DISSERTATION

IMPACTS OF COMPOUND PRECIPITATION EXTREMES ON BELOWGROUND DYNAMICS IN A MESIC GRASSLAND

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ABSTRACT

IMPACTS OF COMPOUND PRECIPITATION EXTREMES ON BELOWGROUND DYNAMICS IN A MESIC GRASSLAND

Climate change is altering precipitation regimes globally and is expected to cause more frequent and extreme droughts as well as intensification of precipitation patterns (e.g., fewer and larger precipitation events) in many regions around the world. Drought has long been a phenomenon of interest to ecologists and has been widely studied as a key driver of ecosystem dynamics. To study drought, ecologists must define or at least operationalize what constitutes drought conditions. How this is accomplished in practice is unclear, so I begin my dissertation with a literature review that assessed how ecologists describe and study drought. I found that few publications explicitly define drought and that many (~30%) provide little quantification of studied droughts at all, simply equating drought with generally dry conditions. This lack of description hampers synthesis and our ability to draw broad ecological conclusions about drought impacts. I suggest that future publications provide detailed descriptions of drought conditions and contextualization within site-specific long-term climatic history, to facilitate more rigorous comparisons among studies.

Our understanding of the ecological impacts of drought is further limited by the fact that most previous research has focused on the impacts of single drought events, and it is increasingly likely that droughts will be compounded with other precipitation changes (e.g., intensified precipitation patterns or previous droughts). To study how the impacts of drought are altered when compounded with other precipitation changes, I imposed a 2-yr extreme drought (growing season precipitation reduced 66%) in two different long-term precipitation experiments at the Konza Prairie Biological Station- one which had intensified precipitation patterns by imposing a treatment of fewer and larger precipitation events with longer intervening dry periods for 16 years (chapter 2), and one which had imposed a previous extreme drought (chapter 3). I found that though precipitation pattern intensification reduced aboveground net primary production (ANPP), it did not alter the response of ANPP to a subsequently imposed drought. In contrast, previous exposure to intensified precipitation patterns reduced belowground net primary production (BNPP) and muted soil CO_2 flux responses to rainfall events during drought. In the case of multiple droughts, I found that repeated drought decreased root mass production more than twice as much as one drought (-63% vs. -27%, respectively, relative to controls). Thus, in both experiments, previous exposure to precipitation change decreased the resistance of BNPP to a subsequent drought. These results suggest that drought impacts might be underestimated if precipitation history and/or belowground impacts are not fully considered. Overall, my dissertation results indicate that understanding and prediction of ecological drought effects can be improved with more detailed and consistent descriptions of drought conditions and greater consideration of past precipitation changes and belowground dynamics.

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CHAPTER 1: INTRODUCTION

Globally, more frequent and extreme droughts are expected as climate change alters precipitation regimes, with evidence for this already emerging (IPCC 2013; USGCRP 2017; Dai 2013). Drought has long been a phenomenon of interest to ecologists and has been studied extensively and shown to impact myriad ecosystem functions (Slette et al. 2019; Dai 2013; Eziz et al. 2017; Gao et al. 2019; Lei et al. 2016; Wu et al. 2011).

Given that drought will continue to be widely studied as a driver of ecosystem dynamics, defining and characterizing drought are important for advancing our understanding of its ecological impacts. Climatologists have struggled to define drought and generally agree that a widely applicable definition has proven elusive (Redmond, 2002), with some even concluding that "... we cannot reasonably expect the existence of any workable generalized objective definition of drought" (Lloyd-Hughes, 2014). Even a cursory review of the ecological drought literature indicates that a universal definition of drought has eluded ecologists as well. Inconsistency in how we define or characterize drought can make it difficult to compare studies and ultimately hampers synthesis (Fraser et al., 2013).

To better understand how ecologists define drought, I reviewed 564 papers published in the last 50 years that evaluated ecological impacts of drought. I assessed how droughts were defined, described, or characterized in these papers and whether definitions varied by research approach or ecosystem type. My goal was to suggest ways in which future studies can better describe and quantify drought conditions, to facilitate synthesis and strengthen inferences drawn from the collective ecological drought literature. This study is presented in Chapter 2.

Much of what we know about the ecological impacts of drought is based on studies of single drought events, but it is increasingly likely that droughts will be compounded with other precipitation changes. Concurrent with increasing drought frequency and severity, climate change is also intensifying precipitation patterns by reducing the number and increasing the size of individual rainfall events (Fischer and Knutti 2016; Fowler et al.2021; Huntington 2006; IPCC 2013; USGCRP 2017). Thus, it is likely that future droughts will occur against a backdrop of intensified precipitation patterns. A shift towards fewer but larger precipitation events and longer intervening dry periods can affect numerous ecosystem processes (Fay et al. 2008; Knapp et al. 2008; Zeppel et al. 2014), but it remains unknown how altered precipitation patterns might affect ecosystem responses to drought, because most research to date has focused on these different aspects of precipitation change individually. In addition, as the time between droughts decreases with climate change, it will be important to understand how ecosystems respond to not only single, but also recurrent drought. Climate anomalies can have persistent effects on ecosystems and leave behind a legacy that alters the impacts of subsequent of climate events, so ecosystem responses to compound weather events are likely not predictable from studies that focus on individual events (Dodd and others 2021; Seneviratne and others 2012; Zscheischler and others 2018; Zscheischler and others 2020). Several previous studies have found amplifying impacts of compound climate extremes, but neutral and mitigating effects have also been reported (Anderegg and others 2020; Backhaus and others 2014; Dreesen and others 2014; Hoover and others 2015, 2021; Hughes and others 2019). Thus, the potential consequences of compounded precipitation changes, ranging from increased acclimation to decreased resistance, remain unresolved.

I performed my dissertation research in a grassland because grasslands are important ecosystems in which to understand the effects of precipitation changes. Grass-dominated systems are globally extensive (Dixon and others 2014; White and others 2000), they play a key role in the global carbon cycle (Pendall and others 2018; Scurlock and Hall 1998), and they are sensitive to changes in precipitation amount and pattern (Felton et al. 2020; Gherardi and Sala 2015; Heisler-White et al. 2008, 2009; Hoover et al. 2014; Huxman et al. 2004; Knapp et al. 2002, 2008, 2015, 2020; Li et al. 2019; Lu et al. 2021; Thomey et al. 2011).

Belowground responses such as belowground net primary production (BNPP) and soil CO_2 flux are of particular interest in grasslands because these systems allocate a substantial portion of total net primary production to roots and store most of their carbon belowground (Hui and Jackson 2006; Risser et al. 1981; Silver et al. 2010; Smith et al. 2008; Soussana and others 2004). Roots are the primary means by which plants acquire water and nutrients, regardless of drought conditions, and are important in ecosystem carbon and nutrient cycling. Root production and soil CO_2 flux are key factors determining the size of the soil carbon pool, which is at least twice as large as the atmospheric carbon pool and plays a key role in global carbon cycling and climate regulation (Köchy et al. 2015; Scharlemann et al. 2014). Understanding grassland root responses to precipitation change will thus help predict both ecosystem- and global-scale changes to carbon dynamics under an increasingly variable climate.

In chapter 3, I present a study in which I tested how long-term intensification of precipitation patterns affected ecosystem responses to a subsequent extreme drought, as well as recovery after drought. I imposed an extreme 2-yr drought (66% reduction in growing season rainfall) in grassland plots with and without previous long-term exposure to an intensified precipitation regime (fewer and larger rainfall events with longer intervening dry periods for 16 years) and assessed key carbon cycling processes (e.g., ANPP, BNPP and soil CO_2 flux) during and after drought. In chapter 4, I report the results of a study focused on assessing root responses to single vs. recurrent extreme droughts, and recovery after drought. I imposed an extreme drought in plots both with and without previous drought exposure and assessed root production and traits during and after drought.

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CHAPTER 2: HOW ECOLOGISTS DEFINE DROUGHT, AND WHY WE SHOULD DO BETTER[1]

Overview

Drought, widely studied as an important driver of ecosystem dynamics, is predicted to increase in frequency and severity globally. To study drought, ecologists must define or at least operationalize what constitutes a drought. How this is accomplished in practice is unclear, particularly given that climatologists have long struggled to agree on definitions of drought, beyond general variants of "an abnormal deficiency of water". We conducted a literature review of ecological drought studies (564 papers) to assess how ecologists describe and study drought. We found that ecologists characterize drought in a wide variety of ways (reduced precipitation, low soil moisture, reduced streamflow, etc.), but relatively few publications (~32%) explicitly define what are, and are not, drought conditions. More troubling, a surprising number of papers (~30%) simply equated "dry conditions" with "drought" and provided little characterization of the drought conditions studied. For a subset of these, we calculated Standardized Precipitation Evapotranspiration Index values for the reported drought periods. We found that while almost 90% of the studies were conducted under conditions quantifiable as slightly to extremely drier than average, ~50% were within the range of normal climatic variability. We conclude that the current state of the ecological drought literature hinders synthesis and our ability to draw broad ecological inferences because drought is often declared

[1]Slette IJ, Post AK, Awad M, Even T, Punzalan A, Williams S, Smith MD, Knapp AK. 2019. How ecologists define drought, and why we should do better. Global Change Biology 25: 3193–3200. https://doi.org/10.1111/gcb.14747

but is not explicitly defined or well characterized. We suggest that future drought publications provide at least one of the following: 1) the climatic context of the drought period based on long-term records, 2) standardized climatic index values, 3) published metrics from drought monitoring organizations, 4) a quantitative definition of what the authors consider to be drought conditions for their system. With more detailed and consistent quantification of drought conditions, comparisons among studies can be more rigorous, increasing our understanding of the ecological effects of drought.

Introduction

Drought has long been a phenomenon of interest to ecologists, with research articles that include “drought” in their title dating back at least to the 1920s (Gorham and Kelly 2018). For many biomes, understanding the dynamics of ecosystem structure and function requires knowledge of their response to periodic droughts (Smith 2011; Vicente-Serrano et al. 2013). Moreover, extreme drought has been associated with regional-scale forest mortality and global carbon cycle anomalies (Breshears et al. 2005; Reichstein et al. 2013). While research detailing the ecological effects of drought has a long history, interest has increased in the last few decades, prompted by climate model forecasts for more frequent, extreme, and spatially extensive droughts (IPCC 2013). Indeed, there is evidence that drought impacts on terrestrial ecosystems have increased globally over the last century (Du et al. 2018; Schwalm et al. 2017).

Given that drought has been and will continue to be a widely studied driver of ecosystem dynamics, defining and characterizing this phenomenon are essential for advancing our understanding of its ecological impacts. Climatologists have grappled with defining drought for decades (both conceptually and operationally, Redmond 2002; Wilhite and Glantz 1985) and have identified many types of drought (meteorological, agricultural, hydrological, socioeconomic, etc.). Numerous standardized indices have also been proposed over the years, to improve objectivity and consistency in quantifying drought conditions (Zargar et al. 2011), and tools have been developed to help provide historical context for drought (e.g., Lemoine et al. 2016). Though the World Meteorological Organization (1992) defines drought as a "period of abnormally dry weather sufficiently prolonged for the lack of precipitation to cause a serious hydrological imbalance", climatologists generally agree that a widely applicable definition of drought has proven elusive (Redmond 2002), with some concluding that "...we cannot reasonably expect the existence of any workable generalized objective definition of drought." (Lloyd-Hughes 2014). If climatologists are unable to agree upon a definition for a climatic phenomenon that is widely recognized as an important driver of ecosystem function and dynamics, how do ecologists define and characterize drought? Ecological drought definitions have recently been proposed (e.g., "an episodic deficit in water availability that drives ecosystems beyond thresholds of vulnerability, impacts ecosystem services, and triggers feedbacks in natural and/or human systems", Crausbay et al. 2017), as have drought vulnerability frameworks (Kovach et al. 2019). However, even a cursory review of the literature indicates there is little consistency in how ecologists define drought, conceptually or operationally. Such inconsistency can make it difficult to compare studies and ultimately hampers synthesis (Fraser et al. 2013).

To better understand how ecologists define and characterize drought, we assessed the current state (last 50 years) of the ecological drought literature by reviewing 564 papers that evaluated the ecological consequences of drought. We specifically addressed the following questions: First, how do ecologists define drought in their research papers? Or, if ecologists do not include an explicit definition, how do they describe or characterize the droughts they study? Second, does the approach ecologists use to study drought (e.g., experiments vs. observations of natural droughts) or the ecosystem type they study (e.g., forests, grasslands, streams, etc.) influence how they define or describe drought? Our goal is not to argue that all ecologists adopt a particular drought definition, but rather to suggest ways in which future studies can better describe and quantify drought conditions in order to facilitate synthesis and strengthen inferences drawn from the collective ecological drought literature.

Methods

We conducted a literature review (Web of Science, Thomson Reuters, Manhattan, NY, USA) of peer-reviewed publications that studied ecological responses to drought. We restricted our search to the last 50 years (1969-2018), to limit this assessment to the time period when standardized indices for quantifying drought conditions have been available (e.g., Palmer Drought Severity Index, PDSI, Palmer 1965). Searching the topics "ecolog*", "ecosystem*", and "drought*" (refined by: categories= ecology or environmental sciences and document type= article) returned 980 papers (as of 22 August 2018). Of these, we deemed 564 publications relevant to our review (Table A1.1). To be considered relevant, a research focus on some ecological aspect of drought had to be evident (i.e. the authors of the paper clearly indicated that they studied drought, drought was a central theme of the study, and, as a result, the authors could reasonably be expected to define what was meant by "drought"). We excluded papers that, for example, simply stated as background information that a site was drought-prone or that a species was drought-tolerant, or papers that tangentially speculated on drought-related implications of their research. We included the search term “ecosystem” to focus our review on larger-scale studies, as we reasoned that studies with this broad-level perspective were more likely to define drought in ways that could be meaningfully applied across systems and studies.

Initially, we classified each publication according to whether the authors explicitly defined the term drought. Explicit definitions of drought included those that were specific and quantitative: e.g., drought was defined as occurring whenever Standardized Precipitation Evapotranspiration Index (SPEI) values were ≤ -1, or when soil water in the top 10 cm was less than 10%, as well as those that were more general: e.g., some authors defined drought as “periods when soil moisture availability does not meet vegetation’s transpiration demand”, or as a “set of exceptional conditions of water shortage” (definitions abridged from papers included in our review). Some authors defined drought in their own terms, whereas others cited a previously published definition of drought or a declaration of drought conditions from a monitoring agency. The common feature was that the authors clearly articulated conditions or criteria for distinguishing drought conditions from non-drought conditions. In contrast to these papers, many publications did not explicitly define drought: e.g., the authors simply declared that a study was performed during (or in response to) drought, but provided no basis for why a period was considered a drought, nor any reference to other sources that described the severity of the drought.

We grouped all reviewed publications (those that explicitly defined drought and those that did not) into eight categories, based on how the authors defined or described the drought(s) studied (Table 2.1). These were (from most to least common): 1) drought used as a synonym for dry; 2) drought used to refer to conditions that differ from normal; 3) drought characterized using a standardized index; 4) drought quantified as a reduction in rainfall (% or amount); 5) drought characterized by low water flow or water table level; 6) drought as evidenced by plant water stress; 7) drought characterized by low soil moisture; or 8) drought used as a synonym for an annual dry season. All of the publications included in category 1 (drought used as synonym for dry) did not fit into any of the other categories. However, several of the other publications described drought in multiple ways and were thus included in multiple categories.

We also categorized each study according to the approach taken to study drought (observational, experimental, modeling, conceptual/theoretical, or review), and according to the ecosystem in which drought was studied (e.g., forest, savannah/woodland, grassland, freshwater, wetland, desert, etc.).

Results and Discussion

How do ecologists define and describe drought? – Ecologists generally do not define drought in their research papers, at least not explicitly. Just 32% of the publications that we reviewed explicitly defined drought or cited a definition of drought (Figure 2.1). Thus, a majority of papers report research focused on drought without explicitly explaining what constitutes a drought. This suggests that many ecologists conceptualize drought very generally, e.g., a “prolonged absence or marked deficiency of precipitation” (the simplest definition provided by the World Meteorological Organization 1992), and thus felt that no definition was needed. Alternatively, drought, similar to many ecological terms, is a pseudocognate (Salt 1979) and authors implicitly assume that readers understand it in the same way they themselves do.

Regardless of whether or not they define drought explicitly, ecologists conceptualize drought in many ways, befitting the breadth of ecological research. Of the eight categories of drought descriptions we identified (Table 2.1), ecologists most often use the term drought as a synonym for generally dry conditions (~30% of papers, Figure 2.1). In other words, authors state they are studying drought without quantifying and/or contextualizing how dry conditions are relative to normal (e.g., by reporting standardized index values, or some measure of deviation from average conditions). This lack of drought characterization inhibits syntheses of drought impacts across studies, and makes reviews and meta-analyses challenging and potentially misleading, when studies of droughts that may vary widely in severity are combined (see below).

When ecologists do provide more quantitative detail about a drought studied, they most commonly do so within the context of long-term precipitation records for their study site or system (e.g., rainfall during the study period was 50% below the long-term mean, Figure 2.1). While most of these papers report the degree of deviation from average conditions which occurred during the study period, they seldom include thresholds for distinguishing drought conditions from dry periods that are part of normal climatic variability.

Despite the number and variety of standardized indices available for quantifying climatic conditions (Zargar et al. 2011), relatively few of the publications reviewed used a standardized index to characterize the drought studied (14% overall and 17% of non-experimental studies, Figure 2.1). However, the use of standardized indices has generally increased over time (up to 22% of non-experimental studies published in the last 5 years, data not shown). The most commonly used indices were the Palmer Drought Severity Index (PDSI, Palmer 1965) and the

Standardized Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano et al. 2010). In some cases, the authors directly calculated these index values, but many more studies instead referenced official drought declarations or a specific category of drought intensity (based on index values) published by a monitoring agency (e.g., The U.S. Drought Monitor, Svoboda et al. 2002, https://droughtmonitor.unl.edu).

Some ecologists use evidence of plant water stress to support the occurrence of drought. Though observed ecophysiological stress may indeed indicate that a drought is occurring, we caution against using a response to drought as the primary evidence of drought. Highly drought tolerant or resistant ecosystems may show little response to drought conditions. Requiring a response to occur would thus preclude the inclusion of such studies in syntheses of ecological drought impacts – and this is valuable information lost.

Finally, some publications equated drought with a predictably dry time of year (i.e., an annual dry season). We find this categorization to be particularly problematic. Although dry seasons include some of the most general attributes of drought ("insufficient water to meet needs", Redmond 2002), from an ecological perspective, such conditions are within the range of normal variability. While some understanding of drought impacts might be inferred from research conducted during annually recurring dry seasons, the relevance of such ecological insight for abnormally dry conditions is unclear, particularly given forecasts for ecosystems to experience drought conditions with no contemporary or historical analog (Williams and Jackson 2007). Similarly, numerous studies used drought as a synonym for aridity (these publications mostly conceptualized drought as generally dry conditions). Like an annual dry season, aridity is a characteristic of an ecosystem and it is not clear that studying arid systems during normal climatic conditions offers useful insight into drought responses of either those or more mesic ecosystems.

Do drought definitions/descriptions vary by study method or ecosystem? – Our review suggests that ecologists most often take an observational approach to studying drought (Figure 2.2), regardless of ecosystem type (Figure 2.3). More than half of the studies included in our review reported research on natural droughts studied opportunistically. When drought was explicitly defined in these studies, it was usually in terms of a standardized index (e.g., PDSI, SPEI, Zargar et al. 2011) and/or a declaration of drought by a monitoring agency (e.g., the U.S. Drought Monitor). The authors of observational studies also frequently characterized drought within the context of a site-specific historical record, usually by comparing precipitation amounts during the drought to the long-term mean. However, almost one third of observational studies did not describe the nature and extent of drought conditions they studied or explain why that time period was considered a drought. In some cases, this could be due to ecologists studying droughts that they considered to be "well-known", e.g., the 2012-2014 California (USA) drought (Griffin and Anchukaitis 2014). However, large-scale drought can vary substantially in space and time, and thus this lack of detailed quantification for specific studies hinders generalizations of drought impacts and comparisons among studies.

Although less common than observational studies, ecologists conduct many drought experiments (Figure 2.2). In experiments, the imposed drought is usually defined or described in terms of reducing precipitation by a specific percent or amount (often, compared to ambient conditions). Experimental droughts are less frequently defined/described in terms of low soil moisture, a more direct measure of water availability than incoming precipitation (Vicca et al.

2012) and even fewer papers (~10% of drought experiments) provided context for drought treatments by comparing them to past droughts or historical precipitation records.

Ecologists study drought in diverse ecosystem types (Figure 2.3), but we did not find any consistent patterns of drought definitions/descriptions varying by ecosystem type among the papers that we reviewed. Terrestrial drought impacts are generally studied more in ecosystems with short-statured vegetation (e.g., grasslands, deserts, savannas) than tall-statured vegetation (e.g., forests) and this is particularly true for experimental drought studies (Figure 2.3 inset). This emphasis on shorter systems is likely due in part to the logistical and cost constraints of deploying such experiments in forests (Asbjornsen et al. 2018; Wullschleger and Hanson 2006). Unequal representation among biomes in the ecological drought literature underscores the need for more diverse drought studies, particularly in systems that have been historically understudied.

Why should ecologists do better when defining or characterizing drought? – Failure to define or characterize drought conditions in the published literature challenges our ability to advance ecological understanding. We highlight this by selecting a subset of terrestrial observational studies in which drought was poorly characterized (i.e., publications that did not include specific information such as a standardized index value or historical context to quantify the drought that they studied) but that did include location coordinates and the specific timeframe of the drought studied. This allowed us to calculate SPEI values for each of 39 different droughts using the Global SPEI database (SPEIbase v2.5, Vicente-Serrano et al. 2010; Begueria et al. 2010; Begueria et al. 2014). We calculated SPEI during the last month of the drought, using the time scale that the authors specified (i.e., for a three-month drought that ended in September 2012, we calculated the three-month SPEI value in September 2012). Results indicate that 87% of the droughts studied were characterized by negative SPEI values (Figure 2.4, negative SPEI values indicate that conditions are drier than average). However, only 50% of the droughts studied were characterized by dry conditions outside of the range of normal climatic variability (SPEI<−1) for the ecosystem, while the other 50% had SPEI values between −1 and +1, a range widely considered to represent normal variability (e.g., Hayes et al. 1999; Li et al. 2014; Li et al. 2015a; Li et al. 2015b; Potop et al. 2014; Potopova et al. 2015; Yu et al. 2014). Surprisingly, 13% of these drought studies occurred during periods that were slightly wetter than average, based on our estimated SPEI values. While it is possible that local-scale drought or shorter, more intense drought periods were the focus of these studies, these results underscore how difficult comparative analyses of the ecological impacts of drought can be when drought conditions are not defined and the effects being compared are in response to droughts ranging in intensity from extreme to dry periods within the range of normal variability.

How can we do better? – It is not surprising that ecological studies of drought would reflect the challenges that climatologists have confronted in determining what constitutes a drought, as well as their disagreement regarding definitions and metrics most appropriate for characterizing drought (e.g., Dracup et al. 1980; Keyantash and Dracup 2002; Quiring 2009; Wilhite 2000; Wilhite and Glantz 1985). Nonetheless, advances in ecological understanding occur not by individual studies but by research consensus and synthesis (Knapp et al. 2004). Given the large and rapidly increasing number of drought studies conducted by ecologists, we offer the following recommendations to improve our ability to draw inferences from this collective research endeavor.

The study of naturally occurring drought has been a dominant contributor to the ecological literature (observational approach in Figure 2.2), and we urge ecologists to utilize standardized indices (e.g., PDSI, SPEI) to characterize these droughts whenever possible. In addition to reporting average and minimum index values during the studied drought, authors should include or reference the threshold index values used to distinguish drought from normal conditions and to determine drought severity. There are numerous online tools available for independently calculating index values for a specific location and time (e.g., SPEIbase, Vicente-Serrano et al. 2010; Begueria et al. 2010; Begueria et al. 2014), and there are published threshold values for classifying drought conditions which are widely referenced (e.g., McKee et al. 1993). We urge ecologists to make use of these tools and references, to improve standardization among studies and expand the inference of their results.

We realize that standardized indices cannot be used in all situations. While calculating SPEI during a natural drought is straightforward, it is difficult to experimentally impose a specific SPEI level. For drought experiments, we recommend that imposed treatment levels be placed in the context of long-term climatic records (means and variability, Knapp et al. 2017), as well as related to ambient conditions. This is particularly important for passive precipitation reduction experiments where ambient conditions during the experiment dictate treatment levels (see Hoover and Rogers 2016). Moreover, justification for why specific treatments were selected to simulate drought should be provided so that drought is defined conceptually, as well as operationally. There are online tools available (Lemoine et al. 2016) to help researchers select experimental treatments with statistical justification based on historical records (e.g., treatments that represent 1-in-10- or 1-in-100-year droughts), or to identify site-specific thresholds of precipitation reduction that must be exceeded to simulate drought of a given severity (Knapp et al. 2017).

Conclusions

Though we found that relatively few ecologists explicitly defined what they consider to be a drought, we are more concerned about the general lack of clear and detailed quantification of studied drought conditions. As stated above, our intention is not to propose a universal definition of drought or to suggest that all ecologists agree to a single definition. Rather, we provide recommendations for describing and quantifying droughts in research publications, in a way that will facilitate comparisons and strengthen inferences drawn from the collective ecological drought literature. We suggest that future publications clearly report both the magnitude and duration of drought within site-specific historical context when possible. We also encourage ecologists to describe the droughts that they study using standardized indices, long-term climate records, drought declarations from monitoring agencies, and published thresholds used to define drought. In light of the growing importance of drought impacts on ecosystems and forecasts for more frequent and extreme droughts in the future, it is essential that ecologists study and describe this phenomenon thoroughly. If future studies provide more consistent and quantitative characterizations of the droughts studied, our understanding of the ecological impacts of drought will advance more rapidly within and among ecosystem types.

Table 2.1: Summary of the categories used to assess how ecologists describe or define the droughts they study. Descriptions and examples are abridged from 564 published papers included in our review. Categories are listed in order from most to least commonly used.

Drought Category	Description	Example(s)
"Dry"	Drought is used as a synonym for generally dry conditions; does not fit into any of the following categories	• Limited water availability and high temperatures • Absence or deficiency of rainfall
Differs from normal	Drought is quantified in the context of site history and refers to conditions that differ from normal	• Precipitation 25% below long-term mean • Precipitation <10th percentile of long-term record
Standardized index	Drought is quantified using an index (e.g., the Standardized Precipitation Evapotranspiration Index [SPEI])	• Negative SPEI values • SPEI values consistently <−1
Reduced rainfall	Drought is quantified as a reduction in rainfall (% or amount)	• Ambient rainfall reduced by 66% in experimental drought treatment
Low water flow/depth	Drought is characterized by low water flow or depth	• Stream flow reduced by 50% in experimental drought treatment • Water depth <5 cm
Plant water stress	Drought is evidenced by plant water stress	• Predawn leaf water potential <−1.0 MPa • Decreased plant water potential
Low soil moisture	Drought is quantified as low soil moisture	• Soil moisture 30% of maximum water holding capacity
Dry season	Drought refers to a predictable, reoccurring dry time of year	• The summer dry period in Mediterranean climates

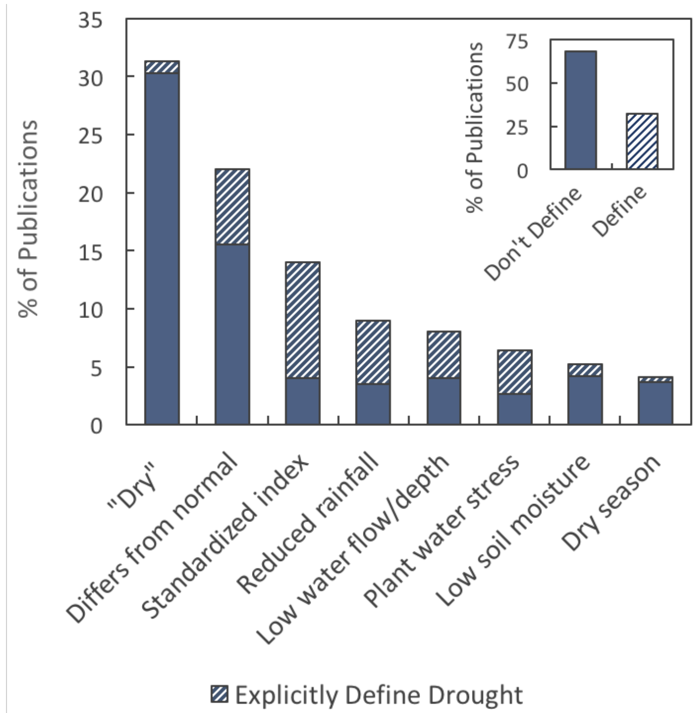

Figure 2.1: How ecologists describe and, in some cases, define the droughts they study, according to the categories identified in Table 2.1. Hatched bars denote the percentage of published papers in which authors provided an explicit definition of drought and solid bars represent publications that did not explicitly define conditions or criteria that constitute a drought. Inset: Total percentage of publications that do or do not explicitly define drought, combined across all categories.

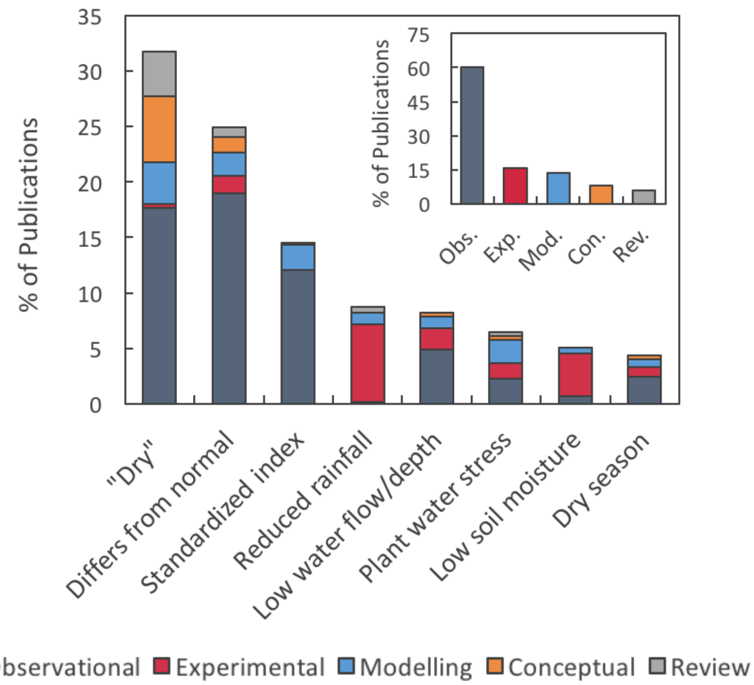

Figure 2.2: Approaches used to study drought, within each of the categories of drought definitions/descriptions identified in Table 2.1. This analysis includes all of the papers that we reviewed, regardless of whether or not they explicitly defined drought. Inset: Approaches used to study drought combined across all categories. Note that some papers used multiple approaches to study drought and multiple categories to describe drought, resulting in the total exceeding 100%.

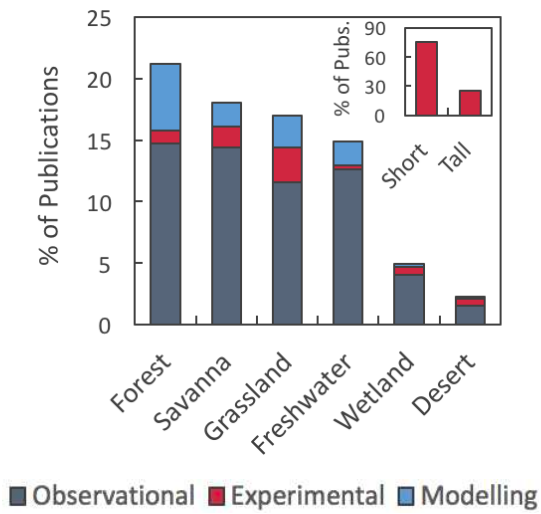

Figure 2.3: Ecosystem types where drought is studied and approaches used to study drought. Shown are the six most common ecosystems in which drought is studied and the three most common approaches used to study drought. "Savanna" also includes woodlands and shrublands. Inset: Drought experiments conducted in terrestrial ecosystems, according to vegetation stature. Short includes grasslands, deserts and shrublands, and tall includes forests and woodlands.

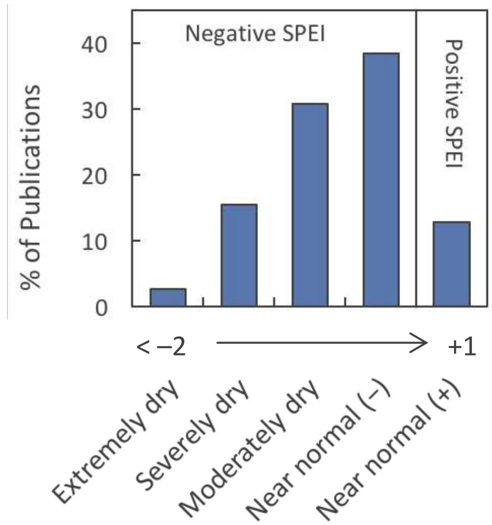

Figure 2.4: Variation in SPEI values for 39 natural droughts studied in a subset of reviewed papers. Papers were selected because they provided precise dates and locations of droughts studied but did not characterize climatic conditions in that time and place well. SPEI values were calculated using SPEIbase (see methods) and droughts were grouped into the following categories: extremely dry (SPEI ≤ −2), severely dry (−2 < SPEI ≤ −1.5), moderately dry (−1.5 < SPEI ≤ −1), and near normal conditions (−1 < SPEI < +1). Droughts in the near normal category were then grouped based on the sign of the SPEI value (positive or negative).

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CHAPTER 3: EFFECTS OF COMPOUDED PRECIPITATION PATTERN INTENSIFICATION AND DROUGHT OCCUR BELOWGROUND IN A MESIC GRASSLAND[2]

Overview

Climate change is altering precipitation regimes globally, with expectations of intensified precipitation patterns (e.g., larger but fewer rainfall events) and more frequent and extreme drought. Both aspects of precipitation change can impact ecosystem function individually, but it is more likely that they will occur in combination. In a central US mesic grassland, we imposed an extreme 2-yr drought (growing season precipitation reduced by 66%) on plots with a long-term (16-yr) history of exposure to either ambient or intensified precipitation patterns (average 3-fold increase in event size and 3-fold decrease in event number during the growing season). While this intensified pattern did not alter total precipitation amount, it generally led to ecosystem responses consistent with a drier environment (e.g., reduced soil moisture, aboveground net primary production (ANPP), and soil CO_2 flux, but little evidence for altered root biomass). Surprisingly, this history of intensified precipitation patterns did not affect the response of ANPP to the subsequent extreme drought. In contrast, previous exposure to intensified precipitation patterns reduced root production and muted soil CO_2 flux responses to rainfall events during drought. Reduced root production in plots experiencing compounded precipitation extremes was driven not by the dominant C_4 grass species, *Andropogon gerardii*, but collectively by the subdominant species in the plant community. Overall, our results reveal

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[2]Slette IJ, Blair JM, Fay PA, Smith MD, Knapp AK. 2021. Effects of Compounded Precipitation Pattern Intensification and Drought Occur Belowground in a Mesic Grassland. Ecosystems. https://doi.org/10.1007/s10021-021-00714-9

that compound changes in precipitation patterns and amount affected this grassland in ways that were less apparent (i.e., belowground) than responses to either change individually and significantly reduced ecosystem carbon uptake.

Introduction

Climate change is expected to intensify precipitation regimes by increasing the size of individual rainfall events as well as the number and length of anomalously dry periods (i.e., droughts), with evidence for these changes already emerging (Dai 2012; Fischer and Knutti 2016; Huntington 2006; IPCC 2013; USGCRP 2017). For example, much of the world is experiencing larger, more intense precipitation events without corresponding increases in total precipitation amount (Fischer and Knutti 2016; Fowler et al. 2021; IPCC 2013). A shift towards fewer but larger precipitation events and longer durations between events can affect myriad ecosystem processes (Fay et al. 2008; Knapp et al. 2008; Zeppel et al. 2014). Concurrently, droughts are becoming more frequent and extreme in many regions. Drought, defined as a period of marked precipitation deficiency relative to the local long-term average, is a well-known climate extreme that has been studied extensively (Dai 2012; Eziz et al. 2017; Gao et al. 2019; Lei et al. 2016; Slette et al. 2019; Wu et al. 2011). Given that both dimensions of precipitation change are increasing, it is likely that future droughts will occur against a backdrop of intensified precipitation patterns (*cf.* Harrison et al. 2018). However, most research to date has focused on these different aspects of precipitation change individually, and their combined effects are thus unresolved.

Ecosystem responses to combined weather events, or compound events (Seneviratne et al. 2012), are likely not predictable from studies that focus on individual events (Dodd et al.

2021; Zscheischler et al. 2018). Instead, one dimension of change might precondition an ecosystem and alter its response to another (Zscheischler et al. 2020). That is, a chronic "press" change such as long-term intensification of precipitation patterns might alter the impacts of a "pulse" event such as a short-term extreme drought. For example, Hoover et al. (2015) found that a short-term extreme "pulse drought" had a larger negative impact on plant production and mortality when it occurred against a backdrop of a milder and longer-term "press drought". Other previous studies have also found amplifying impacts of compound climate extremes more generally, though neutral and mitigating effects have also been reported (Anderegg et al. 2020; Backhaus et al. 2014; Dreesen et al. 2014; Hoover et al. 2021; Hughes et al. 2019). Consensus on the effects of compounded climate changes is therefore lacking. Understanding press-pulse interactions, such as how exposure to intensified precipitation patterns might precondition ecosystem responses to drought, has important implications for improving understanding of carbon cycling in a changing climate.

Grasslands are important ecosystems in which to assess compounded effects of precipitation changes because they are structurally and functionally controlled by water availability (Morgan et al. 2008; Mowll et al. 2015; Sala et al. 1988), they experience high inter- and intra-annual precipitation variability (Knapp and Smith 2001), and they are sensitive to changes in precipitation amount and pattern (Felton et al. 2020; Gherardi and Sala 2015; Heisler-White et al. 2008, 2009; Hoover et al. 2014; Huxman et al. 2004; Knapp et al. 2002, 2008, 2015, 2020; Li et al. 2019; Lu et al. 2021; Thomey et al. 2011). Grass-dominated systems are also globally extensive (Dixon et al. 2014; White et al. 2000) and play a key role in the global carbon cycle (Pendall et al. 2018; Scurlock and Hall 1998). Belowground responses such as belowground net primary production (BNPP) and soil CO_2 flux are of particular interest here because grasslands allocate a substantial portion of total net primary production to roots and store most of their carbon belowground (Hui and Jackson 2006; Risser et al. 1981; Silver et al. 2010; Smith et al. 2008; Soussana et al. 2004). Root production and soil CO_2 flux are key factors determining the size of the soil carbon pool, which is at least twice as large as the atmospheric carbon pool and plays an important role in global carbon cycling and climate regulation (Köchy et al. 2015; Scharlemann et al. 2014). While root mass production is useful for comparing aboveground vs. belowground NPP and their relative contributions to carbon cycling, the capacity of plants to acquire soil resources is likely better reflected by root length than mass because length better reflects the volume of soil that plants can access (Casper and Jackson 1997; Jackson et al. 1996; Wilson 2014). We thus assessed both length and mass production of roots.

The objective of this study was to assess the ecosystem impacts of compounded precipitation changes in a mesic grassland. Specifically, we tested how long-term extreme intensification of precipitation patterns might alter ecosystem responses to a subsequent extreme drought, as well as recovery after drought. Our research builds on the Rainfall Manipulations Plots (RaMPs; Fay et al. 2000) experiment which altered growing season precipitation patterns, but not amount, for 16 years. The RaMPs experiment intensified precipitation patterns by imposing fewer and larger precipitation events with longer intervening dry periods, compared to ambient patterns. Prior results from the RaMPs study revealed that the intensified precipitation pattern resulted in drier soils, increased plant water stress, reduced aboveground net primary production (ANPP) and soil CO_2 flux, altered soil microbial community composition, and altered genotypic structure of the dominant plant species compared to ambient precipitation patterns (Avolio and Smith 2013; Avolio et al. 2013; Evans and Wallenstein 2012; Fay et al. 2002, 2003, 2011; Harper et al. 2005; Knapp et al. 2002; Nippert et al. 2009). We predicted that this history of intensified precipitation patterns would exacerbate the impacts of drought, compared to a history of ambient precipitation patterns. To test this prediction, we imposed an extreme 2-yr drought (66% reduction in growing season rainfall) in grassland plots with and without previous long-term exposure to an intensified precipitation regime and assessed key carbon cycling processes (e.g., ANPP, BNPP and soil CO_2 flux) during and after drought.

Methods

Study site – The Konza Prairie Biological Station (KPBS) is a 3,487-ha unplowed tallgrass prairie in northeast Kansas, USA (39°05’N, 96°35’W) and is a USA Long-Term Ecological Research (LTER) site. The plant community is primarily composed of native C_4 grasses (average 77% of total biomass in the RaMPs experiment over 16 years), dominated by *Andropogon gerardii* and also including *Sorghastrum nutans*, *Sporobolus asper*, and *Panicum virgatum*. The rest of the plant community is composed mostly of an array of C_4 forb species (mainly *Solidago canadensis, Aster ericoides, S. missouriensis*), with woody species accounting for a very small percent of total biomass and cover in the RaMPs experiment (Fay et al. 2001; Knapp et al. 1998). The climate is temperate with warm, wet summers and cold, dry winters. The mean annual temperature is 13°C (Knapp et al. 1998) and the mean annual precipitation is 851 mm, almost 70% of which occurs during the growing season. Our experiment was located on deep silty clay loam soils in the Tully series (Collins and Calabrese 2012; Ransom et al. 1998).

Frequent fires are a historical feature of this grassland and are essential for maintaining grass dominance and reducing woody plant encroachment (Briggs et al. 2005; Knapp et al. 1998), and our experiment was burned annually in mid-March.

The RaMPs experiment design and treatments – The RaMPs experiment included 12 fixed-location shelters (9 × 14 m) arranged in a randomized complete block design (see Fay et al. 2000 for details). Each shelter consisted of a clear (UV transparent) polyethylene roof that excluded all precipitation, gutters and storage tanks for rainfall collection, and an overhead irrigation system for rainfall application. Each RaMP was isolated belowground to a depth of 1.2 m via a subsurface barrier. Sampling occurred in a 6 × 6 m area divided into four 2 × 2 m subplots. Each RaMP received either the ambient or intensified precipitation pattern from 1998-2013. In RaMPs receiving the ambient precipitation pattern, collected rainfall was applied each time a natural rain event occurred. In RaMPs receiving the intensified precipitation pattern, rainfall timing and event size were altered by delaying rainfall applications. The dry interval between rainfall events was increased by 50% and all ambient rainfall during the lengthened dry interval was collected, stored and applied as a single large event. Thus, the ambient and intense treatments received the same amount of rain, but the intense treatment received fewer and larger rainfall events with longer intervening dry periods. Manipulations occurred only during the growing season (May – September). Rainfall events were defined as daily total >5 mm, as smaller amounts are almost entirely intercepted by the canopy (Seastedt 1985). The intense treatment imposed a statistically extreme precipitation pattern, compared to long-term ambient rainfall patterns at the KPBS (Nippert et al. 2006; Smith 2011).

After 16 years of ambient vs. intense precipitation patterns, an extreme drought was imposed on all plots. In 2014 and 2015, total growing season precipitation in all RaMPs was reduced to ~34% of the 1998-2013 experiment average (following Knapp et al. 2017). Each rainfall event was reduced in size by 66% and event timing followed the ambient pattern. Similar reductions have imposed statistically extreme droughts at the KPBS in the past (Hoover et al. 2014). The size and timing of all rainfall events were the same for all plots, to facilitate direct comparisons of how past exposure to intensified precipitation would impact responses to a common drought treatment. To assess recovery after drought, all ambient precipitation was applied to all RaMPs in 2016 with event size and timing matching the ambient pattern.

Field measurements – Key ecosystem processes (e.g., photosynthesis, ANPP, N mineralization) at the KPBS are strongly linked to soil moisture in the top ~30 cm below the surface (Blair 1997; Briggs and Knapp 1995; Knapp et al. 1993; Nippert and Knapp 2007). Thus, soil volumetric water content (VWC) was measured at 15 cm and 30 cm soil depths at 30 min intervals in all RaMPs for the duration of the experiment using Time Domain Reflectometry (TDR) probes (Fay et al. 2000).

Annual ANPP was estimated each year (1998-2016) from end-of-growing-season vegetation harvests of 16 total 0.1 m^2 quadrats per RaMP (four per subplot) performed by clipping all vegetation rooted within the quadrat to the soil surface with scissors. Because the site is burned annually and not grazed, the collected biomass represents ANPP. The dominant species, *A. gerardii*, often drives responses in this system (Smith and Knapp 2003), and it was separated from subdominant species. All biomass was dried at 60°C for 48 hours and weighed.

The cumulative impact of the ambient vs. intense precipitation treatments on total root biomass was estimated by taking four soil cores per RaMP (5 cm diameter, 60 cm deep, one per subplot) at the end of the last growing season before the drought. Each core was divided into 10-cm depth increments. Roots were removed from each increment, washed free of soil, dried at 60°C for 48 hours and weighed. Annual BNPP was estimated during the last year of drought (2015) and first year after drought (2016) by using root ingrowth cores to estimate fine root production. At the start of the growing season (late April), three soil cores (5 cm diameter, 30 cm deep) were taken from each plot, plus 10 from unaltered grassland adjacent to the RaMP (for use as controls) and discarded. This depth captures most root production at our study site and other grasslands (Jackson et al. 1996; Nippert et al. 2012; Schenk and Jackson 2002a; Sun et al. 1997; Weaver and Darland 1949). A cylindrical mesh basket filled with sieved, root-free soil collected adjacent to the RaMPs and packed to approximate field bulk density was placed into each core hole (5 cm diameter, 30 cm deep, 2 × 2 mm mesh holes). Any space between the ingrowth core and intact soil was filled with sieved, root-free soil. Ingrowth cores were removed at the end of the growing season (late September) and stored at 4°C. Each core was divided into 10-cm depth increments. Soil was washed off roots by wet sieving (0.5 mm sieve) under low water pressure, submerging remaining sample in a shallow bowl of water, picking out roots with forceps, and removing attached soil by hand. *A. gerardii* roots are distinctive (Figure A2.1), and they were separated from subdominant species' roots. Roots were scanned using an Epson Perfection photo scanner (Epson America Inc., Long Beach, CA, USA) and scans were analyzed for root diameter and length using WinRhizo (Regent Instruments Inc., Québec, Canada). Roots were dried at 60°C for 48 hours and weighed. BNPP was calculated as root mass production per m^2 ground area.

Soil CO_2 flux was measured in situ between 10:00 am and 2:00 pm local time approximately weekly throughout the 2015 and 2016 growing seasons using a LiCOR 8100A portable gas exchange system (LiCOR Inc., Lincoln, NE, USA). Per RaMP, eight polyvinyl chloride (PVC) collars (two per subplot) were installed (10 cm diameter × 8 cm tall, buried 6 cm into the soil) between plant tillers/stems. Any litter and vegetation within the collar were removed (via clipping with scissors or by hand if loose) so that measurements included only CO_2 flux from the soil. To assess flux responses to rainfall, additional measurements were taken immediately before and approximately 24 hours after individual rainfall applications.

Statistical analyses – We performed all analyses in R (R Core Team 2018), using plot-level and annual-scale data. We used the psych package (Revelle 2020) for summary statistics (Table A2.1). To determine the impacts of ambient vs. intense treatments during 1998-2013 on total, *A. gerardii*, and subdominant species ANPP and on soil moisture at 15 cm and 30 cm, we used linear models (nlme package; Pinheiro et al. 2020) and type 3 sum of squares analyses of variance ("ANOVAs"; car package; Fox and Weisberg 2019) to assess the main effects of treatment (nested within block) and year, and the year × treatment interaction. We similarly assessed the main effect of treatment (nested within block) and depth increment, and the treatment × depth increment interaction on root biomass. To determine the impacts of ambient vs. intense treatment history during the last year of drought and the first year after drought, we used linear models and type 3 sum of squares ANOVAs to assess the main effects of treatment history (nested within block) and year, and the year × treatment history interaction (Table A2.2). We analyzed ANPP, BNPP, NPP, and the BNPP: ANPP ratio for all species, *A. gerardii*, and subdominant species in this way, as well as soil moisture at 15 cm and 30 cm and soil CO_2 flux (growing season average, before rainfall events and after rainfall events). In the BNPP model, we also included the main effect of depth increment and the interactions of depth increment with treatment history and with year. For each dependent variable, we used pairwise contrast comparisons (emmeans package; Lenth 2020) to determine in which years there were differences between treatments. We considered p values <0.05 significant.

Results

Ecosystem responses to an intensified precipitation pattern – Results from various time periods during the RaMPs experiment have been reported previously (e.g., Avolio et al. 2013; Fay et al. 2000, 2002, 2003, 2011; Harper et al. 2005; Knapp et al. 2002), but none from its full 16-yr duration. We updated a subset of past analyses and here report results from the entire experiment. The intense treatment reduced the number of growing season rainfall events almost 3-fold (30 ± 2 ambient vs. 12 ± 1 intense) while increasing rainfall event size by a similar proportion (13 ± 1 mm ambient vs. 33 ± 2 mm intense; Figure 3.1), on average. Despite no differences in total rainfall between treatments, the intense pattern led to drier soils at 15 cm during the growing season (22.2 ± 5.9% vwc intense vs. 25.5 ± 4.5% vwc ambient; F=49.5, p<0.001) and a 14% reduction in ANPP (675 ± 17 g m^{-2} intense vs. 737 ± 18 g m^{-2} ambient; F=4.93, p<0.001), averaged over 16 years. *A. gerardii* composed ~40% of total ANPP on average during this time (Figure 3.2). At the end of the experiment, standing crop root biomass did not differ between treatments overall (792 ± 59 g m^{-2} intense vs. 809 ± 61 g m^{-2} ambient; F=1.01, p=0.32) or in any individual depth increment (Figure A2.2).

How an intensified precipitation pattern affected drought responses – Reducing the size of each ambient precipitation event by 66% resulted in growing season precipitation amounts below the 5^{th} percentile of the RaMPs rainfall record (1998-2013) and the long-term (112-yr) KPBS rainfall record (Hoover et al. 2014). Thus, based on site-specific historical precipitation amounts, we imposed a statistically extreme drought (Smith 2011).

During the last year of the drought (2015), soil moisture did not differ by treatment history at either 15 cm (F=1.13, p=0.30) or 30 cm (F=0.46, p=0.50) depths, but it was 55% (15 cm) and 40% (30 cm) lower than the pre-drought ambient RaMPs average. Similarly, ANPP during the last year of the drought did not differ by treatment history (F=0.086, p=0.78), but it was 36% lower than the pre-drought ambient RaMPs average. Thus, a history of intensified precipitation did not alter the response of ANPP to drought (Figure 3.2). In contrast, BNPP during the last year of the drought was lower in historically intense vs. ambient plots (Figure 3.2; F=7.14, p=0.028). BNPP in historically intense plots was 70% of BNPP in historically ambient plots. This was collectively driven by the subdominant species. BNPP of the subdominant species in the historically intense plots was 46% of that in the historically ambient plots (F=18.19, p=0.0027). Surprisingly, BNPP of the dominant species, *A. gerardii,* did not differ by treatment history (F=2.43, p=0.16). Despite differences in BNPP, NPP (ANPP + BNPP; F=0.64, p=0.45) and the overall ratio of BNPP: ANPP did not differ by treatment history (F=2.17, p=0.18). However, the ratio of subdominant species BNPP: ANPP in historically intense plots was just 50% of that in ambient plots (F=6.09, p=0.039). In the last year of the drought, *A.*

gerardii was 32 and 59% of total BNPP in historically ambient and intense plots, respectively, and it was 44 and 48% of total ANPP in ambient and intense plots, respectively (Figure 3.2).

Historical precipitation intensification reduced subdominant species BNPP in each depth increment (Figure 3.3; 0-10 cm: p=0.046; 10-20 cm: p=0.0099; 20-30 cm: p=0.021) in the last year of drought. In addition, there was a significant effect of depth on subdominant species BNPP (F=4.37, p=0.022) but not *A. gerardii* BNPP (F=1.80, p=0.18). That is*, A. gerardii* BNPP was more evenly distributed among depths. In historically intense plots, *A. gerardii* produced more root mass (p=0.040) and a greater proportion of its total root mass (p=0.014) in the deepest increment sampled, compared to subdominant species.

Similar to BNPP, root length production was lower in historically intense vs. ambient plots during the last year of drought (Figure 3.4; F=29.6, p<0.001). This difference was also due to responses of subdominant species (F=9.65, p=0.038), not of *A. gerardii* (F=2.65, p=0.65). *A. gerardii* made up a smaller proportion of total root length vs. mass production (20% vs. 30% ambient, 30% vs. 60% intense, respectively), due to its smaller specific root length (SRL; 67.4 ± 7.7 m g^{-1}) compared to subdominant species (160 ± 16 m g^{-1}; p<0.001; figure S1). There was no difference in root tissue density (RTD) of *A. gerardii* vs. subdominant species (Figure A2.1; p=0.25). There was also no effect of treatment history and no difference between drought vs. after-drought years on SRL or RTD of *A. gerardii* or subdominant species (p>0.05).

Growing season average soil CO_2 flux during drought did not differ by treatment history during the last year of drought (Figure 3.5; F=1.34, p=0.28), but short-term flux increases after rainfall did. Soil CO_2 flux was higher in historically ambient vs. intense plots after rainfall

(F=1.93, p=0.044). Thus, a history of intensified precipitation dampened the response of soil CO_2 flux to rainfall during drought.

Recovery after drought – The first year after the drought (2016) was wetter than usual, with ambient precipitation almost 40% higher than the pre-drought RaMPs average (Figure 3.1). In this year, soil moisture did not differ by treatment history at either 15 cm (F=0.013, p=0.91) or 30 cm (F=2.96, p=0.13) depths. Total ANPP (F=0.017, p=0.99), *A. gerardii* ANPP (F=0.162, p=0.70), and subdominant species ANPP (F=0.0041, p=0.95) also did not differ by treatment history (Figure 3.2). *A. gerardii* was 50% of total ANPP in both historically ambient and intense plots (Figure 3.2). As expected, total ANPP was higher after vs. during drought, (ambient: p<0.001; intense: p<0.001) as was ANPP of *A. gerardii* and of subdominant species. Compared to the 16-yr pre-drought ambient RaMPs average, ANPP during the wet recovery year was slightly (6%) reduced (F=2.90, p=0.096). However, *A. gerardii* ANPP was higher (9.5%) whereas subdominant species ANPP was lower (26%) than the pre-drought ambient average.

After drought, total BNPP (F=0.29, p=0.61), *A. gerardii* BNPP (F=0.04, p=0.85), and subdominant species BNPP (F=0.59, p=0.47) did not differ by treatment history. *A. gerardii* was 60% of total BNPP in both historically ambient and intense plots (Figure 3.2). Total BNPP (ambient: p=0.049; intense: p=0.025) and *A. gerardii* BNPP (ambient: p=0.014; intense: p=0.048) were higher after vs. during drought, but subdominant BNPP did not differ after vs. during drought (ambient: p=0.14; intense: p=0.10; Figure 3.2). The BNPP: ANPP ratio for all species and for subdominants was lower after vs. during drought in historically ambient (p=0.019, p=0.022, respectively) but not intense plots (p=0.71, p=0.99, respectively), while the

BNPP: ANPP ratio for *A. gerardii* did not differ in either historical treatment (ambient: p=0.18; intense: p=0.78).

Consistent with BNPP, root length production did not differ by treatment history in the first year after drought (Figure 3.4; F=0.35, p=0.58). Total (ambient: p=0.049; intense: p=0.019) and *A. gerardii* (ambient: p=0.014; intense: p=0.045) root length production were higher after vs. during drought, but subdominant species root length production was not different after vs. during drought (ambient: p=0.86; intense: p=0.064).

Finally, growing season average soil CO_2 flux did not differ by treatment history in the first year after drought (Figure 3.5; F=1.19, p=0.31), and was higher after vs. during drought (p<0.001). The short-term flux increase after rainfall did differ by treatment history. Soil CO_2 flux was higher in historically ambient vs. intense precipitation plots after rainfall (F=4.49, p=0.037).

Discussion

Long-term exposure of this mesic grassland to an intensified precipitation pattern reduced soil moisture and ANPP, as reported previously (Fay et al. 2002, 2003, 2011; Knapp et al. 2002). But when exposure to extreme precipitation patterns was compounded with extreme drought, there were no legacy effects of past precipitation pattern on ANPP. This contrasts sharply with responses belowground, where a history of intensified precipitation patterns amplified reductions in BNPP during drought and reduced the size of the soil CO_2 flux increase following rainfall events both during and after drought. Thus, our findings add to growing evidence that grassland belowground responses to precipitation change should not be inferred from aboveground responses (Byrne et al. 2013; Carroll et al. 2021; Chou et al. 2008;

Post and Knapp 2020; Wilcox et al. 2015, 2017). The negative effect of past exposure to intensified precipitation belowground has implications for long-term ecosystem carbon cycling and sequestration, given the important role of soils, especially grassland soils, in global carbon storage (Hui and Jackson 2006; Köchy et al. 2015; Risser et al. 1981; Scharlemann et al. 2014; Silver et al. 2010; Smith et al. 2008; Soussana et al. 2004). Our results thus suggest that, as precipitation patterns continue to intensify, the negative impacts of droughts on plant production and ecosystem carbon uptake may be underestimated if belowground dynamics are not fully considered.

While it is possible that BNPP differed between ambient and intense precipitation plots prior to drought (this was not quantified), root biomass did not differ between treatments in the last year of the experiment (Figures 3.1, A2.2), suggesting that any differences in annual root production between treatments were likely small and did not accumulate to affect standing root biomass. However, we found that root production did differ between ambient and intense treatment plots when precipitation intensification was compounded with drought. The negative effect of intensified precipitation on BNPP during drought was due to responses of the subdominant species. The BNPP distribution of *A. gerardii* was deeper than that of subdominant species, which likely contributed to the different responses during and after drought. Indeed, previous research has linked changes in root distribution within the top ~30 cm to changes in total plant production even when maximum rooting depth is greater than 30 cm (Nippert and Holdo 2015). We also found that *A. gerardii* made up a smaller proportion of total root length production vs. root mass production. The lower dominance of *A. gerardii* root length vs. mass was driven by its low SRL. A lower SRL likely indicates "outsourcing" of resource acquisition to mycorrhizae, vs. a “do-it-yourself” acquisition strategy of plants with higher SRL (Bergmann et al. 2020). We did not assess mycorrhizal abundance, but past research has shown that *A. gerardii* is highly mycorrhizal dependent (Smith et al. 1999; Wilson and Hartnett 1997, 1998). It is thus possible that greater mycorrhizal association of *A. gerardii* vs. subdominant species also contributed to their different responses during and after drought. BNPP of subdominant species differed between historical ambient vs. intense treatments during drought but not after drought, suggesting that the impacts of precipitation pattern intensification are relatively short-lived and reversible. The impact of drought might be longer-lasting, as BNPP of subdominant species remained below control plot levels after drought did not increase after drought, even in a wet year.

Previous research and theory have suggested that increased proportional allocation belowground provides an advantage in dry conditions by increasing water uptake (Bloom et al. 1985; Chapin et al. 1987; Chou et al. 2008; Milchunas and Lauenroth 2001; Poorter et al. 2012). Based on this, we expected to find higher BNPP: ANPP ratios during vs. after drought. However, we only found evidence for this in the former ambient precipitation treatment. This response was driven by an almost two-fold higher BNPP: ANPP ratio of the subdominant species during vs. after drought. That is, whereas BNPP and ANPP of *A. gerardii* changed by the same relative proportion in both historical treatments, subdominant species shifted to produce proportionally more root mass vs. shoot mass during drought, but only in historically ambient precipitation plots. This could indicate greater plasticity of production allocation in response to water availability of subdominant species compared to *A. gerardii*, or that resources other than water (e.g., carbon) were also limiting during drought. The mechanism explaining how a history of intensified precipitation altered the responsiveness of BNPP: ANPP allocation patterns to drought remains to be resolved.

Intensified precipitation patterns decreased average soil CO_2 flux (Harper et al. 2005), but when intensified precipitation patterns were compounded with drought, there was no effect of past precipitation pattern on growing season average soil CO_2 flux. However, previous exposure to intensified precipitation patterns did decrease the response of soil CO_2 flux to individual precipitation events during and after drought. Our results are consistent with well-documented patterns of soil CO_2 flux correlating with soil moisture, e.g., declining during drought and increasing after individual rainfall events, with larger increases after larger rain events and wetter antecedent conditions (e.g., after vs. during drought; Birch 1958; Bremer et al. 1998; Feldman et al. 2021; Fierer and Schimel 2003; Harper et al. 2005; Hoover et al. 2016; Liu et al. 2002; Post and Knapp 2020, 2021). Specifically, the muted response of soil CO_2 flux to precipitation events in historically intense precipitation plots (vs. historically ambient precipitation plots) is consistent with previous research reporting that soils from this treatment were less responsive to moisture pulses pre-drought (Evans and Wallenstein 2012) and had lower microbial respiration following drying and re-wetting (Veach and Zeglin 2020). Thus, this difference in the response of soil CO_2 flux to soil moisture between intense vs. ambient treatments appears to be longer lasting than other pre-drought differences (e.g., lower ANPP in intense vs. ambient treatments). This has important implications for ecosystem carbon dynamics, given that soil CO_2 flux is a large part of the carbon budget in temperate grasslands and a substantial proportion of soil CO_2 flux occurs after rainfall events (Chen et al. 2008, 2009; Gale et al. 1990; Ham et al. 1995; Huxman et al. 2004a, 2004b; Kim et al. 1992; Yan et al. 2014).

Our results indicate that grassland ecosystems might release less total CO_2 from the soil to atmosphere under conditions of increased precipitation pattern intensity and drought.

Drought can have a persistent negative effect on grassland ANPP post-drought, though positive and insignificant impacts of previous droughts have also been reported (Griffin-Nolan et al. 2018; Hoover et al. 2014; Sala et al. 2012). Total ANPP in our study recovered to near the pre-drought average one year after drought. This was likely due at least in part to above-average total precipitation in that year. Regardless, our results are consistent with past research identifying the important role of the dominant species in restoring ecosystem function after drought. One year after drought, ANPP of *A. gerardii* was higher than the long-term pre-drought average, while ANPP of the subdominant species remained below average. Previous grassland drought experiments have reported that, aboveground, grasses recover better than forbs (included in “subdominant species”) after drought (De Boeck et al. 2018; Hoover et al. 2014). We expand on this response by showing that BNPP *of A. gerardii* also recovered more than BNPP of subdominant species after drought.

In summary, we found that the compound effects of long-term precipitation pattern intensification and drought were evident primarily belowground in this mesic grassland. We conclude that as precipitation patterns intensify and drought frequency and severity continue to increase globally, predicting and modeling changes in global terrestrial carbon cycling will require greater understanding of how ecosystems respond to multiple compounded precipitation changes, especially belowground.

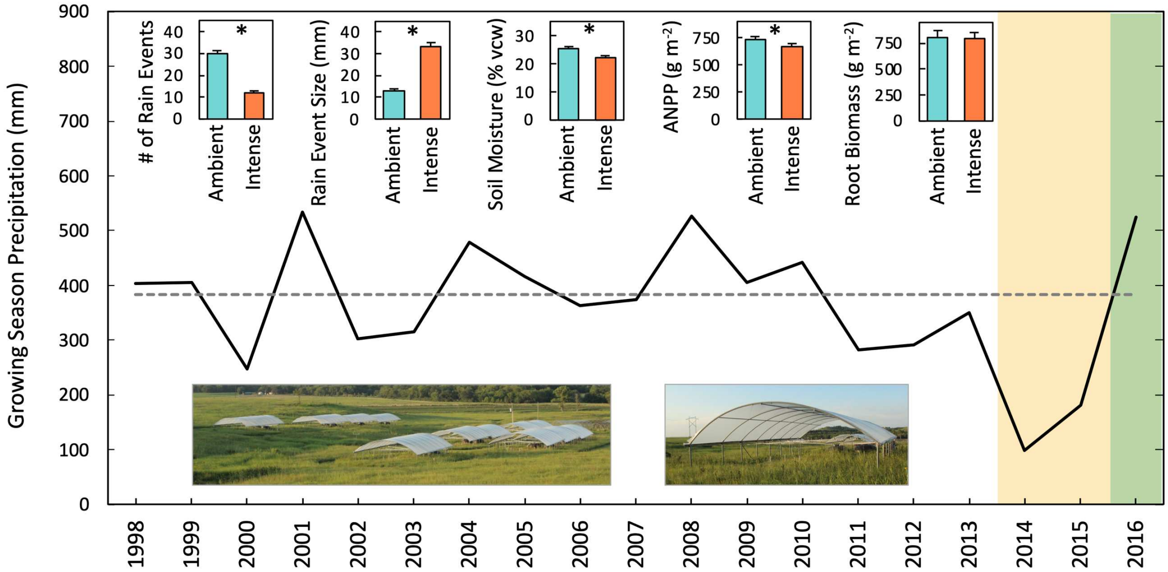

Figure 3.1: Growing season precipitation in each year of the RaMPs experiment (solid line) and 1998-2013 average (dashed line). From 1998-2013 (non-shaded area), the intense treatment received fewer and larger rainfall events. A common drought was imposed on both historical treatments in 2014 and 2015 (yellow-shaded area), and all plots received all ambient rainfall in 2016 (green-shaded area). Insets: 1998-2013 average (+ 1 standard error) growing season number of rain events, size of rain events, soil moisture at 15 cm, aboveground net primary production (ANPP) and root biomass (2013 only) in ambient and intense precipitation pattern treatments. * = significant difference between ambient vs. intense treatments. Photos: The RaMPs experiment (left), closer view of a RaMPs experiment shelter (right).

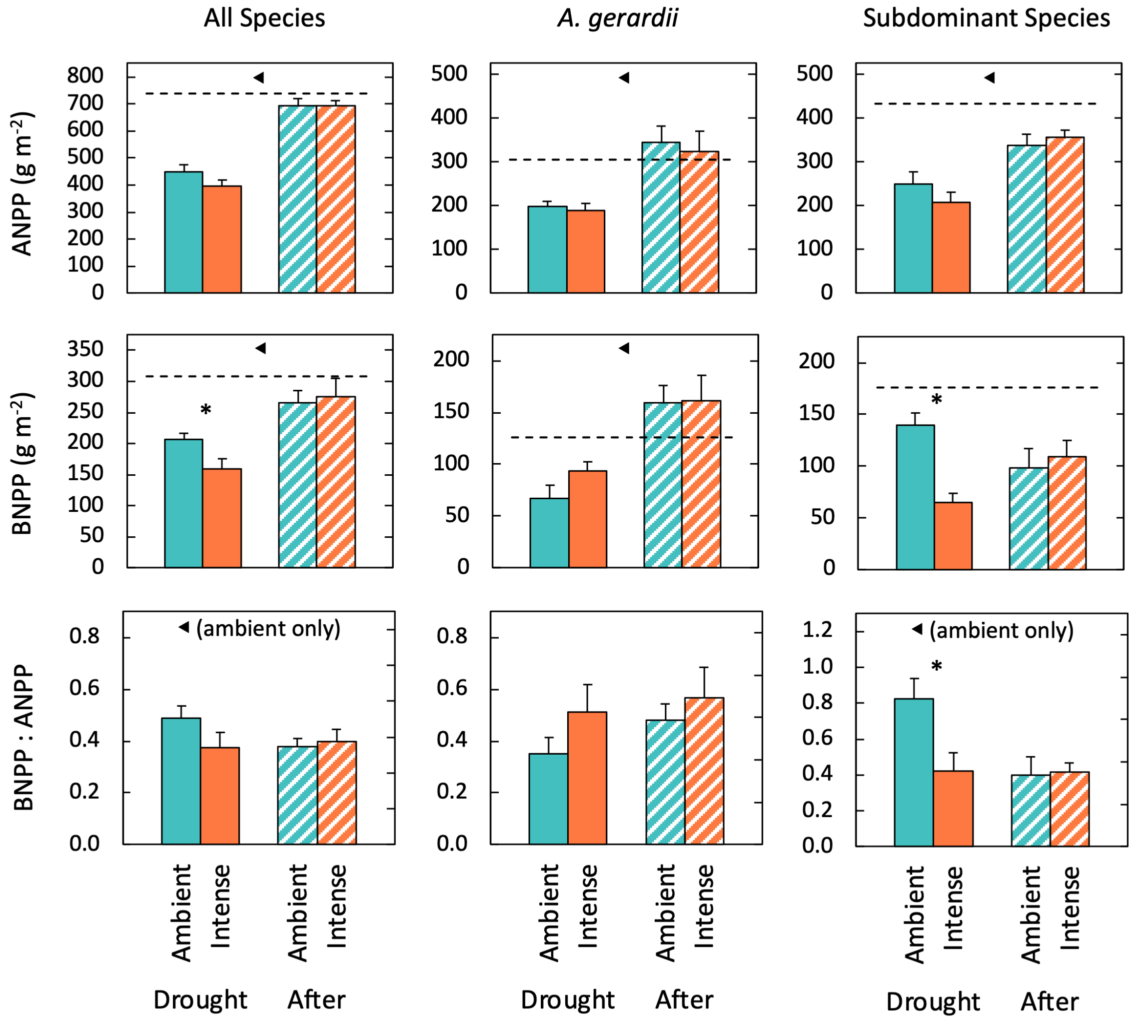

Figure 3.2: Average (+ one standard error) ANPP, BNPP, and ANPP: BNPP ratio of all species, *A. gerardii*, and subdominant species in historically ambient and intense precipitation treatments in the last year of drought (2015) and the first year after drought (2016). Horizontal dashed line = 1998-2013 RaMPs ambient average ANPP or 2015-16 RaMPs-adjacent ambient average BNPP. * = significant difference between historically ambient vs. intense precipitation treatments within a year (drought or after-drought). ◄ = significant difference between drought vs. after-drought years, within historical treatment (ambient or intense).

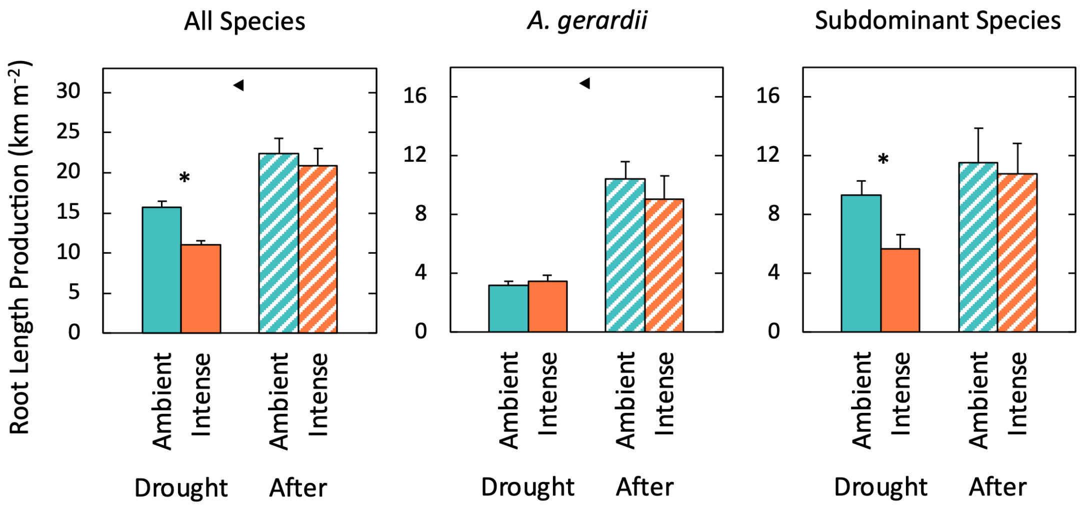

Figure 3.3: Average (+ one standard error) BNPP of *A. gerardii* and subdominant species by depth in historically ambient and intense precipitation treatments during the last year of drought. * = significant difference between historical treatments in a depth increment. ▼ = significant main effect of depth on BNPP. After drought, there were no significant differences between historical treatments in BNPP at any depth, for either *A. gerardii* or subdominant species.

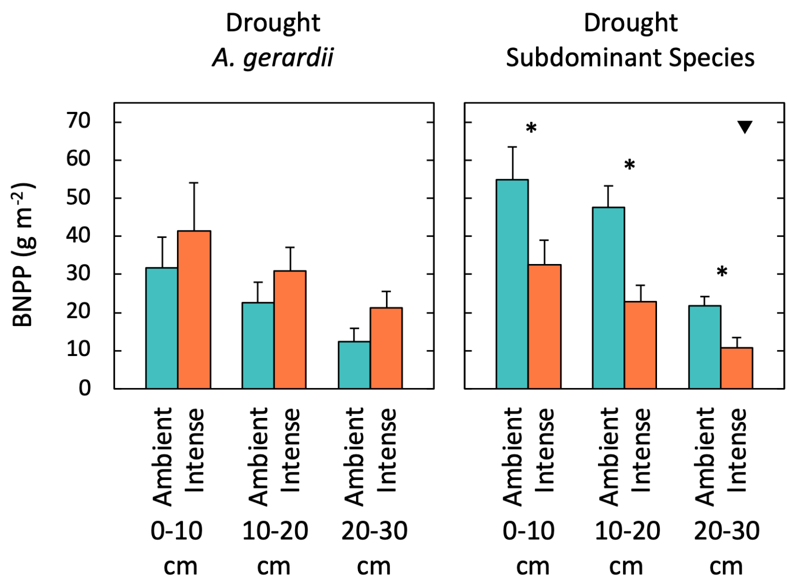

Figure 3.4: Average (+ one standard error) root length production of all species, *A. gerardii*, and subdominant species from historically ambient and intense treatments in the last year of drought and first year after drought. * = significant difference between historically ambient vs. intense precipitation treatments within a year (drought or after-drought). ◂ = significant difference between drought vs. after- drought years, within historical precipitation treatment (ambient or intense).

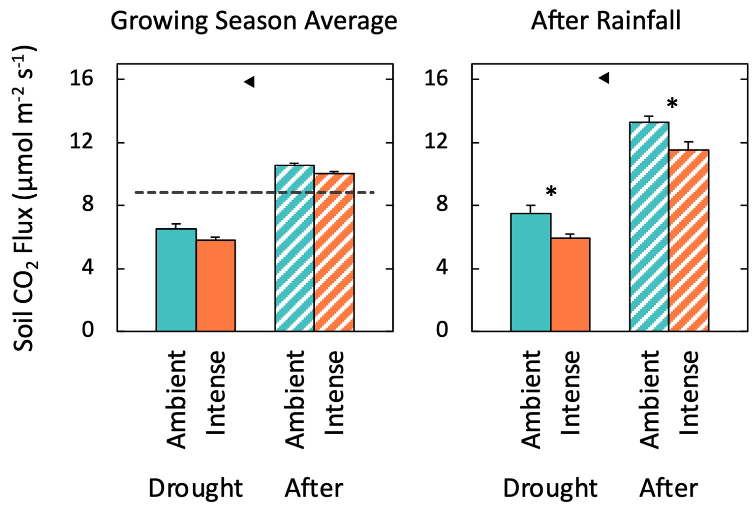

Figure 3.5: Growing season average (+ one standard error) soil CO_2 flux and average (+ one standard error) soil CO_2 flux approximately 24 hours after rainfall in historically ambient and intense treatments in the last year of drought and the first year after drought. Horizontal dashed line = pre-drought ambient RaMPs average. * = significant difference between historically ambient vs. intense precipitation treatments within a year (drought or after-drought). ◄ = significant difference between drought vs. after-drought years, within historical precipitation treatment (ambient or intense).

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CHAPTER 4: REPEATED EXTREME DROUGHTS DECREASE ROOT PRODUCITON, BUT NOT POTENTIAL FOR POST-DROUGHT RECOVERY, IN A MESIC GRASSLAND

Overview

Global climate change is expected to cause more frequent extreme droughts in many parts of the world. Despite the crucial role of roots in water acquisition and plant survival, our understanding of ecosystem vulnerability to drought is primarily based on aboveground impacts. As return intervals between droughts decrease, root responses to one drought might alter responses to subsequent droughts, but this remains unresolved. Thus, we conducted a 7-year experiment that imposed extreme drought (growing season precipitation reduced 66%) on mesic grassland plots during years 1-2, or years 5-6, or both. All plots received ambient precipitation in year 7 and control plots received ambient precipitation in all years. We quantified root production during the last two years of the experiment and found that repeated drought decreased root mass production more than twice as much as one drought (-63% vs. -27%, respectively, relative to controls). Thus, previous drought exposure decreased resistance to a subsequent drought. This was driven by the subdominant species in the community, not by the dominant C_4 grass *Andropogon gerardii*. *A. gerardii* roots were thicker, denser, and deeper than those of the subdominant species across treatments, but root trait values (diameter, tissue density, and specific root length) did not differ among treatments. In year 6, root production in plots droughted 4 years ago had not recovered (-21% vs. control), but root production recovered in all former drought treatments in year 7, when precipitation was above average. Our results highlight the complexity of root responses to drought. Repeated droughts

can have increasingly large negative effects on root production, which might persist for years, but this does not preclude recovery in wet years. Thus, in an increasingly variable climate, the sequence of extreme dry and wet years will determine root dynamics, with important implications for ecosystem functioning.

Introduction

Globally, more frequent and extreme droughts are expected as climate change alters precipitation regimes, with evidence for this already emerging (IPCC 2013; USGCRP 2017; Dai 2013). Drought, defined as a period of marked precipitation deficiency relative to the local long-term average, has been studied extensively and shown to impact myriad ecosystem functions (Slette et al. 2019; Dai 2013; Eziz et al. 2017; Gao et al. 2019; Lei et al. 2016; Wu et al. 2011). But much of what we know is based on aboveground-focused studies of single droughts. As the time between droughts decreases, it will be important to understand how ecosystems respond to not only single, but also recurrent drought. Legacies from past climate anomalies can precondition ecosystems and alter responses to subsequent events, so it is likely that ecosystem responses to recurrent drought, or compound events more generally, are not predictable from studies of individual events (Hughes et al. 2019; Sala et al. 2012; Seneviratne et al. 2012; Zscheischler et al. 2018; Zscheischler et al. 2020). Previous studies of recurrent drought are relatively few and suggest that drought history can impact drought responses in different ways, depending on the ecosystem and species (Anderegg et al. 2020; Backhaus et al. 2014; Dreesen et al. 2014; Hoover et al. 2021). Thus, the potential consequences of repeated drought, ranging from increased acclimation to decreased resistance, remain unresolved.

Roots are the primary means by which plants acquire water and nutrients, regardless of drought conditions, and they are particularly important during drought because of their role in sensing and signaling water deficits (Davies and Zhang 1991; Tardieu and Simonneau 1998). Thus, as the global hydrological cycle intensifies and climates become more variable (Easterling et al. 2000; Huntington 2006; Knapp et al. 2008), resolving how root production responds to drought, and recovers post-drought, is essential for understanding ecosystem dynamics. In addition, roots play many important roles in ecosystem carbon cycling beyond water uptake, providing nutrients via root turnover and contributing greatly to the formation of soil organic matter. Root production and turnover are thus key factors determining the size of the soil carbon reservoir, which is at least twice the size of the atmospheric carbon reservoir and important for global carbon sequestration and climate regulation (Köchy et al. 2015; Scharlemann et al 2014). While belowground net primary production (BNPP) is useful for comparing aboveground vs. belowground NPP and their relative contributions to carbon cycling, the capacity of plants to acquire soil resources may be better reflected by root length than mass because length better reflects the volume of soil that plants can access (Casper and Jackson 1997; Jackson et al. 1996; Wilson 2014). We thus assessed both length and mass production of roots. Despite growing recognition of the importance of root dynamics to ecosystem functioning, root responses to drought are less well-studied than aboveground responses. A framework for predicting root responses to change and linking those responses to broader ecosystem processes could develop from an improved understanding of root traits, and studies that include root trait measurements will therefore be particularly useful in advancing root ecology (Iversen et al. 2017). We thus also assessed root traits in our study.

Grass-dominated ecosystems allocate a substantial portion of total primary production to roots, store most of their carbon belowground (Hui and Jackson 2006; Jones and Donnelly 2004; Risser et al. 1981; Silver et al. 2010; Smith et al. 2008; Soussana et al. 2004), and are globally extensive (Dixon et al. 2014; White et al. 2000). They thus play a key role in the global carbon cycle (Pendall et al. 2018; Scurlock and Hall 1998). Most grassland are water-limited, climatically variable, and sensitive to precipitation, particularly drought (Felton et al. 2020; Knapp and Smith 2001; Knapp et al. 2015, 2020; Li et al. 2019; Morgan et al. 2008; Mowll et al. 2015; Sala et al. 1988). Understanding grassland root responses to drought thus has important implications for predicting both ecosystem- and global-scale changes to carbon dynamics under an increasingly variable climate.

Here we report the results of a study focused on assessing fine root responses to single vs. recurrent extreme droughts, and recovery after drought, in a mesic grassland. Our research builds on the Climate Extremes Experiment (CEE; Hoover et al. 2014a) which imposed an extreme 2-year drought and focused on quantifying primarily aboveground responses during and after drought. Taking advantage of the CEE platform, we imposed another extreme drought in plots both with and without previous drought exposure and assessed root production and traits during and after drought. We predicted that a history of drought exposure would reduce the sensitivity of root production to a second extreme drought, based on the increased relative abundance of C_4 grasses with high water-use-efficiency (Turner and Knapp 1996) and complete recovery of aboveground net primary production (ANPP) after the first extreme drought (Hoover et al. 2014a).

Methods

Study site – The Konza Prairie Biological Station (KPBS) is a 3,487-ha unplowed tallgrass prairie in northeast Kansas, USA (39°05'N, 96°35'W) and is a USA Long-Term Ecological Research (LTER) site. The plant community is composed primarily of native C_4 grasses, dominated by *Andropogon gerardii* (Knapp et al. 1998). The climate is temperate mid-continental with warm, wet summers and cold, dry winters. The mean annual temperature is 13°C (Knapp et al. 1998) and the mean annual precipitation is 851 mm, almost 70% of which falls during the growing season. The CEE was located in a lowland area with deep, silty clay loam soils in the Tully series (Collins and Calabrese 2012; Ransom et al. 1998). Frequent fires are a historical feature of this grassland and are key for maintaining grass dominance and reducing woody plant encroachment (Briggs et al. 2005; Knapp et al. 1998). The CEE was burned annually in mid-March.

The CEE design and treatments – The CEE consisted of four shelters (6 × 24 m) constructed from greenhouse frames with 10 plots (2 × 2 m) in each shelter (see Hoover et al. 2014a for details). Each shelter was hydrologically isolated to a depth of 1 m below the soil surface via a plastic barrier, and via metal flashing installed aboveground. In 2010 and 2011, each rainfall event during the growing season (1 April – 30 August) was reduced in size by ~66% in two shelters by covering the frame with evenly spaced strips of clear polycarbonate plastic, based on Yahdjian and Sala (2002). The other two shelters received ambient precipitation and were covered with deer netting that reduced photosynthetically active radiation by ~10% (equivalent to the reduction in the drought shelters) while allowing all rain to pass through. All plots received all ambient precipitation in 2012 and 2013. Ambient precipitation plots were watered weekly by hand if total rainfall during that week was less than long-term average (in which case the deficit was added). In 2014 and 2015, each rainfall event during the growing season was reduced in size by ~66% in half of each shelter by covering half of the frame with evenly spaced strips of clear polycarbonate plastic (covering 5 of 10 contiguous plots), and the other half was covered with deer netting (Figure 4.1). That is, half of the plots that had been droughted and half of the plots that hadn't been droughted in 2010 and 2011 were droughted in 2014 and 2015. This resulted in four treatments: never droughted (Ambien→ Ambient), droughted only during 2010-11 (Drought→ Ambient), droughted only during 2014-15 (Ambient→ Drought), and droughted during both 2010-11 and 2014-15 (Drought→Drought). To assess recovery after drought, all plots received ambient precipitation in 2016 (Figure 4.1).

Root measurements – We estimated BNPP during the last year of the second drought treatment (2015) and the first year after that drought (2016) by using root ingrowth cores to estimate fine root production. At the start of each growing season, we took a soil core (5 cm diameter, 30 cm deep) from every plot. This depth captures most root production at our site and in other grasslands (Weaver & Darland 1949; Schenk & Jackson 2002; Nippert et al. 2012; Jackson et al. 1996; Sun et al. 1997), and research has linked differences in root distribution within this depth to differences in production even when maximum rooting depth is deeper (Nippert and Holdo 2015). We placed a cylindrical mesh basket filled with sieved, root-free soil (collected adjacent to the CEE) packed to approximate field density into each core hole and filled the space between the ingrowth core and intact soil with sieved, root-free soil. We removed the ingrowth cores at the end of the growing season and stored them at 4°C. We cut each core into 10-cm depth increments that we processed separately. We washed all roots free of soil by wet sieving (0.5 mm sieve) under low water pressure, then submerging remaining sample in a shallow bowl of water, picking out roots with forceps, and removing attached soil by hand. Because roots of the dominant plant species, *A. gerardii*, are visibly distinguishable from roots of other species in this plant community (Figure A3.2), we were able to separate these from the roots of all other species. We scanned all roots using an Epson Perfection photo scanner (Epson America Inc., Long Beach, CA, USA) and analyzed scans for root diameter and length using WinRhizo (Regent Instruments Inc., Québec, Canada). We dried roots at 60°C for 48 hours and weighed them. We calculated BNPP as root mass production per m^2 ground area.

Statistical analyses – We used annual plot-level data for all analyses, which we performed in R (R Core Team 2018). We used the psych package (Revelle 2020) for summary statistics (Table A3.1). To determine the impacts of each of the four precipitation treatments (Ambient→ Ambient, Drought→ Ambient, Ambient→ Drought, Drought→ Drought), during each study year (2015 drought and 2016 recovery), we used linear mixed effects models with plot (nested within shelter) as a random variable (lme4 package, Bates et al. 2015) and type 3 sum of squares analyses of variance ("ANOVAs", car package, Fox and Weisberg 2019) to assess the main effects of treatment and year, as well as the year × treatment interaction. We analyzed total, *A. gerardii*, and other species BNPP and root length production in this way. We used additional models which included the main effect of depth increment and the interactions of depth increment with treatment and with year to assess changes in BNPP depth distribution. We used pairwise contrast comparisons with Holm adjustment to determine in which years there were differences between treatments and in which treatments there were differences between years (emmeans package, Lenth 2021). We considered p values <0.05 indicative of significant effects.

Results

How previous drought exposure affected subsequent drought responses – The 2014 and 2015 drought (66% reduction in the size of each precipitation event), resulted in growing season total precipitation amounts below the 5th percentile of the long-term (112-yr) KPBS rainfall record (Hoover et al. 2014a) in each year. Thus, based on site-specific historic precipitation amounts, the drought that we imposed was statistically extreme (Slette et al. 2019; Smith 2011), similar to the CEE drought imposed in 2010-11 (Hoover et al. 2014a).

A single drought (Ambient→ Drought) reduced BNPP by 27% relative to ambient precipitation (Ambient→ Ambient), and a second drought (Drought→ Drought) reduced BNPP by 63%, more than double the effect of a single drought ($p=0.021$, $p<0.001$, respectively, Figure 4.2). Further, BNPP in plots droughted 4 years earlier (Drought→ Ambient) was 21% lower than in control plots ($p=0.044$).

Reductions in BNPP were most pronounced in shallow soil increments ($F=23.3$, $p<0.01$; Figures 4.2, A3.1). There was an effect of treatment at 0-10 cm ($p=0.002$), but not at 10-20 cm ($p=0.11$) or 20-30 cm ($p=0.28$) below the surface. BNPP in Drought→ Drought plots was reduced from that in Ambient→ Ambient plots by approximately 70%, 60%, and 50% in the 0-10, 10-20, and 20-30 cm depth increments, respectively. As a result of this change in BNPP distribution during drought, BNPP in Drought→ Drought plots was equally distributed among depths, in contrast to Ambient→ Ambient plots, where BNPP declined significantly with depth (Figure 4.2).

Treatment effects on BNPP were driven not by *A. gerardii*, but collectively by the rest of the species in the plant community. Though *A. gerardii* BNPP followed the same pattern as total BNPP, there was no effect of treatment (p=0.32) or of depth (p=0.28) on *A. gerardii* BNPP. In contrast to BNPP, root length production did not differ between Ambient→ Drought and Drought→ Drought plots (p=0.33; Figure 4.3). Compared to Ambient→ Ambient plots, root length production was 52% (p=0.0011) and 63% (p=0.0002) lower in Ambient→ Drought and Drought→ Drought plots, respectively. Thus, while the magnitude of reduction in root mass and length production were the same in Drought→ Drought plots, root length production was reduced more than root mass production in Ambient→ Drought plots. Root length production in Drought→ Ambient plots was reduced from Ambient→ Ambient by 30% (slightly more than root mass production), but this difference was only marginally significant (p=0.056; Figure 4.3). Root diameter, root tissue density (RTD), and specific root length (SRL) all differed between *A. gerardii* vs. other species, across all treatments (p<0.001 for each trait). We did not detect an effect of treatment on diameter, RTD, or SRL of *A. gerardii* or of other species. However, non-significant increases in SRL in Drought→ Drought vs. Ambient→ Drought plots and in Drought→ Ambient vs. Ambient→ Ambient plots likely contributed to the differences in patterns of root mass vs. length production among treatments (Figure A3.3).

Recovery after drought – The first year after the second drought was unusually wet, with ambient growing season precipitation almost 30% above the long-term average (Figure 4.4). Perhaps as a result of this very wet year, there was no effect of the former treatments on BNPP or root length production of either *A. gerardii* (F=0.559, p=0.65 and F=0.708, p=0.56, respectively) or the entire community (F=0.535, p=0.66 and F=2.68, p=0.070, respectively;

Figure 4.5). That is, BNPP and root length production in all former drought treatments recovered from drought (i.e., did not differ from Ambient→ Ambient plots). Compared to the previous year (the last year of the second drought), BNPP and root length production were significantly higher in all formerly droughted plots during the recovery year, regardless of drought history (p=0.0057 A→D, p<0.001 D→D, p=0.020 D→A). BNPP and root length production were also higher in Ambient→ Ambient plots during this wet year vs. the previous average year, but statistical significance was marginal (p=0.059).

Discussion

Our study revealed that recurrent extreme drought, separated by 2 years with average precipitation, decreased BNPP by more than twice as much as a single extreme drought. That is, the history of previous drought exposure decreased root resistance to subsequent drought. Drought impacts in this ecosystem may thus be underestimated if climatic history is not considered. Increasingly larger declines in BNPP with repeated droughts could have important implications for ecosystem carbon cycling and storage, given the role of root production in soil organic matter formation and the role of soils, especially grassland soils, in global carbon sequestration (Köchy et al. 2015; Scharlemann et al. 2014; Hui and Jackson 2006; Risser et al. 1981; Silver et al. 2010; Smith et al. 2008; Soussana et al. 2004).

Root length production declined more than root mass production during a single drought (52% vs. 27%, respectively), while root length and mass production declined equally during a second drought (63%), compared to ambient precipitation plots. Root length production is less commonly quantified than mass production, but it is likely a better indicator of the capacity of plants to acquire soil resources, as length reflects the volume of soil that plants can access (Wilson 2014; Jackson et al. 1996; Casper and Jackson 1997). Although root length is usually related to soil mineral nutrients, the same may apply to soil water, especially when plant growth is limited by soil water deficits. Drought impacts on overall ecosystem function, beyond just net primary production, might thus be underestimated if only root mass production, and not root length production, are quantified.

Declines in root production were not driven by the dominant species, *A. gerardii*, which is responsible for most community and ecosystem dynamics aboveground (Smith and Knapp 2003; Silletti et al. 2004). Instead, responses were due to low drought resistance of the subdominant species in the community (Figure 4.2). This suggests an important role of *A. gerardii*, which has relatively high water use efficiency (Turner and Knapp 1996), in maintaining ecosystem functioning during extreme drought. These differential responses are consistent with results from the first CEE drought, when photosynthesis and production of *A. gerardii* declined less than that of other species (Hoover et al. 2014b). We build upon that finding and extend it to belowground production as well.

In addition to *A. gerardii* root production declining less than that of other species during drought, *A. gerardii* roots were thicker, denser, and deeper than those of the subdominant species in the community (Figure A3.2). This trait combination is likely advantageous during drought. Indeed, given that shallow BNPP was most negatively affected by drought, a deeper BNPP distribution likely increases drought resistance in this grassland. Previous research has linked differences in root depth distribution with differences in plant production (Nippert and Holdo 2015). Thicker, low-SRL roots are generally thought to indicate greater mycorrhizal association and "outsourcing" of resource acquisition to mycorrhizae (Bergmann et al. 2020).

We did not assess mycorrhizal abundance in our study, but previous research has shown that *A. gerardii* is indeed strongly mycorrhizal dependent (Wilson and Hartnett 1997, 1998; Smith et al. 1999), so greater mycorrhizal association of *A. gerardii* vs. other species might thus have also contributed to its greater drought resistance. We did not find any evidence of plasticity in root traits. That is, there was no evidence of either *A. gerardii* or other species altering root traits to adapt to drought conditions (Figure A3.3). Thus, though certain traits appear to be beneficial in maintaining root production during drought, the species in this community might have little capacity to adjust root traits in response to drought. A major goal of trait-based ecology has been to link plant traits with key ecosystem functions but establishing such links has been challenging. Here we show that root production by a dominant mycorrhizal-dependent C_4 grass species with lower SRL, wider root diameter, and a deeper root distribution declined less than the other species in the community during drought. Species with this trait combination should be better able than others to maintain root production under increasing drought frequency and severity.

After the first extreme drought (2010-11), ANPP in the CEE recovered in just one year (Hoover et al. 2014a). In contrast, our results show that BNPP had not fully recovered from that extreme drought even four years later (2015; Figure 4.2). Slow recovery of BNPP was thus a less apparent (i.e., belowground) but more persistent effect of extreme drought in our experiment. Predicted drought impacts might thus be underestimated if belowground dynamics are not fully considered. However, BNPP did recover in the year after the second drought (Figure 4.5), likely due to above-average ambient precipitation in this year, compared to near-average in the previous four years (Figure 4.4). That is, the almost two-thirds reduction in BNPP following two sequential droughts did not preclude rapid post-drought recovery when resource availability was high. This raises the intriguing possibility that while average precipitation amounts appear to be sufficient for ANPP recovery after extreme drought, BNPP recovery may be more resource demanding. Overall, our results add to the growing evidence that precipitation change has different impacts on grassland primary production aboveground vs. belowground (Byrne et al. 2013; Carroll et al. 2021; Chou et al. 2008; Wilcox et al. 2015, 2017; Post and Knapp 2020). It will be important to consider this dissimilarity of aboveground and belowground production responses when forecasting ecosystem responses to increasing climatic variability.

In summary, we found that previous exposure to an extreme drought decreased drought resistance of mesic grassland root production. After drought, root production recovered to ambient levels only when precipitation was above average. As climatic variability increases, causing greater drought frequency and severity as well as more extreme wet years, predicting and modeling changes in key aspects of global terrestrial carbon and water cycling will require understanding the unique dynamics of roots (in addition to more commonly measured aboveground dynamics) and responses during and after not only single but also multiple climate extremes.

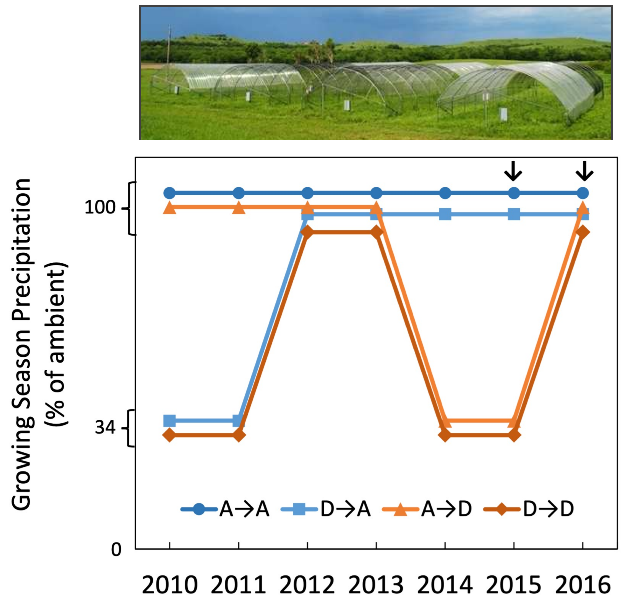

Figure 4.1: Photo and treatment schematic of the Climate Extremes Experiment. Two 2-year droughts (growing season precipitation reduced 66%) were imposed in half of all plots in 2010-11 and 2014-15, separated by 2 years of average ambient precipitation. A=Ambient, D=Drought (in 2010-11 and 2014-15). D→A plots were droughted during the first drought, A→D plots were droughted during the second drought, D→D plots were droughted during both droughts, A→A plots were never droughted. ↓ = year with root measurements.

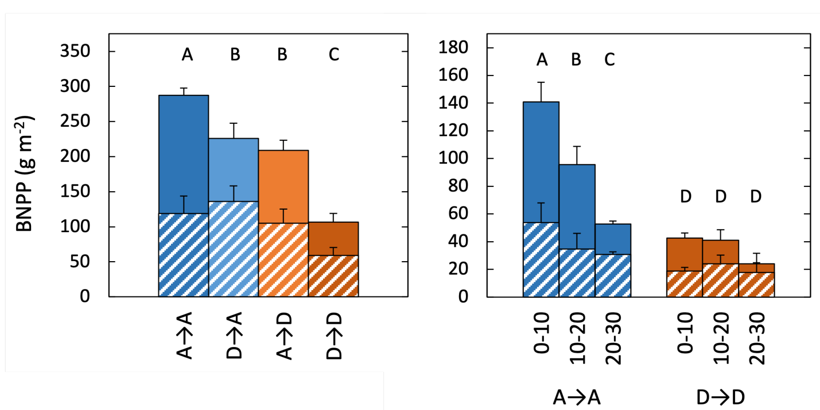

Figure 4.2: Average BNPP (+ one standard error) in the last year of the second 2-year extreme drought, for all treatments (left), and by depth in Ambient→ Ambient and Drought→ Drought treatments (right). The dashed portion of each bar indicates *A. gerardii* BNPP. Different letters indicate significant differences in total BNPP among treatments. There was no effect of either treatment or of depth on *A. gerardii* BNPP (dashed portion of bars), but *A. gerardii* BNPP was higher in A→A vs. D→D plots in the 0-10 cm increment (indicated by *).

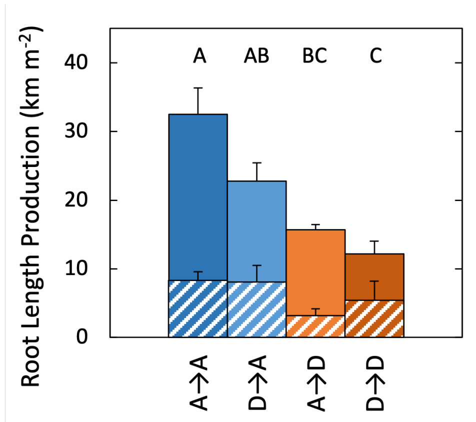

Figure 4.3: Average root length production (+ one standard error) by treatment in the last year of the second 2-year extreme drought. The dashed portion of each bar indicates *A. gerardii* root length production. Different letters indicate significant differences in total root length production among treatments. *A. gerardii* root length production (dashed portion of bars) did not differ among treatments.

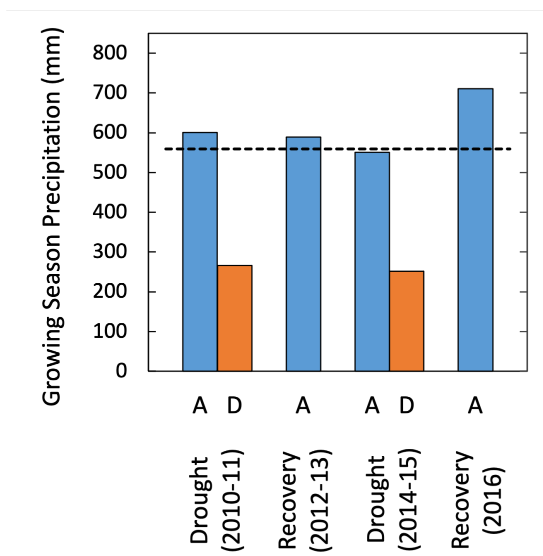

Figure 4.4: Growing season precipitation in Ambient (A) and Drought (D) treatments throughout the Climate Extremes Experiment, and the long-term site average (horizontal dashed line). Ambient precipitation was 30% above average in the first year after the second drought (2016), compared to near average in preceding years. We posit that the wet year allowed root production to recover in all former drought treatments, despite remaining below ambient levels in previous years when precipitation was near average.

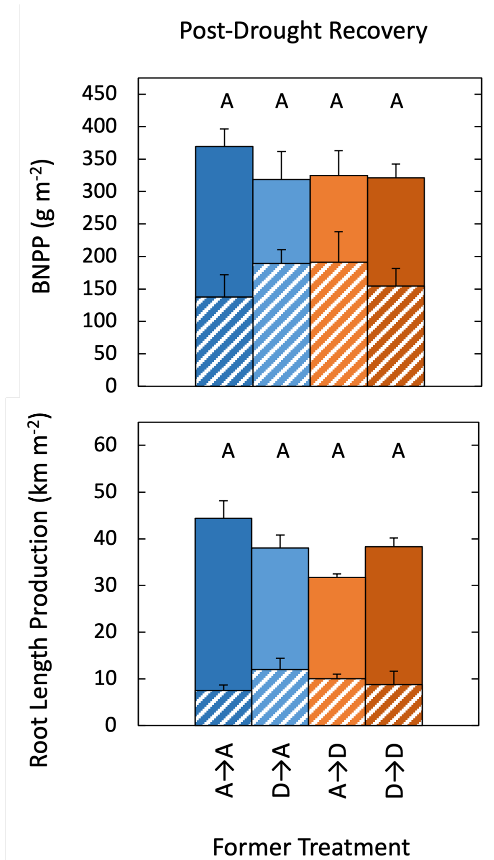

Figure 4.5: Average BNPP and root length production (+ one standard error) in the first year after the second 2-yr extreme drought. Both BNPP and root length production recovered from drought in this year, regardless of drought history. That is, none of the former drought treatments differed significantly from Ambient→ Ambient plots, in terms of BNPP or root length production of the entire community or of *A. gerardii* (dashed portion of each bar).

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CHAPTER 5: CONCLUSIONS

As climate change continues to alter multiple aspects of precipitation regimes, it is important to understand how compounded precipitation changes will affect key ecosystem dynamics (IPCC 2013; Hughes et al. 2019; Seneviratne et al. 2012; Zscheischler et al. 2018; Zscheischler et al. 2020). My dissertation research assessed the impacts of drought and how they are altered when compounded by previous precipitation change. My findings show that predictions of drought impacts can be improved by: more consistent and detailed descriptions of drought condition, considering ecosystem precipitation history, and including belowground dynamics.

My review of the recent ecological drought literature revealed that many authors provide little detail about studied drought conditions and what does or does not constitute a drought, which hampers synthesis and our ability to draw broad ecological conclusions about drought impacts. In chapter 2, I present guidelines to improve standardization of how ecological phenomena are described among studies, with the goal of improving future synthetic research efforts. I suggest that future publications report the magnitude and duration of drought within site-specific historical context, and I encourage ecologists to make use of standardized indices, long-term climate records, drought declarations from monitoring agencies, and published thresholds to define drought. Our understanding of the ecological impacts of drought will advance more rapidly within and among ecosystem types if future studies provide more consistent and quantitative characterizations of the droughts studied.

Concurrently with increasing drought impacts on ecosystems and forecasts for more frequent and extreme droughts in the future, precipitation patterns are intensifying such that much of the world is experiencing larger, more intense precipitation events (Dai 2012; Fischer and Knutti 2016; Fowler et al. 2021; Huntington 2006; IPCC 2013). In the study presented in chapter 3, I found that long-term exposure of a mesic grassland to an intensified precipitation pattern reduced soil moisture and ANPP but did not alter the response of ANPP to a subsequently imposed drought. However, a history of intensified precipitation patterns amplified reductions in BNPP during drought and reduced the size of the soil CO_2 flux increase following rainfall events both during and after drought. From this study, I conclude that as precipitation patterns intensify and drought frequency and severity continue to increase globally, predicting changes in global terrestrial carbon cycling will require greater understanding of how ecosystem belowground dynamics respond to multiple compounded precipitation changes.

As the frequency, severity, and spatial extent of droughts increases with global climate change, it is increasingly likely that ecosystem responses to drought will reflect past as well as current drought conditions (Anderegg et al. 2020; Backhaus et al. 2014; Dreesen et al. 2014; Hoover et al. 2021; IPCC 2013). In the study presented in chapter 4, I found that recurrent extreme drought, separated by 2 years with average precipitation, decreased BNPP by more than twice as much as a single extreme drought. That is, the history of previous drought exposure decreased resistance to subsequent drought. As climatic variability increases, causing greater drought frequency and severity as well as more extreme wet years, predicting changes in key aspects of global terrestrial carbon and water cycling will require understanding the unique dynamics of roots (in addition to more commonly measured aboveground dynamics) during and after multiple extreme climate events.

The findings from both of these studies (chapters 3 and 4) have important implications for long-term ecosystem carbon cycling and sequestration. Root production is key in soil organic matter formation and soils, especially grassland soils, are key in global carbon storage (Hui and Jackson 2006; Köchy et al. 2015; Risser et al. 1981; Scharlemann et al. 2014; Silver et al. 2010; Smith et al. 2008; Soussana et al. 2004). Because root production decreased in both studies, it is possible that the formation of soil organic matter and eventually the amount of soil carbon stored in this ecosystem could decrease with continued precipitation changes.

Both studies also add to growing evidence that grassland belowground responses to precipitation change should not be inferred from aboveground responses (Byrne et al. 2013; Carroll et al. 2021; Chou et al. 2008; Post and Knapp 2020; Wilcox et al. 2015, 2017). In chapter 3, precipitation history altered the response of BNPP, but not ANPP, to extreme drought. In chapter 4, I found that BNPP had not fully recovered from an extreme drought that occurred four years previous, but ANPP recovered from that same drought in just one year (Hoover et al. 2014). Slow recovery of BNPP was thus a more persistent effect of extreme drought than responses observed aboveground. It will be important to consider this dissimilarity of aboveground and belowground production responses when forecasting ecosystem responses to increasing climatic variability.

In addition, both studies suggest an important role of the dominant species, *A. gerardii*, in maintaining ecosystem functioning during drought. In both studies, the declines in root production during drought were driven not by *A. gerardii*, but by the subdominant species in the community. I identified several characteristics that distinguished the roots of *A. gerardii* from those of the subdominant species, which could help explain this difference in responses. Mainly, that the roots of *A. gerardii* were thicker and distributed deeper in the soil than those of the subdominant species. This suggests that root traits could be useful in understanding and predicting ecosystem responses to precipitation change (Iversen et al. 2017).

In summary, I found that understanding and predicting ecological impacts of drought can be improved by ecologists providing more detailed and consistent descriptions of drought conditions in their studies, accounting for precipitation history, and considering changes in belowground dynamics. In light of increasing impacts of precipitation changes, it is essential that ecologists study and describe these changes thoroughly.

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Köchy M, Hiederer R, Freibauer A. 2015. Global distribution of soil organic carbon—part 1: masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world. *Soil* 1: 351–365. https://doi.org/10.5194/soil-1-351-2015

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APPENDIX 1

Table A1.1: List of the publications included in my review of how ecologists define drought, and how I classified each publication. In the classification column, the initial letter(s) refers to the approach(es) used to study drought, abbreviated as the first letter (see Figure 2.2). The number(s) refers to the category of drought description, ordered as they are listed in Table 2.1 (e.g., 1 = “Dry”). The letter(s) after the number(s) refers to the ecosystem(s) in which drought was studied, abbreviated as the first one or two letters (see Figure 2.3, N= not included in the ecosystem assessment because the ecosystem type was not specified, the study was not ecosystem-specific or the ecosystem was not one of the six most common). The publications included in the SPEI analysis (Figure 2.4) are indicated by shading.

Publication	Classification
Aakala, T., Kuuluvainen, T., Wallenius, T., & Kauhanen, H. (2011). Tree mortality episodes in the intact Picea abies-dominated taiga in the Arkhangelsk region of northern European Russia: Episodic tree mortality in intact spruce taiga. *Journal of Vegetation Science*, *22*(2), 322–333.	O, 3, Fo
Abell, S. E., Gadek, P. A., Pearce, C. A., & Congdon, B. C. (2006). Seasonal resource availability and use by an endangered tropical mycophagous marsupial. *Biological Conservation*, *132*(4), 533–540.	O, 8, Fo
Abril, M., Muñoz, I., & Menéndez, M. (2016). Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation. *Science of The Total Environment*, *553*, 330–339.	O, 5, Fr
Acosta Salvatierra, L. H., Ladle, R. J., Barbosa, H., Correia, R. A., & Malhado, A. C. M. (2017). Protected areas buffer the Brazilian semi-arid biome from climate change. *Biotropica*, *49*(5), 753–760.	O, 1, S
Acuña, V., Muñoz, I., Giorgi, A., Omella, M., Sabater, F., & Sabater, S. (2005). Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. *Journal of the North American Benthological Society*, *24*(4), 919–933.	O, 5, Fr
Adams, R. A. (2010). Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology*, *91*(8), 2437–2445.	O, 2, G, S, Fo
Albertson, K., Aylen, J., Cavan, G., & McMorrow, J. (2010). Climate change and the future occurrence of moorland wildfires in the Peak District of the UK. *Climate Research*, *45*, 105–118.	M, 1, S
Alday, J. G., Marrs, R. H., & Martínez-Ruiz, C. (2010). The importance of topography and climate on short-term revegetation of coal wastes in Spain. *Ecological Engineering*, *36*(4), 579–585.	O, 2, G,
Aldridge, C. L., & Boyce, M. S. (2008). Accounting for Fitness: Combining Survival and Selection when Assessing Wildlife-Habitat Relationships. *Israel Journal of Ecology & Evolution*, *54*(3–4), 389–419.	M, 3, G
Alexandre, C. M., Ferreira, T. F., & Almeida, P. R. (2012). Fish assemblages in non-regulated and regulated rivers from permanent and temporary Iberian systems. *River Research and Applications*.	O, 5, Fr
Allen, M. S., & Palmer, M. W. (2011). Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie. *Journal of Vegetation Science*, *22*(3), 436–444.	O, 3, G, Fo
Al-Qaddi, N., Vessella, F., Stephan, J., Al-Eisawi, D., & Schirone, B. (2017). Current and future suitability areas of kermes oak (Quercus coccifera L.) in the Levant under climate change. *Regional Environmental Change*, *17*(1), 143–156.	O, 1, Fo
Amundrud, S. L., & Srivastava, D. S. (2015). Drought sensitivity predicts habitat size sensitivity in an aquatic ecosystem. *Ecology*, *96*(7), 1957–1965.	E, 5, N
Amundrud, S. L., & Srivastava, D. S. (2016). Trophic interactions determine the effects of drought on an aquatic ecosystem. *Ecology*, *97*(6), 1475–1483.	E, 1, N
Anderegg, L. D. L., & HilleRisLambers, J. (2016). Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Global Change Biology*, *22*(3), 1029–1045.	O, 6, Fo
Anthonysamy, W. J. B., Dreslik, M. J., & Phillips, C. A. (2013). Disruptive Influences of Drought on the Activity of a Freshwater Turtle. *The American Midland Naturalist*, *169*(2), 322–335.	O, 2, G, W, Fr
Arce, M. I., Sánchez-Montoya, M. del M., Vidal-Abarca, M. R., Suárez, M. L., & Gómez, R. (2014). Implications of flow intermittency on sediment nitrogen availability and processing rates in a Mediterranean headwater stream. *Aquatic Sciences*, *76*(2), 173–186.	O, 1, Fr
Ariza, C., & Tielbörger, K. (2011). An evolutionary approach to studying the relative importance of plant-plant interactions along environmental gradients. *Functional Ecology*, *25*(4), 932–942.	O, 2, S
Arterburn, J. R., Twidwell, D., Schacht, W. H., Wonkka, C. L., & Wedin, D. A. (2018). Resilience of Sandhills Grassland to Wildfire During Drought. *Rangeland Ecology and Management; Lawrence*, *71*(1), 53–57.	O, 2, G

Audet, P., Arnold, S., Lechner, A. M., & Baumgartl, T. (2013). Site-specific climate analysis elucidates revegetation challenges for post-mining landscapes in eastern Australia. *Biogeosciences*, *10*(10), 6545–6557.	O, 1, N
Bachelet, D., Neilson, R. P., Lenihan, J. M., & Drapek, R. J. (2001). Climate Change Effects on Vegetation Distribution and Carbon Budget in the United States. *Ecosystems*, *4*(3), 164–185.	M, 3, 4, N
Backhaus, S., Kreyling, J., Beierkuhnlein, C., Buhk, C., Nagy, L., Thiel, D., & Jentsch, A. (2014). A transplantation experiment along climatic gradients suggests limitations of experimental warming manipulations. *Climate Research*, *60*(1), 63–71.	E, 6, N
Baho, D. L., Tavşanoğlu, Ü. N., Šorf, M., Stefanidis, K., Drakare, S., Scharfenberger, U., … Angeler, D. G. (2015). Macroecological Patterns of Resilience Inferred from a Multinational, Synchronized Experiment. *Sustainability*, *7*(2), 1142–1160.	O, 1, N
Baker, T. R., Jones, J. P. G., Rendón Thompson, O. R., Cuesta, R. M. R., Del Castillo, D., Aguilar, I. C., … Healey, J. R. (2010). How can ecologists help realise the potential of payments for carbon in tropical forest countries? *Journal of Applied Ecology*, *47*(6), 1159–1165.	M, 1, Fo
Baldocchi, D. D., Ma, S., Rambal, S., Misson, L., Ourcival, J.-M., Limousin, J.-M., … Papale, D. (2010). On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. *Ecological Applications*, *20*(6), 1583–1597.	C, 1, Fo
Baldwin, D. S., Colloff, M. J., Rees, G. N., Chariton, A. A., Watson, G. O., Court, L. N., … Hardy, C. M. (2013). Impacts of inundation and drought on eukaryote biodiversity in semi-arid floodplain soils. *Molecular Ecology*, *22*(6), 1746–1758.	O, 2, Fo
Barbosa, J. M., & Asner, G. P. (2016). Effects of long-term rainfall decline on the structure and functioning of Hawaiian forests. *Environmental Research Letters*, *12*(9), 094002.	O, 1, Fo
Barea, J. M., Palenzuela, J., Cornejo, P., Sánchez-Castro, I., Navarro-Fernández, C., Lopéz-García, A., … Azcón-Aguilar, C. (2011). Ecological and functional roles of mycorrhizas in semi-arid ecosystems of Southeast Spain. *Journal of Arid Environments*, *75*(12), 1292–1301.	R, 6, S, G
Barkaoui, K., Navas, M.-L., Roumet, C., Cruz, P., & Volaire, F. (2017). Does water shortage generate water stress? An ecohydrological approach across Mediterranean plant communities. *Functional Ecology*, *31*(6), 1325–1335.	M, 6, G
Barkaoui, K., Roumet, C., & Volaire, F. (2016). Mean root trait more than root trait diversity determines drought resilience in native and cultivated Mediterranean grass mixtures. *Agriculture, Ecosystems & Environment*, *231*, 122–132.	E, 4, G
Bart, R. R., Tague, C. L., & Dennison, P. E. (2017). Modeling annual grassland phenology along the central coast of California. *Ecosphere*, *8*(7), e01875.	O, 1, G
Barthès, A., Ten-Hage, L., Lamy, A., Rols, J.-L., & Leflaive, J. (2015). Resilience of Aggregated Microbial Communities Subjected to Drought—Small-Scale Studies. *Microbial Ecology*, *70*(1), 9–20.	E, 1, N
Bartholomeus, R. P., Witte, J.-P. M., & Runhaar, J. (2012). Drought stress and vegetation characteristics on sites with different slopes and orientations. *Ecohydrology*, *5*(6), 808–818.	M, 6, N
Bartlett, M. K., Scoffoni, C., & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters*, *15*(5), 393–405.	R, 1, N
Basialashvili, T., Matchavariani, L., & Lagidze, L. (2015). Desertification risk in Kakheti Region, East Georgia. *Journal of Environmental Biology*, *36 Spec No*, 33–36.	C, 2, N
Bauer, J. T., & Reynolds, H. L. (2016). Restoring native understory to a woodland invaded by *Euonymus fortunei* : multiple factors affect success. *Restoration Ecology*, *24*(1), 45–52.	O, 1, S
Baumberger, T., Affre, L., Croze, T., & Mesléard, F. (2012). Habitat requirements and population structure of the rare endangered Limonium girardianum in Mediterranean salt marshes. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *207*(4), 283–293.	O, 1, W
Baumgartner, L. J., Wooden, I. J., Conallin, J., Robinson, W., & Thiem, J. D. (2017). Managing native fish communities during a long-term drought. *Ecohydrology*, *10*(4), e1820.	O, 1, Fr
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Bino, G., Wassens, S., Kingsford, R. T., Thomas, R. F., & Spencer, J. (2018). Floodplain ecosystem dynamics under extreme dry and wet phases in semi-arid Australia. *Freshwater Biology*, *63*(2), 224–241.	O, 5, Fr
Birkett, A., & Stevens-Wood, B. (2005). Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *African Journal of Ecology*, *43*(2), 123–130.	O, 2, S
Bishop-Taylor, R., Tulbure, M. G., & Broich, M. (2017). Surface-water dynamics and land use influence landscape connectivity across a major dryland region. *Ecological Applications*, *27*(4), 1124–1137.	O, 2, N
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APPENDIX 2

Table A2.1: Average (one standard error) dependent variable values from historically ambient and altered precipitation pattern treatments during drought and after drought.

	Drought (2015)		After Drought (2016)	
Variable	Ambient	Intense	Ambient	Intense
Soil moisture (% VWC)				
15 cm	11.7 (0.47)	11.2 (0.68)	21.8 (0.94)	21.6 (1.0)
30 cm	18.4 (0.97)	20.0 (1.4)	28.9 (2.1)	33.3 (1.3)
ANPP (g m^{-2})				
All species	447 (28)	395 (25)	693 (25)	694 (18)
A. gerardii	198 (12)	189 (17)	345 (36)	324 (46)
Subdominant species	250 (16)	206 (23)	338 (26)	355 (38)
BNPP (g m^{-2})				
All species	206 (9.3)	158 (16)	266 (19)	275 (30)
A. gerardii	66.7 (13)	93.5 (9.1)	159 (17)	161 (25)
Subdominant species	140 (11)	64.8 (9.0)	98.8 (18)	109 (15)
BNPP: ANPP				
All species	0.49 (0.04)	0.37 (0.06)	0.38 (0.03)	0.39 (0.05)
A. gerardii	0.35 (0.06)	0.51 (0.10)	0.48 (0.06)	0.57 (0.11)
Subdominant species	0.82 (0.11)	0.42 (0.10)	0.40 (0.10)	0.42 (0.05)
Root length production (km m^{-2})				
All species	15.7 (0.76)	11.1 (0.40)	22.4 (1.9)	20.8 (2.2)
A. gerardii	3.19 (0.30)	3.49 (0.38)	10.4 (1.2)	9.06 (1.6)
Subdominant species	9.32 (1.0)	5.70 (0.93)	11.5 (2.3)	10.8 (2.1)
Soil CO_2 flux (µmol m^{-2} s^{-1})				
Growing season average	6.50 (0.31)	5.81 (0.16)	10.5 (0.14)	10.0 (0.16)
24 hours after rainfall	7.50 (0.49)	5.91 (0.27)	13.3 (0.38)	11.6 (0.48)

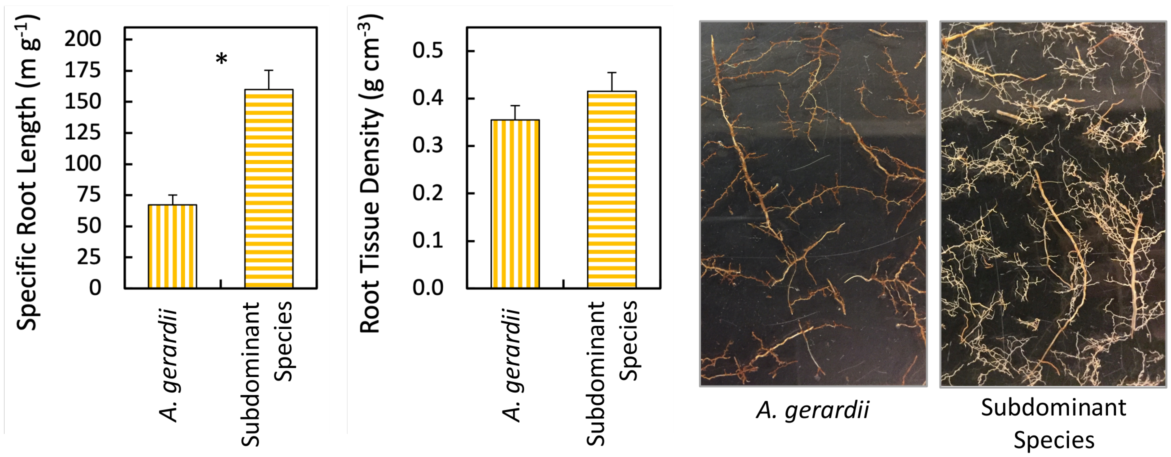

Figure A2.1: Average + one standard error specific root length (SRL) and root tissue density (RTD) of *A. gerardii* vs. subdominant species in the community (historical treatments and sample years combined, because we did not detect any significant differences between historic treatments or between years). * = significant ($p<0.05$) difference between *A. gerardii* vs. subdominant species. Pictures: washed roots of *A. gerardii* and subdominant species.

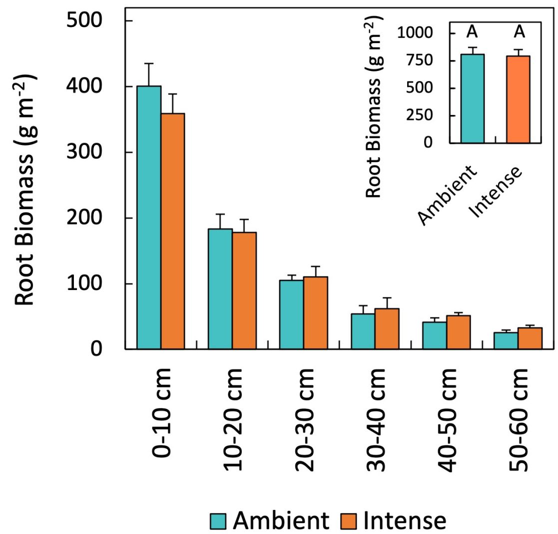

Figure A2.2: Average + one standard error standing crop root biomass in the final year of the RaMPs ambient vs. intense precipitation treatment by 10-cm depth increment. Inset: Average + one standard error total standing crop root biomass in the top 60 cm below the soil surface. There were no differences between treatments overall or in any individual depth increments.

Table A2.2: Results of statistical analyses of the main effects of historical treatment (ambient or intense precipitation pattern), year (2015 drought year and 2016 after-drought year), and the treatment × year interaction on dependent variables from our study.

Variable	Effect	Df	p-value
Total ANPP	Treatment	1, 18	0.743
	Year	1, 18	<0.001
	Treatment × year	1, 18	0.823
A. gerardii ANPP	Treatment	1, 18	0.837
	Year	1, 18	0.010
	Treatment × year	1, 18	0.623
Subdominant species ANPP	Treatment	1, 18	0.642
	Year	1, 18	0.021
	Treatment × year	1, 18	0.779
Total BNPP	Treatment	1, 18	0.023
	Year	1, 18	0.001
	Treatment × year	1, 18	0.092
A. gerardii BNPP	Treatment	1, 18	0.270
	Year	1, 18	0.010
	Treatment × year	1, 18	0.465
Subdominant species BNPP	Treatment	1, 18	0.006
	Year	1, 18	0.030
	Treatment × year	1, 18	0.017
Total ANPP: BNPP	Treatment	1, 18	0.106
	Year	1, 18	0.726
	Treatment × year	1, 18	0.194
A. gerardii ANPP: BNPP	Treatment	1, 18	0.187
	Year	1, 18	0.664
	Treatment × year	1, 18	0.677
Subdominant species ANPP: BNPP	Treatment	1, 18	0.005
	Year	1, 18	0.965
	Treatment × year	1, 18	0.028
Total root length production	Treatment	1, 18	0.024
	Year	1, 18	<0.001
	Treatment × year	1, 18	0.310
A. gerardii root length production	Treatment	1, 18	0.667
	Year	1, 18	0.027
	Treatment × year	1, 18	0.396
Subdominant species root length production	Treatment	1, 18	0.314
	Year	1, 18	0.088
	Treatment × year	1, 18	0.321

Contrast comparisons assessing differences between ambient vs. intense historical treatments within each year of our study (2015 drought year vs. 2016 after-drought year) and differences between years within each historical treatment.

Variable	Effect	p-value
Total ANPP	Ambient vs. intense treatment (2015)	0.78
	Ambient vs. intense treatment (2016)	0.99
	2015 vs. 2016 (ambient treatment)	<0.001
	2015 vs. 2016 (intense treatment)	<0.001
A. gerardii ANPP	Ambient vs. intense treatment (2015)	0.67
	Ambient vs. intense treatment (2016)	0.70
	2015 vs. 2016 (ambient treatment)	0.010
	2015 vs. 2016 (intense treatment)	0.001
Subdominant species ANPP	Ambient vs. intense treatment (2015)	0.59
	Ambient vs. intense treatment (2016)	0.95
	2015 vs. 2016 (ambient treatment)	0.014
	2015 vs. 2016 (intense treatment)	0.044
Total BNPP	Ambient vs. intense treatment (2015)	0.28
	Ambient vs. intense treatment (2016)	0.61
	2015 vs. 2016 (ambient treatment)	0.049
	2015 vs. 2016 (intense treatment)	0.025
A. gerardii BNPP	Ambient vs. intense treatment (2015)	0.16
	Ambient vs. intense treatment (2016)	0.85
	2015 vs. 2016 (ambient treatment)	0.014
	2015 vs. 2016 (intense treatment)	0.048
Subdominant species BNPP	Ambient vs. intense treatment (2015)	0.0027
	Ambient vs. intense treatment (2016)	0.47
	2015 vs. 2016 (ambient treatment)	0.14
	2015 vs. 2016 (intense treatment)	0.10
Total ANPP: BNPP	Ambient vs. intense treatment (2015)	0.18
	Ambient vs. intense treatment (2016)	0.62
	2015 vs. 2016 (ambient treatment)	0.019
	2015 vs. 2016 (intense treatment)	0.71
A. gerardii ANPP: BNPP	Ambient vs. intense treatment (2015)	0.24
	Ambient vs. intense treatment (2016)	0.82
	2015 vs. 2016 (ambient treatment)	0.18
	2015 vs. 2016 (intense treatment)	0.78
Subdominant species ANPP: BNPP	Ambient vs. intense treatment (2015)	0.039
	Ambient vs. intense treatment (2016)	0.62
	2015 vs. 2016 (ambient treatment)	0.022
	2015 vs. 2016 (intense treatment)	0.99

Total root length production	Ambient vs. intense treatment (2015)	<0.001
	Ambient vs. intense treatment (2016)	0.58
	2015 vs. 2016 (ambient treatment)	0.049
	2015 vs. 2016 (intense treatment)	0.019
A. gerardii root length production	Ambient vs. intense treatment (2015)	0.65
	Ambient vs. intense treatment (2016)	0.81
	2015 vs. 2016 (ambient treatment)	0.014
	2015 vs. 2016 (intense treatment)	0.045
Subdominant species root length production	Ambient vs. intense treatment (2015)	0.038
	Ambient vs. intense treatment (2016)	0.85
	2015 vs. 2016 (ambient treatment)	0.86
	2015 vs. 2016 (intense treatment)	0.064

APPENDIX 3

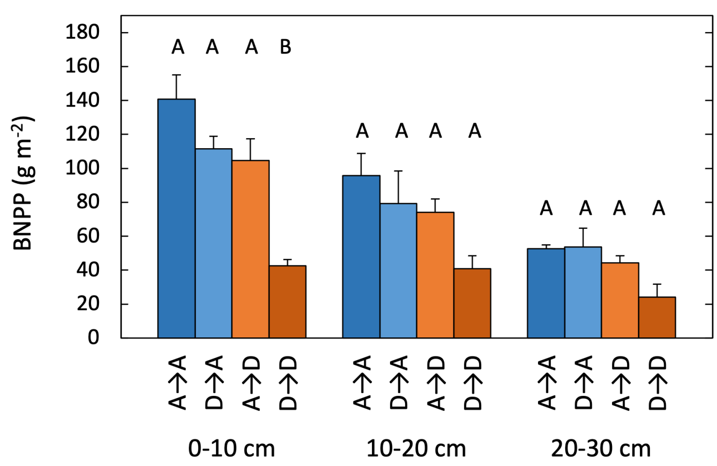

Figure A3.1: Average BNPP (+ one standard error) by depth increment in all treatments during the last year of the second 2-year drought. The largest declines in BNPP during drought were in the shallowest soil increments. Different letters indicate significant differences among treatments within a depth increment.

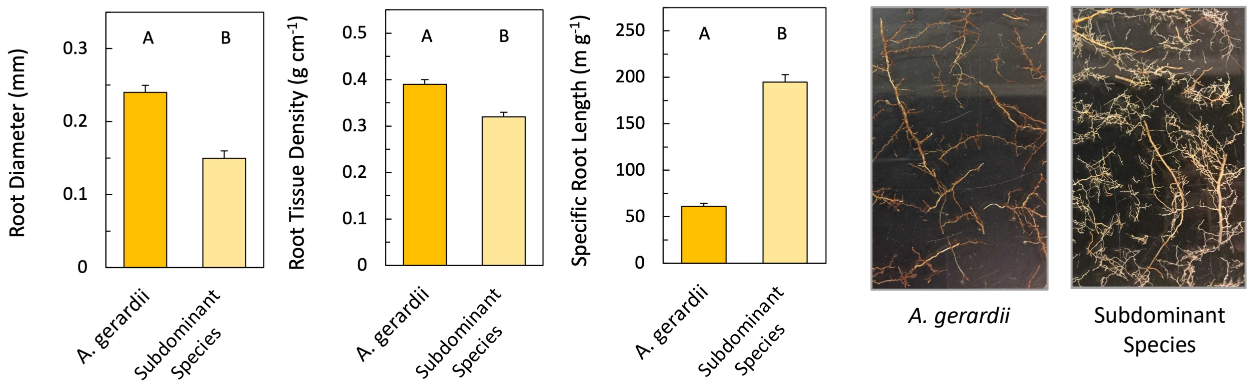

Figure A3.2: Left: Average (+ one standard error) root diameter, specific root length, and root tissue density of *A. gerardii* and of subdominant species. Values are averaged across treatments and years because there were no differences among treatments or between years. Compared to the rest of the species in the community (collectively), *A. gerardii* has a larger diameter, lower SRL and higher RTD. Different letters indicate significant differences between *A. gerardii* vs. the rest of the species in the community. Right: pictures of washed roots of *A. gerardii* and of subdominant species.

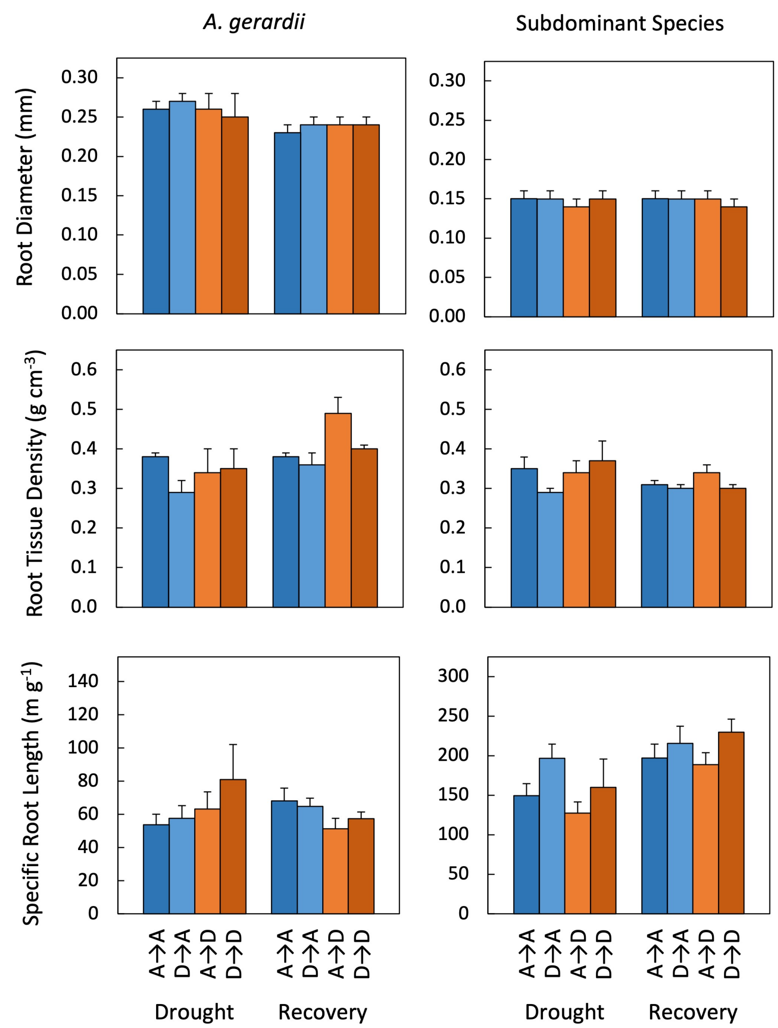

Figure A3.3: Average (+ one standard error) root diameter, root tissue density, and specific root length of *A. gerardii* and of subdominant species in all treatments during the last year of the second 2-year drought and during the first year after that drought. Root traits were overall quite stable. There were no significant effects of year or of treatment on any of these traits. SRL of the subdominant species did increase (non-significantly) during the second drought and after drought, altering the drought responses of BNPP vs. root length production.

Table A3.1: Average (one standard error) dependent variable values from each treatment during drought and after drought.

	During Drought (2015)				After Drought (2016)			
Variable	A→ A	D→ A	A→ D	D→ D	A→ A	D→ A	A→ D	D→ D
BNPP (g m^{-2})								
All species	287 (10)	226 (22)	209 (15)	106 (13)	370 (27)	319 (43)	325 (38)	321 (21)
A. gerardii	119 (25)	136 (22)	105 (20)	59 (11)	138 (34)	189 (21)	191 (47)	154 (28)
Subdominant species	159 (23)	90 (17)	104 (15)	47 (7)	231 (35)	156 (26)	134 (32)	172 (31)
Root length production (km m^{-2})								
All species	32.5 (3.8)	22.8 (2.7)	15.7 (0.8)	12.2 (1.9)	44.3 (1.9)	38.1 (3.8)	31.7 (3.7)	38.3 (3.1)
A. gerardii	8.33 (1.2)	8.11 (2.4)	3.19 (1.0)	5.42 (2.8)	7.48 (2.2)	12.0 (1.1)	10.0 (2.9)	8.82 (1.6)
Subdominant species	21.0 (1.4)	14.7 (2.4)	9.32 (1.1)	7.01 (0.9)	36.9 (3.9)	27.8 (3.7)	21.7 (3.4)	29.5 (3.2)