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Experimental droughts with rainout shelters: a methodological review

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Abstract. Forecast increases in the frequency, intensity, and duration of droughts with climate change may have extreme and extensive ecological consequences. There are currently hundreds of published, ongoing, and new drought experiments worldwide aimed to assess ecological sensitivity to drought and identify the mechanisms governing resistance and resilience. To date, the results from these experiments have varied widely, and thus, patterns of drought sensitivities and the underlying mechanisms have been difficult to discern. Here we examined 89 published drought experiments, along with their associated historical precipitation records to (1) identify where and how drought experiments have been imposed, (2) determine the extremity of drought treatments in the context of historical climate, and (3) assess the influence of ambient precipitation variability on the magnitude of drought experiments. In general, drought experiments were most common in water-limited ecosystems, such as grasslands, and were often short-term, as 80% were 1–4 yr in duration. When placed in a historical context, the majority of drought experiments imposed extreme drought, with 61% below the 5th, and 43% below the 1st percentile of the 50-yr annual precipitation distribution. We also determined that interannual precipitation variability had a large and potentially underappreciated effect on the magnitude of drought treatments due to the co-varying nature of control and drought precipitation inputs. Thus, detecting significant ecological effects in drought experiments is strongly influenced by the interaction between experimental drought magnitude, precipitation variability, and key ecological thresholds. The patterns that emerged from this study have important implications for the design and interpretation of drought experiments and also highlight critical gaps in our understanding of the ecological effects of drought.

Key words: drought sensitivity; experimental design; precipitation manipulation; rainout shelters; resilience; resistance.

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INTRODUCTION

Rising temperatures and changes in precipitation due to climate change are projected to increase the frequency, severity, and duration of droughts (Dai 2012, Trenberth 2012, IPCC 2013, Cook et al. 2015). Such alterations in water availability can have large and potentially long-lasting ecological consequences, depending on the extremity of the climatic conditions and the resistance and resilience of the ecosystem (Smith 2011, Hoover et al. 2014). Indeed, observed ecological responses to drought have included reductions in net primary productivity (Zscheischler et al. 2014, Knapp et al. 2015*a*) and species richness (Tilman and El Haddi 1992, Copeland et al. 2016), altered carbon cycling (Ciais et al. 2005, Reichstein and Ciais 2007), and in some cases, extensive mortality (Breshears et al. 2005). Changes in ecosystem structure and function that develop during drought can also have prolonged effects even after conditions improve (Weaver 1954, Haddad et al. 2002). Thus, understanding ecological responses to drought and identifying driving mechanisms is key to forecasting ecosystem dynamics in drying regions of the world.

Observations of the ecological responses to naturally occurring droughts have been complemented by a growing body of research that experimentally imposes droughts (Grime et al. 2008, Plaut et al. 2012, Reichmann et al. 2013). Over the past two decades, experimental droughts have become one of the leading methods to examine how reduced water availability affects ecosystem processes. Such experiments allow for greater control over factors that often co-occur with droughts (Déry and Wood 2005, Trenberth and Shea 2005, De Boeck and Verbeeck 2011) and thus have enhanced our mechanistic understanding of ecological responses to drought. Experimental droughts are most commonly imposed using passive rainout shelters that are placed over an intact community to exclude or reduce rainfall (Fig. 1), and are compared to a control treatment receiving ambient rainfall. The methodology of a rainout shelter was first developed in agricultural studies, which deployed large roofed structures over target plants during rainfall events (Horton 1962). Eventually, this method was adopted in

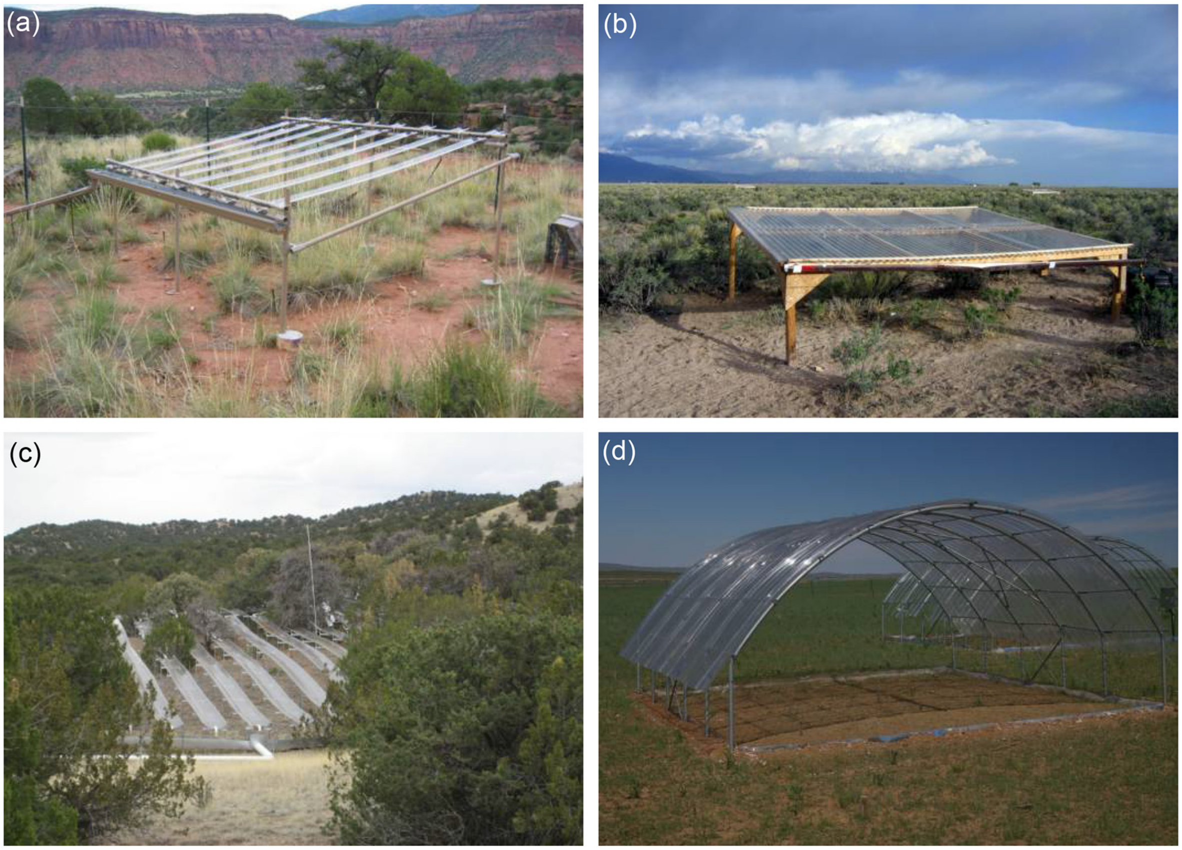

Fig. 1. Diversity in rainout shelter methods and scales. Two types of drought experiment shelters are shown here: (1) reduction shelters (a, c), where a fixed proportion of ambient rainfall (<100%) is intercepted and removed by clear gutters, and (2) exclusion shelters (b, d) where all ambient rainfall (100%) is intercepted and removed. Shelter scales range from small (a, b) to large (c, d). Shelter photographs: (a) Adam Kind, Colorado Plateau, Utah, USA; (b) Jules Kray, San Luis Valley, Colorado, USA; (c), Jennifer Plaut, Sevilleta National Wildlife Refuge, New Mexico, USA; and (d) Alan Knapp, Hohhot, China.

ecology in the late 1990s by Reynolds et al. (1999) in the form of a precipitation exclusion shelter, in which a clear, solid plastic roof removed 100% of ambient rainfall (Fig. 1b, d). In 2002, Yahdjian and Sala designed a rainout shelter capable of intercepting different amounts of rainfall, or a precipitation reduction shelter in which a shelter covered with strips of clear plastic gutters removed <100% of ambient rainfall (Fig. 1a, c). These methods have been applied in hundreds of published, ongoing, and new drought experiments in a wide range of ecosystems globally (Fig. 1; Beier et al. 2012).

Despite the abundance of drought experiments in the literature, and the relative simplicity of the method, ecological responses have been highly variable, and thus, patterns and mechanisms of drought sensitivities across ecosystems have been difficult to discern (Wu et al. 2011, Zhou et al. 2016, Smith et al. 2017, Wilcox et al. 2017). For example, within the ecoregion of the U.S. Great Plains, a 50% reduction in ambient rainfall had different treatment effects on aboveground net primary production (ANPP) across six different experimental sites, despite using the same drought treatment magnitude (Cherwin and Knapp 2012, Byrne et al. 2013, Koerner and Collins 2014). Divergent responses within ecoregions may be attributed to local site-level differences, such as soil properties or plant community composition. For example, differing nitrogen availabilities across ecosystems may alter responses to changes in precipitation through co-limitation (Burke et al. 1997). Additionally, differences in ANPP responses to precipitation can be driven by differences in plant community composition (Smith et al. 2009, Wilcox et al. 2015, 2016). Another complicating factor in drought experiments is the variation in the amount of precipitation that is reduced across experiments (Zhou et al. 2016). However, even when the amount of rainfall alteration is accounted for, there can still be significant variation in patterns of ecosystem responses (Wu et al. 2011, Smith et al. 2017, Wilcox et al. 2017).

A key question that emerges is: Does the variability in ecological responses to drought represent fundamental differences in drought sensitivities across ecosystems, or does it reflect the magnitude of the drought treatment imposed? In this study, we address the latter part of the question by focusing on how control and drought treatments are affected by the interaction between experimental drought magnitude (i.e., percent precipitation reduction) and variability in ambient precipitation amount. Since the drought treatment is a fixed percentage of the control, the fundamental design of passive rainout shelters results in co-varying control and drought treatments, and thus, the experimental drought magnitude alone does determine treatment precipitation inputs. For example, control and drought treatments will receive different precipitation amounts depending on ambient precipitation in a given year; a 50% reduction will yield very different precipitation amounts in a wet vs. a dry year (Knapp et al. 2017*a*). Another layer of complexity involved in drought experiments is whether the water availability in control and drought treatments span key ecological thresholds. Large ecological responses are predicted to occur when dominant species or key plant functional types cross critical thresholds, leading to reduced growth or even mortality (Smith 2011, Kardol et al. 2012, Hoover et al. 2014). However, due to the co-varying nature of control and drought treatments, the magnitude of the ecological responses will depend largely on whether the treatments span such thresholds.

Here we review the methodologies of experimental droughts with rainout shelters using 89 published studies and their associated long-term precipitation records. We address three main objectives. First, we surveyed the literature to assess where and how experimental droughts have been imposed and to identify potential methodological gaps. Second, we determined the extremity of the experimental drought treatments using historical precipitation records. Third, we assessed the influence of interannual precipitation variability on drought experiments. Overall, the results of this study will aid in interpreting and designing drought experiments, with implications for our understanding of the ecological responses to predicted future climates.

METHODS

Literature search and study database

The literature search was conducted on papers published prior to February 2016 through the Web of Science (see Appendix S1: Table S1 for keywords and search results). A total of 566 papers were selected based on our search terms, screened by abstract, and were retained if they contained references to drought experiments. Of them, 173 papers were selected as potentially suitable, which were then filtered down to 109 papers based on the following criteria: (1) The study was conducted in a native plant community, and (2) the experiment consisted of a drought treatment where ambient precipitation was reduced or excluded and compared to a control receiving ambient precipitation. Given that some drought experiments had multiple papers or levels of drought treatments, we developed a criterion to define an independent drought experiment and then treated it as the experimental unit for analyses. First, experiments with multiple papers were identified by experimental names and/or locations, and the most recent paper was used in the study. Second, if a paper had multiple sites, each site was treated as an independent experiment. Third, if a study had multiple levels of experimental drought magnitude (e.g., 25% and 50% reductions), each level of drought was treated as an independent drought experiment, even if they shared a common control. Using this criterion, there were a total of 89 drought experiments for this analysis (Appendix S1: Table S2). For each experiment, the following information was entered into a database: latitude and longitude, mean annual precipitation (MAP) and mean annual temperature (MAT), ecosystem type, experimental drought magnitude, experiment duration (length of study), and timing of the drought treatment.

Climate data

One of the main goals of this study was to place experimental droughts into the context of historical droughts. To do this, we obtained daily long-term precipitation records from the Global Historical Climatology Network (https://www.ncdc.noaa.gov/ghcn-daily-description), which is a large database (75,000 stations) of daily climate summaries from around the world. Site-based daily precipitation records were selected for each drought experiment using the following criteria: (1) It was the nearest weather station within 100 km, (2) it spanned a common 50-yr period (1960–2010) with the other precipitation records, and (3) the missing daily precipitation values comprised <10% of the total number of days in a given year and <10% of years missing (45 out of 50 yr). Based on these criteria, 53 out of the 89 experiments (~60%) had an associated climate record (n = 36 stations, since some weather stations were associated with multiple drought experiments). To evaluate potential topographical mismatches between weather stations and drought experiments, we examined elevation differences for each pair with a 1 arc second (~30 m) near-global digital elevation model derived from the NASA Shuttle Radar Topography Mission (Farr et al. 2007), using Google Earth Engine (Gorelick et al. 2017). Based on this analysis, we believed there were no major topographical mismatches between weather stations and drought experiment sites (mean elevation difference = 213 m; standard deviation = 330 m; maximum difference = 1297 m), and retained all pairs in the analysis.

Each daily climate record was assessed for normality using the Shapiro–Wilk test, and those stations not fitting a normal or lognormal distribution were removed. Means, standard deviations, and probability distributions were then calculated for each station. For each experiment and year (n = 186 total experiment years), the timing of the drought treatments was determined from the dates contained in each manuscript and the annual precipitation for the control and drought treatments was calculated as follows:

1. Control treatment annual precipitation = PPT

2. Drought treatment annual precipitation $= \mathrm{PPT}_{\mathrm{ND}} + (\mathrm{PPT}_{\mathrm{D}} \times \mathrm{RED\%})$

where PPT = ambient precipitation; $\mathrm{PPT}_{\mathrm{ND}}$ = ambient precipitation during the non-drought period; $\mathrm{PPT}_{\mathrm{D}}$ = ambient precipitation during the drought period; and RED% = the percent reduction of the drought treatment.

In order to quantify the historical drought magnitude, we calculated the percentiles of annual precipitation of each experiment and year based on the probability distribution from the 50-yr historical record. This approach is consistent with the focus on manipulating precipitation inputs in drought experiments, and the World Meteorological Organization’s (2006) definition of a meteorological drought as a “precipitation deficiency threshold over a predetermined period of time.” Therefore, we are defining extreme drought as an annual precipitation total below the 5th percentile of historical precipitation, or a 1-in-20 yr event. While we recognize the limitation of focusing solely on precipitation inputs, given the lack of other common metrics across drought experiments (e.g., soil water potential; Vicca et al. 2012), we believe this is a justified approach. Furthermore, it is important to note that drought conditions can develop due to factors other than precipitation deficits, such as increased temperatures, altered precipitation patterns, and human modifications of hydrological processes (Dai 2012, Trenberth et al. 2014, Knapp et al. 2015*b*, Crausbay et al. 2017).

Drought experiment simulation

Given the short duration of most published drought experiments, our comparisons between control and drought treatments consisted of precipitation data from many sites with a limited number of years and thus lacked broad temporal resolution. In order to fully examine the influence of interannual variability on the relationship between control and drought treatments at the site level, we conducted a simulation using long-term precipitation data from three sites in this study. The sites spanned a range in MAP and ecosystem type and consisted of: Jornada, New Mexico, USA (grassland, MAP = 240 mm), GLOWA, Israel (shrubland, MAP = 540 mm) and Walker Branch, Tennessee, USA (forest, MAP = 1353 mm). In this simulation, we used the natural interannual variability in precipitation across the 50-yr climate records at each site to impose simulated experimental droughts of varying historical drought magnitude. For each year in the 50-yr climate record, we calculated the annual precipitation percentiles for a control and 20%, 50%, and 80% reductions, representing the broad range of experimental drought magnitude in published experiments (Fig. 3a). This allowed us to compare the co-varying relationship between control and drought treatments across a wider range of annual precipitation and experimental drought magnitude.

RESULTS

Location of drought experiments

Of the 89 published drought experiments, the vast majority were located in North America ($n = 43$) and Europe ($n = 33$), with a few in Africa ($n = 7$), South America ($n = 4$), and Asia ($n = 2$; Fig. 2a). Grasslands were the dominant ecosystem for drought experiments, occurring in 52.6% of the studies, while shrubs (25.8%), forests (17.5%), and other (4.1%) comprised the remainder (Fig. 2b). Climatically, all of the experiments were conducted in areas where MAT was greater than freezing (MAT ranged ~0–25°C) and 82% had MAP <1000 mm/yr (Fig. 2c).

Magnitude and duration of drought experiments

There were four types of drought experiments based on the percent precipitation reduction (exclusion or reduction) and intra-annual drought duration (annual or seasonal) including: 3 annual exclusions, 31 seasonal exclusions, 24 annual reductions, and 31 seasonal reductions. In terms of experimental drought magnitude, there was a fairly wide range in the percent of rainfall excluded (10–100%, Fig. 3a), with the 50% being the most common type of reduction experiment (Fig. 3a). On average, seasonal reductions were imposed for a longer duration within a year than seasonal exclusions (188 ± 62 vs. 113 ± 39 d, respectively), though there was substantial variability. While the total duration of experiments ranged from 1 to 15 yr, there was a strong tendency toward short-term experiments, with 55% only 1–2 yr long and 80% were 1–4 yr long (Fig. 3b).

Experimental droughts vs. historical climate

For each experiment and year, we determined the precipitation inputs for the control and drought treatments and compared them to nearby historical precipitation records. Across all the experiment years, control treatments received a fairly wide and variable distribution of rainfall (Fig. 4a), which was expected given that the control treatments represent a random sampling of annual ambient precipitation for 189 yr across the world. On the other hand, the drought treatments were heavily skewed toward the extreme end; 61% of the experiment years were below the 5th percentile (Fig. 4b) and 43% were below the 1st percentile (Fig. 4b inset).

Experimental drought simulations

In order to examine the role of interannual precipitation variability on drought experiments with a greater temporal resolution, we ran a series of drought simulations at three sites (grassland, shrubland, and forest) under three different

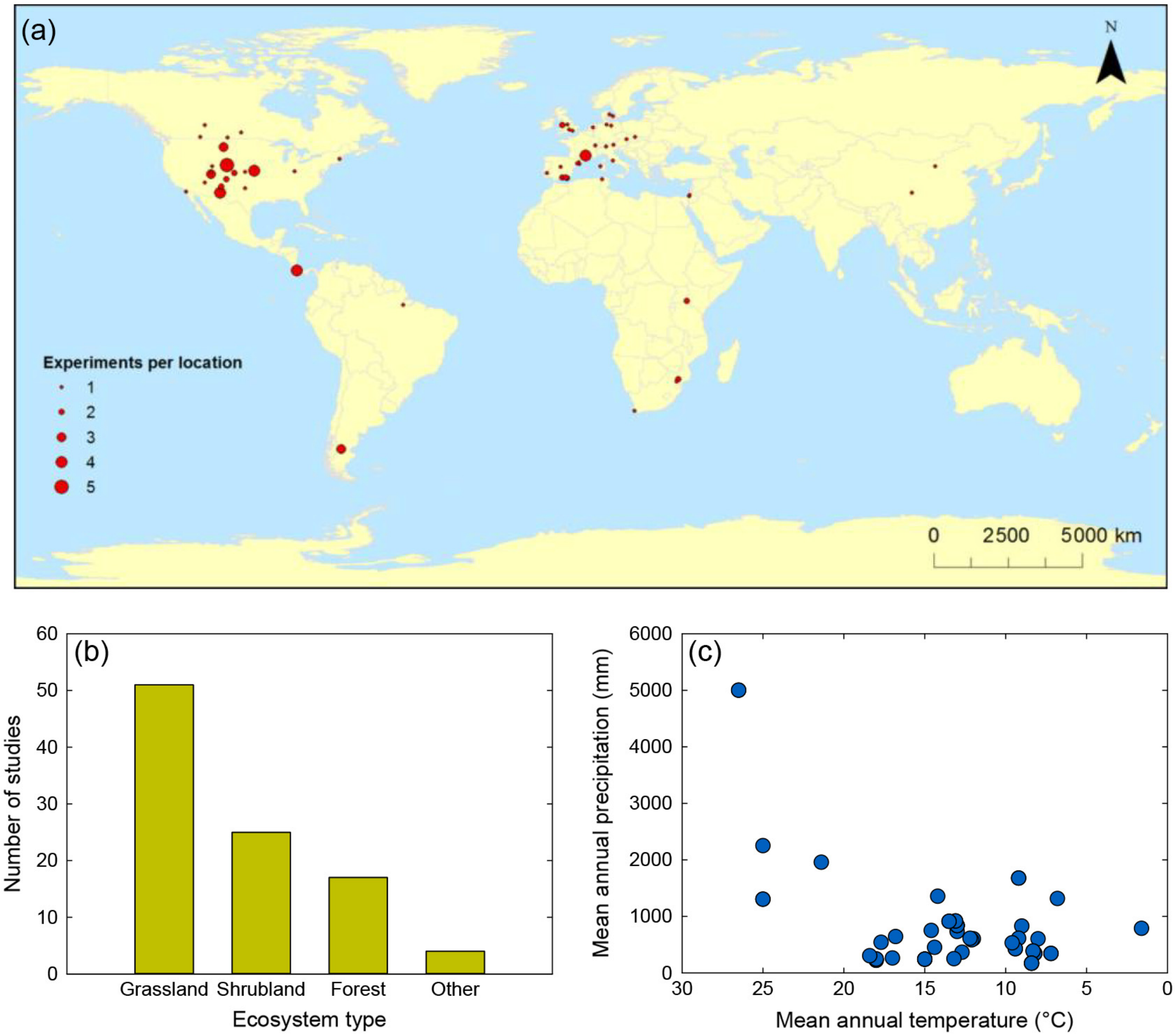

Fig. 2. Geographical and ecological distribution of drought experiments. (a) Global distribution of drought experiments with each point representing a study location and the size of the point representing the number of experiments per location. Experiments with multiple publications were only counted once, but those with more than one level of precipitation reduction were counted for each level of precipitation reduction. (b) The frequency of ecosystem types described for all drought experiments, including all ecosystems described. (c) Mean annual temperature vs. mean annual precipitation for each experiment when both data were reported in the methods.

experimental drought magnitudes (20%, 50%, and 80% annual reductions) over 50 yr (Fig. 5). There were three key results. First, and unsurprisingly, experimental drought magnitude had a large effect on the extremity of the drought treatment. The difference between control and drought treatments increased with increasing ambient (control) precipitation. More notably, across the three sites, the majority of years for the 20% reduction were not extreme, while almost all years for the 80% reduction were extreme (Fig. 5). Second, in the 25% and 50% reductions, the divergence between control and drought treatments increased with MAP (Fig. 5). Finally, we emphasized the effect of interannual variability on short-term drought experiments by highlighting three years at each site (2008–2010; filled symbols in Fig. 5), as if experimental droughts were being imposed at the three sites at the same time. This resulted in three contrasting precipitation regimes

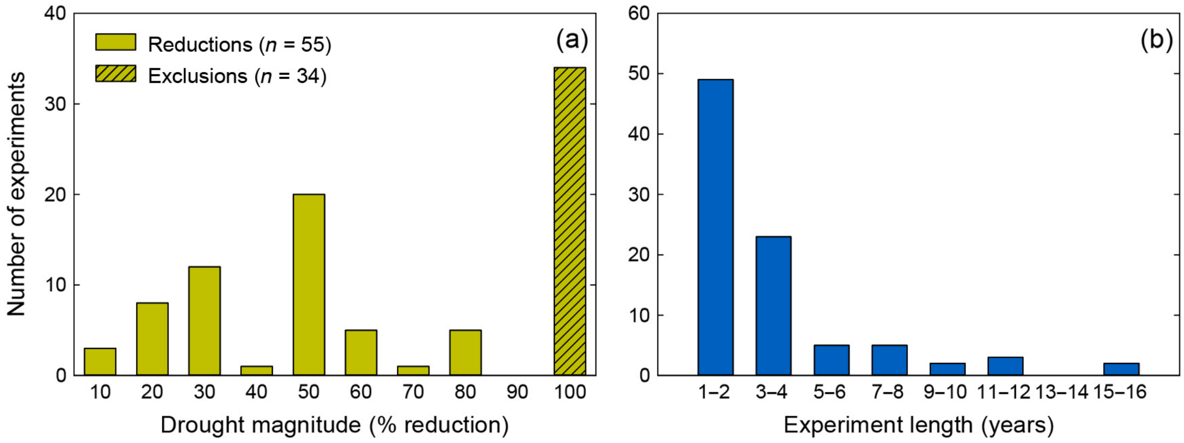

Fig. 3. Drought experiment magnitude and duration. (a) Distribution of drought magnitude (percent reduction from ambient precipitation) across the different experiments. (b) Distribution of experiment lengths across the different experiments. For experiments with multiple publications per experiment, only the most recent publication was used to determine experiment length.

across the different sites for these simulated drought experiments. The grassland site had two dry and one wet year, the shrubland site had three dry years, and the forest site had one near average and two wet years (Fig. 5). As a result of this variability in ambient precipitation, these systems experienced varying levels of precipitation inputs in the context of historical precipitation. For example, during the driest year in the grassland, the control's annual precipitation was in the 20th percentile, while the 20%, 50%, and 80% reductions were in the, 11th, 3rd, and 1st, respectively (Fig. 5a). Contrast those values with the wettest year, when the control's annual precipitation was

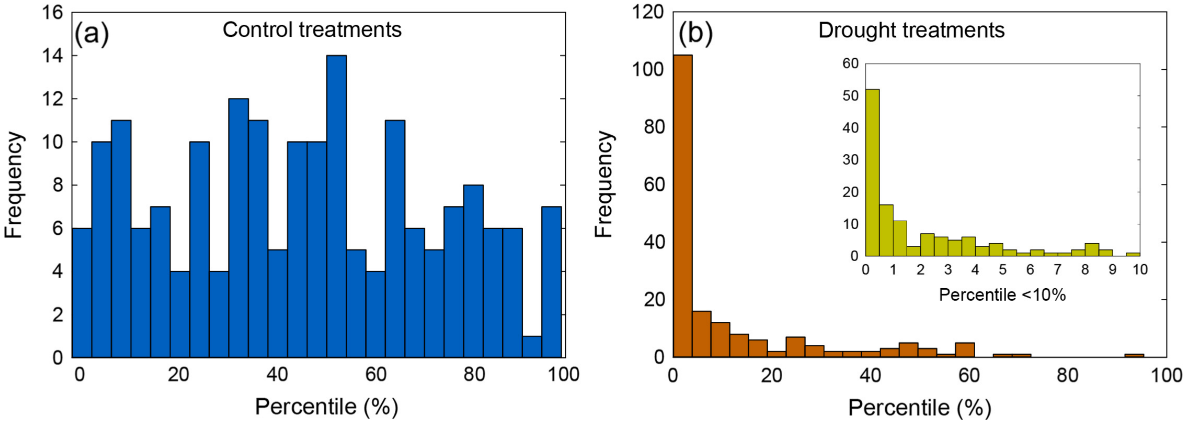

Fig. 4. Historical perspective of control and drought treatments across many different drought experiments (n = 54 experiments) and years (186 experiment years). Precipitation records were obtained, and probability distributions were calculated for experiments within 100 km of a long-term weather station (50-yr records obtained from the Global Historical Climatology Network). For each experiment and year, we determined the precipitation inputs for control treatments (equal to ambient) and drought treatments (based on the percent reduction and shelter timing). These inputs were compared to the historical probability distribution to calculate the percentile for each experiment, year, and treatment. (a) Frequency distribution for experimental control treatments. (b) Frequency distribution for experimental drought treatments, with the inset graph highlighting the distribution of droughts experimental inputs below the 10th percentile.

in the 77th percentile, while the 20%, 50%, and 80% reductions were in the 51st, 14th, and 2nd percentile, respectively (Fig. 5a). Therefore, the differences between the control and drought treatments, when placed in a historical context, varied drastically, depending on the ambient precipitation for that year.

DISCUSSION

In this study, we used the available literature to identify where and how drought experiments have been imposed and then used long-term precipitation records to determine the extremity of the drought treatments and evaluated the influence of precipitation variability on control and drought treatments. There were several clear methodological trends in the location, duration, and magnitude of the experimental droughts, which may limit our understanding of drought sensitivities across different ecosystems and drought scenarios. When placed in a context of historical precipitation, the majority of experimental droughts were extreme, but interannual precipitation variability had a large impact on the drought treatment relative to the control treatment.

Methodological gaps in drought experiments

In the literature review, we found drought experiments were dominated by short-term, extreme droughts imposed over short-statured vegetation in water-limited ecosystems. Similar trends were found in a review on all types of precipitation manipulation experiments by Beier et al. (2012); we propose these trends exist for several reasons. First, funding and time constraints often limit the duration and scale of experimental droughts. It is much easier and cheaper to install

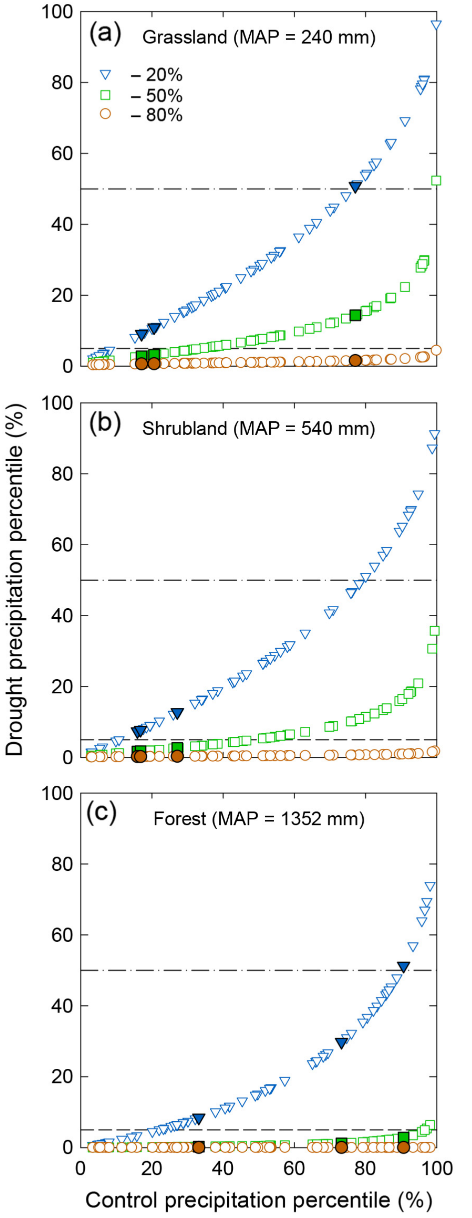

Fig. 5. Simulated precipitation inputs for experimental droughts at different magnitudes and across three ecosystem types (a–c) that also vary in mean annual precipitation (MAP). For each site, we obtained a 50-yr historical precipitation record (from the Global Historical Climatology Network) and simulated precipitation reductions of 20%, 50%, and 80%. For each year, the percentiles for control and drought treatment amounts were calculated based on the historic probability distribution. For example, in 1968 at the grassland site, the control treatment received an average year (~50th percentile), while the 20%, 50%, and 80%

(Fig. 5. *Continued*)

reductions received precipitation equivalent to the 29th, 8th, and 1st percentiles, respectively. Dotted and dashed lines indicate average precipitation (50th percentile) and extreme drought (5th percentile) for the drought treatment, respectively. To emphasize the effect of interannual variability on short-term experiments, we highlighted three common years for each site (2008–2010, filled), resulting in three contrasting precipitation regimes across the different sites. For example, in the shrubland, all three years were below average precipitation, while the grassland and forest varied.

a 2 × 2 m rainout shelter over a grassland for two years than a 50 × 50 m throughfall experiment in a forest for a decade. Second, the tendency toward more extreme historical drought magnitude may be a result of researchers hoping to test the limits of resistance and resilience of their focal ecosystems, or an unanticipated interaction between the experimental drought magnitude and interannual variability in precipitation. Finally, ecologists tend to focus on the resource or process that is most limiting in their ecosystem (Tilman 1982), hence a trend toward water-limited ecosystems in drought experiments.

While geographical gaps may limit our abilities to detect patterns of drought sensitivities across different ecosystems, the tendency toward imposing short-term extreme droughts results in a critical lack of information on the effects of prolonged water stress on ecosystems. This is unfortunate for two reasons. First, in addition to short-term extreme pulse-droughts, climate change is predicted to cause chronic water shortages or long-term press-droughts due to increased evaporative demand with elevated temperature (IPCC 2013, Trenberth et al. 2014, Hoover and Rogers 2016). Second, the mechanisms governing drought resistance may respond differently depending on the duration of the drought. Chronic changes in resources can lead to non-linear responses including species reordering and immigration (Smith et al. 2009); mechanisms that may not be observed in short-term droughts. Therefore, by emphasizing short-term over long-term droughts in these experiments, our understanding of drought sensitivity remains incomplete.

Effects of interannual precipitation variability on drought experiments

The results from this study suggest that interannual precipitation variability has a large and potentially underappreciated influence on drought experiments. The simulations in this study showed that in most years, removing 50% or 80% of ambient precipitation will result in an extreme historical drought. But while many experimental droughts were extreme in the context of historical droughts, the ecological responses have varied dramatically, as has been shown by previous meta-analyses of precipitation experiments. For example, Wu et al. (2011) found substantial variation of ANPP responses to drought treatments across 10 studies, even when standardizing the responses by the magnitude of the precipitation reduction through calculations of sensitivity (i.e., the amount of ANPP that is reduced for each mm of precipitation reduced). They found 95% confidence intervals of sensitivity values spanned from 0.04 to 0.33 $\text{g}\cdot\text{m}^{-2}\cdot[\text{mm precipitation}]^{-1}$ across studies and were unable to relate sensitivity with any site-level attribute, such MAP and MAT. Similarly, Wilcox et al. (2017) examined 39 studies that assessed primary production responses to drought treatments, and found the sensitivity of ANPP to drought varied from -0.95 (meaning productivity increased under drought) to 1.1 $\text{g}\cdot\text{m}^{-2}\cdot[\text{mm precipitation}]^{-1}$ with no relationships between sensitivity and MAP or MAT. The question then arises: Do these ambiguous responses to drought reflect varying levels of drought resistance among different ecosystems, or is it an artifact of the experimental method and/or interpretation?

We hypothesize that such inconsistent ecological sensitivities among drought experiments are in part due to the co-varying nature of the control and drought treatments. As seen in the simulation (Fig. 5), the relationship between control and drought treatments is non-linear. During wet years, the difference in absolute precipitation amounts and precipitation percentiles is greater than in dry years (Fig. 5). Thus, while the imposed reduction is consistent (e.g., 50% reduction), the relationship between precipitation in control and drought treatments varies with interannual precipitation amounts. Another important factor to consider is how experimental drought magnitude interacts with interannual variability in precipitation. For example, in the simulation, the relationship between control and drought treatments is flat in an 80% precipitation reduction, but curvilinear in a 20% precipitation reduction, with the greatest variability occurring during wetter years (Fig. 5). This suggests that lower experimental drought magnitude may experience greater variability in the differences between precipitation inputs in control and drought treatments than higher experimental drought magnitudes.

While much of this analysis has focused on the influence of variation in precipitation inputs on ecological responses, it is also important to also consider how the ecological responses themselves may further complicate interpreting the results from drought experiments. The ecological response to an extreme event, such as drought, is predicted to be greatest if it pushes organisms past key thresholds (Smith 2011, Kardol et al. 2012, van de Pol et al. 2017), and many relationships between and environmental driver and an ecological response are non-linear (e.g., precipitation and ANPP—Hsu et al. 2012, Zhou et al. 2016, Knapp et al. 2017*b*, soil respiration and temperature—Lloyd and Taylor 1994).

Here we present a conceptual model to demonstrate how the relationship between ambient precipitation variability and ecological function may influence the treatment effects of drought experiments (Fig. 6). For each level of ambient precipitation (dry, normal, and wet years), we show the precipitation inputs for the control and drought treatments, as well as the response of and treatment differences in ecological function. Based on this model, it is clear that treatment differences can vary widely depending on ambient precipitation amounts and the nature of the relationship between precipitation and ecological function. There are two factors driving this variability. First, the absolute difference in precipitation inputs between control and drought treatments is larger in wet years than dry years (Fig. 6). Therefore, if the relationship between precipitation inputs and ecological function is linear (Fig. 6a, b), treatment differences will be greatest in wetter years due to the high absolute difference in precipitation inputs. Second, under non-linear relationships, the greatest treatment difference will occur when control and drought precipitation inputs span a critical ecological threshold, and smallest when they are both above or below such a threshold. For example, the sigmoidal relationship (Fig. 6e, f) has the greatest treatment difference under average precipitation, and very little effect under wet and dry conditions because both control and drought treatments are above or below critical thresholds. Therefore, we believe that some of the unexplained variation among drought experiments may be driven by the interaction between variability in precipitation and the relationship between precipitation and a given ecological function.

SUMMARY AND RECOMMENDATIONS

Over the past two decades, drought experiments have provided key insights into how various ecosystems respond to drought and the mechanisms governing those responses. Here, our analyses suggest that gaps in the location, duration, and magnitude of experimental droughts, as well as the influence of precipitation variability, may lead to highly variable results across studies; thus, patterns and mechanisms of drought sensitivities have been difficult to discern. Based on the results of this study, we provide five recommendations for the design and interpretation of drought experiments.

1. In echoing recommendations from past studies (Wu et al. 2011, Beier et al. 2012), new experiments should aim to broaden the geographic and ecological extent of drought experiments to advance our understanding of how drought sensitivity varies across ecosystems. In addition to expanding traditional site-based experiments, coordinated distributed networks (Fraser et al. 2013) can help to improve our understanding how and why ecosystems differ in their sensitivity to droughts at regional and global scales.
2. Greater variety is needed in the combinations of drought duration and experimental drought magnitude of new and existing experiments. As we have shown, there is an abundance of short-term, extreme droughts in the literature, yet detailed understanding of the effects of drought duration and experimental drought magnitude is needed to fully assess the impacts of the multitude of predicted drought scenarios (IPCC 2013). For example, imposing low-magnitude, long-term drought (e.g., a 20% precipitation reduction over 10 yr) could simulate chronic water shortages due to increase evaporative demand with warming and/or reductions in MAP (IPCC 2013, Trenberth et al. 2014). Furthermore, the likelihood of multi-decade megadroughts is predicted to increase with climate change (Woodhouse and Overpeck 1998, Cook et al. 2015). Such events have never been observed in the instrumental record or imposed experimentally (e.g., a 75% reduction 10–20 yr), yet have the potential to transform ecosystems and even civilizations (Hoggarth et al. 2016).
3. Researchers designing new drought experiments should carefully consider local precipitation variability when selecting the experimental drought magnitude and duration

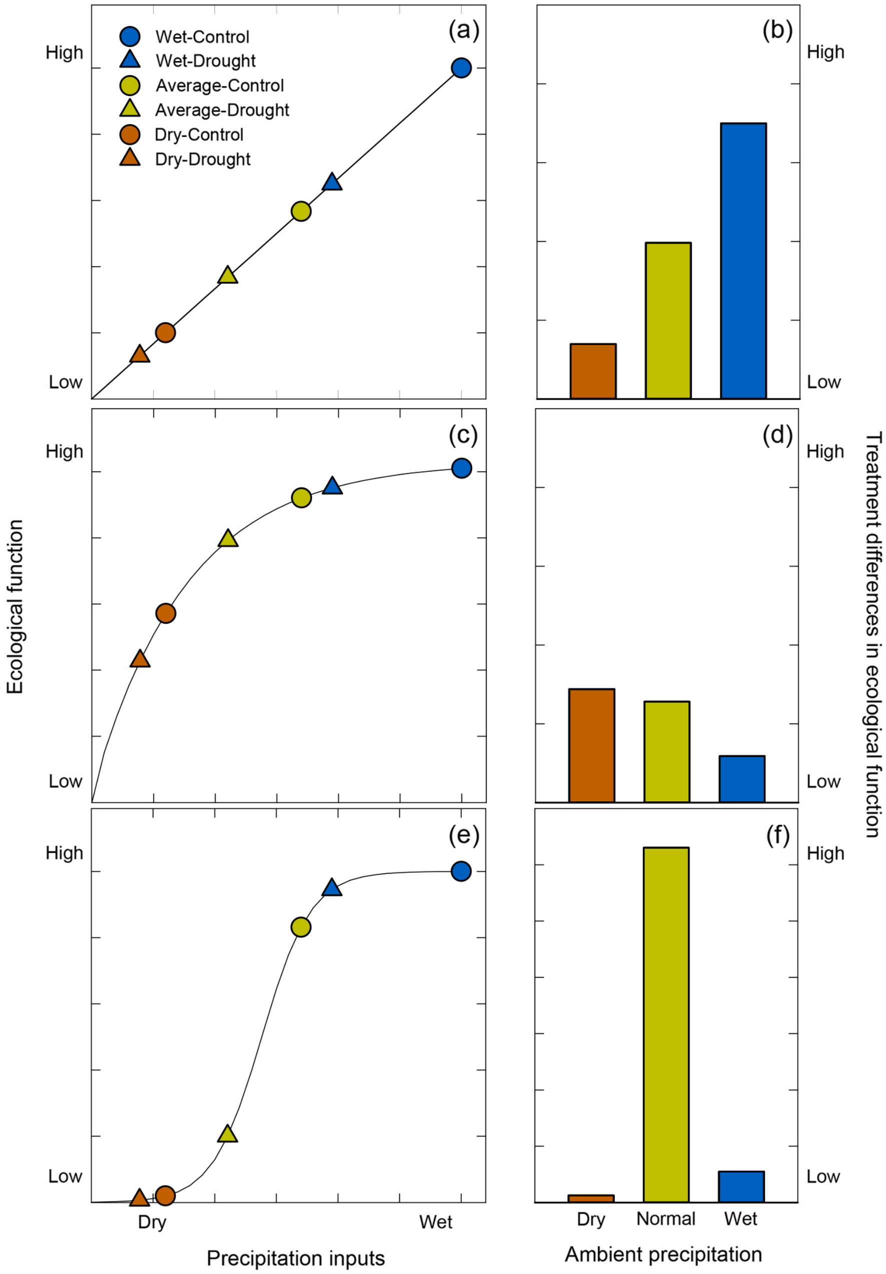

Fig. 6. A conceptual model depicting the interaction between ambient precipitation variability and key ecological thresholds on potential treatment effects on ecological function. We selected three relationship types: linear (a), threshold (c), and sigmoidal (e), between a given ecological function (e.g., leaf water potential, photosynthesis, soil respiration, productivity) and precipitation inputs. The symbols overlaying these relationships represent the precipitation inputs for control and drought treatments for a given annual ambient precipitation regime. Variation in treatment differences, shown here as the absolute difference in ecological function (b, d, and f), across the three theoretical relationships and ambient precipitation. This conceptual figure highlights the potential variation in experimental drought treatment effects that may arise due to: (1) the co-varying nature of the control and drought treatments, (2) the influence of interannual precipitation variability, and (3) different relationships between precipitation and ecosystem function that may exist across ecosystems or levels biological organization.

of the experimental treatments. Simulating treatment scenarios from local historical precipitation records (Fig. 5) or analyzing precipitation using software packages (e.g., Terrestrial Precipitation Analysis; Lemoine et al. 2016) will allow researchers to select treatments that will likely achieve desired drought scenarios, given local interannual variability in precipitation. In addition, certain types of drought (e.g., pulse vs. press drought) may be more prevalent in certain regions, and within a region, the magnitude of extreme events may continue to shift under climate change (Christidis et al. 2015, Stott et al. 2016). Therefore, researchers should consider predicted future hydrological regimes to guide which combinations of experimental drought magnitude and duration.

4. Drought experiments should be designed to buffer against the co-varying nature of control and drought treatments by including multiple levels of experimental drought magnitude and/or water additions. For example, instead of one or two levels of drought and a typical ANOVA approach, researchers can utilize a regression/gradient approach with few replicates but multiple levels of drought treatments to examine response surfaces and better identify key drought thresholds (Kreyling et al. 2014). Also, supplementing control plots with water during dry years (Hoover et al. 2014) or including water addition treatment (Gherardi and Sala 2015) may help buffer drought experiments from naturally dry years.
5. When interpreting results from experimental droughts, researchers should carefully consider the interaction between experimental drought magnitude, ambient precipitation variability, and key ecological thresholds. It is critically important that a lack of treatment effect is not misinterpreted as high drought resistance (Fig. 6), rather than a potential experimental artifact due to the co-varying nature of control and drought treatments. Knowing the connection between precipitation, soil moisture, and physiological thresholds of key or dominant species in a given ecosystem or region is essential in avoiding such pitfalls.

We hope that the results from this study and our recommendations will provide guidance in the design and interpretation of drought experiments and lead toward a better understanding of ecological sensitivity to drought.

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