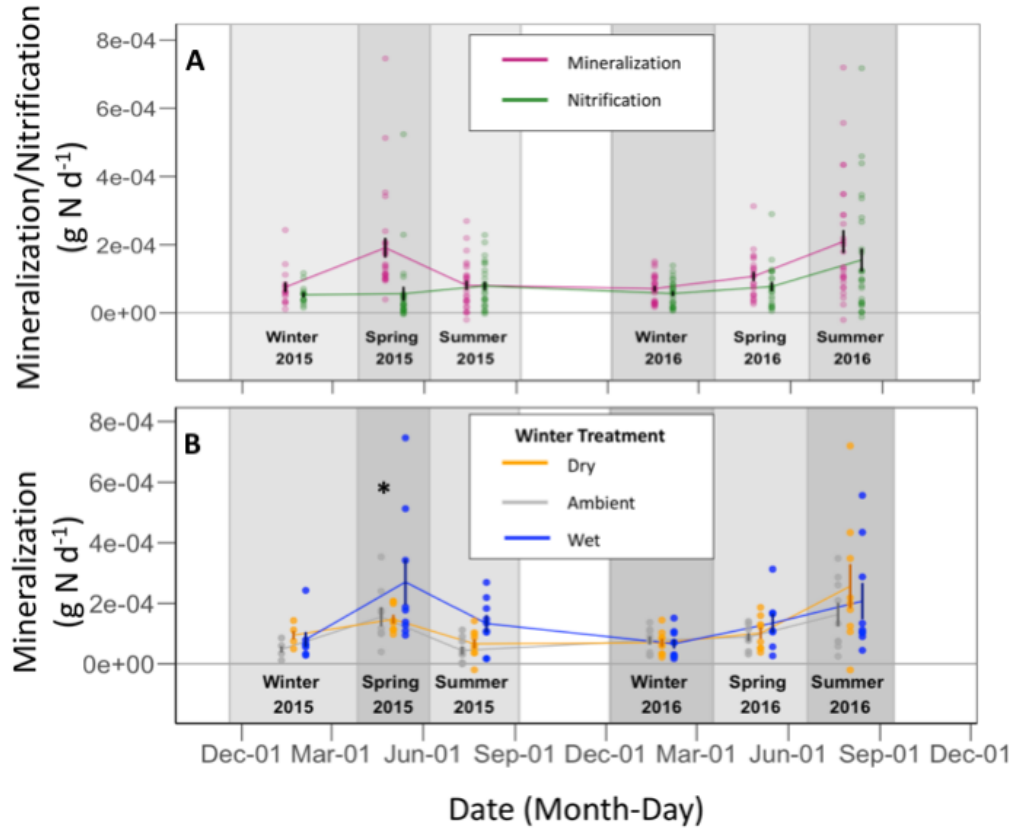


Fig. 2.3.: Daily mineralization and nitrification rates over each of the 6 incubation periods, winter, spring, and summer of 2015 and 2016, with standard error bars. Each dot represents an individual sample taken during each incubation period. (A) Average daily mineralization or nitrification rates (g N d<sup>-1</sup>). Mineralization values are denoted by the color purple, and nitrification values are denoted by the color green. (B) Average daily mineralization rates (g N d<sup>-1</sup>) of winter treatments: winter-dry = orange, winter-control = gray, and winter-wet = blue. The asterisks represents statistically significant differences (Tukey HSD,  $\alpha = 0.05$ ).

$r^2 = 0.14$ ; Fig. 2.4A; Table A5), and total precipitation over the incubation period ( $P + P^2$ ,  $F_{2, 168.02} = 4.192$ ,  $p = 0.0167$ ,  $r^2 = 0.09$ ; Fig. 2.4B). There was an interactive effect between the total precipitation and average soil temperature ( $P + P^2 * ST + ST^2$ ,  $p = 0.0305$ ,  $r^2 = 0.19$ ; Fig. 2.4C; Table A5). Daily nitrification rates varied from  $-2.40 \times 10^{-4}$  to  $1.44 \times 10^{-4}$  g N d<sup>-1</sup> (Table A3). Winter and summer treatments did not affect daily nitrification rates but rates varied temporally (Table A4). Incubation period (IP,  $F_{2, 138.31} = 5.812$ ,  $p = 0.0038$ ) and year (Year,  $F_{2, 138.33} = 4.171$ ,  $p = 0.0431$ )

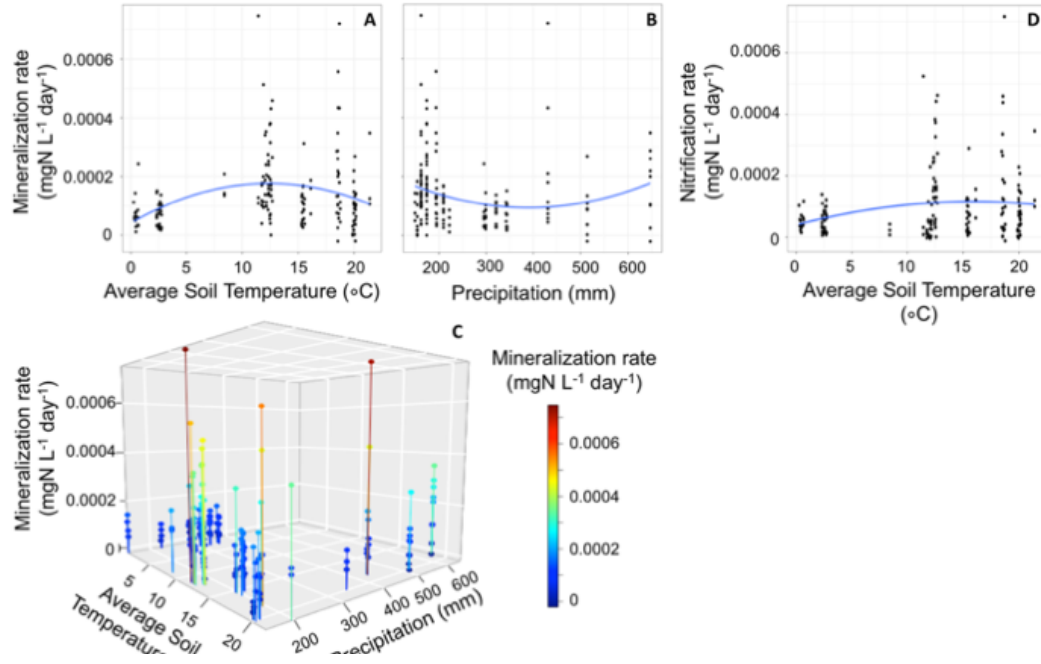


Fig. 2.4.: Relationships between environmental variables and mineralization or nitrification rates. Each point represents an individual sample. (A) Daily mineralization rates (DMR) as a function of average soil temperature during the incubation period of a sample. The blue line represents a quadratic relationship,  $DMR = ST + ST^2$  ( $r^2 = 0.14$ ). (B) Daily mineralization rates as a function of average precipitation during the incubation period of a sample. The blue line represents a quadratic relationship,  $DMR = P + P^2$  ( $r^2 = 0.09$ ). (C) Mineralization as a function of average soil temperature and precipitation during the sample incubation period,  $DMR = \ln(P) + \ln(P^2) * ST + ST^2$  ( $r^2 = 0.19$ ). Dots with warmer color tones indicate higher mineralization rates and cooler colors indicate lower mineralization rates. (D) Daily nitrification rates (DNR) as a function of average soil temperature during the incubation period of a sample. The blue line represents a quadratic relationship,  $DNR = ST + ST^2$  ( $r^2 = 0.10$ ).

were found to significantly affect nitrification rates (Table A4). Nitrification rates were higher during summer incubation periods compared to other incubation periods (IP,  $p < 0.05$ , Tukey HSD), and in 2016 versus 2015 (Year,  $p < 0.05$ , Tukey HSD; Fig. 2.3A). Nitrification rates were quadratically related to average soil temperatures during the incubation period ( $ST + ST^2$ ,  $F_{1, 168.16} = 4.521$ ,  $p = 0.0012$ ,  $r^2 = 0.10$ ; Fig. 2.4D; Table A5).

### 2.3.3 Plant Recruitment and Community Composition

Although we followed the stratification and scarification methods outlined in the Woody Plant Seed Manual [63] the only species that germinated in significant numbers were *L. benzoin* and *A. petiolata*. Germination of *L. benzoin* took place between the end of May and September of 2015, and no new plants germinated in 2016. Germination rates of *L. benzoin* were reduced in subplots that received dry winter treatments (Winter treatment,  $F_{2,22} = 7.682$ ,  $p = 0.0295$ ) but were unaffected by summer treatments (Table A6). Germination rates were approximately 24% lower in winter-dry plots compared to the other winter treatments (Winter treatment,  $p < 0.05$ , Tukey HSD; Fig. 2.5A). Emergence time of *L. benzoin* was unaffected by both winter and summer treatments. Mortality rates of *L. benzoin* were not affected by the applied treatments but changed over the course of time (Date,  $F_{2,52} = 6.882$ ,  $p = 0.0022$ ; Table A6). Mortality rates were similar across treatments in the first growing season of the *L. benzoin* plants and declined by the end of the second growing season (Date,  $p < 0.05$ , Tukey HSD; Fig. 2.5B). The RGR of *L. benzoin* was affected by the summer treatment (Summer treatment,  $F_{2,263.13} = 12.042$   $p < 0.001$ ; Fig. 2.5 C; Table A6) but not by the winter treatment. Summer-dry plots had approximately 21% higher RGRs than the other summer treatments (Summer treatment,  $p < 0.05$ , Tukey HSD; Fig. 5C). Germination rates and aboveground productivity of *A. petiolata* were unaffected by alterations to winter and summer precipitation. After plants were thinned, the remaining plants did not survive long enough to take additional measurements.

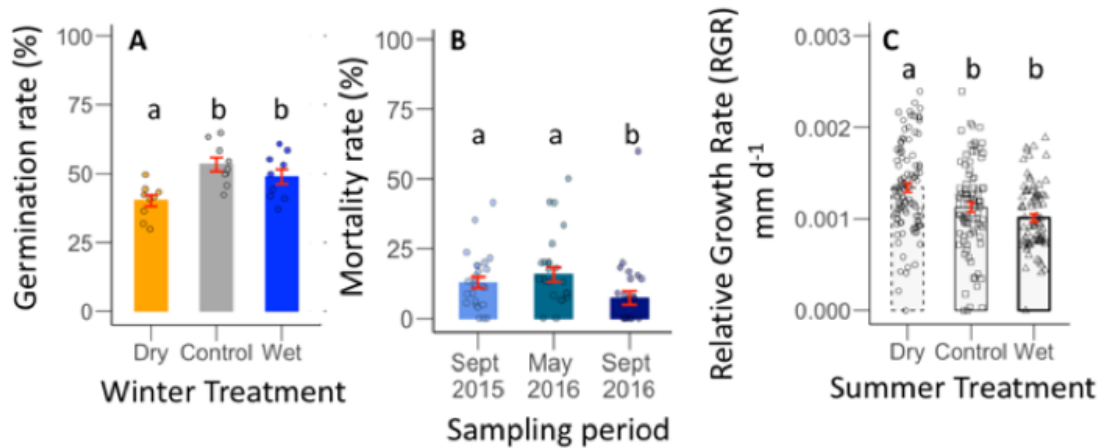


Fig. 2.5.: Germination, mortality, and relative growth rate of *Lindera benzoin* seedlings. Error bars indicate standard errors of the mean and letters represent statistically similar groups (Tukey HSD,  $\alpha = 0.05$ ). Dots are individual data points. (A) Germination rates averaged over winter treatments, where orange = winter-dry, gray = winter-control, and blue = winter-wet. (B) Mortality rates by sampling period. (C) Relative growth rates (RGR) averaged over summer treatments, where bar lines indicate the following treatments: dashed = summer-dry, solid, thin = summer-control, and solid, thick = summer-wet.

Understory plant species richness (Winter treatment,  $F_{2,93} = 6.632$ ,  $p = 0.0020$ ) and diversity (Winter treatment,  $F_{2,93} = 4.012$ ,  $p = 0.0213$ ) were affected by winter snow manipulations, and there was a marginal difference in richness between years (Winter treatment:Year,  $F_{2,93} = 2.552$ ,  $p = 0.0832$ ; Table A7). Winter-dry treatments had 27% greater richness and 22% greater diversity than winter-wet treatments (Winter treatment,  $p < 0.05$ , Tukey HSD; Fig. 2.6A,B). The same trend for richness was found for the winter of 2015, but in 2016, richness was not different among treatments (Winter treatment:Year,  $p < 0.05$ , Tukey HSD; Table A7). Evenness was affected by summer treatments (Summer treatment,  $F_{2,99} = 3.232$ ,  $p = 0.0485$ ; Table A8; Fig. 2.6C), and changed depending upon the month (Month,  $F_{2,99} = 7.811$ ,  $p = 0.0063$ ).

Richness and diversity (invD) were driven by the timing of the sampling period in both years (Month,  $p < 0.001$ ),  $F_{2,93} = 60.642$ ,  $F_{2,99} = 35.752$ , respectively, and were found to be lower in September than June in both sampling years (Month,  $p <$

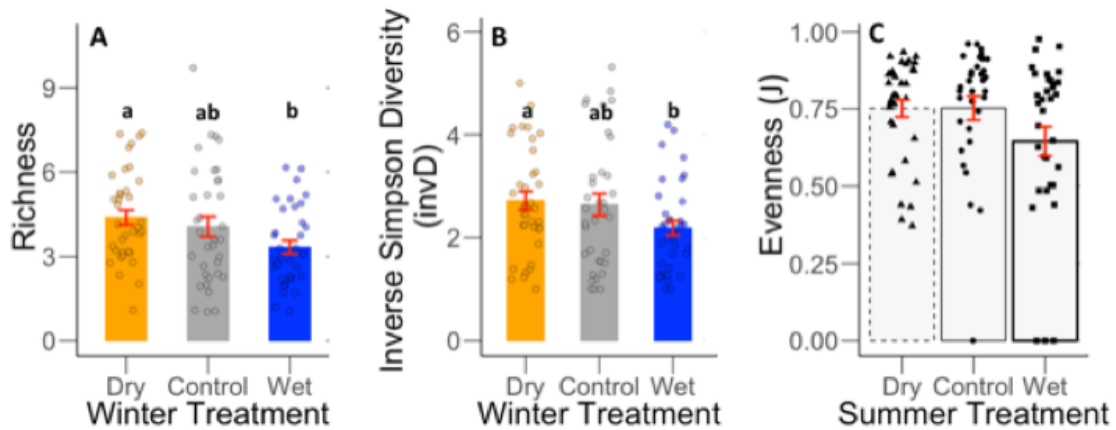


Fig. 2.6.: Mean species richness (A), diversity (B; inverse D), and evenness (C; J) of the understory community. Error bars indicate standard errors of the mean and letters represent statistically similar groups (Tukey HSD,  $\alpha = 0.05$ ). Results for richness and diversity are averaged over winter treatments and years; winter-dry = orange, winter-control = gray, and winter-wet = blue. Results for evenness are averaged over summer treatments and years; winter-dry = dashed line, winter-control = solid, thin line, and winter-wet = solid, thicker line.

0.05, Tukey HSD). Richness was lower in 2015 in winter-dry plots compared to other winter treatments but was similar in 2016 (Winter treatment:Year,  $p < 0.05$ , Tukey HSD; Fig. B4). When species were grouped into PFT, neither the winter nor the summer treatments had an effect on PFT composition, but PFT composition changed temporally throughout the experiment (PFT:Month,  $F_{3,1052} = 7.993$ ,  $p < 0.001$ ).

## 2.4 Discussion

In the face of large increases and decreases in summer and winter precipitation over two years, forest understory composition, recruitment, and inorganic N supplies were generally resistant to change. During the experimental period, the region experienced above-average summer precipitation rates (Fig. B1,B2), which suggests that even during the periods for which we have no VWC data, the summer-dry treatments likely did not result in water stress for plants or microbes. Above-average precipitation

in both years likely created extremely wet soils in the summer-wet treatments that could have led to hypoxic conditions during the growing season, particularly after a watering event. Even with these extreme wet conditions created by the summer-wet treatments, most differences in plant or microbial activity appeared to arise as a result of the applied winter treatments and/or varied temporally.

#### **2.4.1 Mineralization and Nitrification Rates**

Daily mineralization rates were not affected by changes to summer precipitation and were moderately altered by changes to winter snowpack. During the spring 2015 incubation period, plots receiving additional snow had higher mineralization rates. This is potentially the result of the lower variability in winter soil temperatures during the previous months, as the snow acted as an insulator. The winter of 2016 was warmer and received less snowfall, and winter treatments did not result in differences in daily or yearly soil temperature variability. We suspect that the warmer and drier conditions prevented positive effects that snow additions may have had on plant or microbial activity, for instance through nutrient flush from snow melt early in the growing season and insulation from extreme cold.

Our results are consistent with those of previous precipitation manipulation studies in the Hubbard Brook Experimental Forest that found that snow removal treatments had no significant effect on rates of N mineralization and nitrification [28, 69–72]. In our study, we found that additional snow in the colder winter of 2015 increased mineralization rates, which is consistent with the findings of Durn et al. [53], who found that more snowpack resulted in higher mineralization rates in the spring. While other studies have found that snow removal reduced mineralization rates [53], we did not find that pattern. We also did not detect an effect of the previous years precipitation on mineralization and nitrification rates, as the values for inorganic nitrogen transformations remained relatively consistent over the course of our experiment.

Mineralization and nitrification were likely impacted by the differences in precipitation between the two years, as air temperatures did not vary between the two years. We speculate that the wet summer incubation period of 2015 (469 mm of precipitation) may have created longer periods where microbial activity was suppressed by hypoxic conditions than the drier (323 mm) summer incubation period of 2016. Wetter conditions, non-hypoxic conditions, in summer-ambient and summer-dry treatments could explain the higher mineralization rates found during 2016. This is consistent with the concept that nitrification tends to be higher in more aerobic conditions, whereas denitrification takes place in very wet conditions [48, 73].

Despite increased mineralization rates in the spring of 2015 in winter-wet treatments, overall, we found that the winter treatment had minimal effects on mineralization rates. In this system, it appears that mineralization and nitrification rates are primarily affected by environmental conditions, particularly precipitation and soil temperature, experienced during the incubation period. This result is consistent with other studies that confirm the importance of water availability, temperature, and the interactive effects between the two, on mineralization rates [45].

#### **2.4.2 Plant Recruitment and Community Composition**

Plant germination from seed varied widely depending on the species, and most species did not germinate in significant numbers in this experiment. This could have been a result of seed predation, inability to break dormancy, or loss of viability. Interestingly, although the shrub *L. maackii* is regarded as highly invasive, its seeds did not germinate in significant numbers in either year. While some have suggested that *L. maackii* requires cold stratification (0-10 °C) for 60-90 days to break dormancy, non-stratified seeds have been found to germinate in light or dark conditions [74, 75]. Luken and Goessling [74] found that most seeds of *L. maackii* do not have a well-developed dormancy mechanism [74]. These studies suggest that conditions provided in this study should have enabled the germination of *L. maackii* seeds. Most studies

that explore germination of *L. maackii* are conducted in laboratory or greenhouse setting, so we do not know why our seeds failed to germinate in the field, but our results provide a cautionary example to others planning fieldwork with this invasive species.

The two species that did germinate in relevant numbers were *L. benzoin*, a common native shrub, and *A. petiolata*, a common invasive herb. *L. benzoin* seeds were stratified over the winter of 2015 and were less likely to germinate in plots with more variable soil temperatures and cooler daily temperatures. *L. benzoin* seeds have a dormant embryo that responds to a warm incubation for 30 days at 25 °C, which was done in the lab before planting the seeds in the field, followed by 90 days of moist stratification at 1 to 5 °C [63]. In 2015, the winter-dry treatments created more variable soil temperatures that often fell below 0C, which may have caused some seeds to remain in a dormant state. Seeds of *L. benzoin* did not germinate in 2016, which was to be expected because these seeds lose viability shortly after maturity [63].

Current projections for the Midwestern United States suggest that winters will become wetter and summers will become drier [5, 36]. While these projections, particularly those for summer, are less certain than projections of rising global mean temperatures, projected reductions in snowfall in a warmer world could create colder soils leading to increases in soil freezing and increased stress for fine roots [28]. Differential resistance to freezing stress among species may alter woody plant recruitment in forests [7, 28]. In this experiment, the winter-dry treatments imposed in 2015 created greater soil temperature variability and lowered the germination rates of the woody plant species *L. benzoin*. If germination of other woody plant species, particularly shade-tolerant species, is compromised by greater freezing stress in the winter, this could result in changes in forest succession and species composition [7].

In this community, understory richness and diversity were impacted by winter treatments, and evenness was altered by summer treatments. The only response of the community to treatments was a change in richness, which was affected by winter treatments and varied temporally depending on the month and year. Generally

speaking, winter-wet treatments lowered richness in the winter of 2015. We speculate that this may be the result of snow remaining on the ground for a longer period of time, suppressing emergence of certain species. PFT composition was not affected by the treatments.

While we found statistically significant responses of some aspects of community structure to the precipitation treatments, we find it difficult to discern ecologically significant patterns. Understory richness was only reduced by 1-2 species in winter treatments, but there was no consistency in the species that were lost. Diversity was also minimally reduced in winter treatments. Evenness was impacted by summer treatments, but post-hoc analysis of evenness did not identify any specific differences between treatments.

## 2.5 Conclusions

In the forest community in this study, changes in precipitation affected recruitment of a woody plant species, *L. benzoin*, but had little effect on understory composition. We found that *L. benzoin* could be compromised by cold, relatively dry winters, and by wet summers. Cold winters with limited snowfall reduced germination rates, and wet summers reduced RGRs. We had difficulty getting other species to germinate, so we cannot offer more general insights into the effect of precipitation on forest succession. In the short term, changes to germination and RGRs of woody plant species such as those found in this study may have little impact on long-term succession, but over longer periods of time persistent changes would have the potential to alter the direction of succession [76].

Conversely, understory plants and some microbial processes in this forest appear to be resistant to large changes in winter and summer precipitation. The treatments in this study had little effect on diversity and community composition, and mineralization rates were only marginally impacted by winter snowpack. Understory richness

was affected by reduced winter snowfall, but this may have resulted from the relatively cold winter conditions of 2015.

While previous studies have found that alterations to winter and summer precipitation can affect exotic species and their interactions with native species [10,12], our study found inconclusive results for whether the major understory invaders in this forest would benefit from altered precipitation regimes. *A. petiolata* germinates and grows well within this forest community, and precipitation changes did not alter its success. The other major invasive species in this forest community, *L. maackii*, surprisingly did not germinate under any of our experimental conditions.

In this study, large changes in winter and summer precipitation seemed to affect the system independently of one another. Forest understory composition resisted change in the short time frame of this experiment, but responses of *L. benzoin* suggested woody plant recruitment may be sensitive to changes in seasonal precipitation. We expect that larger and/or longer-term changes in precipitation patterns would be required to cause ecologically significant effects on inorganic N supply, understory compositional changes, and forest succession in temperate deciduous forests.

Forests tend to have a general inertia to species turnover and recover quickly after a disturbance (Lloret et al. 2012), which is consistent with our findings. However, as communities experience more variable precipitation patterns over the longer-term, this resistance and resilience to extreme climatic events will likely be reduced and may lead to increases in background tree mortality rates or the frequency of rapid die-off events [77,78]. Recently, MAP has been found to be positively related to resistance and negatively related to resilience in forest systems [79]. This finding will be important for management practices in different climatic conditions, particularly by understanding stabilizing mechanisms of the dominant species within the community that reduce mortality or enhance recruitment [78]/

Further, forest communities interact in complex ways, and species vary dramatically in their interactions with one another and their environment [78,80]. More experimental studies as well as long-term monitoring of forests can provide useful in-

formation about how climate change will affect mortality, vegetation responses, and stabilizing processes that maximize survival or enhance recruitment [78]. This is particularly important for the dominant species within the system. Plant communities dominated by long-lived species may be resistant to change, but persistent extreme climatic events could affect the dominant species, altering community structure and function [78]. Determining the plant functional traits and systems that are sensitive to climate change will help inform and support policy decisions and forest management practices.

### 3. TIMING, NOT DURATION, OF DROUGHT DRIVES GRASSLAND PRODUCTIVITY AND COMMUNITY RESPONSES

#### 3.1 Introduction

Climate models project changes in hydrological processes that will result in more frequent and intense drought events in some regions, and increases in rainfall variability in other regions, which could also lead to more frequent dry periods [9,26]. While mean annual precipitation (MAP) is expected to increase in the Midwestern United States, the number of consecutive dry days, days receiving less than 1 mm of precipitation, is increasing, and the seasonality of precipitation is projected to change [5,36]. While seasonal precipitation projects are less certain and disagreements with models are still an issue, it is expected that at least part of the Midwest will experience increases in precipitation during the winter and spring and decreases in precipitation during the summer and fall. Currently, evidence suggests that longer intervals between rainfall events and seasonal timing, particularly less rainfall during the summer months, are more likely to reduce ANPP than a reduction in MAP [16,81].

These projections suggest that drought will become more frequent during the growing season, causing rapid and lasting effects on the terrestrial carbon cycle and plant community structure [3,9,13]. Drought can reduce plant growth and increase mortality, leading to changes in productivity and plant community composition [3,8,20,38,82]. Drought-induced changes to community composition can have significant effects on local ecosystems, such as reduced productivity, changes to biodiversity, state changes, extirpation, and increases in the spread of invasive species [3,8]. Grasslands are often used for drought experiments as they tend to be the most responsive of terrestrial ecosystems to changes in precipitation, and drought is anticipated to have

the largest effect on the carbon cycle in these systems [9, 14]. Ecosystem processes and services provided by grasslands include high productivity, making them important carbon sinks, and high biodiversity, which can buffer ecosystem functioning against climate [7, 8, 32, 83]. These ecosystem services have been shown to benefit organisms and processes across trophic levels [84]. Many studies have explored the effects of drought on ecosystem and community responses, but the effects that the timing and duration of drought have on these responses remain largely unknown [3].

The current body research in plant communities has focused primarily on productivity, a major currency in global ecology, but results from these studies have been inconsistent [3, 19]. While some natural and simulated droughts led to decreases in aboveground primary productivity (ANPP) (e.g. [20, 85], others have found no change in ANPP, even following severe drought (e.g. [19, 86]. To the best of our knowledge, there has not been research investigating the effects that both the timing and duration of growing season drought will have on productivity or diversity.

Limited research has been conducted exploring the impacts that the timing of growing season droughts will have on ecosystems. Drought studies investigating one grassland site found that timing is an important factor for ecosystem productivity [16, 17]. These studies found that drought reduced ANPP in mid- and late-summer droughts. However, the experimental study found that early-season droughts, occurring between mid-April and mid-June, had no impact on ANPP [17]. Long-term data from the site indicated that drought reduced productivity during this same timeframe, but droughts past August had no effect [17].

Studies exploring different lengths of dry periods tend to use rainfall variability experiments, which may or may not create drought conditions, i.e. water stress (e.g. [15, 87]). An experiment manipulating the duration of dry intervals between rainfall events found that longer dry periods decreased productivity in a mesic tallgrass prairie, but increased productivity in less mesic sites [15]. Based upon a thorough review of the literature, research has not been conducted to explore the impacts that the timing or length of drought have on community composition. However, other

drought research suggests that productivity and diversity are inversely related [32], and plant diversity can increase the stability of aboveground vegetative C stocks during drought [40].

As projected by climate models, in the central United States, the patterns of drought episodes will change in the future, making it important to understand how the timing and length of growing season drought will impact ecosystem functioning and community composition [3, 5]. The questions we explored in this study are: (1) does the timing and/or the length of drought during the growing season alter productivity and community structure? and (2) is the timing of drought or the length of drought more important in predicting these responses? To explore these questions, we established an experiment in a restored tallgrass prairie that varied the timing and duration of drought to understand the effects on ANPP and plant community composition.

We predicted that both the timing and length of drought would drive changes in productivity and community composition. We hypothesized that early-season drought would have the least effect on productivity, as plants would have time to recover from drought stress. We also expected that early-season droughts would result in greater shifts in community composition. We hypothesized that stunted growth early in the season would reduce competition for light and enable species typically shaded out by the tall-statured dominant species in this system to grow into these open spaces, increasing diversity.

We predicted that mid-season droughts would result in greater losses to productivity, as plant growth is highest during this time, but we also predicted that plants would also be more established by this time, resulting in minimal changes to species composition. We anticipated the effects on productivity would become progressively diminished as plants reached peak biomass, and therefore, late-season droughts would have minimal to no effect on productivity or composition. Finally, we expected that the longer droughts would have increasingly negative effects on productivity and diversity, as a result of increased plant mortality and reductions of plant growth. We

predicted that plants growing in the 21-week drought treatments would become extremely water stressed and would have the greatest reduction in productivity and diversity.

## 3.2 Materials and Methods

### 3.2.1 Experimental Site

We conducted our research in a restored tallgrass prairie growing on silt loam soil (27.5% clay, 20.8% sand, and 51.7% silt) at the Purdue Wildlife Area (PWA) in West Lafayette, Indiana, USA (40°26'50.1"N, 87°03'7.3"W). Restoration at the site began in 2008 using a mixture of native grass and forb species (Table C.1) that did not include *S. canadensis* seeds. Prescribed burns have been conducted on the property regularly, and the site was burned in April 2016, prior to the start of this experiment. The dominant species at the site are *S. canadensis* (perennial, C3 clonal forb) and *A. gerardii* (perennial, C4 grass).

The site has a humid continental climate and receives 975 mm MAP, with an average of 500 mm falling during the experimental period (Apr-Sept; Fig. S1A), which is a large portion of the growing season at this site. The experimental periods in 2016 and 2017 had 512 mm and 744 mm of rain, which fall into the 50th and 95th percentile for this region, respectively (Fig. S1B). The mean annual temperature (MAT) during the experimental period is 19.3C, and both years had temperatures close to this average. Precipitation and air temperature data were obtained from a weather station at the Purdue Agronomy Center for Research and Education (ACRE), located approximately 8 km from PWA ([iclimete.org](http://climate.org)).

### 3.2.2 Experiment treatments

In April 2016, we established 32 plots (3.4 m x 3.2 m) that were randomly assigned one of eight experimental drought treatments in a blocked design with four replicates.

The perimeters of each plot were trenched to a depth of 75 cm and lined with a double layer of 6 mil plastic sheeting before structures were put in place. At all times during the course of the experiment, each plot was covered with either a rainout shelter or an infrastructure control structure (mid-April to early-September in 2016 and 2017). Treatments included 7-, 14-, and 21-week droughts that varied in timing, including either early- (E), mid- (M), or late-season droughts (L; Fig. 3.1), and a control treatment that received ambient (A) precipitation throughout the year. The times that the shelters were in place were for: E treatments from April 20th June 8th in 2016 and April 19th June 7th in 2017, M treatments from June 8th July 27th in 2016 and June 7th July 26th in 2017, and L treatments from July 27th September 14th in 2016 and July 26th September 13th in 2017. Climate diagrams represent the approximate treatments in each year (Fig. D.1-3).

<b>Treatment</b>	<b>7 weeks (Apr-Jun)</b>	<b>7 weeks (Jun-Jul)</b>	<b>7 weeks (Jul-Aug)</b>
Ambient control (A)			
Early (E)			
Middle (M)			
Late (L)			
EM			
ML			
EL			
EML			

Fig. 3.1.: Applied drought treatments. Dark shaded areas in the table indicate when rainout shelters were in place, and light shaded areas indicated when infrastructure control shelters were in place. A indicates ambient precipitation conditions, E indicates early-season drought, M indicates mid-season drought, and L indicates late-season drought.

Drought was simulated using rainout shelters that covered the plot entirely with clear, corrugated polycarbonate sheets (Fig. D.4). Infrastructure control structures

were built with the same materials but were covered with orange construction fencing in lieu of polycarbonate sheets (Fig. D.4). The fencing simulated the shading effects of the plastic sheets, providing similar reductions in photosynthetically active radiation (PAR). Using a ceptometer (ACCUPAR LP-80; METER environment, Pullman, WA), we measured PAR directly above and 15 cm below the shelters and found that the fencing simulated PAR within 5% of the rainout shelters. A gutter and pipe system was established to divert excess water away from all plots.

### 3.2.3 Soil Moisture

Volumetric water content (VWC) of the soil was measured every 6 hours in each plot using soil moisture sensors (10HS; Decagon Devices, Pullman, WA, USA) connected to a datalogger (CR1000; Campbell Scientific, Logan, UT, USA). Sensors were installed at a soil depth of approximately 15 cm. Daily soil moisture was taken by averaging each value in each plot. Values were removed as needed as a result of sporadic sensor malfunction. Soil moisture measurements were also taken manually twice a week in ambient (A) and 21-week (EML) plots at 100, 200, 300, 400, 600, and 1000 mm depths (PR2/6; Dynamax, Fresno, CA, USA).

### 3.2.4 Productivity

Each plot consisted of 0.5 m-wide buffer strip surrounding a 0.25 m-wide strip used for biomass harvests. A 1.5 m x 1.5 m area in the center of the plot remained for vegetation surveys. Biomass harvests took place in August and October in each sampling year using a 0.25 m x 1.75 m quadrat. Clippings were taken at a height of 10 cm and from different areas of the plot for each harvest. Immediately following the harvest, biomass was sorted into species and senesced material. Plant material was dried at 65C for 48+ hours then weighed. ANPP ( $\text{g m}^{-1}$ ) was calculated by taking the weight of each species and dividing by the sampled area (1.75 m x 0.25 m). Total

ANPP was calculated by taking the sum of both live and senesced plant material, and live ANPP did not include senesced material.

### 3.2.5 Community Composition

Community composition was explored using plant functional type (PFT) composition and diversity. Each species was assigned to one of five PFTs: grasses, clonal forbs, legumes (N-fixing forbs), other forbs (non-N fixing and non-clonal forbs), and shrubs (Table C.2). The relative abundance of each PFT was calculated by dividing the amount of the PFT ( $\text{g m}^{-1}$ ) by the amount of live biomass ( $\text{g m}^{-1}$ ) in each plot. Diversity was calculated using the inverse Simpsons diversity index ( $\text{invD}$ ),

$$\text{invD} = \frac{1}{\sum_{i=1}^R p_i^2}$$

where  $S$  is the number of species and  $p_i$  is the percentage cover of the  $i$ th species in the plot [64]. The percent cover of the species was calculated by dividing the ANPP of the species by the total ANPP of all living material.

### 3.2.6 Data Analysis

Data were analyzed using repeated-measures, mixed-model analysis of variance with the `lmer` function in the `lme4` package in R version 3.3.0 [65,66]. Tukey HSD post-hoc analyses were performed on all models using the `lsmeans` package [68]. All models used year as a fixed effect and block as a random variable. Continuous variables were transformed when necessary to meet model assumptions. Some models included treatment as a categorical variable with 8 levels: A, E, M, L, EM, ML, EL, and EML. Separate models were run to explore differences in the impacts of timing or length of drought. Models exploring the timing of drought included 3 categorical values, E, M, or L, where a 0 or 1 was input if a rainout shelter was in place during that part of the experimental period. Length was also considered as a continuous variable in weeks

for each model. Models run for total ANPP used the maximum value from one of the two harvests collected each year, either August or October, leaving one total ANPP value for each of the 32 plots for each year. Separate models were run for each PFT.

### 3.3 Results

#### 3.3.1 Soil Moisture

Daily soil moisture in the top 15 cm of soil varied by treatment and year (Treatment:Year;  $F = 44.97_{7, 9941}$ ,  $p < 0.0001$ ; Table C.3). Soil moisture was different in all treatments in 2016, and in 2017, soil moisture was different in all treatments, except that early- (E) and late-season (L) droughts had similar reductions in soil moisture (Treatment:Year; Tukey HSD  $< 0.05$ , Fig. 3.2). Soil moisture measurements taken at soil depths from 100 to 1000 mm in A and EML plots varied between years, treatments, and soil depth (Treatment:Depth:Year;  $F = 3.31_{5, 5555.1}$ ,  $p = 0.0054$ ; Table C.4). Soil moisture was reduced in EML compared to A in both years and at all soil depths (Treatment:Depth:Year; Tukey HSD  $< 0.05$ , Fig. 3.3).

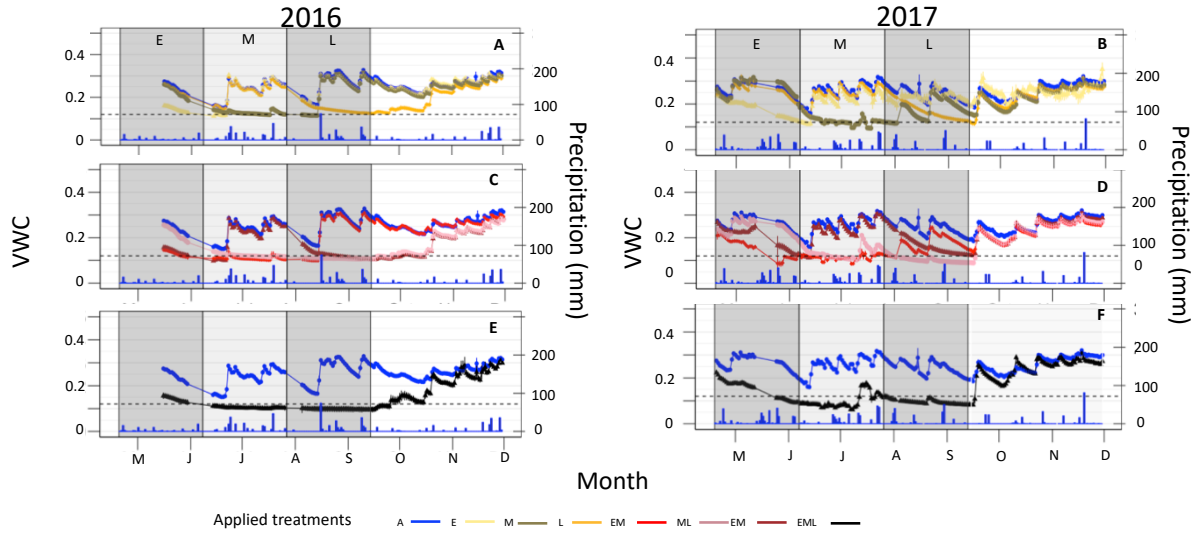


Fig. 3.2.: Daily soil moisture in volumetric water content (VWC) and precipitation by treatment. The left-y axis of each graph represents the VWC, and the right y-axis of each graph represents daily precipitation (mm). The grey rectangles represent the three time periods for this experiment: early (E), middle (M), and late (L) season droughts. Month on the x-axis begins with May and ends with December. The dotted line represents an estimate of the wilting point for plants in this system. Ambient (A) = blue, E = light yellow, M = brown, L = orange, EM = red, ML = pink, EL = dark red, and EML = black. (A) VWC of 7-week droughts compared to A and precipitation in 2016 and (B) 2017, (C) VWC of 14-week droughts compared to A and precipitation in 2016 and (D) 2017, (E) VWC of 21-week droughts compared to A and precipitation in 2016 and (F) 2017.

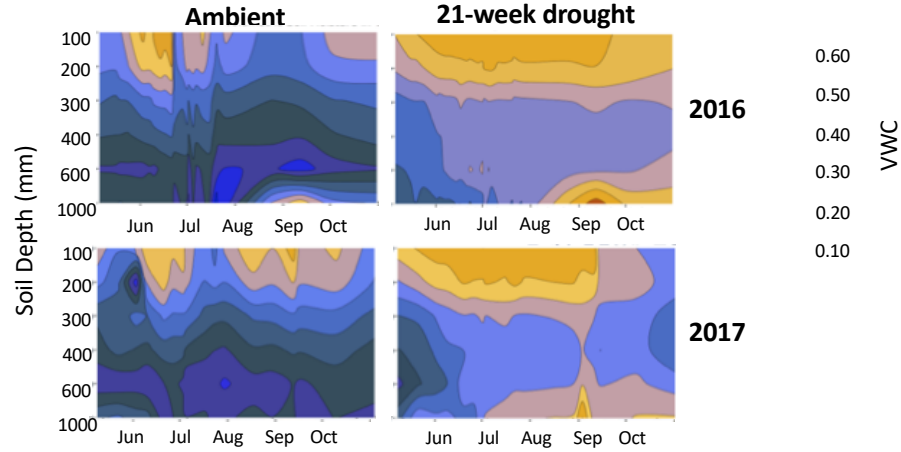


Fig. 3.3.: Soil moisture (VWC) at multiple soil depths (100-1000 mm) in ambient (A) and 21-week drought (EML) plots. The top plots represent VWC in 2016, and the bottom plots represent VWC in 2017. Warmer colors indicate drier soils and cooler colors represent wetter soils.

### 3.3.2 Productivity

ANPP was linearly related to soil moisture (Average soil moisture;  $F = 4.63_{1, 44}$ ,  $p = 0.0370$ ,  $r^2 = 0.42$ ; Table C.5), and the model including the timing of drought (E, M, L) as a categorical variable, ANPP ~ Average soil moisture\*E\*M\*L, increased both AIC and  $r^2$  values of the model (without timing  $r^2 = 0.19$ ; Fig. 3.4). This relationship was driven by the interactions of soil moisture and mid-season drought (Average soil moisture:M;  $F = 4.82_{1, 44}$ ,  $p = 0.0335$ ; Table C.5). Late-season drought was also related to ANPP (L;  $F = 4.54_{1, 44}$ ,  $p = 0.0388$ ; Table C.5). When drought length was included in the model relating ANPP to soil moisture, no relationship was found. However, ANPP did have a weak non-linear relationship with the length of drought (Length;  $F = 4.52_{2, 61}$ ,  $p = 0.0148$ ,  $r^2 = 0.13$ ; Table C.6; Fig. 3.5).

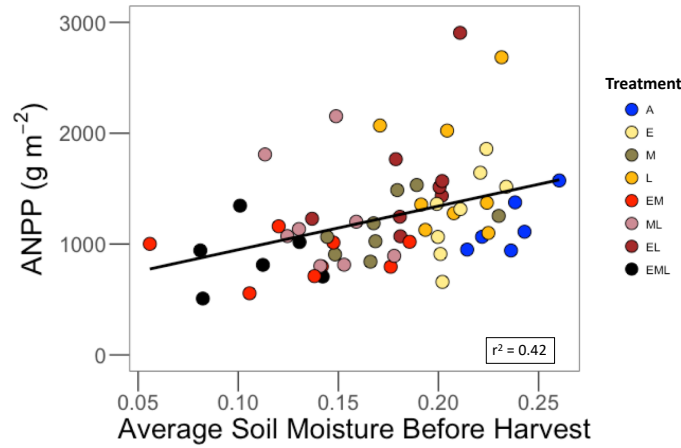


Fig. 3.4.: Linear relationship between productivity (ANPP) and average soil moisture at a depth of 15 cm before the biomass harvest of each experimental year based on the timing of the drought. Points represent individual data points for the maximum ANPP for biomass harvests in 2016 and 2017. Colors represent the applied treatments: ambient (A) = blue, early (E) = light yellow, middle (M) = brown, late (L) = orange, EM = red, ML = pink, EL = dark red, and EML = black. The  $r^2$  value for this relationship,  $\text{ANPP} \sim \text{Average soil moisture} * E * M * L$ , is in the box in the bottom, right corner of the graph.

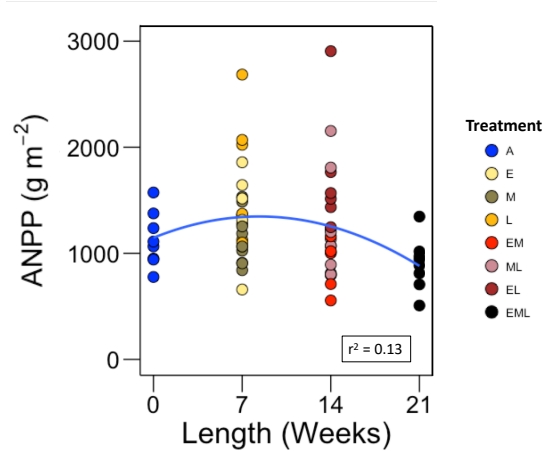


Fig. 3.5.: Non-linear relationship between productivity (ANPP) and average soil moisture before the biomass harvest of each experimental year according to the length of the drought. Each point is grouped by the length of the drought, a continuous variable. Points are represented the same way as described in Figure 4. The  $r^2$  value for this relationship,  $\text{ANPP} \sim \text{Length} + \text{Length}^2$ , was 0.13.

ANPP was altered by some of the drought treatments (Treatment;  $F_{7,44} = 4.73$ ,  $p = 0.0003$ ; Table C.7; Fig. 3.6A). In general, droughts that occurred early- through mid-season (EM, EML) reduced ANPP by 58 % compared to late-season drought treatments (L) or early-season and late-season drought treatments (EL) ( $p < 0.05$ , Tukey HSD; Fig. 3.6A). ANPP was 23 % greater in 2017 compared to 2016 (Year;  $F = 11.07_{1,44}$ ,  $p = 0.0018$ ; Table C.7 and C.8; Fig. D.5A).

Interestingly, the timing of experimental droughts affected ANPP, but the duration of drought did not. Combined early and mid-season droughts (E:M;  $F_{1,44} = 4.91$ ,  $p = 0.0319$ ; Table C.8) and mid-season droughts (M;  $F = 18.12_{1,44}$ ,  $p = 0.0001$ ; Table C.8) both reduced ANPP compared to all other treatments. Plots receiving both early- and mid-season drought (EM,EML) experienced a reduction in ANPP of 42% compared to all other treatments (Tukey HSD,  $p < 0.05$ ; Fig. 3.6B). Plots receiving late-season, but not mid-season, droughts (L,EL) had 42% greater ANPP than plots receiving mid-season drought (M,EM,ML,EML;  $p < 0.05$ ; Tukey HSD; Fig. 3.6C).

### 3.3.3 Plant Community Composition

The proportion of total live biomass contributed by clonal forbs and grasses varied by year and were inversely related (Year:  $F = 7.00_{1,45}$ ,  $p = 0.0112$ ; Table C.9 & Year:  $F_{1,45} = 4.31$ ,  $p = 0.0437$ , Table C.10, respectively). *S. canadensis*, the dominant clonal forb, made up a greater proportion in 2017 ( $56 \pm 4\%$ ) than 2016 ( $41 \pm 5\%$ ), and *A. gerardii*, the dominant grass, was greater in 2016 ( $52 \pm 5\%$ ) than 2017 ( $36 \pm 4\%$ ; Year; Tukey HSD,  $p < 0.05$ ; Fig. D.5B).

The timing of drought, but not its duration, affected the abundances of clonal forbs, other forbs, and legumes. Mid-season and late-season droughts altered relative abundance of clonal forbs (M:L;  $F_{1,45} = 4.30$ ,  $p = 0.0439$ ; Table C.9). Late-season droughts (L,EL) after an ambient-precipitation middle period decreased clonal forb abundance by about 15% compared to late-season droughts that immediately followed mid-season droughts (ML,EML) and by 17% compared to treatments that did not

experience a mid-season or late-season drought (A,E; M:L; Tukey HSD,  $p < 0.05$ ; Fig. D.6A). Non-clonal forbs increased by 4% in late-season droughts (L,EL,ML,EML) compared to other drought treatments in 2017 (L; Tukey HSD,  $p < 0.05$ ; Table C.11; Fig. D.6B). Legumes were altered by early- and late-season droughts depending on the year (E:L:Year;  $F_{1,45} = 5.00$ ,  $p = 0.0309$ , Table C.12; Fig. D.6C), but Tukey HSD tests were unable to reveal any differences between groups. Neither grass nor shrub proportions were affected by drought.

Diversity (invD) was affected by the timing of drought but not the duration of drought. Mid-season and late-season droughts altered diversity within the community depending on the year (M:L:Year;  $F_{1,45} = 6.21$ ,  $p = 0.0165$ ; Table C.13). In 2016, late-season droughts (L,EL) reduced diversity by 30% compared to droughts that either did not (A,E) or did occur from mid-season to late-season (ML, EML; Tukey HSD,  $p < 0.05$ ; Fig. 3.7A). Diversity was impacted by both early-season (E:Year;  $F_{1,45} = 7.87$ ,  $p = 0.0074$ ; Table C.13) and late-season droughts (L:Year;  $F_{1,45} = 9.61$ ,  $p = 0.0033$ ) depending on the sampling year. Diversity was 18% greater in plots that experienced an early-season drought (E,EL,EM,EML) compared to those that did not in 2016 (Tukey HSD,  $p < 0.05$ ; Fig. 3.7B). These differences were no longer apparent in 2017. In 2017, diversity was 17% greater in late-season drought plots (L,EL,ML,EML) compared to all other treatments (Tukey HSD,  $p < 0.05$ ; Fig. 3.7C).

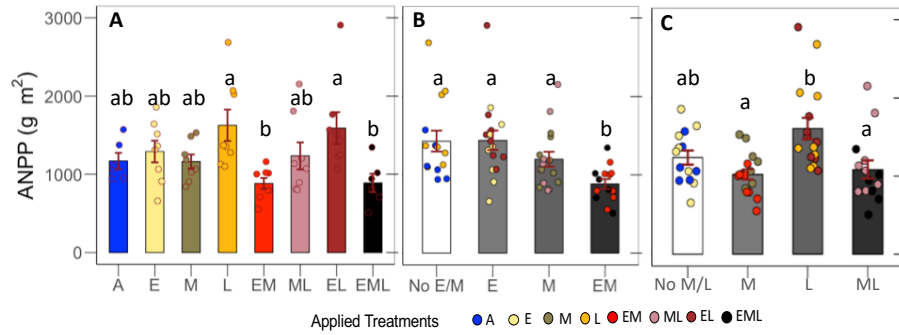


Fig. 3.6.: ANPP by drought treatment. Lowercase letters represent treatments that are statistically similar. Points are represented the same way as described in Figure 4. Bars represent the mean ANPP for each treatment, and error bars represent standard error. (A) ANPP of each applied treatment, (B) ANPP of early- and middle-season droughts, where No E/M includes A and L treatments, E includes E and EL treatments, M includes M and ML treatments, and EM represents EM and EML treatments, (C) ANPP of middle- and late-season droughts, where No M/L includes A and E treatments, M includes M and EM treatments, L includes L and EL treatments, and ML includes ML and EML treatments.

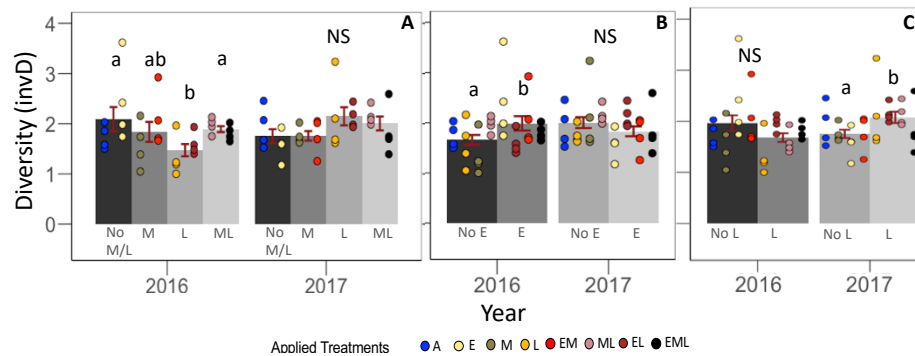


Fig. 3.7.: Timing of drought and diversity (invD). Letters represent statistically significant differences between treatments. Points are represented the same way as described in Figure 4. Bars represent the mean diversity for each treatment group, and error bars represent standard error. (A) Diversity by mid- and late-season drought treatment in 2016 and 2017, where No M/L includes A and E treatments, M includes M and EM treatments, L includes L and EL treatments, and ML includes ML and EML treatments. (B) Diversity by early-season drought treatment in 2016 and 2017, where No E includes A, M, L, ML and E includes E, EM, EL, EML. (C) Diversity by late-season drought treatment in 2016 and 2017, where No L includes A, E, M, EM and L includes L, ML, EL, EML.

### 3.4 Discussion

Contrary to our hypotheses, productivity and diversity were not altered by both the timing and length of drought, as only the timing of drought had an effect on these factors in this system. This is a noteworthy result, as we predicted that longer droughts would have a greater impact on productivity and diversity. It is especially remarkable that the 21-week drought treatment was resistant to changes in productivity and community composition even after two years of extreme drought. To the best of our knowledge, this study suggests that the main driver of productivity and diversity in grasslands is the timing of drought within the growing season, and the length of drought may be inconsequential.

#### 3.4.1 Soil Moisture

Soil moisture measurements in the top 15 cm indicated that treatments created similar droughts in both years and that soil moisture levels were at or near the approximate wilting point of the system. Despite this apparent water stress, the system remained resistant to change in regard to the length of drought. Soil moisture measured at deeper depths in A and EML plots may indicate that plants were receiving water from lower in the profile, although we are uncertain why soil moisture levels were greater below 20 cm. Regardless of the cause of these spatial patterns in soil moisture, these results demonstrate that there was a reduction in soil moisture in EML plots compared to A plots down to at least 1 m in depth.

#### 3.4.2 Productivity

Results from two years of drought treatments show that changes in productivity in this system were driven by the timing of drought, not the length. ANPP was positively correlated with average soil moisture and including the timing of drought in the model significantly improved the fit of this linear regression. Total average ANPP

was greater in 2017 compared to 2016, which was likely the result of the larger amount of precipitation in 2017. Both of these findings align with other grassland studies that found ANPP increases with increasing precipitation (e.g. [38]). An unforeseen aspect of the relationship found in this study was that the timing of drought improved the fit of the linear regression between ANPP and soil moisture, but the addition of length in the model resulted in no relationship.

Mid- and late-season droughts affected the relationship between soil moisture and ANPP. As we predicted, mid-season droughts decreased ANPP, which corresponds with other studies manipulating droughts during similar time periods within the growing season [16, 17, 88]. We hypothesized that mid-season droughts would experience the greatest reductions in ANPP, because this time period corresponds with increased photosynthesis and growth of many species [89, 90]. Numerous studies have demonstrated that drought can reduce ANPP (e.g. [20, 38, 91], but we were not able to find studies that explored the effect of both the timing and duration of drought have on productivity. The few drought studies that explore the how timing of drought impacts ANPP also found that mid-season drought reduced ANPP, but they did not explore how the duration affected productivity [16, 17].

Our study suggests late-season droughts ranging from late-July to early-September have the potential to increase or maintain ANPP compared to droughts at other times during the growing season and ambient conditions, respectively. This is consistent with results of Craine et al. [16], who found that ANPP had no detectable impact on productivity after August. Interestingly, we found that when an early-season drought occurred in conjunction with late-season droughts, ANPP had similar patterns to short, late-season droughts. This indicates that early-season droughts only reduced ANPP in this system when they occurred consecutively with a mid-season drought, but otherwise had no effect on productivity. This supports the results from Denton et al. [17] who found no change in ANPP when a drought occurred early in the growing season, but contradictory to an analysis of a dataset from the same site, including

27 years of data, suggesting that productivity can be reduced during this same time frame [16].

The non-linear relationship found between ANPP and drought length suggests that shorter droughts may actually increase ANPP in this system, and we suspect that this increase was driven by late-season droughts, as early-season droughts did not affect ANPP and mid-season droughts decreased ANPP. Positive growth responses to late-season or shorter droughts were not found for any specific PFT but emerged as the response of the community as a whole. At the community level, ecophysiological and demographic stabilizing processes can minimize and stabilize the effects of drought [78]. These stabilizing processes can include mechanisms related to stress memory, plant interactions, which can include reductions in competition and facilitative effects through plant traits related to temperature and water buffering, and drought tolerance/avoidance [78, 92, 93]. Stabilizing processes are often related to the dominant species of the system [78], in this case, *S. canadensis* and *A. gerardii*, both of which have been found to have mechanisms to tolerate and/or avoid drought stress [94–97].

### 3.4.3 Plant community composition

The plant community had a higher proportion of clonal forbs, primarily *S. canadensis*, in 2017 than 2016, but a lower proportion of grasses, which were primarily represented by *A. gerardii*. *S. canadensis* (clonal forb) and *A. gerardii* (grass) are generally co-dominant in this system with some variation in dominance between years. These shifts in dominance likely resulted from the two major disturbances in 2016, a prescribed burn and trenching of plots. *A. gerardii* has been documented to have vigorous growth post-fire, which explains the high percentage in 2016 [98]. We suspect that the clonal nature of *S. canadensis* resulted in a reduction in growth in the first year, as trenching severed the rhizomes of the clones of this species. In the second year, *S. canadensis* was able to reestablish the rapid growth and vigorous vegetative

reproduction characteristic of this species, particularly during secondary succession, the state of this field site [99]. These two species remained dominant throughout the experiment in all plots, likely the result of the drought-tolerant and/or avoidant nature of both of these species [100, 101].

Alterations to community diversity were also driven by the timing of drought, with no responses associated with the length of drought. Composition of some PFTs was altered by drought timing, but post-hoc analysis did not reveal differences between groups. As expected, early-season droughts resulted in an increase in diversity in the first year of drought, but contrary to our expectations, this difference was no longer found after the second year of drought. This is consistent with other studies that found that plants can become more resistant to repeated exposure to drought through physiological, genetic, or biochemical acclimation, which can be considered a type of stress memory [102–104].

Late-season drought treatments had some expected and unexpected effects on diversity. We expected that there would be a reduction in diversity in late-season droughts, which is consistent with our findings in 2016. Both dominant species, *S. canadensis* and *A. gerardii*, are fast-growing, tall species (approx. max. height 1.3 m and 2.4 m, respectively [99, 105]). These characteristics could have created greater competition for light and space with other species before they could become established, as we originally hypothesized. Late-season droughts were relatively highly productive, and previous studies have demonstrated a negative relationship between ANPP and diversity further supporting the findings from 2016 [32, 106]. In contrast, diversity increased after the second year of late-season drought treatments, regardless of length. We speculate that this may have been a result of stabilizing mechanisms within the plant community, such as stress memory of other species and species coexistence processes [78, 93, 102, 103]. Ecological stress memory consist of species, their interactions soil properties, and other site characteristics and determines how a community reacts to stress. Stress memory involves mechanisms, including epigenetics

and acclimation, that improves the response of a plant to a future stress experience after being exposed to a similar stress [103].

### 3.5 Conclusions

Timing of drought was a better indicator of productivity and plant community responses than length of drought in this mesic prairie ecosystem. The length of drought had a weak relationship with productivity, but not with community properties. Early-season droughts had no impact on productivity, and diversity increased as a result of early-season drought in the first year, but not the second. Mid- and late-season droughts had the greatest impact on productivity, where mid-season droughts decreased productivity and late-season droughts either had no effect or increased productivity. Mid-season drought did not alter diversity, but late-season droughts altered community structure after a second year of similar drought conditions. These results appear to indicate that there are some stabilizing mechanisms occurring in this system, including drought tolerance/avoidance, species co-existence (plant-plant interactions), and stress memory [78, 93, 102, 103].

As the climate continues to change and precipitation becomes increasingly variable, it will be important to understand how drought conditions impact ecosystem and community responses, particularly because drought research has found conflicting responses in similar ecosystems [3, 19]. The results from this study highlight two aspects of drought that has been largely ignored, the timing and length of drought, may play an important role in future C cycling and plant community composition in restored grasslands. If the major driver of ecosystem and community responses is the timing of drought, then researchers should consider timing when designing drought-related or rainfall variability experiments.

Plants in grassland communities interact in complex ways, and interactions between species and their environment vary dramatically [3, 8, 78]. More experimental studies that explore the relationship between drought duration and timing will pro-

vide greater insight into the potential importance of the timing of drought and can be used to improve models and restoration techniques. Further, a better understanding of the traits that correspond to drought tolerance/avoidance, species co-existence process, and stress memory will enhance our understanding of the stabilizing mechanisms that allow for resistance and resilience of grassland community. This information can be used to better inform management practices for prairie restoration.

## 4. COMMUNITY RESPONSE TO EXTREME DROUGHT (CRED): A FRAMEWORK FOR DROUGHT-INDUCED SHIFTS IN PLANT-PLANT INTERACTIONS

### 4.1 Introduction

#### 4.1.1 Current research on drought-induced plant community reordering

Climatic change is creating new abiotic and biotic conditions in many terrestrial ecosystems, inducing community shifts that alter ecosystem structure and function [3, 107]. Many regions are expected to experience increases in the frequency and/or magnitude of droughts and in regions where drought intensification does not occur, increased precipitation variability may lead to more frequent dry periods [26, 38, 108]. Episodic disturbances like droughts are anticipated to cause more rapid and lasting effects on plant communities than more gradual but chronic changes, such as rises in atmospheric CO<sub>2</sub> or decreases in mean annual precipitation (MAP) [13, 20, 21, 26, 38, 82, 107]. While abiotic stressors caused by drought drive community change, plant-plant interactions influence community-level responses to drought by mediating the effects of these stressors [109].

Studies examining changes in community composition following drought often focus on species richness, but few address the mechanisms of abundance change (species re-ordering, Smith, 2011) and species turnover through time [110]. Focusing solely on richness can mask biologically important changes in species composition, which can have lasting legacy effects on plant communities, potentially affecting post-drought recovery and responses to future drought conditions [107]. For example, Hoover et al. [20] found that species richness was not altered by drought; however, the system shifted from a grass-forb co-dominated community to a grass-dominated community.

Concurrent environmental stressors, such as drought, may cause communities to cross thresholds that delay or prevent recovery [21, 107, 111, 112]. The underlying mechanisms for changes in community composition may be physiological or may act at the community level through alterations to plant-plant interactions that guide the direction of succession after drought [112, 113].

Drought-induced vegetation shifts have been captured in paleohistorical records as well as contemporary observational and experimental studies across a variety of biomes [108]. While these studies have furthered our understanding of drought-induced community reorganization, each has limitations. Paleorecords, such as pollen in sediment cores, describe the existence of vegetation changes at centennial scales, but their temporal resolutions are commonly too coarse to be ecologically informative [108]. Experimental droughts provide important information about community change at finer timescales; however, they rarely observe the community for extended periods of time and do not mimic important aspects of natural drought, such as increased vapor pressure deficit (VPD) and high heat conditions [114, 115]. Observational studies that explore historical, natural droughts provide insight into the temporal trends of community reordering both during and after drought. These studies allow us to observe changes at fine temporal scales that are ecologically relevant and include abiotic conditions that are difficult to simulate. In Table 4.1, we highlight several studies in herbaceous systems, which typically respond more rapidly to environmental change than systems dominated by longer-living species, e.g. forests. In these examples, plant communities shifted substantially and composition stabilization took several years. These studies demonstrate that variability in response times in similar community types, providing evidence that resistance and resilience of community composition varies depending on drought severity and the biotic and abiotic characteristics of the system [78].

The mechanisms for the temporal evolution of community drought responses are not fully understood, but biotic interactions are increasingly recognized as potentially important drivers of community composition [22–25]. Previous studies examining the

roles of biotic interactions and community composition have focused on interactions between trophic levels, such as herbivory (e.g. [116,117], while the role of plant-plant interactions, notably facilitation, have been largely ignored.

Table 4.1.: Papers quantifying the response and recovery of herbaceous communities experiencing naturally occurring droughts

<i>Authors</i>	<i>Location &amp; System</i>	<i>Drought Conditions Duration (years)</i>	<i>Recovery (years)</i>	<i>Definition</i>	<i>Compositional Change Greatest During drought change</i>	<i>After drought</i>
<b>Stampfli &amp; Zetter (2004)</b> [18]	Mesobromion Grassland; Ne- grentino, Switzer- land; MAP: 1300 mm	3	9	Max of days with less than 10 mm of rain	After No shift in relative cover of grasses and forbs	Grasses decreased following drought. Forbs replaced grasses. System stabilized in 4 years
<b>Tilman [118]</b>	Grassland; Min- nesota, USA; MAP 815 mm	2	6	3rd worst drought in 150 years	During Grasses: C4 increased, C3 decreased. Legumes de- clined	C4 & C3 grasses returned to pre-drought levels after 6 years; legumes increased
<b>Rondeau et al. (2013)</b> [119]	Short grass steppe; Colorado, USA; MAP: 302 mm	2	7	Worst drought in 1100 years; 2003: 60% below average	Both Shrubs: decreased slightly; all species declined equally; Grasses: Total cover de- creased dramatically; sub- dominant species becomes dominant	Shrubs: Total cover 38% higher; driven by 59% increase in one species; Grasses: Total cover did not recover, subdominant species maintained new domi- nance
<b>Albertson &amp; Tomaneck, 1965</b> [120]	Schizachyrium scoparium dom- inated commu- nity; Kansas, USA; MAP: 582 mm S. scoparium and Andro- pogon gerardii co-dominated community; Kansas, USA; MAP: 582 mm				Both Drought 1: S. scoparium decreased; rare more xeric grass increased; Drought 2: Only slight changes  Both Drought 1: Initial co- dominant grasses decrease; replaced by different co- dominants. Drought 2: No dramatic change	Recovery 1: S. scoparium increased; 3 co-dominant grasses. Recovery 2: S. sco- parium rebounds, one of other co-dominants persists, other declines. Recovery 1: One of initial co- dominants recovers, the new co- dominants decrease. Recovery 2: Grass increased in recovery 1 continues to increase, and the two new grasses stabilize

#### 4.1.2 The role of plant-plant interactions in shaping communities

Competition is the most studied biotic interaction both within and between species, but fewer studies explore the balance between competition and facilitation [121]. While the concept of facilitation, positive interactions among species, was originally proposed over a century ago [122], the introduction of the stress-gradient hypothesis (SGH; [123, 124] led to heightened interest in the topic [22, 121]. The SGH proposes competitive interactions are more prevalent and intense under low-stress conditions, while facilitative interactions are more frequent under high-stress conditions [123]. Refinements to the SGH acknowledge that the intensity and importance of facilitation may be highest under moderate stress and may decrease or even collapse under severe conditions [125–128].

Empirical studies and meta-analyses have found support for [24, 126, 129–134] and evidence contradicting [135–137] the SGH, which have led to refinements of the model [137]. A meta-analysis by He et al. [24] found increasing stress led to shifts towards facilitation or decreased competition across climates and ecosystems, though the strength of facilitation was system-dependent, and few studies have examined tropical dry forests and rainforests.

Despite evidence for increased facilitation under increasing stress, the vast majority of plant-plant interaction studies still focus on competition [121]. Generally, the literature on facilitation is dominated by variations in interactions along environmental gradients [121]. Few studies have explored plant-plant interactions across time (e.g. [138], as they apply to drought stress (e.g. [139]), or under more favorable conditions (e.g. [109]). Even fewer studies have explored plant-plant interactions as water stress decreases after drought (e.g. [139]).

Stress tolerance and competition for resources are often considered the primary determinants of compositional change in response to drought [121]. Competition is a negative response that hinders growth or survival of other plants within the community, whereas stress tolerance is an individual's ability to buffer against stress and

involves physiological responses to drought [140]. While there are many physiological responses to drought (e.g. stomatal closure), these tend to be species-specific and can manifest as facilitative mechanisms for neighboring plants [141, 142].

Facilitation can protect communities against drought through habitat modification, resource enhancement, provision of a refuge from predators and competitors, and recruitment enhancement (Fig. 4.1; [23, 121, 143]). While competition and stress tolerance clearly play important roles in community reorganization, facilitation may also have a strong influence. Thus, frameworks for community-level drought responses across time should incorporate facilitative plant-plant interactions, as stress levels change continuously and often dramatically during and after drought.

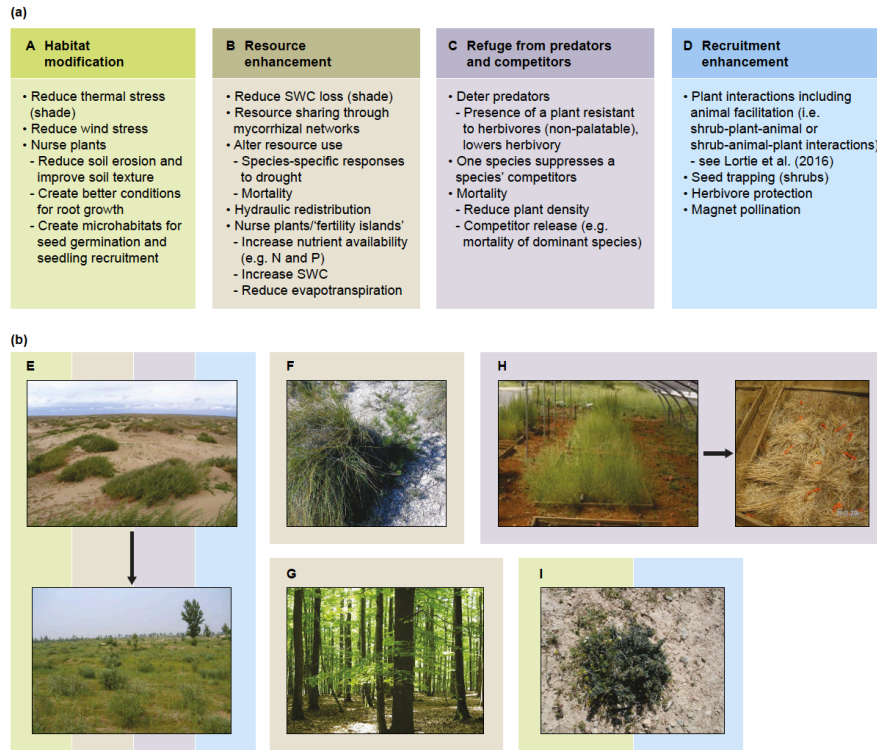


Fig. 4.1.: (a) Potential facilitative mechanisms that occur within plant communities [23, 121, 129, 143]. (b) These pictures provide examples for the outlined facilitative mechanisms. The colors behind each picture corresponds to the mechanisms outlined in part (a). (E) Shifting sand dune (top) were restored using remnant shrub canopies (Photo from Zhao et al., 2007 [144]). (F) Adult individuals of tussock grass facilitated saplings (Maestre et al., 2003 [145]; photo from Brooker et al., 2008 [23]). (G) *Fagus sylvatica* was more resistant and resilient to drought stress when *Quercus petraea* were present (Photo from Hans Pretzsch; [146]Pretzsh et al., 2013). (H) Live grasses (left), competitors of shrubs, become facilitative through mortality (right; labeled with orange tape) (Photo from Victor Resco de Dios; Resco de Dios et al., 2014 [139]) (I) *Gymnocarpus decander* facilitated annual vegetation (Photo from Pierre Liancourt; Brooker et al., 2008 [23]).

## 4.2 The Community Response to Extreme Drought (CRED) framework

Measures of ecosystem function, such as aboveground net primary productivity (ANPP), often respond rapidly to the onset of extreme drought and recover rapidly [20, 79, 147]. Conversely, plant community reordering can persist for years following an extreme drought (e.g. Table 4.1; [148, 149], suggesting that community-level effects may be better indicators of drought severity [107]. Altered plant-plant interactions may play an important role in driving community dynamics and species co-existence during and following drought [109, 149].

Recent research has shown that plant-plant interactions can shift towards facilitation not only in locations with permanently harsh climates, but also during and after episodic drought in a variety of settings (Table 4.2; [23, 24, 78, 121]). Here, we propose the Community Response to Extreme Drought (CRED) framework, which transfers some of the spatial concepts from the SGH to the temporal progression of drought. CRED explores plant-plant interactions as water stress increases during drought and decreases through recovery and suggests how these interactions may influence community reorganization and stabilization after drought (Fig. 4.2).

Table 4.2.: Studies exploring plant-plant interactions in during drought.

Authors	Natural system (x) /# of species	Natural drought	Removal experiment	Seeds planted	Assessment of facilitation	During drought	After drought (years)	Observed mechanisms
<b>During drought</b>								
Cipriotti, et al. 2008 [150]	x			x	Seedling success	x		Facilitative role of adult plants on grass seedlings during drought
Grant et al. 2014 [109]	5				Individual and community biomass	x		Positive effect on all species except the legume during drought due to release from competition
Jentsch et al. 2011 [19]	2-4				Productivity	x		Drought induced complementary plant-plant interactions; Increase in facilitative and competitive effects, species-specific
Khan, et al. 2014 [151]	3				Productivity	x		No facilitation of community productivity under drought; Species-specific facilitation from legumes under climate manipulations
Kitzberger et al. 2000 [152]	x	x			Seedling success	x		Establishment of species requires nurse shrubs during years with substantial drought stress
Mariotte et al. 2013 [153]	x		x		Productivity			Presence of subordinates facilitated regrowth of dominant and transient neighbors during drought
Resco de Dios et al. 2014 [139]	x			x	Seedling success	x		Drought positive effect on woody plant recruitment through mortality of competitive grasses passive facilitation
Sthultz et al. 2007 [154]	x	x			Growth and survival of juveniles	x		Positive effects on juvenile tree survival and growth in high-stress sites with shrub cover; opposite effect in low-stress sites

Table 4.3.: Studies exploring plant-plant interactions after drought and during and after drought.

Authors	Natural system (x) / # of species	Natural drought	Removal experiment	Seeds planted	Assessment of facilitation	During drought	After drought (years)	Observed mechanisms
<b>After drought</b>								
del Ca-cho & Lloret, 2012 [155]	x	x			Seedling success		x	Drought-induced canopy dieback increased establishment of woody species; pioneer shrubs facilitate establishment of late-successional species
Lloret et al., 2013 [149]	x	x			Plant growth juveniles		x	Juveniles less damaged beneath dense vegetation canopy during drought; Post-drought growth higher in juveniles in open-spaces
<b>During and after drought</b>								
Pretzsh et al., 2013 [146]	x	x			Annual basal area of trees	x	27/8	Species-specific facilitation in mixed stands (oak positive effect on beech); Temporal example of SGH
Seifan, et al., 2010 [130] (b)	x		x		Seedling success	x	x	Positive effect of drought on shrub seedling establishment (competitive release from annuals)
Tielborger & Kadmon, 2000 [135]	x	x			Demographic responses of 4 annual species	x	2	Shrubs limited emergence and reproduction of understory plants during drought; Facilitation increased following drought

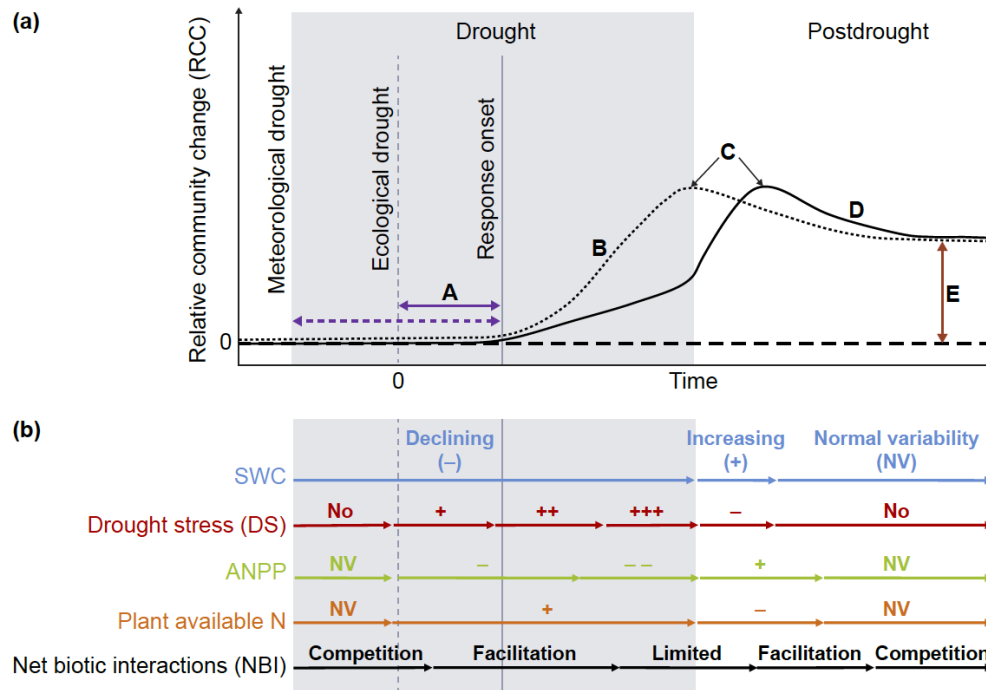


Fig. 4.2.: (a) Conceptual framework for plant community responses to extreme drought (top panel). The grey area indicates the start of a meteorological drought. At time = 0, plants start to respond to the drought at an individual level. The time between individual to community level response (A) depends on a specific systems ability to resist drought stress. The purple lines indicate the two ways that resistance can be viewed from: the start of the ecological drought (solid line) or the start of the meteorological drought (dashed line). The rate of RCC (B) is system-dependent, here illustrated by a fast-responding(dotted line) and slow-responding(solid line) system. The timing of peak community change (C) may vary between systems. Rate and magnitude of post-drought recovery (D) is system-dependent and varies with the rewetting scenario (see also Fig. 4.4). The community finally stabilizes at a state similar to pre-drought or may experience lasting changes in composition (E). (b) The bottom panel shows temporal trajectories and stages of five key drivers for RCC: soil water content (SWC), drought stress (DS), aboveground net primary productivity (ANPP), plant available nitrogen (N) and net biotic interaction (NBI).

#### 4.2.1 Assumptions and definitions

In CRED, the general term net biotic interactions (NBI) refers to the balance between interactions, as facilitation and competition occur simultaneously within a

community [123]. NBI can shift along a continuum from net negative (competitive) to net positive (facilitative). The SGH initially proposed that the frequency of interactions changes under stressful conditions; however, frequency does not necessarily translate into the intensity of interactions and only qualitatively addresses the importance of interactions [127, 130, 156, 157]. Intensity describes the absolute impact of interactions on plants, whereas importance describes the effects of neighbors on a plant in relation to abiotic factors. This distinction between intensity and importance allows for the differentiation between biotic and abiotic drivers of community change, respectively [127, 130, 156, 157].

Drought can be defined from multiple viewpoints, so we define drought from two perspectives: (1) meteorological, a prolonged absence or marked deficiency of precipitation [26] and (2) ecological, an episodic deficiency in water availability that pushes ecosystems beyond their threshold of vulnerability and, in plants, results in the continuous loss of water through transpiration until stomatal shutdown [158–160]. Prolonged meteorological drought will eventually elicit physiological responses of plants to water limitation, and this indication of drought stress marks the onset of ecological drought. In CRED, we only consider droughts that qualify as extreme climatic events (ECEs; *sensu* [107]); that is, events that result in changed community composition.

Time in CRED is a relative measure, as plant communities can respond to extreme drought in time frames of weeks or months (e.g. [161]) or years (e.g. Table 4.1). While time frames vary, the reference period is considered to be the typical generation time of the dominant species, including its persistence in the seed bank [78, 108]. If there is a shift in vegetation, we would expect an abrupt change in the abundance of species or plant functional types (PFT), e.g. grasses, forbs, trees, etc., exceeding the range of natural temporal variability [20, 78].

We use the term relative community change (RCC) to illustrate the degree of compositional change arising through changes in abundance, extirpation and/or immigration. RCC can be visualized, or measured, as the distance between two commu-

nities in multivariate space, and is a generalizable way to describe temporal variation in community composition [162].

Resistance is the capacity of the system to withstand change during extreme drought, and resilience is the degree to which the system recovers to its initial composition [79]. In the theoretical communities used for this framework, both communities have the same resistance (A in Fig. 4.2a) and resilience (E in Fig. 4.2a) to drought, but the trajectory of community change is different (B-D in Fig. 4.2a), where one community experiences most of the change during drought (dotted-line; e.g. [118] Tilman, 1996) and the other experiences most of the change after drought (solid-line; e.g. [18]). For systems that are highly resistant, we expect a longer lag time between the onset of ecological drought and changes in the relative abundance of species (i.e. a greater distance of A solid, line in Fig. 4.2a). In practice, the onset of ecological drought is rarely recorded; therefore, resistance can also be considered from the start of the meteorological drought (A dashed, line in Fig. 4.2a).

#### 4.2.2 Shifting from meteorological to ecological drought

At the onset of meteorological drought, soil water content (SWC) begins to decline, but plants are not drought stressed. During this phase, the NBI is negative, as plants compete for limiting resources at normal rates and water stress remains low. As the meteorological drought continues, SWC declines to a point at which plants begin to respond physiologically and ecological drought begins, indicated by time zero in Fig. 4.2. As plants become increasingly drought-stressed, we hypothesize that NBI will shift from competitive to facilitative (Fig. 4.2b). The intensity of competition will likely relax because of mortality and differential use of resources [125], which could increase the importance of physiological responses and lead to stronger relative facilitation.

Plant functional traits (hereafter traits) such as growth forms, life histories, life stage, physiological characteristics, and origin, can provide insight into the strength

and nature of plant interactions in low stress conditions [24]. For example, in low stress conditions, grasses and herbs are often highly competitive, whereas trees exhibit strong facilitative mechanisms. As conditions become highly stressful, regardless of traits or magnitude of competitive responses, plants typically show decreasing competition and increasing facilitation [24].

While changes to plant-plant interactions are system-dependent, we expect facilitative mechanisms to increase in intensity and importance during drought, particularly resource enhancement, habitat modification, increase in space/light availability, refuge from predators and competitors (Fig. 4.1a (A-D), Fig. 4.3b). As mortality increases and growth decreases, we expect competitive release. We anticipate that these facilitative mechanisms will outweigh competition for resources. Reductions in competition can manifest as indirect facilitation when species-specific responses to drought leave behind resources for other species (Fig. 4.1b). For example, isohydric behavior has been observed in  $C_4$  grasses, temperate hardwoods, and other species of gymnosperms, where plants reduce water consumption and growth in the early phases of drought stress, leaving behind unused resources for anisohydric plants [92, 146].

Drought-resistant systems, such as those with many drought-tolerant species, will likely maintain net competitive interactions for longer periods during the early stages of a drought. In some cases, the presence of a single species can enhance the drought resistance of a community (Fig. 4.1). For example, in a removal experiment in a grassland, the presence of a subordinate species facilitated the growth of dominant and transient species in the community during drought, increasing the resistance of the system [153]. These examples demonstrate that plant-plant interactions may be an important factor in determining a community's resistance to drought.

### 4.2.3 Onset of community change

As a drought extends over time, we anticipate that more species will reach drought tolerance thresholds [125, 127]. Thus, we expect that both intra- and interspecific com-

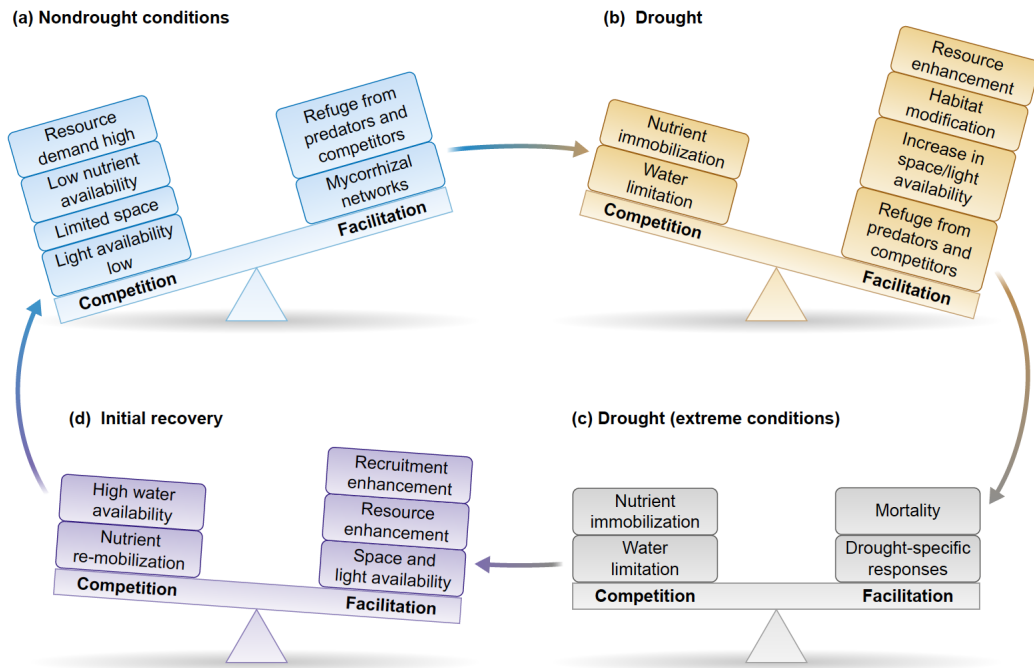


Fig. 4.3.: Temporal transitions of net biotic interactions (NBI) through the course of an extreme drought. NBI refers to the balance between plant-plant interactions, as facilitation (+) and competition (-) occur simultaneously within a community. Letters a-d correspond to different time periods over the course of an extreme drought. The angle at which the scale is leaning represent the relative importance and/or strength of the plant-plant interaction. The boxes on the scale suggest the potential mechanisms driving the interactions towards either negative, positive, or NBI.

petition will continue to relax, as growth is reduced further and mortality increases (B in Fig. 4.2a). The combined effects of habitat modification, competition release through increases in mortality, reduced competition for available resources, and resource modification cause NBI to become more facilitative (Fig. 4.1a (A-C)). In a savanna, Resco de Dios et al. [139] found active competition continued under drought conditions when live grasses were present, but once grass canopies died, strong passive facilitation for shrubs occurred because areas with dead grasses had higher SWC than bare soils.

As the meteorological drought persists beyond the point at which NBI shifts from competitive to facilitative, we predict that plants will still experience net facilitative

NBI, although the strength of the facilitative interactions may diminish through time as drought intensifies [125,127]. As ANPP declines, nitrogen (N) begins to accumulate in the soil as plant and microbial activity decouple and reduced SWC limits the mobility of N [14,41].

Plant interactions are expected to weaken as the drought intensifies, and traits and drought tolerance become the biotic determinants for plant survival, further increasing RCC. Under very extreme droughts, we expect the importance of biotic interactions to be reduced and interactions to be minimal. As proposed in the hump-shaped model for plant-plant interactions [125], if stress levels become extreme enough, facilitative mechanisms may decrease or even collapse; the intensity and importance of facilitation is highest under moderate stress [125, 127, 128]. Therefore, in line with the hump-shaped model, if conditions become extreme enough, we hypothesize that NBI will be near zero or may become negative (Fig. 4.3c; Fig. 4.4d, red line).

#### 4.2.4 Post-drought recovery

We define the end of a meteorological drought as the time at which the SWC rises above the wilting point of the dominant species in the community, which will depend on the nature of rewetting event(s) and site-specific characteristics. Plant communities do not immediately respond to the amelioration of water stress, and the response time of the community will vary, depending on a variety of potential modifiers (D in Fig. 4.2a; see also Fig. 4.3 and Table 4.3). As stress is alleviated, we expect that plant-plant interactions will respond in a manner that is essentially the inverse of the SGH, and facilitative NBI will increase (Fig. 4.2b), although interactions will likely be weaker than before or during the drought, as competition is ameliorated by both the reduction in competitors and relatively high resource availability (Fig. 4.3d; Fig 4d). Primary facilitation mechanisms at this stage will differ from those during the drought including a shift from mechanisms that facilitate survival to those that facilitate growth and recruitment (Fig 4.1).

As favorable growth conditions persist, plant competition likely increases, generally resulting from the reduction of available resources through increased N uptake by both plants and microbes, and increased plant growth [163]. The rate of N reduction and increase in productivity likely depend on the post-drought rewetting rate of the soil [164, 165]; Fig. 4.4). As climate, nutrient availability, productivity, and other conditions return to normal (i.e., within their previous ranges), compositional changes begin to stabilize.

We consider the community to have stabilized when it maintains normal variability in community composition from year to year with clear dominant and subdominant species, and NBI shifts back to its pre-drought status (E in Fig. 4.2a). Drought-induced changes to plant composition can result in changes at the community level, through the establishment of a new dominant species or PFT, such as a shift from a grass-dominated community to a forb-dominated community [18]. These effects can also shift the community to a new ecosystem type, such as from grassland to savanna [139]. These types of community changes (i.e., state changes) will likely generate new plant-plant interactions and could have important implications for ecosystem processes and trophic interactions.

Table 4.4.: Factors influencing community resistance and resilience to drought and related studies.

Potential Modifier	Related Observational Studies
<b>Ecosystem</b>	
1. Precipitation regime (MAP and variability)	[38, 79, 126, 133, 134]
2. Ecosystem fertility	[34, 151, 166, 167]
<b>Soil Properties</b>	
1. Texture, depth, and infiltration rates	[168–171]
2. Plants roles in infiltration rates	[150, 172]
<b>Environmental conditions contributing to stress</b>	
1. Time-scale and intensity of drought	[120, 173]
2. Vapor pressure deficit	[115]
3. Heat	[76, 104]
4. Disturbance (e.g. fire/grazing)	[76, 174]
<b>Landscape</b>	
1. Land use/age	[175, 176]
2. Heterogeneity	[177, 178]
<b>Plant assemblage</b>	
1. Niche partitioning (resources, predators, time, and space)	[179–182]
a. Diversity (PFT/species)	[19, 118, 183, 184]
b. Community composition/species-specific traits	[109, 146, 151, 185]
c. Storage Effect	[173, 186]
2. Stability of dominant functional type/species	[20, 82, 119]
3. Timing of drought (life stage)	[128, 187]
4. Intraspecific trait variability/Stress memory	[161, 188]
5. Lifespan of community/plants	[148, 166, 189]
<b>Multi-trophic interactions</b>	[116, 117]

### 4.3 Post-drought rewetting rates: system and community recovery

#### 4.3.1 Recovery and the importance of abiotic and biotic conditions

The recovery period immediately following a drought or multiple drought events is a critical time for community reorganization, as exhibited by changes in plant community composition highlighted in the case studies in Table 4.1. These case studies demonstrate that drought events are often not a singular event, can occur over multiple years, and lapses between drought events can create multiple recovery periods (e.g. [120]). The exact relevant time period for recovery depends on site-specific variables influencing infiltration rates, such as soil texture, climate, and community composition (see section IV), and on the temporal sequence of drought events, such as frequency, recurrence, and lapses between drought events. While specific characteristics of plant taxa can determine their ability to respond to post-drought conditions, variability in resource dynamics will influence which suites of traits are most advantageous, thereby driving compositional changes during the recovery period [142].

The effects of post-drought rewetting rates on plant-plant interactions and community composition have received relatively little attention, but many ecosystem processes are heavily reliant on water availability [190]. Rewetting rates will influence the temporal dynamics of water, nutrient, and light availability, plant growth, and, therefore, the dynamics of NBI during community recovery. Nutrient limitation is common in many ecosystems, most frequently in the form of limitations in N or phosphorous (P), or NP-co-limitations [191]. We focus on soil N during post-drought rewetting as a result of its mobility in the soil and because it is more directly affected by climatic conditions than P [191].

During a drought, inorganic N typically accumulates in the soil as a result of decreased plant and microbial uptake, despite lower mineralization rates [41, 190, 192] (. Whether this translates into enhanced productivity or a lag in productivity response depends on whether the community is able to capitalize on the accumulated N, or if this N is lost from the system before plants can benefit (Fig. 4.3; [193] .

Different rewetting scenarios, through their effects on SWC and soil N, are likely to influence not only the temporal dynamics of plant-plant interactions, but also the relative strength of plant-microbe interactions, affecting community composition, retention of ecosystem N, and carbon sequestration [41].

### 4.3.2 CRED and resource recovery following drought

We predict that rewetting rates are negatively associated with N availability, through both abiotic mechanisms, such as volatilization, leaching, and resource remobilization, and biotic mechanisms by affecting N demand and the plant community's uptake ability (Fig. 4.3b). During recovery, maximum water and N availability may occur at different times, and this asynchrony could explain observed lags in the response of ANPP to increases in water availability [193]

When dry soils are rewetted, there is an increase in decomposition of organic matter, which may increase N mineralization [190]. In contrast to the rapid metabolic response of microbes to rewetting, recovery of maximum photosynthetic rates in plants is a slower process. For example, perennial C<sub>4</sub> grasses of a tallgrass prairie did not attain maximum photosynthetic rates for a week or more following drought, despite recovery of leaf water status and stomatal conductance [194]. Reduced leaf N concentrations can persist for a similarly long time after rewetting [194]. A result of the differential responses of plants and microbes to rewetting rates is additional N accumulation, which we predict are more prominent under slower rewetting scenarios (Fig. 4.3b; dotted and dashed lines); this consequently drives the dynamics of NBI during the post-drought period (Fig. 4.3d).

During rewetting, plant available N is susceptible to loss, which is likely exacerbated by faster rewetting (Fig. 4.3b, solid line; [192]). Under the faster rewetting scenario, we expect faster initial recovery of ANPP, as photosynthesis and water uptake ability can respond relatively quickly to increased SWC [40, 194] (. However, recovery of N uptake ability is not immediate, and the lag can vary widely across

taxa [40, 195]. Relatively high ANPP early in the recovery period increases aboveground competition for space and light, while low available N increases belowground competition for N [196]. Combined, these processes accelerate the transition back to net competitive plant-plant interactions (Fig. 4.3d; solid line). As the recovery period progresses following rapid rewetting, reduced N availability likely drives stronger competition belowground and depresses ANPP recovery rates (Fig. 4.3c; solid line).

Conversely, at slower rewetting rates, we expect soils to retain more inorganic N prior to and during ANPP recovery, as less leaching is likely to occur (Fig. 4.3b, dashed and dotted lines; [40]). When SWC is limiting for an extended period, we expect slower initial ANPP recovery as water may still limit growth (Fig. 4.3c, dashed line). We expect competition for aboveground resources (space/light) and plant available N to be relaxed and develop more slowly and for facilitative mechanisms to remain the primary NBI for a longer period of time under slower rewetting scenarios (Fig 3d, dashed and dotted lines). Gradual rewetting may reduce the competitive advantage of species that respond rapidly to renewed soil water availability by increasing the strength of facilitation during this period and may benefit taxa that use N less efficiently in the longer term [192, 197].

### 4.3.3 Mechanisms for positive NBI during initial recovery

Many lines of evidence suggest that facilitation plays important roles at times of increasing stress (e.g. [129–134, 146, 150]); however, studies that examine the role of facilitation as drought stress becomes relaxed are less common (Table 4.2). We hypothesize that facilitative interactions will be more important than competitive interactions both during and immediately after drought (Fig. 4.1; Fig. 4.3d; Fig. 4.4d). Lloret & Granzow-de la Cerda [149] found that seedling establishment of dominant shrubs was enhanced following drought and suggested that facilitative interactions may enhance species co-existence and drive community dynamics. The processes in post-drought plant communities are expected to be similar to those identified during early suc-

cession, and interactions would lead to the eventual dominance and co-existence of superior competitors [113]. Following a severe disturbance such as a drought, forest sites maintain high levels of structural complexity and spatial heterogeneity and retain legacy materials, such as a seed bank [198]. In non-forest systems, we might similarly expect recovery to be characterized by high species diversity, including survivors, opportunists, and drought-tolerant species, and organic material/structures that can create habitats for surviving and colonizing species [78, 112, 198].

Due to limited direct evidence for facilitation following extreme drought, we also include a null hypothesis that NBI will not become positive after drought (Fig. 4.4d, red line). In this scenario, facilitative mechanisms still act simultaneously with competitive mechanisms, but net competitive mechanisms are either equal to or greater than net facilitative mechanisms. While this may be the case, we suggest that at least in some systems NBI will lean towards the positive side after a drought. Figure 4.3d illustrates how this may occur using the facilitative mechanisms outlined in Figure 4.1a (A, B, D). Post-drought facilitation may become the dominant interaction following a drought through several mechanisms: (1) species composition (e.g. [144, 185]), (2) reduced competition (e.g. [18, 148]), (3) enhanced recruitment (e.g. [18, 144]), and (4) altered resource availability (e.g. [144, 199]). For example, in a *Sphagnum* peatland, seedling emergence was enhanced in the vicinity of tussocks [185]. This phenomenon was observed both before and after the drought but collapsed during the drought, providing evidence for recruitment enhancement following drought (Fig. 4.1a (D)), as well as the collapse of facilitation under extreme drought (also see Fig. 4.3c).

During the initial phases of recovery, the intensity of competition is relaxed compared to non-stressful conditions (Fig. 4.3d vs. 3a). Drought-induced mortality results in reduced plant densities and therefore reduced competition [78]. Plant traits have been linked to facilitative effects, and physical traits related to temperature and water buffering may reduce mortality during ECEs, such as drought. In forests, per capita soil water availability can increase with mortality, which may promote survival after the drought (Fig. 4.1a (A); [78, 199]). A recent modelling study es-

established a physiologically meaningful metric for hydraulic failure risk for chaparral species in southern California and species-specific changes in hydraulic risk that could induce shifts in composition [200]. These types of models may be beneficial for understanding species sensitivity across timescales of rainfall variability to improve our understanding of community responses to drought.

#### **4.4 Site-specific characteristics influencing community resistance and resilience**

While we expect extreme droughts to induce similar shifts in NBI across ecosystems, the timing and rate of change will be affected by the intensity, duration, timing, and recurrence of drought, by ecosystem characteristics, and by their interaction. These site-specific characteristics drive community resistance and resilience following extreme drought can be highly system-specific and require a deep understanding of the mechanisms driving community composition in a particular system [38]. We present a non-exhaustive overview of these factors (Table 4.3), which aims to emphasize the most widely recognized and generalizable characteristics influencing community reorganization. In the following sections, we highlight some of the main abiotic and biotic factors thought to influence drought-induced community composition change and system-wide resistance and resilience. We also discuss how ecosystem factors may modify the rate of drying and rewetting within a system and ways plant community composition at the onset of drought may affect the intensity and importance of plant-plant interactions.

##### **4.4.1 Ecosystem properties contributing to resistance/resilience and drying/rewetting rates**

Physical attributes such as moisture regime and soil characteristics can strongly influence a community's resistance and resilience to drought conditions [79, 171]. Climatic gradients (e.g. MAP) drive spatial variation in richness and composition of

plant communities and generate differential sensitivity in responses to drought; systems with a higher MAP generally support higher diversity, which in turn increases community stability [38]. In a synthesis of grassland sites across the U.S., Cleland et al. [189] found that species turnover rates were higher in arid systems that had a high proportion of annual species. Hallett et al. [201] suggest that mechanisms behind community stability vary in importance across environmental gradients, and the key driver of stability in sites with high MAP was species richness. Conversely, in systems with high precipitation variability, compensatory dynamics were more important for stability, such that a decline of stress-intolerant species was compensated for by growth of others [201].

A recent meta-analysis found that MAP was a good predictor of resistance to extreme drought in both grasslands and forests and indicated that physiological mechanisms may determine resistance [79]. However, the relationship for resilience to extreme drought with MAP was positive in grasslands and negative in forests, which may be driven by differences in plant residence time, plant architecture, and drought strategies. Dry grasslands may have low resistance and resilience as a result of general water-limitation or greater mortality than mesic systems [79]. Butterfield et al. [137] found that the difference between soil moisture under shrubs and in gaps decreased along an aridity gradient when long-term averages were considered, contradicting the SGH. However, when extreme years were considered, positive effects of shrubs on soil moisture were greatest at intermediate points along the aridity gradient, which is consistent with the hump-shaped model of plant-plant interactions [125, 137, 202]. These patterns were contingent on soil type, where plants had stronger effects on water availability in coarse soils, whereas physical properties were more important in fine soils [137].

While few studies have focused on the role of soil texture in modulating the effect of droughts on community composition, [203] found that soil texture affected the proportion of ANPP contributed by different PFTs, demonstrating that soil texture plays a role in community compositional changes. In a semi-arid desert grassland, [170]

found that coarse-textured soils rewetted faster, had lower soil water potential, and did not maintain soil water content as long as finer soils. Soils with more silt and clay retain more N, in the form of  $\text{NO}_3^-$ , than sandy soils [204]. Drought was found to reduce the maximum water-holding capacity of hydric and mesic heathland soils, apparently as a result of changes to soil texture [205]. These findings demonstrate how soil texture could play an important role in SWC and nutrient availability under drought-induced community change, altering resource availability both during drought and under different rewetting scenarios (Fig. 4.4).

Differences in community structure along precipitation gradients can also impact soil hydraulic properties through the presence of macropores, or soil cavities that can be created by decaying roots. Macropores can increase infiltration capacity and rate and, therefore, speed up soil rewetting. Macropores created by roots depend largely on root architecture [172,206]. Perennials generally have deeper and thicker roots and an extensive root network compared to annual species, hence creating more macropores than annual species [172]. In contrast, some grasses may decrease hydraulic conductivity when roots form thick matting near the soil surface [207]. Rooting depth, and the ability of roots to penetrate different substrates, can also affect post-drought recovery and community resilience [208]. Species also differ in their contributions to soil organic matter which affects nutrient content, water holding capacity and infiltration rates [167, 209, 210].

#### **4.4.2 The role of plant community composition in species coexistence and plant-plant interactions**

In times of water limitation, community responses are products of species and/or PFT composition and traits, which can strongly filter species within a community [78]. Partitioning of available resources can mediate community responses to drought stress and is affected by the specific plant community composition at the time of drought and by the amount of diversity of the system [211, 212]. Demographic tradeoffs in

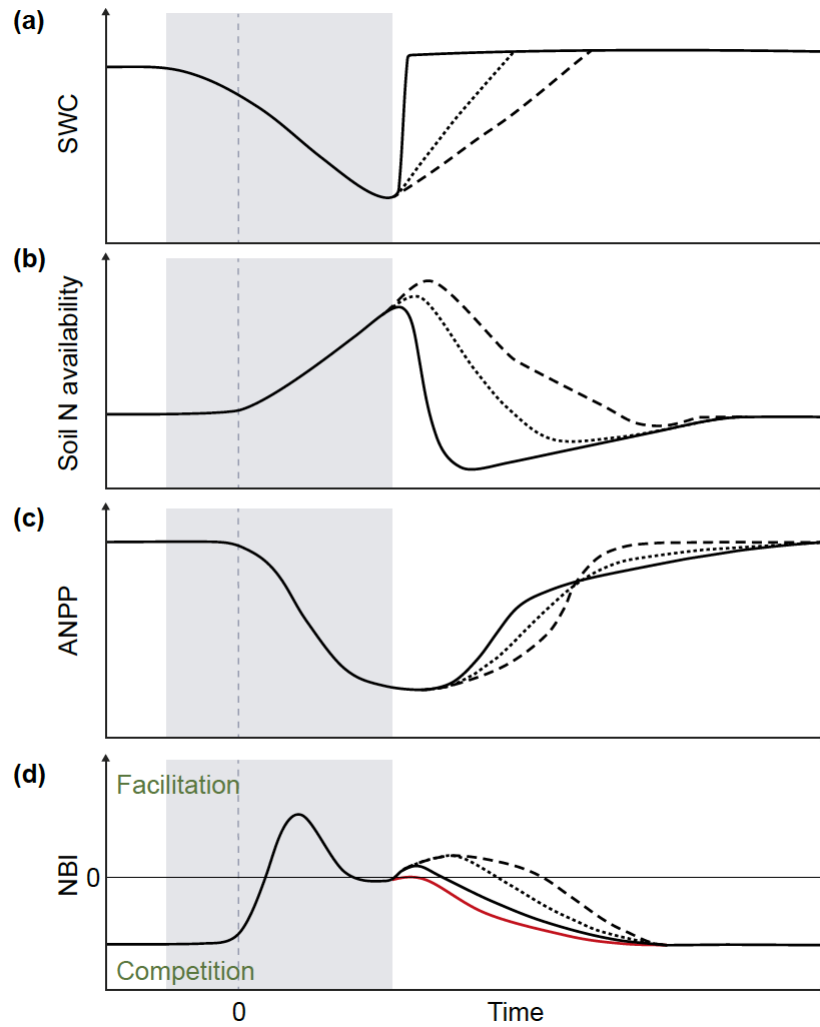


Fig. 4.4.: Conceptual diagram showing different post-drought rewetting scenarios, and their hypothesized effects on (a) soil water content (SWC), (b) soil nitrogen (N) availability, and community-level drought recovery as measured by (c) aboveground net primary production (ANPP), and (d) net biotic interactions (NBI). Solid lines represent the most rapid rewetting scenario, dotted lines represent the slowest, and dashed lines represent an intermediate rewetting rate. The grey box and red line are meant to correspond to those in Figure 1 and represent the extent of meteorological drought. Similarly, because we aimed to illustrate relative differences in rates of change at various stages of post-drought recovery, time is relative and continuous, but not intended to be linear.

growth and survival can promote niche partitioning and the distribution of limiting resources during a drought [182].

Understanding the relationship between traits and the trajectories and strengths of plant-plant interactions may provide insight into the resistance and resilience of a system [24,78,80,213,214]. Partitioning of resources and species co-existence depends on the composition of PFTs and intraspecific phenotypic plasticity [211,215]. Soil water partitioning can be achieved through utilization of water from different soil layers or greater plasticity in water uptake strategies [179,181]. Drought can also act as a means to filter out species with traits that are unable to cope with water stress. In grassland ecosystems, species with low resource acquisition strategies tend to be favored, and competitors are more facilitated than stress-tolerant species under water stress, highlighting the importance of understanding traits within a community [109,125,161]. Intraspecific trait variability may also be an important driver in short-term functional responses of plant communities [161].

High inter- and intraspecific trait variability in resource acquisition increases niche differentiation and has a role in stabilizing a community [147,161,184]. This is particularly true in systems with high PFT diversity as opposed to species diversity, *per se*. With a broad range of water use and resource acquisition strategies, functionally diverse plant communities could be expected to resist changes in community structure [161,183]. Indeed, in a drought study manipulating PFT diversity, temperate grasslands with greater ranges of PFTs were more resistant to changes in key ecosystem processes and vegetative losses than systems with lower diversity [183]. Drought stress can alter interactions between PFTs, but these changes are system-specific. Legumes, which often act as complementary or facilitative species under normal or wet conditions, can become competitive in drought conditions [109,151]. Conversely, PFTs that typically confer competitiveness under ideal soil water conditions tend to become more facilitative under drought conditions [151]. While the resistance of a system is generally greater in systems with high PFT diversity, the dominant species or PFT tends to play an important role in community restructuring. For example, following a natural drought in a mesic grassland, the dominant PFT, grasses, were replaced by forbs [18], but in an experimental drought in a similar ecosystem, Hoover

et al. [20] found the opposite pattern. These differences are most likely the result of the traits of the dominant species, and its interactions with neighboring species.

He et al. [24] found that regardless of traits, or the intensity of an individuals competitive effects or responses, there was consistently a decrease in competition and an increase in facilitation with increasing stress (Fig. 4.4b). During drought, highly competitive species likely decrease their competitive effects and less competitive species increase their facilitative effects. Species composition therefore determines the specific mechanisms of plant-plant interactions at play in a community (Fig. 4.1; [24]). The intensity and magnitude of these community effects/responses is an important component in the resistance (Fig. 4.2a, A-B) and resilience (Fig. 4.2a, D-E) of a community. Modified plant behavior in the form of facilitation may promote recovery (Fig. 4.4d; [216]. For example, delayed recovery of a dominant species may release other species from competition, which can induce change in community dominance [216].

Following drought, resilience will depend on several mechanisms, but stabilization will likely occur faster under scenarios that minimize mortality (i.e. increase survival) and/or enhance recruitment, particularly in those dominated by long-lived species [78, 108]. Physiological mechanisms, such as enhanced stress tolerance, and phenotypic plasticity and variability can reduce mortality. Stress tolerance can also be influenced by the historic environmental conditions experienced by a community [78].

Leaf, root and seed traits were found to affect mortality in a Mediterranean shrubland, where plant cover resilience was positively related to higher water use efficiency (WUE) and lower specific leaf area (SLA). Conversely, resistance was characterized by higher SLA and lower WUE [213]. Phenotypic plasticity can also reduce mortality [78, 215]. This variability can be related to age, where early developmental stages are more sensitive to drought stress than adult stages and can create a major bottleneck in recruitment [35, 155].

Resilience to drought will also be impacted by the recruitment ability of the dominant PFT(s). Recruitment can be reduced through low fecundity, self-incompatibility, low genotype diversity, and through increases in seed mortality via processes such as

desiccation or seed age [217]. More frequent and intense droughts may favor long-lived clonally spreading species and reduce populations of species that depend on frequent recruitment from seed (e.g. [217]). Positive interactions between adult plants and seedling establishment may occur when the adult plant provides protection and improves abiotic conditions for germination [155]. Recruitment has also been found to be positively related to mortality and seed size in a Mediterranean shrubland [213]. Seed bank richness has been found to be lower in drier years, and the total number of established seedlings is negatively influenced by drought [155, 213]. These effects are also species-specific and therefore result in changes in species composition within the seedling pool [155].

#### 4.5 Conclusions

Extreme climatic events (ECEs) are anticipated to increase in the future, and drought intensification can drive rapid responses at both the ecosystem and community levels. Empirical evidence demonstrates that drought can lead to community reordering, result in changes to the dominant species or PFT (e.g. [20]), or cause transitions to new ecosystem types (e.g. [139]), and alter important ecosystem functions and processes [107], but the mechanisms behind these changes are still not fully understood. Species turnover can also lead to increases in invasive species and extinction of rare species [12, 218]. Changes to a plant community are rarely immediate, and community stabilization can take years following an extreme drought (e.g. Table 4.1).

Many studies discuss mechanisms underlying the relatively slower rates of community stabilization compared to the productivity recovery, but few have explicitly explored the mechanisms proposed in CRED, namely the temporal evolution of plant-plant interactions during and after drought. While only a fraction of drought research has explored the role of NBI in community reordering (Table 4.2), the few studies that have been conducted demonstrate that plant-plant interactions can at least partially

explain community changes that result from an extreme drought (e.g. [109,139,146]). However, these studies did not monitor the community long enough to detect community stabilization. Plant responses to ECEs are highly variable and idiosyncratic, highlighting the value of long-term monitoring following drought [78]. While more extreme climate does not necessarily result in shifts in vegetation, it is likely that as droughts become more frequent and intense more systems will experience compositional changes [78].

Plant communities engage in a complex set of interactions, within and between trophic levels (e.g. herbivory), and species vary dramatically in their interactions with one another and their environment. These interactions can sometimes be categorized or predicted based on plant traits, and taking a functional comparative approach to facilitation could improve our ability to identify general patterns and consequences of positive interactions [80,214,219]. Tests of the hypotheses in the CRED framework could provide relevant information for communities that are sensitive to extreme drought, which could be used to inform management and conservation efforts, maintain ecosystem function, and slow species extinctions.

Targeted research into the role of plant-plant interactions in drought responses will provide insight into mechanisms responsible for changes in community composition and increase our understanding of local adaptation to drought and other factors that contribute to localized extinction under drought intensification. We advocate for the establishment of drought experiments that manipulate neighborhood interactions (e.g. [109]) and explore plant-plant interactions during drought and recovery. These experiments should be careful to use standardized definitions and protocols to test plant-plant interactions and use multi-factorial approaches that consider variables such as PFT, traits, and diversity [23,24,80,130,157]. Further, indices for competition and facilitation need to incorporate the relative importance and intensity of these plant-plant interactions to help differentiate between the abiotic and biotic drivers of community change [130,156,157].

The CRED framework organizes some of the mechanisms hypothesized to cause drought-induced shifts in community composition. Currently, though, little evidence is available to show how NBI changes over time with drought (see Table 4.2). Even less is known about how NBI may respond in a shifting climate, as droughts become warmer, and more frequent and intense in some regions. While it might be expected that communities experiencing more frequent droughts would become progressively more resistant/resilient to them, for now this remains an untested hypothesis.

Recently, land-surface models and remotely sensed data have been used to explore recovery of gross primary productivity (GPP) after drought [111]. Model data suggest drought impacts have increased over the twentieth century, with longer recovery times of GPP following drought, which could lead to a chronic state of incomplete recovery of GPP. Many ecological processes, including species turnover, may act to buffer impacts to GPP in the future, but the effectiveness and timescales on which these processes act relative to new drought regimes is unknown [111]. There are limitations of this study, namely that land-surface models do not represent many relevant dynamic processes of drought impacts and recovery, such as plant mortality [220]. Regardless, Schwalm, et al. [111] highlight an underappreciated dimension of drought impacts on GPP: timescale of recovery and its relationship to the occurrence of drought events [111]. These factors will likely be important for community dynamics after as well.

We suggest that the CRED framework will be applicable in some systems that experience more frequent droughts, but the trajectories and intensity/importance of plant-plant interactions may change based on the new community structure, prior baseline climatic conditions, and new drought conditions, particularly in relation to droughts that occur during recovery. Long-term surveys of vegetation responses and multi-site research studies can provide the data needed to identify key characteristics influencing community composition response to drought or other stressors [21, 212]. These coordinated distributed experiments and surveys hold the potential to test some CRED hypotheses and provide further insight into the role of site-specific characteristics that alter the trajectory of NBI during and after drought. These datasets

will expand our knowledge of how drought affects plant communities, and how recurrent droughts (some of which may occur during the recovery phase) and changes to recovery timescales will alter the trajectories of future communities.

## 5. CONCLUSIONS

While I found some ecosystem and community level responses to altered precipitation regimes in mesic, terrestrial ecosystems in the Midwestern United States, it appears that these systems tend to be fairly resistant to change. For instance, in chapter 1, I found that forest understory communities and N cycling were not affected by two years of changes in winter snow or summer precipitation. Other studies have found similar results in forest ecosystems and suggest that forests tend to have a general inertia to species turnover and recover quickly following disturbances [78], particularly mesic ecosystems [79]. Conducting a similar experiment over a longer period of time and/or conducting long-term monitoring of forest sites could provide better insight into the resistance of these systems, as it has been suggested that the longer a forest community experiences more variable precipitation, the more likely that resistance will be reduced [77, 78].

From this study, I also found it difficult to get woody plant seeds to germinate in the field, despite following guidelines outlined by the USDA [63]. Only one species germinated successfully, *L. benzoin*, and this species recruitment was affected by both winter and summer treatments, although independently of one another. This raises many questions regarding successful germination in the field, and the impacts that changes in precipitation patterns will have on the recruitment of other woody plants species. Unfortunately, without more species germinating and the short timeframe of this experiment, it is difficult to offer more general insights into the effects of precipitation variability on forest succession. But over longer periods of time persistent changes could have the potential to alter the direction of succession [76].

In chapter 2, I found the system less resistant to changes in precipitation than the forest system, as some drought treatments altered both productivity and diversity. The most surprising result was that two years of plots receiving 21-week drought treat-

ments from Apr-Sep did not alter productivity nor diversity. However, when I considered whether it was the timing or length of drought that resulted in changes in this system, I found that the timing of drought was a better indicator of productivity and community-level responses than the length of drought. Mid- and late-season droughts had the greatest impact on productivity, where mid-season droughts decreased productivity and late-season droughts may have increased or maintained productivity. Early-season drought did not affect productivity nor diversity, and only late-season droughts had an effect on community diversity. These results appear to indicate that there are some stabilizing mechanisms occurring in this system, including drought tolerance/avoidance, species co-existence, and stress memory [78, 93, 102, 103]. Further, my study highlights the importance of exploring the timing of drought events when exploring the impacts of drought on terrestrial ecosystems.

Conflicting results on the effects of drought on ecosystem and community level responses from other studies suggest that there is still a lack of understanding of the effects that future precipitation patterns will have on terrestrial ecosystems [3, 19]. Plants in grassland and forest communities interact in complex ways, and interactions between species and their environment vary dramatically [3, 8, 78]. Understanding stabilizing mechanisms within these communities may enable us to understand why we find such a variety of responses. In chapter 3, I suggest some potential mechanisms that should be explored further to understand species coexistence and the resistance/resilience of a system. This review suggests that plant-plant interactions, both facilitative (+) and competitive (-), should be explored further as potential mechanisms for community responses to drought.

Ultimately, my research and other studies demonstrate that the effects of precipitation changes on plant communities and ecosystem processes, such as C and N cycling, vary depending on the system, and the mechanisms behind these different response remain largely unknown. Long-term surveys of vegetation responses and multi-site research studies may provide the data needed to identify key characteristics influencing plant responses to altered precipitation regimes [17, 21, 78]. Larger

datasets will expand our knowledge of how altered precipitation regimes will affect plant communities and could provide insight on system-specific responses.

## REFERENCES

## REFERENCES

- [1] IPCC, “IPCC special report on the impacts of global warming of 1.5 C - Summary for policy makers,” Incheon, Republic of Korea, Tech. Rep., 2018. [Online]. Available: <http://www.ipcc.ch/report/sr15/>
- [2] Y. Zhang, M. Susan Moran, M. a. Nearing, G. E. Ponce Campos, A. R. Huete, A. R. Buda, D. D. Bosch, S. a. Gunter, S. G. Kitchen, W. Henry McNab, J. a. Morgan, M. P. McClaran, D. S. Montoya, D. P. Peters, and P. J. Starks, “Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes,” *Journal of Geophysical Research: Biogeosciences*, vol. 118, no. 1, pp. 148–157, mar 2013. [Online]. Available: <http://doi.wiley.com/10.1029/2012JG002136>
- [3] M. J. B. Zeppel, J. V. Wilks, and J. D. Lewis, “Impacts of extreme precipitation and seasonal changes in precipitation on plants,” *Biogeosciences*, vol. 11, pp. 3083–3093, 2014.
- [4] K. Byun and A. F. Hamlet, “Projected changes in future climate over the Midwest and Great Lakes region using downscaled CMIP5 ensembles,” *International Journal of Climatology*, vol. 38, no. January, pp. e531–e553, 2018.
- [5] A. Hamlet, K. Byun, S. Robeson, M. Widhalm, and M. Baldwin, “Impacts of Climate Change on the State of Indiana: Future Projections Based on CMIP5,” *Climate Change Publications*, vol. Paper 1, 2018.
- [6] A. K. Knapp, C. Beier, D. D. Briske, A. T. Classen, Y. Luo, M. Reichstein, M. D. Smith, S. D. Smith, J. E. Bell, P. a. Fay, J. L. Heisler, S. W. Leavitt, R. Sherry, B. Smith, and E. Weng, “Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems,” *BioScience*, vol. 58, no. 9, p. 811, 2008. [Online]. Available: <http://bioscience.oxfordjournals.org/cgi/doi/10.1641/B580908>
- [7] J. F. Weltzin, M. E. Loik, S. Schwinning, D. G. Williams, P. A. Fay, B. M. Haddad, J. Harte, T. E. Huxman, A. K. Knapp, G. Lin, W. T. Pockman, M. R. Shaw, E. E. Small, M. D. Smith, S. D. Smith, D. T. Tissue, and J. C. Zak, “Assessing the Response of Terrestrial Ecosystems to Potential Changes in Precipitation,” *BioScience*, vol. 53, no. 10, pp. 941–952, 2003. [Online]. Available: [http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568\(2003\)053\[0941:ATROTE\]2.0.CO;2](http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568(2003)053[0941:ATROTE]2.0.CO;2)
- [8] C. P. O. Reyer, S. Leuzinger, A. Rammig, A. Wolf, R. P. Bartholomeus, A. Bonfante, F. de Lorenzi, M. Dury, P. Gloning, R. Abou Jaoudé, T. Klein, T. M. Kuster, M. Martins, G. Niedrist, M. Riccardi, G. Wohlfahrt, P. de Angelis, G. de Dato, L. François, A. Menzel, and M. Pereira, “A plant’s perspective of extremes: terrestrial plant responses to changing climatic variability.”

- Global change biology*, vol. 19, no. 1, pp. 75–89, jan 2013. [Online]. Available: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3857548&tool=pmcentrez&rendertype=abstract>
- [9] D. Frank, M. Reichstein, M. Bahn, K. Thonicke, D. Frank, M. D. Mahecha, P. Smith, M. van der Velde, S. Vicca, F. Babst, C. Beer, N. Buchmann, J. G. Canadell, P. Ciais, W. Cramer, A. Ibrom, F. Miglietta, B. Poulter, A. Rammig, S. I. Seneviratne, A. Walz, M. Wattenbach, M. A. Zavala, and J. Zscheischler, “Effects of climate extremes on the terrestrial carbon cycle: Concepts, processes and potential future impacts,” *Global Change Biology*, vol. 21, no. 8, pp. 2861–2880, 2015.
  - [10] D. Blumenthal, R. A. Chimner, J. M. Welker, and J. A. Morgan, “Increased snow facilitates plant invasion in mixedgrass prairie,” *New Phytologist*, vol. 179, no. 2, pp. 440–448, 2008.
  - [11] R. A. Chimner, J. M. Welker, J. Morgan, D. Lecain, and J. Reeder, “Experimental manipulations of winter snow and summer rain influence ecosystem carbon cycling in a mixed-grass prairie , Wyoming , USA,” *Ecohydrology*, vol. 293, no. March, pp. 284–293, 2010.
  - [12] J. S. Prevéy and T. R. Seastedt, “Seasonality of precipitation interacts with exotic species to alter composition and phenology of a semi-arid grassland,” *Journal of Ecology*, no. October 2015, pp. n/a–n/a, 2014. [Online]. Available: <http://dx.doi.org/10.1111/1365-2745.12320%5Cn>
  - [13] J. S. Dukes, N. R. Chiariello, E. E. Cleland, L. a. Moore, M. R. Shaw, S. Thayer, T. Tobeck, H. a. Mooney, and C. B. Field, “Responses of grassland production to single and multiple global environmental changes.” *PLoS biology*, vol. 3, no. 10, p. e319, oct 2005. [Online]. Available: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1182693&tool=pmcentrez&rendertype=abstract>
  - [14] M. Reichstein, M. Bahn, P. Ciais, D. Frank, M. D. Mahecha, S. I. Seneviratne, J. Zscheischler, C. Beer, N. Buchmann, D. C. Frank, D. Papale, A. Rammig, P. Smith, K. Thonicke, M. Van Der Velde, S. Vicca, A. Walz, and M. Wattenbach, “Climate extremes and the carbon cycle,” *Nature*, vol. 500, no. 7462, pp. 287–295, 2013.
  - [15] J. L. Heisler-White, J. M. Blair, E. F. Kelly, K. Harmony, and A. K. Knapp, “Contingent productivity responses to more extreme rainfall regimes across a grassland biome,” *Global Change Biology*, vol. 15, no. 12, pp. 2894–2904, 2009.
  - [16] J. M. Craine, J. B. Nippert, A. J. Elmore, A. M. Skibbe, S. L. Hutchinson, and N. A. Brunsell, “Timing of climate variability and grassland productivity,” *Proceedings of the National Academy of Sciences*, vol. 109, no. 9, pp. 3401–3405, 2012. [Online]. Available: <http://www.pnas.org/cgi/doi/10.1073/pnas.1118438109>
  - [17] E. M. Denton, J. D. Dietrich, M. D. Smith, and A. K. Knapp, “Drought timing differentially affects above- and belowground productivity in a mesic grassland,” *Plant Ecology*, no. 218, pp. 317–328, 2017.

- [18] A. Stampfli and M. Zeiter, "Plant regeneration directs changes in grassland composition after extreme drought : a 13-year study in southern Switzerland," *Journal of Ecology*, vol. 92, pp. 568–576, 2004.
- [19] A. Jentsch, J. Kreyling, M. Elmer, E. Gellesch, B. Glaser, K. Grant, R. Hein, M. Lara, H. Mirzae, S. E. Nadler, L. Nagy, D. Otieno, K. Pritsch, U. Rascher, M. Schädler, M. Schloter, B. K. Singh, J. Stadler, J. Walter, C. Wellstein, J. Wöllecke, and C. Beierkuhnlein, "Climate extremes initiate ecosystem-regulating functions while maintaining productivity," *Journal of Ecology*, vol. 99, no. 3, pp. 689–702, 2011.
- [20] D. Hoover, A. Knapp, and M. Smith, "Contrasting sensitivities of two dominant C 4 grasses to heat waves and drought," *Plant Ecology*, vol. 215, pp. 721–731, 2014.
- [21] M. D. Smith, A. K. Knapp, and S. L. Collins, "A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change," *Ecology*, vol. 79, no. 1, pp. 3–24, 2009.
- [22] R. W. Brooker, "Plant plant interactions and environmental change," *New Phytologist*, vol. 171, no. 2, pp. 271–284, 2006.
- [23] R. W. Brooker, F. T. Maestre, R. M. Callaway, C. L. Lortie, L. a. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffrers, M. Seifan, B. Touzard, and R. Michalet, "Facilitation in plant communities: The past, the present, and the future," *Journal of Ecology*, vol. 96, no. 1, pp. 18–34, 2008.
- [24] Q. He, M. D. Bertness, and A. H. Altieri, "Global shifts towards positive species interactions with increasing environmental stress," *Ecology Letters*, vol. 16, no. 5, pp. 695–706, 2013.
- [25] J. HilleRisLambers, M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald, "How will biotic interactions influence climate change induced range shifts ?" *Annals of the New York Academy of Sciences*, vol. 1297, pp. 112–125, 2013.
- [26] IPCC, *Summary for Policymakers. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. Midgley, Eds. Cambridge, UK & New York, NY, USA: Cambridge University Press, 2013.
- [27] V. V. Kharin, F. W. Zwiers, X. Zhang, and M. Wehner, "Changes in temperature and precipitation extremes in the CMIP5 ensemble," *Climatic Change*, vol. 119, no. 2, pp. 345–357, 2013.
- [28] P. M. Groffman, C. T. Driscoll, T. J. Fahey, J. P. Hardy, D. Ross, G. L. Tierney, and R. D. Filtzhugh, "Colder soils in a warmer world : A snow manipulation study in a northern hardwood forest ecosystem," *Biogeochemistry*, vol. 56, pp. 135–150, 2001.

- [29] S. Czóbel, O. Szirmai, J. Nagy, J. Balogh, Z. Ürmös, E. Péli, and Z. Tuba, “Effects of irrigation on community composition and carbon uptake in Pannonian loess grassland monoliths,” *Community Ecology*, vol. 9, no. December 2016, pp. 91–96, 2008. [Online]. Available: <http://www.akademiai.com/openurl.asp?genre=article&id=doi:10.1556/ComEc.9.2008.S.13>
- [30] S. L. Collins, S. E. Koerner, J. a. Plaut, J. G. Okie, D. Brese, L. B. Calabrese, A. Carvajal, R. J. Evansen, and E. Nonaka, “Stability of tallgrass prairie during a 19-year increase in growing season precipitation,” *Functional Ecology*, vol. 26, pp. 1450–1459, 2012.
- [31] K. F. Gimbel, K. Felsmann, M. Baudis, H. Puhlmann, A. Gessler, H. Bruehlheide, Z. Kayler, R. H. Ellerbrock, A. Ulrich, E. Welk, and M. Weiler, “Drought in forest understory ecosystems - A novel rainfall reduction experiment,” *Bio-geosciences*, vol. 12, no. 4, pp. 961–975, 2015.
- [32] A. K. Knapp, P. a. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron, “Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland.” *Science (New York, N.Y.)*, vol. 298, no. 5601, pp. 2202–5, dec 2002. [Online]. Available: <http://www.ncbi.nlm.nih.gov/pubmed/12481139>
- [33] S. B. Clair, E. A. Sudderth, C. Castanha, M. S. Torn, and D. D. Ackerly, “Plant responsiveness to variation in precipitation and nitrogen is consistent across the compositional diversity of a California annual grassland,” *Journal of Vegetation Science*, vol. 20, no. 5, pp. 860–870, 2009.
- [34] N. G. Smith, M. J. Schuster, and J. S. Dukes, “Rainfall variability and nitrogen addition synergistically reduce plant diversity in a restored tallgrass prairie,” *Journal of Applied Ecology*, pp. 1–8, 2016. [Online]. Available: <http://doi.wiley.com/10.1111/1365-2664.12593>
- [35] J. L. Walck, S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschlod, “Climate change and plant regeneration from seed,” *Global Change Biology*, vol. 17, pp. 2145–2161, 2011.
- [36] J. Walsh, D. Wuebbles, K. Hayhoe, J. Kossin, K. Kunkel, G. Stephens, P. Thorne, R. Vose, M. Wehner, J. Willis, D. Anderson, S. Doney, R. Feely, P. Hennon, V. Kharin, T. Knutson, F. Landerer, T. Lenton, J. Kennedy, and R. Somerville, “Ch. 2: Our Changing Climate. Climate Change Impacts in the United States: The Third National Climate Assessment,” U.S. Global Change Research Program, Tech. Rep., 2014.
- [37] J. L. Heisler-White, A. K. Knapp, and E. F. Kelly, “Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland,” *Oecologia*, vol. 158, no. 1, pp. 129–140, 2008.
- [38] A. K. Knapp, C. J. W. Carroll, E. M. Denton, K. J. La Pierre, S. L. Collins, and M. D. Smith, “Differential sensitivity to regional-scale drought in six central US grasslands,” *Oecologia*, vol. 177, no. 4, pp. 949–957, 2015.
- [39] J. D. Dietrich and M. D. Smith, “The effect of timing of growing season drought on flowering of a dominant C4 grass,” *Oecologia*, vol. 181, no. 2, pp. 391–399, 2016.

- [40] J. M. G. Bloor and R. D. Bardgett, "Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: Interactions with plant species diversity and soil nitrogen availability," *Journal of PPEES Sources*, vol. 14, no. 3, pp. 193–204, 2012. [Online]. Available: <http://dx.doi.org/10.1016/j.ppees.2011.12.001>
- [41] F. A. Dijkstra, M. Z. He, M. P. Johansen, J. J. Harrison, and C. Keitel, "Plant and microbial uptake of nitrogen and phosphorus affected by drought using N-15 and P-32 tracers," *Soil Biology & Biochemistry*, vol. 82, pp. 135–142, 2015.
- [42] D. R. Zak, P. M. Groffman, K. S. Pregitzer, S. Christensen, and J. M. Tiedje, "The Vernal Dam: Plant-Microbe Competition for Nitrogen in Northern Hardwood Forests," *Ecology*, vol. 71, no. 2, pp. 651–656, 1990.
- [43] J. P. Kaye and S. C. Hart, "Competition between plants and soil microorganisms," *Trends in Ecology & Evolution*, vol. 12, no. 4, pp. 139–143, 1997.
- [44] Q. Liu, N. Qiao, X. Xu, X. Xin, J. Y. Han, Y. Tian, H. Ouyang, and Y. Kuzyakov, "Nitrogen acquisition by plants and microorganisms in a temperate grassland," *Scientific Reports*, vol. 6, no. February, pp. 1–10, 2016. [Online]. Available: <http://dx.doi.org/10.1038/srep22642>
- [45] J. Sierra, "Temperature and Soil Moisture Dependence of N mineralization in intact soil cores," *Soil Biology and Biochemistry*, vol. 29, no. 9, pp. 1557–1563, 1997.
- [46] Y. Tian, H. Ouyang, Q. Gao, X. Xu, M. Song, and X. Xu, "Responses of soil nitrogen mineralization to temperature and moisture in alpine ecosystems on the Tibetan Plateau," *Procedia Environmental Sciences*, vol. 2, no. 5, pp. 218–224, 2010. [Online]. Available: <http://linkinghub.elsevier.com/retrieve/pii/S1878029610000599>
- [47] M. Guntiñas, M. Leirós, C. Trasar-Cepeda, and F. Gil-Sotres, "Effects of moisture and temperature on net soil nitrogen mineralization: A laboratory study," *European Journal of Soil Biology*, vol. 48, pp. 73–80, jan 2012. [Online]. Available: <http://linkinghub.elsevier.com/retrieve/pii/S1164556311000732>
- [48] Y. Li, Y. Liu, Y. Wang, L. Niu, X. Xu, and Y. Tian, "Interactive effects of soil temperature and moisture on soil N mineralization in a *Stipa krylovii* grassland in Inner Mongolia, China," *Journal of Arid Land*, vol. 6, no. 5, pp. 571–580, 2014.
- [49] S. Wang and M. Loreau, "Biodiversity and ecosystem stability across scales in metacommunities," *Ecology Letters*, pp. 1–9, 2016. [Online]. Available: <http://doi.wiley.com/10.1111/ele.12582>
- [50] L. E. Rustad, J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. Cornelissen, J. Gurevitch, R. Alward, C. Beier, I. Burke, J. Canadell, T. Callaghan, T. R. Christensen, J. Fahnestock, I. Fernandez, J. Harte, R. Hollister, H. John, P. Ineson, M. G. Johnson, S. Jonasson, L. John, S. Linder, A. Lukewille, G. Masters, J. Melillo, A. Mickelsen, C. Neill, D. M. Olszyk, M. Press, K. Pregitzer, C. Robinson, P. T. Rygielwicz, O. Sala, I. K. Schmidt, G. Shaver, K. Thompson, D. T. Tingey, P. Verburg, D. Wall, J. Welker, and R. Wright, "A meta-analysis of the response of soil respiration,

- net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming,” *Oecologia*, vol. 126, no. 4, pp. 543–562, 2001.
- [51] E. Bai, S. Li, W. Xu, W. Li, W. Dai, and P. Jiang, “A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics,” *New Phytologist*, vol. 199, no. 2, pp. 431–440, 2013.
  - [52] P. M. Groffman, J. P. Hardy, M. C. Fisk, T. J. Fahey, and C. T. Driscoll, “Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest,” *Ecosystems*, vol. 12, pp. 927–943, 2009.
  - [53] J. Durán, J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, M. J. Mitchell, and P. H. Templer, “Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests,” *Global change biology*, vol. 20, no. 11, pp. 3568–77, nov 2014. [Online]. Available: <http://www.ncbi.nlm.nih.gov/pubmed/24796872>
  - [54] J. Durán, A. Rodríguez, J. L. Morse, and P. M. Groffman, “Winter climate change effects on soil C and N cycles in urban grasslands,” *Global Change Biology*, vol. 19, no. 9, pp. 2826–2837, 2013.
  - [55] T. H. DeLuca, D. R. Keeney, and G. W. McCarty, “Effect of freeze-thaw events on mineralization of soil nitrogen,” *Biology and Fertility of Soils*, vol. 14, no. 2, pp. 116–120, oct 1992. [Online]. Available: <http://link.springer.com/10.1007/BF00336260>
  - [56] J. L. Campbell, P. M. Groffman, L. Christenson, and J. P. Hardy, “Winter in northeastern North America: a critical period for ecological processes,” *Frontiers in Ecology and the Environment*, vol. 3, no. 6, pp. 314–322, 2005. [Online]. Available: <c:%5CPDFs%5Ci1540-9295-003-06-0314.pdf>
  - [57] M. Schütt, W. Borken, C. F. Stange, and E. Matzner, “Substantial net N mineralization during the dormant season in temperate forest soils,” *Journal of Plant Nutrition and Soil Science*, vol. 177, no. 4, pp. 566–572, aug 2014. [Online]. Available: <http://doi.wiley.com/10.1002/jpln.201300644>
  - [58] I. C. Burke, W. K. Lauenroth, and W. J. Parton, “Regional and Temporal Variation in Net Primary Production and Nitrogen Mineralization in Grasslands,” *Ecology*, vol. 78, no. 5, pp. 1330–1340, 1997.
  - [59] M. Giese, Y. Z. Gao, S. Lin, and H. Brueck, “Nitrogen availability in a grazed semi-arid grassland is dominated by seasonal rainfall,” *Plant and Soil*, vol. 340, no. 1, pp. 157–167, 2011.
  - [60] S. S. Staff, “Web soil survey,” Natural Resources Conservation Service, United States Department of Agriculture, Report.
  - [61] J. DiStefano and H. Gholz, “A proposed use of ion exchange resins to measure nitrogen mineralization and nitrification in intact soil cores,” *Communications in Soil Science and Plant Analysis*, vol. 17, no. February 2015, pp. 989–998, 1986.
  - [62] G. B. Noe, “Measurement of Net Nitrogen and Phosphorus Mineralization in Wetland Soils Using a Modification of the Resin-Core Technique,” *Soil Science Society of America Journal*, vol. 75, no. 2, p. 760, 2011.

- [63] F. Bonner and R. E. Karrfalt, *The Woody Plant Seed Manual*, agricultur ed. United States Department of Agriculture Forest Service, 2008, no. July.
- [64] J. Oksanen, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner, "vegan: Community Ecology Package," 2016. [Online]. Available: <https://cran.r-project.org/package=vegan>
- [65] D. Bates, M. Maechler, B. Bolker;, and S. Walker, "Fitting Linear Mixed-Effects Models Using lme4," *Journal of Statistical Software*, vol. 67, no. 1, pp. 1–48, 2015.
- [66] R Core Team, "R: A language and environment for statistical computing," Vienna, Austria, 2016. [Online]. Available: <https://www.r-project.org/>
- [67] B. M. Bolker, M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White, "Generalized linear mixed models: a practical guide for ecology and evolution," *Trends in Ecology and Evolution*, vol. 24, no. 3, pp. 127–135, 2009.
- [68] R. V. Lenth, "Least-squares means: The R package lsmeans," *Journal of Statistical Software*, vol. 69, no. 1, pp. 1–33, 2016.
- [69] R. D. Fitzhugh, C. T. Driscoll, P. M. Groffman, G. L. Tierney, T. J. Fahey, J. P. Hardy, R. D. Hitzhughl, and M. Peter, "Effects of soil freezing disturbance on soil solution nitrogen , phosphorus , and carbon chemistry in a northern hardwood ecosystem," *Biogeochemistry*, vol. 56, no. 2, pp. 215–238, 2001.
- [70] P. M. Groffman, C. T. Driscoll, T. J. Fahey, J. P. Hardy, D. Ross, G. L. Tierney, and J. Timothy, "Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest," *Biogeochemistry*, vol. 56, no. 2, pp. 191–213, 2001.
- [71] J. P. Hardy, P. M. Groffman, R. D. Fitzhugh, K. S. Henry, T. Adam, J. D. Demers, T. J. Fahey, C. T. Driscoll, G. L. Tierney, J. P. Hardy, P. M. Groffman, R. D. Fitzhugh, K. S. Henry, A. T. Welman, J. D. Demers, T. J. Fahey, C. T. Driscoll, L. Geraldine, and S. Nolan, "Snow Depth Manipulation and Its Influence on Soil Frost and Water Dynamics in a Northern Hardwood Forest," *Biogeochemistry*, vol. 2, no. 56, pp. 151–174, 2001.
- [72] G. L. Tierney, T. J. Fahey, P. M. Groffman, J. P. Hardy, R. D. Fitzhugh, and C. T. Driscoll, "Soil freezing alters fine root dynamics in a northern hardwood forest," *Biogeochemistry*, vol. 56, pp. 175–190, 2001.
- [73] S. Pajares and B. J. Bohannan, "Ecology of nitrogen fixing, nitrifying, and denitrifying microorganisms in tropical forest soils," *Frontiers in Microbiology*, vol. 7, no. JUL, pp. 1–20, 2016.
- [74] J. O. Luken and N. Goessling, "Seedling Distribution and Potential Persistence of the Exotic Shrub *Lonicera maackii* in Fragmented Forests," *The American Midland Naturalist*, vol. 133, no. 1, pp. 124–130, 1995.
- [75] S. N. Hidayati, J. M. Baskin, and C. C. Baskin, "Dormancy-breaking and germination requirements of seeds of four *Lonicera* species (Caprifoliaceae) with underdeveloped spatulate embryos," *Seed Science Research*, vol. 10, no. 4, pp. 459–469, 2000.

- [76] P. Prieto, J. Peñuelas, F. Lloret, L. Llorens, and M. Estiarte, “Experimental drought and warming decrease diversity and slow down post-fire succession in a Mediterranean shrubland,” *Ecography*, vol. 32, no. 4, pp. 623–636, 2009.
- [77] C. D. Allen, A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. T. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb, “A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests,” *Forest Ecology and Management*, vol. 259, no. 4, pp. 660–684, 2010.
- [78] F. Lloret, A. Escudero, J. M. Iriondo, J. Martínez-Vilalta, and F. Valladares, “Extreme climatic events and vegetation: The role of stabilizing processes,” *Global Change Biology*, vol. 18, no. 3, pp. 797–805, 2012.
- [79] E. Stuart-Haëntjens, H. J. De Boeck, N. P. Lemoine, P. Mänd, G. Kröel-Dulay, I. K. Schmidt, A. Jentsch, A. Stampfli, W. R. Anderegg, M. Bahn, J. Kreyling, T. Wohlgemuth, F. Lloret, A. T. Classen, C. M. Gough, and M. D. Smith, “Mean annual precipitation predicts primary production resistance and resilience to extreme drought,” *Science of The Total Environment*, vol. 636, no. April, pp. 360–366, 2018. [Online]. Available: <http://linkinghub.elsevier.com/retrieve/pii/S0048969718314670>
- [80] B. J. Butterfield, “Effects of facilitation on community stability and dynamics: synthesis and future directions,” *Journal of Ecology*, vol. 97, pp. 1192–1201, 2009.
- [81] P. A. Fay, J. D. Carlisle, A. K. Knapp, J. M. Blair, L. Scott, and S. L. Collins, “Altering Rainfall Timing and Quantity in a Mesic Grassland Ecosystem: Design and Performance of Rainfall Manipulation Shelters,” *Ecosystems*, vol. 3, no. 3, pp. 308–319, 2000.
- [82] P. Kardol, C. E. Campany, L. Souza, R. J. Norby, J. F. Weltzin, and A. T. Classen, “Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem,” *Global Change Biology*, vol. 16, no. 10, pp. 2676–2687, 2010.
- [83] J. Kreyling, D. Jürgen, J. Walter, N. Velez, E. Ururlu, D. Sopotlieva, C. Picon-Cochard, I. Nijs, P. Hernandez, B. Guler, H. J. De Boeck, J. M. Bloor, S. Berwaers, C. Beierkuhnlein, M. A. S. Arfin Khan, I. Apostolova, Y. Altan, M. Zeiter, C. Wellstein, M. Sternberg, A. Stampfli, G. Campetella, S. Bartha, M. Bahn, and A. Jentsch, “Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment,” *Ecology Letters*, pp. 1–9, 2017.
- [84] C. Scherber, N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E.-D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Bessler, M. Bonkowski, N. Buchmann, F. Buscot, L. W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A.-M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D. Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. Petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tscharnkte, “Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment.” *Nature*, vol. 468, no. 7323, pp. 553–6, nov 2010. [Online]. Available: <http://www.ncbi.nlm.nih.gov/pubmed/20981010>

- [85] K. Grant, J. Kreyling, C. Beierkuhnlein, and A. Jentsch, "Importance of Seasonality for the Response of a Mesic Temperate Grassland to Increased Precipitation Variability and Warming," *Ecosystems*, vol. 20, no. 8, pp. 1–14, 2017.
- [86] D. A. Frank, "Drought effects on above- and belowground production of a grazed temperate grassland ecosystem." *Oecologia*, vol. 152, no. 1, pp. 131–9, may 2007. [Online]. Available: <http://www.ncbi.nlm.nih.gov/pubmed/17180369>
- [87] P. A. Fay, D. M. Kaufman, J. B. Nippert, J. D. Carlisle, and C. W. Harper, "Changes in grassland ecosystem function due to extreme rainfall events: Implications for responses to climate change," *Global Change Biology*, vol. 14, no. 7, pp. 1600–1608, 2008.
- [88] P. A. Fay, J. D. Carlisle, A. K. Knapp, J. M. Blair, L. Scott, and S. L. Collins, "Productivity responses to altered rainfall patterns Productivity in a C4-dominated grassland," *Oecologia*, vol. 137, no. 2, pp. 245–251, 2003.
- [89] D. Ode, L. Tieszen, and J. Lerman, "The Seasonal Contribution of C<sup>3</sup> and C<sup>4</sup> Plant Species to Primary Production in a Mixed Prairie," *Ecology*, vol. 61, no. 6, pp. 1304–1311, 1980.
- [90] S. Piao, P. Friedlingstein, P. Ciais, N. Viovy, and J. Demarty, "Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades," *Global Biogeochemical Cycles*, vol. 21, no. 3, pp. 1–11, 2007.
- [91] P. Ciais, M. Reichstein, N. Viovy, a. Granier, J. Ogée, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, a. Carrara, F. Chevallier, N. De Noblet, a. D. Friend, P. Friedlingstein, T. Grünwald, B. Heinesch, P. Keronen, a. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J. F. Soussana, M. J. Sanz, E. D. Schulze, T. Vesala, and R. Valentini, "Europe-wide reduction in primary productivity caused by the heat and drought in 2003." *Nature*, vol. 437, no. 7058, pp. 529–533, 2005.
- [92] N. McDowell, W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams, and E. A. Yezzer, "Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought?" *New Phytologist*, vol. 178, no. 4, pp. 719–739, 2008.
- [93] S. Niu, Y. Luo, D. Li, S. Cao, J. Xia, J. Li, and M. D. Smith, "Plant growth and mortality under climatic extremes: An overview," *Environmental and Experimental Botany*, vol. 98, pp. 13–19, 2014. [Online]. Available: <http://dx.doi.org/10.1016/j.envexpbot.2013.10.004>
- [94] P. Barnes, "Adaptation to Water Stress in the Big BluestemSand Bluestem Complex," *Ecology*, vol. 66, no. 6, pp. 1908–1920, 1985.
- [95] M. Nolf, K. Pagitz, and S. Mayr, "Physiological acclimation to drought stress in *Solidago canadensis*," *Physiologia Plantarum*, vol. 150, no. 4, pp. 529–539, 2014.

- [96] M. L. Avolio, A. M. Hoffman, and M. D. Smith, "Linking gene regulation, physiology, and plant biomass allocation in andropogon gerardii in response to drought," *Plant Ecology*, vol. 219, no. 1, pp. 1–15, 2018.
- [97] D. L. Kramer, K. L. Maricle, C. J. Hilt, N. M. Martin, A. D. Urban, C. M. Smart, S. G. Baer, L. C. Johnson, and B. R. Maricle, "Drought tolerance in ecotypes of big bluestem (*Andropogon gerardii*) relates to above-ground surface area: Results from a common garden experiment," *Flora: Morphology, Distribution, Functional Ecology of Plants*, vol. 246-247, no. July, pp. 52–60, 2018. [Online]. Available: <https://doi.org/10.1016/j.flora.2018.07.005>
- [98] A. K. Knapp, "Effect of Fire and Drought on the Ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a Tallgrass Prairie Author ( s ): Alan K . Knapp Published by : Wiley on behalf of the Ecological Society of America Stable URL : <http://www.jstor.org/stable/19>," *Ecology*, vol. 66, no. 4, pp. 1309–1320, 1985.
- [99] P. A. Werner, I. A. N. K. Bradburyt, and R. S. Grossi, "The biology of Canadian weeds. *Solidago canadensis* L." *Canadian Journal of Plant Science*, vol. 60, pp. 1393–1409, 1980.
- [100] J. E. Weaver, "Classification of Root Systems of Forbs of Grassland and a Consideration of Their Significance," *Ecology*, vol. 39, no. 3, p. 393, 1958. [Online]. Available: <http://www.jstor.org/stable/1931749?origin=crossref>
- [101] R. Uchytíl, "Andropogon gerardii," USDA, Tech. Rep., 1988.
- [102] T. J. Bruce, M. C. Matthes, J. A. Napier, and J. A. Pickett, "Stressful "memories" of plants: Evidence and possible mechanisms," *Plant Science*, vol. 173, no. 6, pp. 603–608, 2007.
- [103] J. Walter, L. Nagy, R. Hein, U. Rascher, C. Beierkuhnlein, E. Willner, and A. Jentsch, "Do plants remember drought? Hints towards a drought-memory in grasses," *Environmental and Experimental Botany*, vol. 71, no. 1, pp. 34–40, apr 2011. [Online]. Available: <http://linkinghub.elsevier.com/retrieve/pii/S0098847210002182>
- [104] F. E. Dreesen, H. J. De Boeck, I. A. Janssens, and I. Nijs, "Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages," *Biogeosciences*, vol. 11, pp. 109–121, 2014.
- [105] "Plant Fact Sheet: Big bluestem (*Andropogon gerardii* Vitman)," *USDA NRCS Plants Materials Program*, 2002.
- [106] J. d. D. Miranda, F. Padilla, R. Lazaro, and F. Pugnaire, "Do changes in rainfall patterns affect semiarid annual plant communities ?" *Journal of Vegetation Science*, vol. 20, pp. 269–276, 2009.
- [107] M. D. Smith, "An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research," *Journal of Ecology*, vol. 99, no. 3, pp. 656–663, 2011.
- [108] J. Martínez-Vilalta and F. Lloret, "Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics," *Global and Planetary Change*, vol. 144, pp. 94–108, 2016. [Online]. Available: <http://dx.doi.org/10.1016/j.gloplacha.2016.07.009>

- [109] K. Grant, J. Kreyling, H. Heilmeyer, C. Beierkuhnlein, and A. Jentsch, “Extreme weather events and plant-plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall,” *Ecological Research*, vol. 29, pp. 991–1001, 2014.
- [110] A. E. Magurran, “How ecosystems change,” *Science*, vol. 351, no. 6272, pp. 448–449, 2016.
- [111] C. R. Schwalm, W. R. Anderegg, A. M. Michalak, J. B. Fisher, F. Biondi, G. Koch, M. Litvak, K. Ogle, J. D. Shaw, A. Wolf, D. N. Huntzinger, K. Schaefer, R. Cook, Y. Wei, Y. Fang, D. Hayes, M. Huang, A. Jain, and H. Tian, “Global patterns of drought recovery,” *Nature*, vol. 548, no. 7666, pp. 202–205, 2017. [Online]. Available: <http://dx.doi.org/10.1038/nature23021>
- [112] S. P. Harrison, M. L. LaForgia, and A. M. Latimer, “Climate-driven diversity change in annual grasslands: Drought plus deluge does not equal normal,” *Global Change Biology*, vol. 24, no. 4, pp. 1782–1792, 2018.
- [113] F. Bazzaz, “PlantPlant Interactions in Successional Environments,” in *Perspectives on Plant Competition*, J. Grace and D. Tilman, Eds. San Diego: Academic Press, Inc., 1990, ch. 12, pp. 239–263. [Online]. Available: <http://linkinghub.elsevier.com/retrieve/pii/B9780122944529500163>
- [114] H. J. De Boeck, F. E. Dreesen, I. A. Janssens, and I. Nijs, “Whole-system responses of experimental plant communities to climate extremes imposed in different seasons,” *New Phytologist*, vol. 189, no. 3, pp. 806–817, 2011.
- [115] K. A. Novick, D. L. Ficklin, P. C. Stoy, C. A. Williams, G. Bohrer, A. Oishi, S. A. Papuga, P. D. Blanken, A. Noormets, B. N. Sulman, R. L. Scott, L. Wang, and R. P. Phillips, “The increasing importance of atmospheric demand for ecosystem water and carbon fluxes,” *Nature Climate Change*, vol. 6, no. 11, pp. 1023–1027, 2016. [Online]. Available: <http://www.nature.com/doi/10.1038/nclimate3114>
- [116] S. N. Johnson, J. T. Staley, F. A. L. Mcleod, and S. E. Hartley, “Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions,” *Journal of Ecology*, vol. 99, no. 1, pp. 57–65, 2011.
- [117] M. a. Lee, P. Manning, C. S. Walker, and S. a. Power, “Plant and arthropod community sensitivity to rainfall manipulation but not nitrogen enrichment in a successional grassland ecosystem,” *Oecologia*, vol. 176, pp. 1173–1185, 2014.
- [118] D. Tilman, “Biodiversity: Population Versus Ecosystem Stability,” *Ecology*, vol. 77, no. 2, pp. 350–363, 1996.
- [119] R. J. Rondeau, K. T. Pearson, and S. Kelso, “Vegetation Response in a Colorado Grassland-shrub Community to Extreme Drought: 1999–2010,” *The American Midland Naturalist*, vol. 170, no. 1, pp. 14–25, 2013.
- [120] F. W. Albertson and G. W. Tomanek, “Vegetation Changes During a 30-Year Period in Grassland Communities Near Hays, Kansas,” *Ecology*, vol. 46, no. 5, pp. 714–720, 1965.

- [121] R. Michalet and F. I. Pugnaire, "Facilitation in communities : underlying mechanisms, community and ecosystem implications," *Functional Ecology*, vol. 20, pp. 3–9, 2016.
- [122] F. Clements, *Plant succession: an analysis of the development of vegetation*. Washington, DC: Carnegie Institute Publication, 1916.
- [123] R. M. Callaway and L. R. Walker, "Competition and facilitation: A synthetic approach to interactions in plant communities," *Ecology*, vol. 78, no. 7, pp. 1958–1965, 1997.
- [124] M. D. Bertness and R. Callaway, "Positive interactions in communities," *Trends in Ecology & Evolution*, vol. 9, no. 5, pp. 191–193, 1994.
- [125] R. Michalet, R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway, "Do biotic interactions shape both sides of the humped-back model of species richness in plant communities?" *Ecology Letters*, vol. 9, no. 7, pp. 767–773, 2006.
- [126] R. Michalet, C. Sch??b, C. J. Lortie, R. W. Brooker, and R. M. Callaway, "Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change," *Functional Ecology*, vol. 28, no. 1, pp. 75–86, 2014.
- [127] F. T. Maestre, R. M. Callaway, F. Valladares, and C. J. Lortie, "Refining the stress-gradient hypothesis for competition and facilitation in plant communities," *Journal of Ecology*, vol. 97, no. 2, pp. 199–205, 2009.
- [128] C. T. Castanho, A. A. Oliveira, and P. I. K. L. Prado, "Does extreme environmental severity promote plant facilitation? An experimental field test in a subtropical coastal dune," *Oecologia*, vol. 178, no. 3, pp. 855–866, 2015. [Online]. Available: <http://dx.doi.org/10.1007/s00442-015-3285-7>
- [129] C. J. Lortie and R. M. Callaway, "Re-analysis of meta-analysis: Support for the stress-gradient hypothesis," *Journal of Ecology*, vol. 94, no. 1, pp. 7–16, 2006.
- [130] M. Seifan, T. Seifan, C. Ariza, and K. Tielbörger, "Facilitating an importance index," *Journal of Ecology*, vol. 98, no. 2, pp. 356–361, 2010.
- [131] C. Ariza and K. Tielbörger, "An evolutionary approach to studying the relative importance of plant-plant interactions along environmental gradients," *Functional Ecology*, vol. 25, no. 4, pp. 932–942, 2011.
- [132] J. Dohn, F. Dembélé, M. Karembé, A. Moustakas, K. A. Amévor, and N. P. Hanan, "Tree effects on grass growth in savannas: Competition, facilitation and the stress-gradient hypothesis," *Journal of Ecology*, vol. 101, pp. 202–209, 2013.
- [133] J. Ziffer-Berger, P. J. Weisberg, M. E. Cablk, and Y. Osem, "Spatial patterns provide support for the stress-gradient hypothesis over a range-wide aridity gradient," *Journal of Arid Environments*, vol. 102, pp. 27–33, 2014. [Online]. Available: <http://dx.doi.org/10.1016/j.jaridenv.2013.11.006>
- [134] R. P. Lopez, F. A. Squeo, C. Armas, D. A. Kelt, and J. R. Guti??rrez, "Enhanced facilitation at the extreme end of the aridity gradient in the Atacama Desert: A community-level approach," *Ecology*, vol. 97, no. 6, pp. 1593–1604, 2016.

- [135] K. Tielborger and R. Kadmon, "Temporal Environmental Variation Tips the Balance between Facilitation and Interference in Desert Plants," *Ecology*, vol. 81, no. 6, pp. 1544–1553, 2000.
- [136] F. T. Maestre, F. Valladares, and J. F. Reynolds, "Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments," *Journal of Ecology*, vol. 93, no. 4, pp. 748–757, 2005.
- [137] B. J. Butterfield, J. B. Bradford, C. Armas, I. Prieto, and F. I. Pugnaire, "Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems," *Functional Ecology*, vol. 30, pp. 10–19, 2016.
- [138] S. R. Biswas and H. H. Wagner, "A temporal dimension to the stress gradient hypothesis for intraspecific interactions," *Oikos*, vol. 123, no. 11, pp. 1323–1330, 2014.
- [139] V. Resco de Dios, J. F. Weltzin, W. Sun, T. E. Huxman, and D. G. Williams, "Transitions from grassland to savanna under drought through passive facilitation by grasses," *Journal of Vegetation Science*, vol. 25, no. 4, pp. 937–946, 2014.
- [140] J. Harper, *Population biology of plants*. London ; New York: Academic Press, 1977.
- [141] M. Holmgren, M. Scheffer, and M. Huston, "The interplay of facilitation and competition in plant communities," *Ecology*, vol. 78, no. 7, pp. 1966–1975, 1997.
- [142] F. Volaire, "A unified framework of plant adaptive strategies to drought: crossing scales and disciplines," *Global Change Biology*, no. December 2017, pp. 1–10, 2018. [Online]. Available: <http://doi.wiley.com/10.1111/gcb.14062>
- [143] J. J. Stachowicz, "Mutualism, Facilitation, and the Structure of Ecological Communities," *BioScience*, vol. 51, no. 3, pp. 235–246, 2001.
- [144] H. L. Zhao, R. L. Zhou, Y. Z. Su, H. Zhang, L. Y. Zhao, and S. Drake, "Shrub facilitation of desert land restoration in the Horqin Sand Land of Inner Mongolia," *Ecological Engineering*, vol. 31, no. 1, pp. 1–8, 2007.
- [145] F. T. Maestre, I. S. Bautista, and I. J. Cortina, "Positive, Negative, and Net Effects in Grass-Shrub Interactions in Mediterranean Semiarid Grasslands," *Ecology*, vol. 84, no. 12, pp. 3186–3197, 2003.
- [146] H. Pretzsch, G. Schütze, and E. Uhl, "Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation," *Plant Biology*, vol. 15, no. 3, pp. 483–495, 2013.
- [147] D. Tilman and A. E. Haddi, "Drought and biodiversity in Grasslands," *Oecologia*, vol. 89, pp. 257–264, 1992.
- [148] L. M. Suarez and T. Kitzberger, "Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests," *Canadian Journal of Forest Research*, vol. 38, pp. 3002–3010, 2008.

- [149] F. Lloret and I. Granzow-de la Cerda, "Plant competition and facilitation after extreme drought episodes in Mediterranean shrubland: Does damage to vegetation cover trigger replacement by juniper woodland?" *Journal of Vegetation Science*, vol. 24, no. 6, pp. 1020–1032, 2013.
- [150] P. A. Cipriotti, P. Flombaum, O. E. Sala, and M. R. Aguiar, "Does drought control emergence and survival of grass seedlings in semi-arid rangelands? An example with a Patagonian species," *Journal of Arid Environments*, vol. 72, no. 3, pp. 162–174, 2008.
- [151] A. M. A. S. Khan, K. Grant, C. Beierkuhnlein, J. Kreyling, and A. Jentsch, "Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland," *Plant and Soil*, pp. 1–15, 2014.
- [152] T. Kitzberger, D. F. Steinaker, and T. T. Veblen, "Effects of Climatic Variability on Facilitation of Tree Establishment in North Patagonia," *Ecology*, vol. 81, no. 7, pp. 1914–1924, 2000.
- [153] P. Mariotte, C. Vandenberghe, P. Kardol, F. Hagedorn, and A. Buttler, "Subordinate plant species enhance community resistance against drought in semi-natural grasslands," *Journal of Ecology*, vol. 101, no. 3, pp. 763–773, 2013.
- [154] C. M. Sthultz, C. A. Gehring, and T. G. Whitham, "Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland," *New Phytologist*, vol. 173, no. 1, pp. 135–145, 2007.
- [155] M. del Cacho and F. Lloret, "Resilience of Mediterranean shrubland to a severe drought episode: The role of seed bank and seedling emergence," *Plant Biology*, vol. 14, no. 3, pp. 458–466, 2012.
- [156] C. W. Welden and W. L. Slauson, "The Intensity of Competition Versus its Importance : An Overlooked Distinction and Some Implications," *The Quarterly Review of Biology*, vol. 61, no. 1, pp. 23–44, 1986.
- [157] R. Brooker, Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet, "The importance of importance," *Oikos*, vol. 109, no. 1, pp. 63–70, 2005.
- [158] C. A. Jaleel, P. Manivannan, A. Wahim, M. Farooq, J. Al-Juburi, R. Somasundaram, and R. Panneerselvam, "Drought Stress in Plants : A Review on Morphological Characteristics and Pigments Composition," *International Journal of Agriculture & Biology*, vol. 11, no. 1, pp. 100–105, 2009.
- [159] Z. Hao and V. P. Singh, "Drought characterization from a multivariate perspective: A review," *Journal of Hydrology*, vol. 527, pp. 668–678, 2015. [Online]. Available: <http://dx.doi.org/10.1016/j.jhydrol.2015.05.031>
- [160] S. D. Crausbay, A. R. Ramirez, S. L. Carter, M. S. Cross, K. R. Hall, D. J. Bathke, J. L. Betancourt, S. Colt, A. E. Cravens, M. S. Dalton, J. B. Dunham, L. E. Hay, M. J. Hayes, J. McEvoy, C. A. McNutt, M. A. Moritz, K. H. Nislow, N. Raheem, and T. Sanford, "Defining ecological drought for the twenty-first century," *Bulletin of the American Meteorological Society*, vol. 98, no. 12, pp. 2543–2550, 2017.

- [161] V. Jung, C. H. Albert, C. Violle, G. Kunstler, G. Loucougaray, and T. Spiegelberger, "Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events," *Journal of Ecology*, vol. 102, pp. 45–53, 2014.
- [162] M. L. Avolio, C. C. Chang, J. J. Weis, and M. D. Smith, "The effect of genotype richness and genomic dissimilarity of *Andropogon gerardii* on invasion resistance and productivity," *Plant Ecology and Diversity*, vol. 8, no. 1, pp. 61–71, 2015. [Online]. Available: <http://dx.doi.org/10.1080/17550874.2013.866990>
- [163] J. P. Schimel and J. Bennett, "Nitrogen Mineralization: Challenges of a Changing Paradigm," *Ecology*, vol. 85, no. 3, pp. 591–602, 2004.
- [164] N. Fierer and J. P. Schimel, "Effects of drying - rewetting frequency on soil carbon and nitrogen transformations," *Soil Biol Biochem*, vol. 34, pp. 777–787, 2002.
- [165] P. M. Homyak, S. D. Allison, T. E. Huxman, M. L. Goulden, and K. K. Treseder, "Effects of Drought Manipulation on Soil Nitrogen Cycling: A Meta-Analysis," *Journal of Geophysical Research: Biogeosciences*, vol. 2100, no. i, 2018.
- [166] J. Kreyling, M. Wenigmann, C. Beierkuhnlein, and A. Jentsch, "Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition," *Ecosystems*, vol. 11, no. 5, pp. 752–763, 2008.
- [167] R. Michalet, R. W. Brooker, C. J. Lortie, J.-p. Maalouf, and F. I. Pugnaire, "Disentangling direct and indirect effects of a legume shrub on its understorey community," *Oikos*, vol. 124, pp. 1251–1262, 2015.
- [168] O. E. Sala, W. J. Parton, L. A. Joyce, and W. K. Lauenroth, "Primary production of the central grassland region of the United States," *Ecology*, vol. 69, no. 1, pp. 40–45, 1988.
- [169] S. M. Buckland, J. P. Grime, J. G. Hodgson, and K. Thompson, "A Comparison of Plant Responses to the Extreme Drought of 1995 in Northern England," *Journal of Ecology*, vol. 85, no. 85, pp. 875–882, 1997. [Online]. Available: <http://www.jstor.org/stable/2960608> <http://about.jstor.org/terms>
- [170] N. B. English, J. F. Weltzin, A. Fravolini, L. Thomas, and D. G. Williams, "The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland," *Journal of Arid Environments*, vol. 63, no. 1, pp. 324–343, 2005.
- [171] E. Weng and Y. Luo, "Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: A modeling analysis," *Journal of Geophysical Research: Biogeosciences*, vol. 113, no. 3, pp. 1–16, 2008.
- [172] A. H. Marshall, R. P. Collins, M. W. Humphreys, and J. Scullion, "A new emphasis on root traits for perennial grass and legume varieties with environmental and ecological benefits," *Food and Energy Security*, vol. 5, no. 1, pp. 26–39, 2016.
- [173] P. B. Adler, J. HilleRisLambers, P. C. Kyriakidis, Q. Guan, and J. M. Levine, "Climate variability has a stabilizing effect on the coexistence of prairie grasses." *Proceedings of the National Academy of Sciences of the United States of America*, vol. 103, no. 34, pp. 12 793–12 798, 2006.

- [174] S. E. Koerner and S. L. Collins, “Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa,” *Ecology*, vol. 95, no. 1, pp. 98–109, 2014.
- [175] M. D. Morecroft, G. J. Masters, V. K. Brown, I. P. Clarke, M. E. Taylor, and A. T. Whitehouse, “Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland,” *Functional Ecology*, vol. 18, no. 5, pp. 648–655, 2004.
- [176] E. Forey, B. Touzard, and R. Michalet, “Does disturbance drive the collapse of biotic interactions at the severe end of a diversity-biomass gradient?” *Plant Ecology*, vol. 206, no. 2, pp. 287–295, 2009.
- [177] A. R. Gitlin, C. M. Sthultz, M. A. Bowker, S. Stumpf, K. L. Paxton, K. Kennedy, A. Muñoz, J. K. Bailey, and T. G. Whitham, “Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought,” *Conservation Biology*, vol. 20, no. 5, pp. 1477–1486, 2006.
- [178] C. Ovalle, A. Del Pozo, M. A. Casado, B. Acosta, and J. M. De Miguel, “Consequences of landscape heterogeneity on grassland diversity and productivity in the Espinal agroforestry system of central Chile,” *Landscape Ecology*, vol. 21, no. 4, pp. 585–594, 2006.
- [179] O. E. Sala, R. A. Golluscio, W. K. Lauenroth, and A. Soriano, “Resource partitioning between shrubs and grasses in the Patagonian steppe,” *Oecologia*, vol. 81, no. 4, pp. 501–505, 1989.
- [180] T. R. Pearson, D. F. Burslem, R. E. Goeriz, and J. W. Dalling, “Regeneration niche partitioning in neotropical pioneers: Effects of gap size, seasonal drought and herbivory on growth and survival,” *Oecologia*, vol. 137, no. 3, pp. 456–465, 2003.
- [181] J. B. Nippert and A. K. Knapp, “Soil water partitioning contributes to species coexistence in tallgrass prairie,” *Oikos*, vol. 116, no. 6, pp. 1017–1029, 2007.
- [182] R. K. Shriver, “Rainfall variability and fine-scale life history tradeoffs help drive niche partitioning in a desert annual plant community,” *Ecology Letters*, vol. 20, pp. 1231–1241, 2017.
- [183] E. L. Fry, P. Manning, D. G. P. Allen, A. Hurst, G. Everwand, M. Rimmler, and S. A. Power, “Plant Functional Group Composition Modifies the Effects of Precipitation Change on Grassland Ecosystem Function,” *PLoS ONE*, vol. 8, no. 2, 2013.
- [184] D. Tilman, P. B. Reich, and J. M. H. Knops, “Biodiversity and ecosystem stability in a decade-long grassland experiment,” *Nature*, vol. 441, no. 7093, pp. 629–632, 2006.
- [185] A. Koyama and S. Tsuyuzaki, “Facilitation by tussock-forming species on seedling establishment collapses in an extreme drought year in a post-mined Sphagnum peatland,” *Journal of Vegetation Science*, vol. 24, no. 3, pp. 473–483, 2013.

- [186] M. L. Peterson, K. J. Rice, and J. P. Sexton, "Niche partitioning between close relatives suggests trade-offs between adaptation to local environments and competition," *Ecology and Evolution*, vol. 3, no. 3, pp. 512–522, 2013.
- [187] K. Schiffrers and K. Tielbörger, "Ontogenetic shifts in interactions among annual plants," *Journal of Ecology*, vol. 94, no. 2, pp. 336–341, 2006.
- [188] A. V. Malyshev, M. A. S. Arfin Khan, C. Beierkuhnlein, M. J. Steinbauer, H. A. L. Henry, A. Jentsch, J. Dengler, E. Willner, and J. Kreyling, "Plant responses to climatic extremes: Within-species variation equals among-species variation," *Global Change Biology*, pp. 449–464, 2015.
- [189] E. E. Cleland, S. L. Collins, T. L. Dickson, E. C. Farrer, K. L. Gross, L. A. Gherardi, L. M. Hallett, R. J. Hobbs, J. S. Hsu, L. Turnbull, and K. N. Suding, "Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation," *Ecology*, vol. 94, no. 8, pp. 1687–1696, 2013.
- [190] M. He and F. A. Dijkstra, "Drought effect on plant nitrogen and phosphorus : a meta-analysis," *New Phytologist*, vol. 204, pp. 924–931, 2014.
- [191] L. Augusto, D. L. Achat, M. Jonard, D. Vidal, and B. Ringeval, "Soil parent materialA major driver of plant nutrient limitations in terrestrial ecosystems," *Global Change Biology*, vol. 23, no. 9, pp. 3808–3824, 2017.
- [192] S. E. Evans and I. C. Burke, "Carbon and Nitrogen Decoupling Under an 11-Year Drought in the Shortgrass Steppe," *Ecosystems*, vol. 16, pp. 20–33, 2013.
- [193] L. Yahdjian, O. E. Sala, and A. T. Austin, "Differential controls of water input on litter decomposition and nitrogen dynamics in the patagonian steppe," *Ecosystems*, vol. 9, no. 1, pp. 128–141, 2006.
- [194] S. A. Heckathorn, E. H. Delucia, and R. E. Zielinski, "The contribution of drought-related decreases in foliar nitrogen concentration to decreases in photosynthetic capacity during and after drought in prairie grass," *Physiologia Plantarum*, vol. 101, pp. 173–182, 1997.
- [195] A. C. Franco and P. S. Nobel, "Influences of root distribution and growth on predicted water uptake and interspecific competition," *Oecologia*, vol. 82, no. 2, pp. 151–157, 1990.
- [196] S. D. Wilson and D. Tilman, "Plant Competition and Resource Availability in Response to Disturbance and Fertilization," *Ecology*, vol. 74, no. 2, pp. 599–611, 1993.
- [197] M. A. Vinton and I. C. Burke, "Interactions Between Individual Plant Species and Soil Nutrient Status in Shortgrass Steppe," vol. 76, no. 4, pp. 1116–1133, 1995.
- [198] M. E. Swanson, J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. a. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson, "The forgotten stage of forest succession: Early- successional ecosystems on forest sites," *Frontiers in Ecology and the Environment*, vol. 9, no. 2, pp. 117–125, 2011. [Online]. Available: <http://www.esajournals.org/doi/abs/10.1890/090157>

- [199] V. H. Dale, L. a. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. Michael Wotton, "Climate Change and Forest Disturbances," *BioScience*, vol. 51, no. 9, p. 723, 2001. [Online]. Available: [http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568\(2001\)051\[0723:CCAFD\]2.0.CO;2](http://bioscience.oxfordjournals.org/cgi/doi/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2)
- [200] X. Feng, T. E. Dawson, D. D. Ackerly, L. S. Santiago, and S. E. Thompson, "Reconciling seasonal hydraulic risk and plant water use through probabilistic soilplant dynamics," *Global Change Biology*, vol. 23, no. 9, pp. 3758–3769, 2017.
- [201] L. M. Hallett, J. S. Hsu, E. E. Cleland, S. L. Collins, T. L. Dickson, E. C. Farrer, L. A. Gherardi, K. L. Gross, R. J. Hobbs, L. Turnbull, and K. N. Suding, "Biotic mechanisms of community stability shift along a precipitation gradient," *Ecology*, vol. 95, no. 6, pp. 1693–1700, 2014.
- [202] M. Holmgren and M. Scheffer, "Strong facilitation in mild environments: The stress gradient hypothesis revisited," *Journal of Ecology*, vol. 98, no. 6, pp. 1269–1275, 2010.
- [203] D. R. Lane, D. P. Coffin, and W. K. Lauenroth, "Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States," *Journal of Vegetation Science*, vol. 9, no. 2, pp. 239–250, 1998.
- [204] T. P. Gaines and S. T. Gaines, "Soil texture effect on nitrate leaching in soil percolates," *Communications in Soil Science and Plant Analysis*, vol. 25, no. 13-14, pp. 2561–2570, 1994.
- [205] A. Sowerby, B. A. Emmett, A. Tietema, and C. Beier, "Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils," *Global Change Biology*, vol. 14, no. 10, pp. 2388–2404, 2008.
- [206] D. A. Devitt and S. D. Smith, "Root channel macropores enhance downward movement of water in a Mojave Desert ecosystem," *Journal of Arid Environments*, vol. 50, no. 1, pp. 99–108, 2002.
- [207] N. A. L. Archer, J. N. Quinton, and T. M. Hess, "Below-ground relationships of soil texture, roots and hydraulic conductivity in two-phase mosaic vegetation in South-east Spain," *Journal of Arid Environments*, vol. 52, pp. 535–553, 2002.
- [208] F. Lloret, J. Penuelas, and M. Estiarte, "Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community," *Global Change Biology*, vol. 10, no. 2, pp. 248–258, 2004.
- [209] F. Pugnaire, P. Haase, and J. Puigdefábregas, "Facilitation between higher plant species in a semiarid environment," *Ecology*, vol. 77, no. 5, pp. 1420–1426, 1996.
- [210] F. I. Pugnaire, C. Armas, and F. Valladares, "Soil as a mediator in plant-plant interactions in a semi-arid community," *Journal of Vegetation Science*, vol. 15, pp. 85–92, 2004.

- [211] P. B. Reich, “The world-wide fastslow’ plant economics spectrum: a traits manifesto,” *Journal of Ecology*, vol. 102, no. 2, pp. 275–301, 2014. [Online]. Available: <http://onlinelibrary.wiley.com/doi/10.1111/1365-2745.12211/abstract%5Cnhttp://onlinelibrary.wiley.com/doi/10.1111/1365-2745.12211/full>
- [212] A. J. Felton, M. D. Smith, and A. J. Felton, “Integrating plant ecological responses to climate extremes from individual to ecosystem levels,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, no. 372, 2017.
- [213] F. Lloret, E. G. de la Riva, I. M. Pérez-Ramos, T. Marañón, S. Saura-Mas, R. Díaz-Delgado, and R. Villar, “Climatic events inducing die-off in Mediterranean shrublands: are species’ responses related to their functional traits?” *Oecologia*, vol. 180, no. 4, pp. 961–973, 2016.
- [214] G. Kunstler, D. Falster, D. A. Coomes, F. Hui, M. Kooyman, Robert, D. C. Laughlin, L. Poorter, M. Vanderwel, G. Vieilledent, S. J. Wright, M. Aiba, C. Baraloto, J. Caspersen, J. H. C. Cornelissen, S. Gourlet-Fleury, M. Hanewinkel, B. Herault, J. Kattge, H. Kurokawa, Y. Onoda, J. Penuelas, H. Poorter, M. Uriarte, S. Richardson, and P. Ruiz-Benito, “Plant functional traits have globally consistent effects on competition,” *Nature*, vol. 529, pp. 1–15, 2015. [Online]. Available: <http://dx.doi.org/10.1038/nature16476>
- [215] A. B. Nicotra, O. K. Atkin, S. P. Bonser, a. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, M. D. Purugganan, C. L. Richards, F. Valladares, and M. van Kleunen, “Plant phenotypic plasticity in a changing climate.” *Trends in plant science*, vol. 15, no. 12, pp. 684–92, dec 2010. [Online]. Available: <http://www.ncbi.nlm.nih.gov/pubmed/20970368>
- [216] S. J. Brotherton and C. B. Joyce, “Extreme climate events and wet grasslands: plant traits for ecological resilience,” *Hydrobiologia*, vol. 750, no. 1, pp. 229–243, 2015.
- [217] A. Stampfli and M. Zeiter, “Mechanisms of structural change derived from patterns of seedling emergence and mortality in a semi-natural meadow,” *Journal of Vegetation Science*, vol. 19, no. 4, pp. 563–574, 2008.
- [218] L. Van Peer, I. Nijs, D. Reheul, and B. De Cauwer, “Species richness and susceptibility grassland ecosystems: compositional vs physiological effects,” *Functional Ecology*, vol. 18, pp. 769–778, 2014.
- [219] B. J. Butterfield and R. M. Callaway, “Mechanisms of Plant Competition: A functional comparative approach to facilitation and its context dependence,” *Functional Ecology*, vol. 27, pp. 907–917, 2013.
- [220] S. I. Seneviratne and P. Ciais, “Environmental science: Trends in ecosystem recovery from drought,” *Nature*, vol. 548, no. 7666, pp. 164–165, 2017.

## APPENDICES

## APPENDICES

## Appendix A: Supplementary Tables Chapter 2

Table A.1.: Soil temperature models and the resulting p-values, F statistic/chi-square, and degrees of freedom. Dashed lines in a box indicate that the variable was excluded from the model. Models were first run with all variables. Variables were excluded when they were found to be insignificant, and the new model improved the AIC value. Winter refers to the winter treatment applied to the subplot. Values represent p-values (\*\*\*p<0.001, \*\*p<0.01, \*p<0.05). Values in parentheses are the F statistic with degrees of freedom based on the Kenward-Roger method for daily soil temperature and soil temperature variability. Freeze-thaw event models were based on a binomial distribution, and degrees of freedom were calculated using type II Wald chi-squared tests. Values in parentheses are the chi-square statistic followed by degrees of freedom.

Daily Soil Temperature	
Transformation/distribution used	log(x+273) - Gaussian
Winter (W)	-
Month (M)	<0.001 (94.392, 1219)***
Year (Y)	<0.001 (223.972, 1219)***
W:Y	-
W:M	-
M:Y	<0.001 (61.602, 1219)***
W:M:Y	-

Table A.2.: Soil moisture models and the resulting p-values, F statistic and degrees of freedom. Summer refers to the summer treatments applied to the plots. Continuous measurements were taken using a datalogger, and manual measurements were taken using before and after watering events. See Table A.1 for p-values and F-statistics.

	Continuous	Manual
Transformation	ln(x )	
Summer (S)	1 (-0.0442,0)	< 0.001 (98.992,2372)***
Date	< 0.001 (145.7849,1641)***	< 0.001 (240.7417,2372)***
S:D	< 0.001 (5.1698,1641)***	< 0.001 (8.1034,2372)***

Table A.3.: Daily mineralization and nitrification rates ( $\text{g N d}^{-1}$ ) for each incubation period. Mineralization was averaged over winter treatment and the incubation period and over the incubation period for total mineralization. Nitrification was averaged over the incubation period for total nitrification. Numbers in parentheses are the standard error of the mean. See Table A.1 for p-values and F-statistics.

Mineralization per day (g N d <sup>-1</sup> )									
Winter Treatment		Winter 2015	Spring 2015	Summer 2015	Winter 2016	Spring 2016	Summer 2016		
Dry		9.49 10 <sup>-5</sup> (2.06 x 10 <sup>-5</sup> )	1.48 10 <sup>-4</sup> (1.48 x 10 <sup>-5</sup> )	6.64 x 10 <sup>-5</sup> (1.58 x 10 <sup>-5</sup> )	7.00 10 <sup>-5</sup> (1.31 x 10 <sup>-5</sup> )	1.02 10 <sup>-4</sup> (1.98 x 10 <sup>-5</sup> )	2.57 x 10 <sup>-4</sup> (7.28 x 10 <sup>-5</sup> )		
Control		4.78 10 <sup>-5</sup> (1.61 x 10 <sup>-5</sup> )	1.56 10 <sup>-4</sup> (3.13 x 10 <sup>-5</sup> )	4.40 x 10 <sup>-5</sup> (1.36 x 10 <sup>-5</sup> )	7.77 10 <sup>-5</sup> (1.32 x 10 <sup>-5</sup> )	8.88 10 <sup>-5</sup> (1.39 x 10 <sup>-5</sup> )	1.63 x 10 <sup>-4</sup> (3.88 x 10 <sup>-5</sup> )		
Wet		8.07 10 <sup>-5</sup> (2.79 x 10 <sup>-5</sup> )	2.71 10 <sup>-4</sup> (7.46 x 10 <sup>-5</sup> )	1.33 x 10 <sup>-4</sup> (2.81 x 10 <sup>-5</sup> )	6.64 10 <sup>-5</sup> (1.55 x 10 <sup>-5</sup> )	1.35 10 <sup>-4</sup> (3.56 x 10 <sup>-5</sup> )	2.07 x 10 <sup>-4</sup> (5.97 x 10 <sup>-5</sup> )		
Total		7.57 10 <sup>-5</sup> (1.47 x 10 <sup>-5</sup> )	1.91 10 <sup>-4</sup> (2.86 x 10 <sup>-5</sup> )	8.13 x 10 <sup>-5</sup> (1.35 x 10 <sup>-5</sup> )	7.14 10 <sup>-5</sup> (7.82 x 10 <sup>-6</sup> )	1.07 10 <sup>-4</sup> (1.37 x 10 <sup>-5</sup> )	2.09 x 10 <sup>-4</sup> (3.35 x <sup>-5</sup> )		
Nitrification per day (g N d <sup>-1</sup> )									
Total		5.32 10 <sup>-5</sup> (7.18 x 10 <sup>-6</sup> )	5.65 10 <sup>-5</sup> (2.02 x 10 <sup>-5</sup> )	7.92 x 10 <sup>-5</sup> (1.23 x 10 <sup>-5</sup> )	5.69 10 <sup>-5</sup> (7.28 x 10 <sup>-6</sup> )	7.74 10 <sup>-5</sup> (1.32 x 10 <sup>-5</sup> )	1.55 x 10 <sup>-4</sup> (3.39 x 10 <sup>-5</sup> )		

Table A.4.: Mineralization and nitrification models and the resulting p-values with degrees of freedom. Dashed lines in a box indicate that the variable was excluded from the model. Incubation period refers to the 6 incubation periods for the in-situ soil cores (winter, spring, summer of 2015 and 2016). See Table A.1 for p-values and F-statistics.

Transformation	Mineralization per day	Nitrification per day
	(g N d <sup>-1</sup> )	(g N d <sup>-1</sup> )
	ln(x + 1)	
Winter Treatment (W)	0.0689 (2.732, 126.08)	-
Summer Treatment	-	-
Incubation period (IP)	0.0024 (6.342, 126.27)**	0.0038 (5.81, 138.31)**
Year (Y)	0.4916 (0.481, 126.30)	0.0431 (4.171, 138.33)*
IP:Y	<0.001 (13.152, 109.383)***	0.1613 (1.882, 138.31)
W:IP	0.4012 (1.024, 126.05)	-
W:Y	0.3016 (1.212, 126.04)	-
W:IP:Y	0.7593 (0.474, 126.07)	-

Table A.5.: Total precipitation and average soil temperature mineralization and nitrification models using orthogonal polynomial and the resulting p-values with degrees of freedom. See Table A.1 for p-values and F-statistics.

Formula	Mineralization per day	Nitrification per day
	(g N d <sup>-1</sup> )	(g N d <sup>-1</sup> )
	ln(x + 1)	
Model with ST		NS
ST + ST <sup>2</sup>	<0.001 (9.992, 168.20)***	0.0012 (4.521, 168.16)**
Model with P		
P + P <sup>2</sup>	0.0167 (4.192, 168.02)*	
Model with P & ST		NS
P + P <sup>2</sup>	0.2562 (1.372, 162.07)	-
ST + ST <sup>2</sup>	0.0856 (2.502, 162.06)	-
P + P <sup>2</sup> * ST + ST <sup>2</sup>	0.0305 (2.744, 162.06)*	-

Table A.6.: Models for *Lindera benzoin* germination, emergence, and mortality rates and relative growth rate (RGR) with resulting p-values with F statistic and degrees of freedom in parentheses. See Table A.1 for p-values and F-statistics.

	<b>Germination</b>	<b>Mortality</b>	<b>RGR</b>
<b>Transformation</b>	$\ln(x+1)$		-
<b>Winter Treatment</b>	0.00295 (7.7, 22)**	NS	-
<b>Summer Treatment</b>	-	NS	< 0.001 (12,263)***
<b>Winter:Summer</b>	-	NS	-
<b>Date</b>	-	0.0022 (6.9,52)**	-

Table A.7.: Plant community models with resulting p-values and degrees of freedom. See Table A1 for p-values and F-statistics.

	Richness		Inverse Simpsons Diversity		Plant functional type (PFT)
Transformation	$\sqrt{x}$		$\ln(x)$		$\ln(x+1)$
Winter Treatment (W)	0.0020 (6.632, 93.001)**		0.0213 (4.012, 99.01)*		-
Summer	-		-		-
Month (M)	<0.001 (60.642, 93.001)***		<0.001 (35.752, 99.01)*		<0.001 (12.721, 1052)***
Year (Y)	0.9027 (0.0151, 93.001)		-		0.08833 (2.891, 1052)
M:Y	0.2924 (1.211, 93.001)		-		0.0723 (3.241, 1052)
W:M	0.7076 (0.3472, 93.001)		0.9008 (0.105 (2, 99.01)		-
W:Y	0.0832 (2.552, 93.001)		-		-
W:M:Y	0.9533 (0.0482, 93.001)		-		-
PFT	-		-		<0.001 (93.073, 1052)***
PFT:M	-		-		<0.001 (7.993, 1052)***
PFT:Y	-		-		0.1591 (1.733, 1052)
PFT:M:Y	-		-		0.2866 (1.133, 1052)

Table A.8.: Plant community evenness with resulting p-values and degrees of freedom.  
See Table A1 for p-values and F-statistics.

Transformation	Evenness (J)
	$\sqrt{x}$
Winter Treatment (W)	-
Summer Treatment (S)	0.0485 (3.232, 99.005)*
Month (M)	0.0063 (7.811, 99.005)**
S:M	0.7933 (3.232, 99.005)

## Appendix B: Supplementary Figures Chapter 2

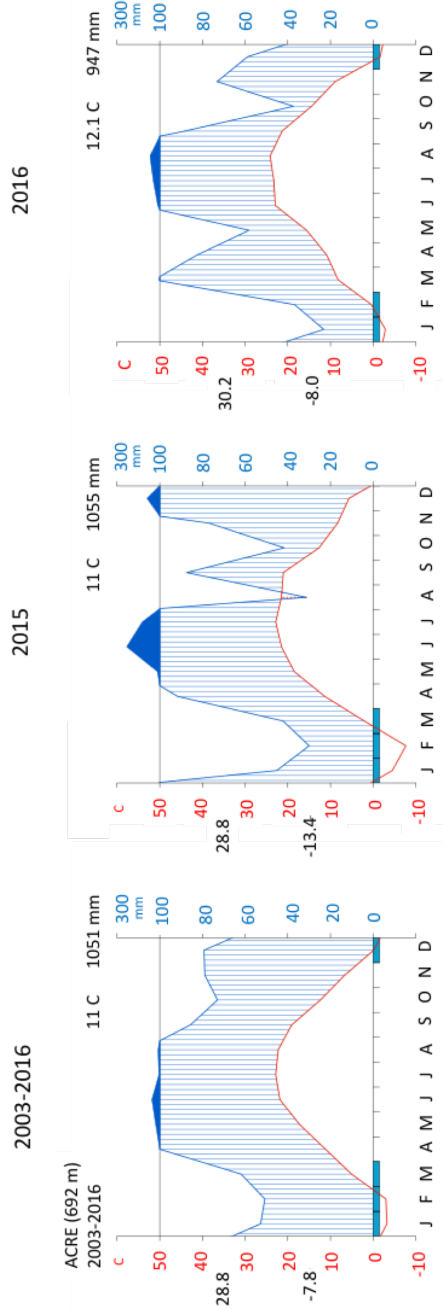


Fig. B.1.: Climate diagrams for the site using data collected from a nearby weather station at ACRE. The blue line represents the precipitation (mm) time series, and values are on the left y-axis. The red line represents the temperature curve, and values are on the x-axis. The black numbers to the left of each diagram represent the mean daily minimum temperature of the warmest month (top) and the mean daily maximum temperature of the coldest month (bottom). The black numbers on the top of each diagram represent the MAT and MAP. The blue-boxes on the x-axis are indicators of frost periods. The climate diagram on the left is for the time period from 2003-2016 (13 years) and the middle and right diagrams are for each of the years for the experiment, 2015 and 2016, respectively.

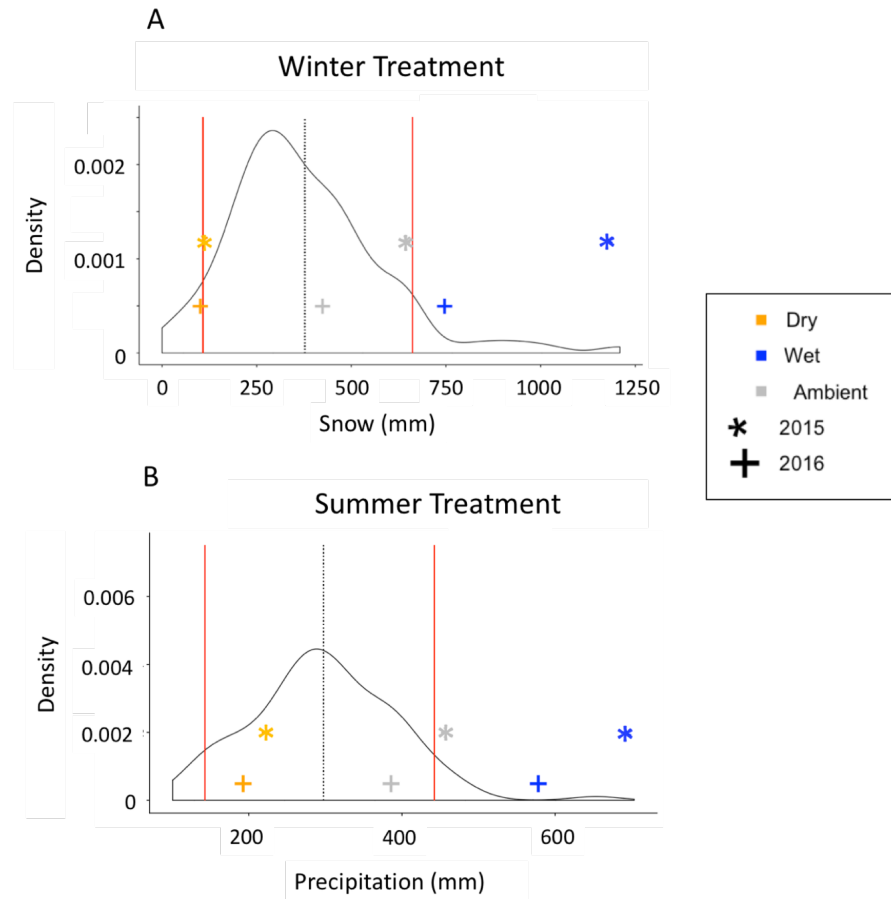


Fig. B.2.: Density curve of the precipitation record from the area from 1901-2016. The \* and + indicate the treatments for 2015 and 2016, respectively. The colors indicate the treatment applied in each season: orange = dry, blue = wet treatments, and gray = winter, control (ambient) conditions (A) Snowfall distribution for the months of January-March. (B) Summer precipitation distribution for the months of June-August.

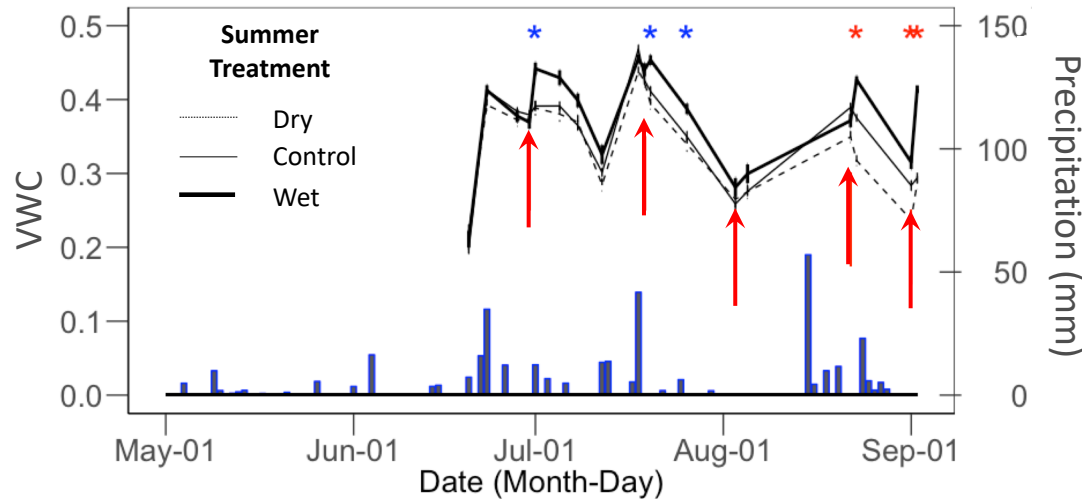


Fig. B.3.: Soil moisture (mean and SE) collected manually and precipitation for 2016, grouped by summer treatment ( $N=9$ ). The dashed line represents summer-dry subplots, the thin, solid line represents summer-control plots, and the thick, solid line represents summer-wet treatments. The red arrows indicate the dates on which a watering event occurred. The asterisks indicate statistically different VWC, where blue indicates that summer-wet was different from summer-dry and red indicates that summer-dry was different from both control and summer-wet. The blue bars on the bottom represent daily precipitation values.

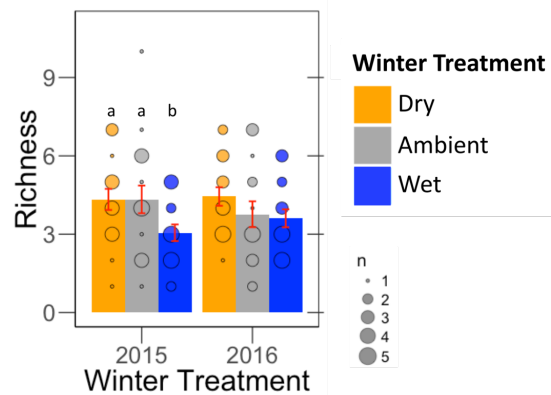


Fig. B.4.: Mean of richness of the understory community averaged over month ( $N=18$ ). Error bars indicate standard errors of the mean and letters represent statistically similar groups (Tukey HSD,  $\alpha = 0.05$ ). The circles represent the number of individual data points, with the same richness.

### Appendix C: Supplementary Tables Chapter 3

Table C.1.: Species planted as seeds during the 2008 restoration of the experimental site.

#### Seeds planted during restoration

*Andropogon gerardii* - (Big Blue Stem)  
*Asclepias tuberosa* (Butterfly Weed)  
*Aster nova-angliae* (New England Aster)  
*Aster oolentangiensis* (Sky Blue Aster)  
*Baptisa australis* (Blue False Indigo)  
*Cassia fasciculata* (Partridge Pea)  
*Coreopsis lanceolata* - (Lance-leaf Coreopsis)  
*Coreopsis palmata* (Prairie Coreopsis)  
*Dalea candidum* (White Prairie Clover)  
*Dalea purpurea* (Purple Prairie Clover)  
*Desmanthus illinoensis* - (Prairie Bundelflower)  
*Desmodium canadenses* (Showy Tick-trefoil)  
*Echinacea purpurea* - (Purple Coneflower)  
*Elymus canadensis* - (Wild Rye)  
*Helianthus grosseserratus* (Saw-Tooth Sunflower)  
*Heliopsis helianthoides* (False Sunflower)  
*Lespedeza capitata* - (Round-head Lespedeza )  
*Liatris aspera* (Rough Blazingstar)  
*Liatris pycnostachya* (Prairie Blazingstar)  
*Liatris spicata* (Spiked Liatris)  
*Rudbeckia hirta* - (Black-eyed Susan)  
*Rudbeckia triloba* (Brown-eyed Susan)  
*Schizachyrium scoparium* - (Little Blue Stem)  
*Schizachyrium virginicus* - (Broomsedge)  
*Solidago rigida* (Stiff Goldenrod)  
*Solidago speciosa* (Showy Goldrod)  
*Sorghastrum nutans* - (Indian Grass)  
*Sporobolus heterolepis* - (Prairie Dropseed)  
*Tripsacum dactyloides* - (Eastern Gama)  
*Vernonia fasciculata* (Common Ironweed)

Table C.2.: Classification of plant functional types (PFT).

Plant functional type (PFT)	Description	Species
Clonal forb	Non-nitrogen fixing dicotyledonous perennial forb capable of asexual reproduction	<i>Solidago canadensis</i>
		<i>Ambrosia psilostachya</i>
		<i>Solidago speciosa</i>
		<i>Solanum carolinense</i>
		<i>Echinacea purpurea</i>
		<i>Cirsium arvense</i>
		<i>Euthamia graminifolia</i>
Other forb	Non-nitrogen fixing dicotyledonous forb not capable of asexual reproduction, reproduces sexually	<i>Symphotrichum pilosum</i>
		<i>Symphotrichum novae-angliae</i>
		<i>Heliopsis helianthoides</i>
		<i>Erigeron annuus</i>
		<i>Rudbeckia triloba</i>
		<i>Daucus pusillus</i>
		<i>Asclepias tuberosa</i>
Grass	Monocotyledonous grasses with C3 or C4 photosynthetic system	<i>Andropogon gerardii</i>
		<i>Festuca spp.</i>
		<i>Setaria spp.</i>
		<i>Sorghastrum nutans</i>
		<i>Elgmus spp.</i>
Legume	Nitrogen-fixing dicotyledonous forb	<i>Desmodium canadense</i>
		<i>Lotus corniculatus</i>
		<i>Trifolium spp.</i>
Shrub	Non-nitrogen fixing dicotyledonous woody plant	<i>Rubus idaeus</i>

Table C.3.: Model results for daily soil moisture at 15 cm depth. DF represents degrees of freedom of the numerator and denominator, respectively. Symbols next to p-values indicate the following:  $\leq 0.1$ , \*  $\leq 0.05$ , \*\*  $\leq 0.01$ , and \*\*\*  $\leq 0.001$ .

	F statistic	DF	p-value
Treatment	304.22	(7, 9873)	<0.0001***
Year	19.5	(1, 9940.3)	<0.0001***
Treatment:Year	44.97	(7, 9941)	<0.0001***

Table C.4.: Model results for daily soil moisture at 100-1000 mm depths. DF and symbols as in Table C.2

	F statistic	DF	p-value
Treatment	2773.96	(1, 5556)	< 0.0001***
Depth	1158.41	(5, 5555)	< 0.0001***
Year	0.53	(1, 5556)	0.468
Treatment:Depth	35.37	(5, 5555)	< 0.0001***
Treatment:Year	19.59	(1, 5556)	< 0.0001***
Depth:Year	3.67	(5, 5555)	0.0026
Treatment:Depth:Year	3.31	(5, 5555)	0.0054

Table C.5.: Model results for relationship of ANPP to average soil moisture before the harvest date and timing of drought. DF and symbols as in Table C.2

	F statistic	DF	p-value
Average Soil Moisture	4.6292	(1,44)	0.0370*
E	1.3392	(1,44)	0.2534
M	3.7962	(1,44)	0.0578
L	4.5362	(1,44)	0.0388*
Average Soil Moisture:E	1.3823	(1,44)	0.246
Average Soil Moisture:M	4.8176	(1,44)	0.0335*
E:M	0.3132	(1,44)	0.5786
Average Soil Moisture:L	3.4169	(1,44)	0.0713
E:L	0.3168	(1,44)	0.5764
M:L	1.342	(1,44)	0.2529
Average Soil Moisture:E:M	0.494	(1,44)	0.4859
Average Soil Moisture:E:L	0.4732	(1,44)	0.4951
Average Soil Moisture:M:L	0.4583	(1,44)	0.502
E:M:L	0.3486	(1,44)	0.5579
Average Soil Moisture:E:M:L	0.64	(1,44)	0.428
<hr/>			
$r^2 = 0.4162$			

Table C.6.: Model results for relationship of ANPP and the length of drought. DF and symbols as in Table C.2

	F-statistic	DF	p-value
Length + Length <sup>2</sup>	4.5219	(2, 61)	0.0148 *
<hr/>			
$r^2 = 0.1255$			

Table C.7.: Model results for relationship between ANPP and the treatment, including both timing and duration, and the year of the harvest. DF and symbols as in Table C.2

	F statistic	DF	p-value
Treatment	4.7257	(7, 44)	0.0003***
Year	11.0659	(1, 44)	0.0018**
Treatment:Year	0.4857	(7, 44)	0.8398

Table C.8.: Model results for relationship between ANPP and timing of drought (Early (E), Middle (M), and Late (L). DF and symbols as in Table C.2

	F statistic	DF	p-value
E	3.4637	(1, 44)	0.06942
M	18.1186	(1, 44)	0.0001***
L	3.1785	(1, 44)	0.08151
Year	11.0659	(1, 44)	0.0018**
E:M	4.9109	(1, 44)	0.0319*
E:L	0.1747	(1, 44)	0.678
M:L	2.9944	(1, 44)	0.0906
E:Year	0.2759	(1, 44)	0.602
M:Year	1.038	(1, 44)	0.3139
L:Year	0.1418	(1, 44)	0.7083
E:M:L	0.037	(1, 44)	0.8483
E:M:Year	1.167	(1, 44)	0.2859
E:L:Year	0.5646	(1, 44)	0.4564
M:L:Year	0.0004	(1, 44)	0.9849
E:M:L:Year	0.2103	(1, 44)	0.6488

Table C.9.: Model results for percentage of clonal forbs in live biomass. DF and symbols as in Table C.2

	F statistics	DF	p-value
E	0.6739	(1, 45)	0.416
M	0.8034	(1, 45)	0.3748
L	0.941	(1, 45)	0.3372
Year	6.9964	(1, 45)	0.0112*
E:M	0.1935	(1, 45)	0.6621
E:L	0.066	(1, 45)	0.7984
M:L	4.3004	(1, 45)	0.0439*
E:Year	0.0104	(1, 45)	0.9191
M:Year	1.7791	(1, 45)	0.189
L:Year	0.1834	(1, 45)	0.6705
E:M:L	0.6688	(1, 45)	0.4178
E:M:Year	0.0787	(1, 45)	0.7804
E:L:Year	1.1898	(1, 45)	0.2812
M:L:Year	0.2777	(1, 45)	0.6008
E:M:L:Year	1.4755	(1, 45)	0.2308

Table C.10.: Model results for percentage of grasses in live biomass. DF and symbols as in Table C.2

	F statistic	DF	p-value
E	0.2596	(1,45)	0.6129
M	0.122	(1,45)	0.7285
L	0.1414	(1,45)	0.7087
Year	4.3067	(1,45)	0.0437*
E:M	0.0001	(1,45)	0.9928
E:L	0.1431	(1,45)	0.707
M:L	1.9691	(1,45)	0.1674
E:Year	0.3229	(1,45)	0.5727
M:Year	0.2976	(1,45)	0.5881
L:Year	0.0047	(1,45)	0.9459
E:M:L	0.0092	(1,45)	0.9239
E:M:Year	0.1722	(1,45)	0.6802
E:L:Year	1.8901	(1,45)	0.176
M:L:Year	0.5795	(1,45)	0.4505
E:M:L:Year	0.8233	(1,45)	0.3691

Table C.11.: Model results for percentage of other forbs in live biomass. DF and symbols as in Table C.2

	F statistic	DF	p-value
E	0.0726	(1, 45)	0.7888
M	0.4596	(1, 45)	0.5013
L	0.9945	(1, 45)	0.324
Year	2.1703	(1, 45)	0.1477
E:M	0.6548	(1, 45)	0.4227
E:L	0.0549	(1, 45)	0.8159
M:L	0.4291	(1, 45)	0.5158
E:Year	0.9552	(1, 45)	0.3336
M:Year	0.1033	(1, 45)	0.7494
L:Year	5.6801	(1, 45)	0.0214*
E:M:L	0.0333	(1, 45)	0.8561
E:M:Year	1.2734	(1, 45)	0.2651
E:L:Year	0.0148	(1, 45)	0.9036
M:L:Year	0.2825	(1, 45)	0.5977
E:M:L:Year	0.0545	(1, 45)	0.8165

Table C.12.: Model results for percentage of legumes in live biomass. DF and symbols as in Table C.2

	F statistic	DF	p-value
E	0.4947	(1, 45)	0.4855
M	0.0937	(1, 45)	0.7609
L	0.4315	(1, 45)	0.5146
Year	1.1829	(1, 45)	0.2826
E:M	1.7901	(1, 45)	0.1876
E:L	0.2615	(1, 45)	0.6116
M:L	0.35	(1, 45)	0.5571
E:Year	0.0025	(1, 45)	0.9606
M:Year	0.4745	(1, 45)	0.4945
L:Year	0.0373	(1, 45)	0.8478
E:M:L	0.6434	(1, 45)	0.4267
E:M:Year	0.1678	(1, 45)	0.684
E:L:Year	4.9683	(1, 45)	0.0309*
M:L:Year	3.7917	(1, 45)	0.0578
E:M:L:Year	0.0235	(1, 45)	0.8788

Table C.13.: Model results for timing of drought and diversity. DF and symbols as in Table C.2

	F statistic	DF	p-value
E	0.7788	(1, 45)	0.3822
M	0.2084	(1, 45)	0.6502
L	0.091	(1, 45)	0.7643
Year	1.6621	(1, 45)	0.2039
B:M	0.6235	(1, 45)	0.4339
E:L	1.0432	(1, 45)	0.3125
M:E	2.8658	(1, 45)	0.0974
E:Year	7.8725	(1, 45)	0.0074**
M:Year	0.964	(1, 45)	0.3314
L:Year	9.6073	(1, 45)	0.0033**
E:M:L	2.7152	(1, 45)	0.1064
E:M:Year	0.5215	(1, 45)	0.4739
E:L:Year	1.9886	(1, 45)	0.1654
M:L:Year	6.2053	(1, 45)	0.0165*
E:M:L:Year	0.102	(1, 45)	0.7509

## Appendix D: Supplementary Figures Chapter 3

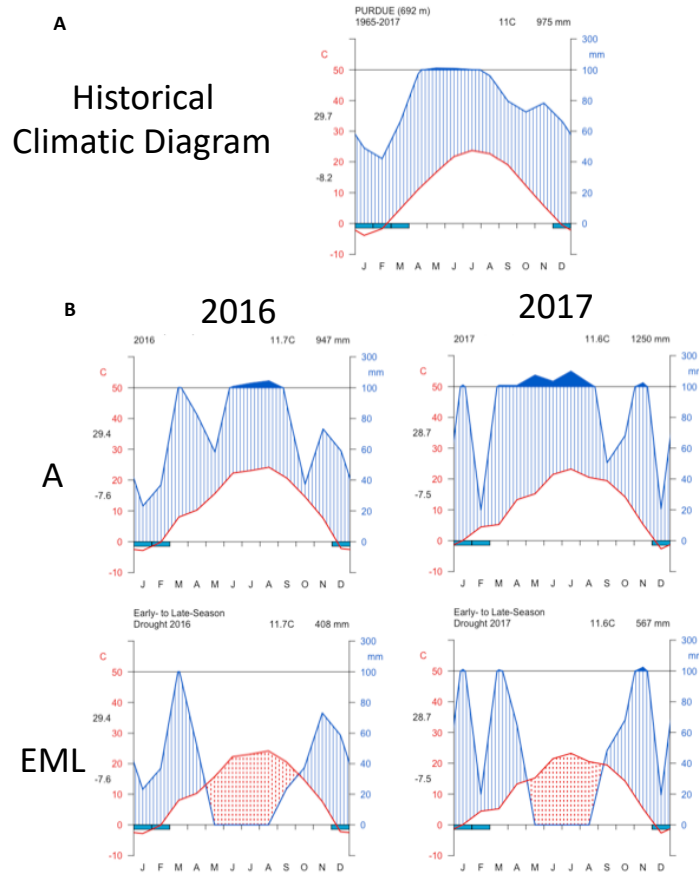


Fig. D.1.: Climate diagrams for the field site and the treatments applied at the site. Climate diagrams for the site use data collected from a nearby weather station at ACRE. Values on the right y-axis represent monthly precipitation (mm), and the blue line represents the time series of monthly precipitation. Values on the left y-axis represent monthly average air temperature (C), and the red line represents the time series of monthly temperatures. The black numbers at the top of each diagram represent the annual temperature and precipitation averaged across the experimental year, respectively. The black numbers on the left-side of each diagram are the mean daily maximum temperature of the warmest month (top) and the mean daily minimum temperature of the coldest month (bottom). The blue-boxes on the x-axis indicate frost periods. (A) Historical climate diagram for the time period from 1965-2017. (B) Climate diagrams for each year of the experiment, 2016 (left) and 2017 (right).

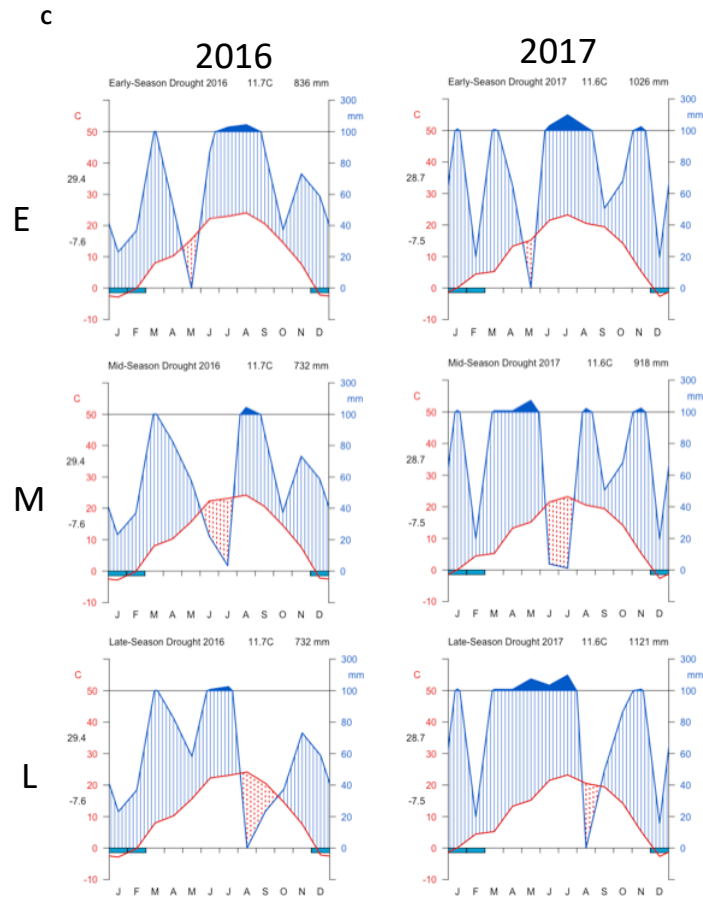


Fig. D.2.: Climate diagrams for the 7-week treatments applied at the site. See Fig. D.1 explanation.

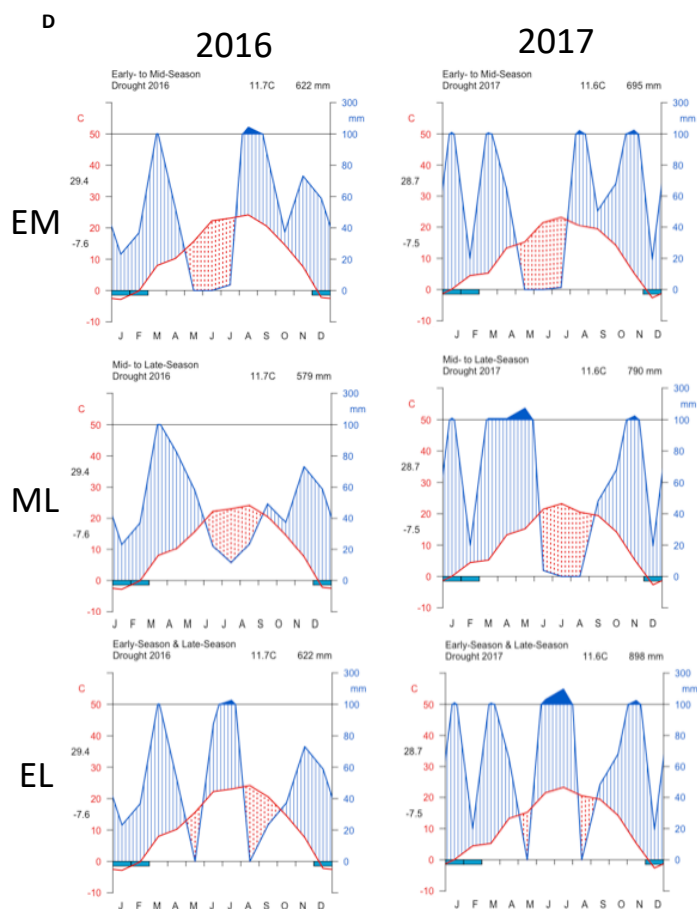


Fig. D.3.: Climate diagrams for the 14-week treatments applied at the site. See Fig. D.1 explanation.

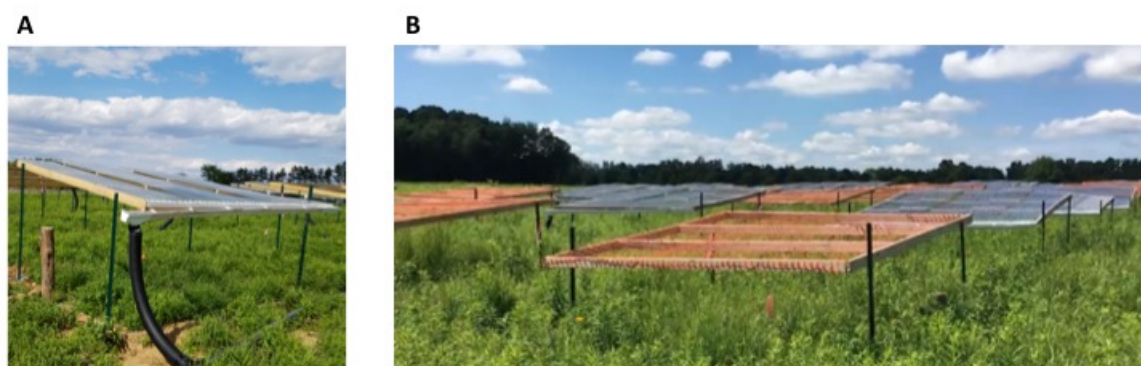


Fig. D.4.: Pictures of experimental site. (A) Rainout shelter showing gutter and drainage system. (B) Picture of several plots, including an infrastructure control with construction fencing.

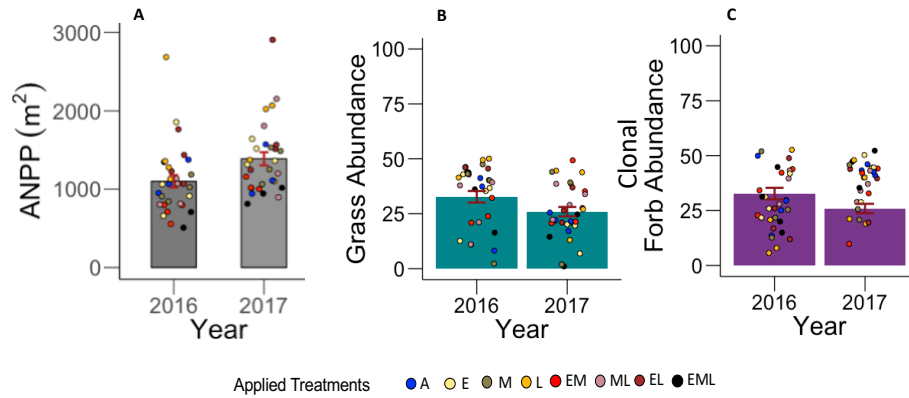


Fig. D.5.: Total ANPP(A) for each year and relative abundance of (B) grasses and (C) clonal forbs for the total ANPP of each year. Dots represent individual data points for each plot in each year. Colors represent the applied treatments: ambient (A) = blue, early (E) = light yellow, middle (M) = brown, late (L) = orange, EM = red, ML = pink, EL = dark red, and EML = black. Bars represent the mean ANPP or percentage for each year, and error bars represent standard error.

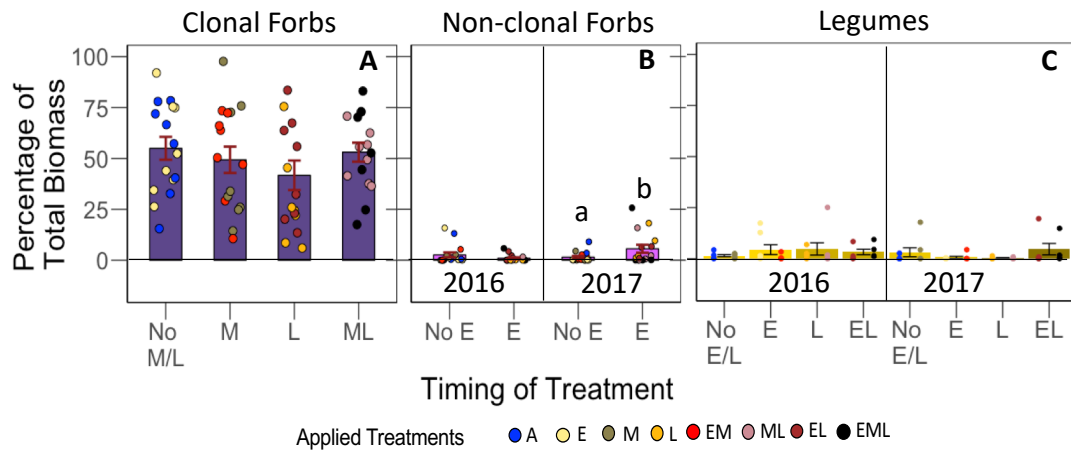


Fig. D.6.: Relative abundance of plant functional types (PFT) in the drought treatment groups. Letters identify treatment groups that are statistically similar. Dots represent individual data points for relative abundance (%) of each PFT in each treatment. Treatment colors, bars, and error bars as in Figure S3. (A) Percentage of clonal forbs in mid- to late-season droughts, where No M/L includes A and E treatments, M includes M and EM treatments, L includes L and EL treatments, and ML includes ML and EML treatments. (B) Percentage of non-clonal forbs in early-season droughts in 2016 and 2017, where No E includes A, M, L, ML and E includes E, EM, EL, EML. (C) Percentage of legumes in early- and late-season droughts in 2016 and 2017, where No E/L includes A and M treatments, E includes E and EL treatments, L includes L and ML treatments, and EL includes EL and EML treatments.