PLANT ECOLOGY

Drought intensity and duration interact to magnify losses in primary productivity

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As droughts become longer and more intense, impacts on terrestrial primary productivity are expected to increase progressively. Yet, some ecosystems appear to acclimate to multiyear drought, with constant or diminishing reductions in productivity as drought duration increases. We quantified the combined effects of drought duration and intensity on aboveground productivity in 74 grasslands and shrublands distributed globally. Ecosystem acclimation with multiyear drought was observed overall, except when droughts were extreme (i.e., ≤1-in-100-year likelihood of occurrence). Productivity losses after four consecutive years of extreme drought increased by ~2.5-fold compared with those of the first year. These results portend a foundational shift in ecosystem behavior if drought duration and intensity increase, from maintenance of reduced functioning over time to progressive and profound losses of productivity when droughts are extreme.

Drought, defined meteorologically as "a prolonged absence or marked deficiency of precipitation" (*1*), is a frequent and impactful disturbance in many terrestrial ecosystems globally. Although most droughts are short term and moderate in intensity (*2*), the most damaging and costly droughts from the perspective of ecological, societal, and economic impacts are both prolonged, unfolding over multiple years, and extreme with respect to long-term variation in climate conditions [e.g., (*3,4*)]. Although such drought events have historically occurred infrequently and, in some places, are absent from the recent historical record (*2*, *5*), there is evidence that longer-duration, intensified droughts are becoming more common (*6*, *7*) and will further increase in magnitude and frequency with global climate change (*5*, *8*, *9*). Yet, the impacts of multiyear, extreme droughts remain understudied, and past research is equivocal for how long-term droughts impact terrestrial ecosystems (*2*).

Theory predicts that as drought duration increases, the impacts of drought on ecosystem functioning (e.g., primary production) should accumulate or be magnified over time, resulting in more substantial losses in functioning, even for ecosystems that appear resistant to short-term drought (*2*, *10*). Several past studies report this expected cumulative pattern of response: a progressively more negative effect of drought on ecosystem functioning as duration increases (*11*, *12*). However, others find little evidence that increasing drought duration reduces functioning beyond that of a single-year drought [e.g., (*13*–*15*)]. Indeed, some research suggests that ecosystem function can "acclimate" or stabilize in response to multiyear drought [i.e., ecosystem acclimation; (*16*)], characterized by the impacts of drought remaining relatively constant or even diminishing over time (*11*, *16*–*19*). These variable responses to drought duration may result from differences in the magnitude (or intensity) of drought imposed. Indeed, drought duration and intensity are expected to interact in important ways (*2*, *10*). Droughts that are both prolonged and extreme are more likely to result in large impacts on ecosystem functioning (*10*, *20*, *21*). By contrast, short-term drought or prolonged moderate drought may result in lesser impacts on ecosystem functioning than extreme drought (*10*, *13*, *15*). Thus, to fully understand patterns of ecosystem response to drought duration, we need to also assess its interaction with drought intensity.

Our goals for this study were to 1) determine if prolonged drought results in a pattern of ecosystem response consistent with ecosystem acclimation (constant or lessening over time) vs. progressive losses (continuous decline over time), 2) quantify losses of ecosystem function attributable to each pattern, and 3) assess whether these patterns of loss change with the magnitude of drought imposed. We achieved these goals with results from the International Drought Experiment (IDE), a multiyear global-scale study of drought effects on aboveground net primary productivity (hereafter referred to as "productivity"), a key measure of ecosystem functioning and a major component of the terrestrial carbon cycle (*22*).

The International Drought Experiment

The International Drought Experiment (IDE) is a coordinated drought experiment established in grassland and shrubland ecosystems across the globe [Fig. 1A and table S1; (*23*)]. These ecosystems cover ~40% of Earth's land surface, provide crucial ecosystem services [e.g., food, forage, fiber (*24*, *25*)], and their productivity is among the most responsive to

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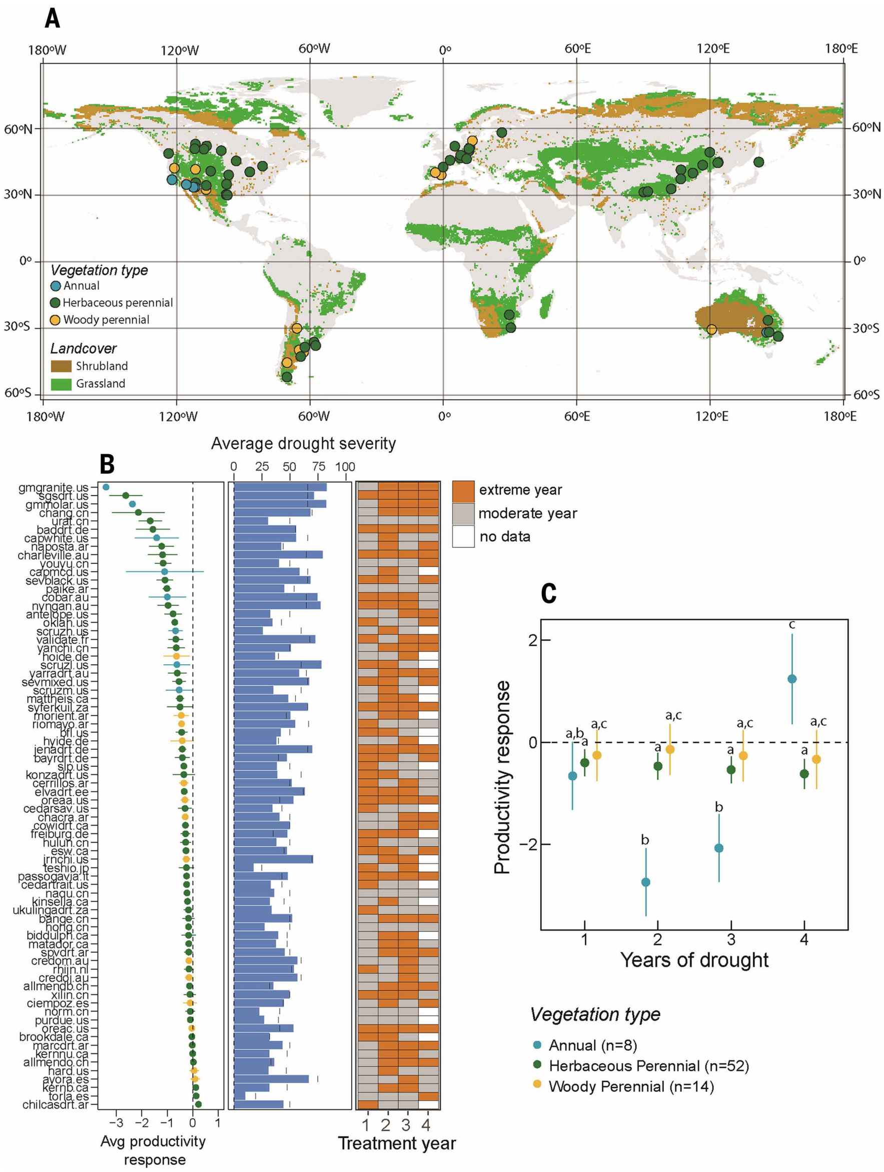

Fig. 1. Overview of the IDE: geographic locations, drought treatments, and effects on aboveground productivity. (**A**) Locations of the 74 IDE sites included in this study and their distribution across six continents (site names are given in table S1). Background shading denotes Moderated Resolution Imaging Spectroradiometer–derived landcover types (*50*), and the colors of the points denote the vegetation type of each site: annual, herbaceous perennial, or woody perennial (*23*). (**B**) (Left) IDE sites ordered by the average productivity response to drought over the 3- to 4-year duration of the experiment. Error bars represent the standard error for each site. (Middle) The average drought severity [defined as (MAP – precipitation received by drought treatment plots)/MAP; (*23*)] experienced over the duration of the experiment (blue bars). The expected average drought severity for the target 1-in-100–year drought treatment is indicated by the vertical black line. Overall, 53% of sites experienced an average precipitation reduction equivalent to the level expected with the target 1-in-100–year extreme drought treatment over the duration of the experiment. (Right) The temporal sequence of extreme (orange) versus moderate (gray) drought years imposed at each site. Note that 21 sites imposed only 3 years of drought treatment, and, therefore, the designation for the fourth year of treatment is left empty (white). (**C**) Average productivity response to drought (moderate and extreme combined) over time for three vegetation types. Productivity response was calculated as the natural log of the ratio of productivity during drought to long-term mean productivity (*23*). For example, a productivity response of –1 equates to a change in productivity due to drought of about 63% of the long-term mean. Error bars represent standard error, and letters denote statistical differences among groups based on a linear mixed effect model and post hoc comparison (table S3).

precipitation variability [e.g., (*26*)]. IDE sites were established on six continents and span broad precipitation, temperature, and environmental gradients [Fig. 1A and table S1; (*27*, *28*)]. All IDE sites utilize a common experimental approach: passive rainfall manipulation shelters (*29*) that simulated year-round drought [365 days; (*27*)] for up to 4 years. This allows for drought-duration impacts to be assessed in a cost-effective manner while still representing key characteristics of natural drought events [i.e., smaller and fewer rainfall events accompanied by longer periods between rainfall events; (*29*)]. At the time of this analysis, there were 74 grassland and shrubland IDE sites that had imposed 3 ($n = 21$) or 4 ($n = 53$) years of drought (Fig. 1B).

In addition to drought duration, IDE was designed to capture another way in which drought events are changing: increased intensity (or magnitude). To accomplish this, we selected a statistically extreme target level of drought intensity tailored for each IDE site: a 1-in-100–year drought based on long-term annual precipitation amounts available from site-level historical records (Fig. 1B) (*23*). By choosing this target level, our intent was to impose a scenario of extreme drought that is currently predicted to become more common with climate change in the near future, yet not so extreme as to be unrealistic [e.g., a 1-in-100–year drought will become more common well before a 1-in-1000–year drought does; (*30*)]. Thus, the goal with IDE was to apply drought treatments that (i) were historically and statistically rare for most if not all sites included in our study but also (ii) are forecast to become more common with climate change (*31*).

The IDE passive rainfall manipulation shelters rely on ambient precipitation to achieve drought (*29*). However, because ambient precipitation varied each year of the study, the target 1-in-100–year drought treatment was realized only when ambient rainfall was less than or equal to mean annual precipitation (MAP) for a site (*23*). When this criterion was met, we categorized the drought treatment as "extreme" [following (*27*)]. By contrast, when ambient annual rainfall was greater than MAP for a site, the target 1-in-100–year drought was not met, but drought was still imposed. For this scenario, we categorized the drought treatment as "moderate." The extreme and moderate categories of drought intensity align with those used in well-recognized drought classification systems, such as the US Drought Monitor (*23*). We also quantified the IDE drought treatments as a continuous variable using a common and comparable drought severity metric (*32*), calculated as the relative reduction in rainfall in the drought treatment from MAP (*23*). Average drought severity was substantially greater (~60%) for the extreme versus moderate drought intensity categories (fig. S1). An additional feature of the IDE design is that, in any given year, approximately half of the sites experienced extreme, 1-in-100–year drought, and after multiple years, sites experienced different combinations of moderate and extreme drought years (Fig. 1B). This allowed us to contrast distinct sequences of moderate and extreme drought impacts over multiple years.

Variability in drought response over time

Previously, we showed that average productivity reductions were ~60% greater when a single-year drought was extreme versus not extreme; however, variability among IDE sites in their response to short-term drought was notably high, ranging from complete resistance (i.e., no reduction in productivity) to large declines in productivity (*27*). Much of this variability in response was related to variation in drought severity, with productivity decreasing, as expected, with increasing drought severity (*27*). As drought duration was increased from 1 to 4 years in this study, we expected that variation in productivity responses among sites would decrease. However, average productivity responses to multiple (3 to 4) years of drought remained notably variable, ranging from little response to as much as a 97% decline in productivity (Fig. 1B).

We examined a broad set of biotic and abiotic variables previously hypothesized to explain variation in drought response (*23*), including differences in plant species richness, abundance of key growth forms (i.e., graminoids), soil texture, MAP, mean annual temperature, mean aridity index (AI), interannual precipitation variability, precipitation seasonality, and previous and current year drought severity (figs. S2 to S5 and table S2). We found that, as drought extended over multiple years, previous years' drought severity (years 2 and 3), MAP (years 2 to 4), mean AI (year 3), interannual variation (year 4) and seasonality in precipitation (year 3), and plant species richness (years 1 and 4) were major predictors of variation in drought response (figs. S2 to S5). Thus, as found in other studies (*27*, *33*), drier and less biodiverse sites, as well as those with more variable or more seasonal precipitation, experienced greater losses in productivity with drought. However, drought severity was the best and most consistent predictor of variation in drought response, as observed with single-year droughts (*27*).

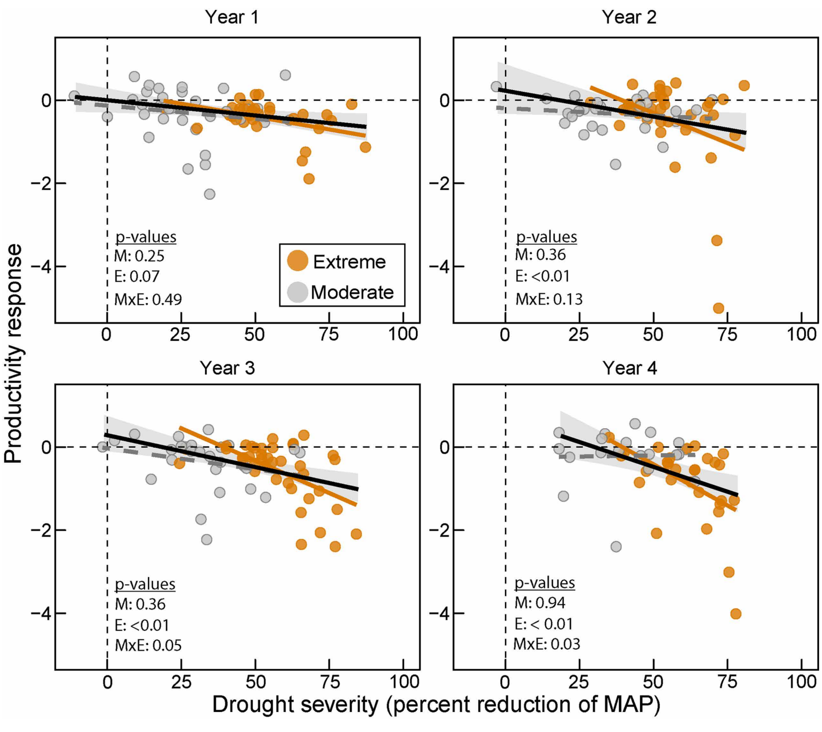

Fig. 2. Relationships between ecosystem productivity response to drought and drought severity across all sites (black line) and moderate (gray dots) versus extreme (orange dots) drought intensities for each of the 4 years of the experiment. Productivity response was calculated as the natural log of the ratio of productivity during drought to long-term mean productivity (*23*). Drought severity was calculated as: (MAP – precipitation received by drought treatment plots)/MAP (*23*). The regression across all sites was significant for all years (table S4). *P* values for moderate and extreme regressions are shown in the bottom left corner of each panel (table S5): M, moderate regression; E, extreme regression; MxE, the interaction between moderate and extreme regressions (i.e. whether the slopes differ from each other).

Pattern of productivity loss with multiyear drought

Despite variation in drought response among sites, we expected that a pattern of progressive (or cumulative) losses of productivity would emerge at most sites as drought continued over multiple years. After a significant decline in productivity in the first year of drought (29%), when averaged across all sites and drought intensity categories, productivity did not continue to decrease over time (Fig. 1C and table S3). Instead, ecosystem acclimation was generally observed. Notably, annual grasslands responded distinctly from perennial grasslands and shrublands, exhibiting a much larger initial response, but with the response lessening over time (table S3). Previous studies in annual-dominated systems have also found similar responses as well as strong drought resistance (*34*, *35*). Unfortunately, given the small number of annual-dominated IDE sites ($n = 8$) and their limited geographic coverage (seven were in the southwestern United States, and six experienced above-average precipitation in year 4), it is difficult to draw substantive conclusions about the nature of drought-duration effects based on these annual ecosystems. As such, we focused all subsequent analyses on the more widely represented perennial-dominated grassland and shrubland sites.

Interaction of drought duration and severity

The above analysis of drought duration effects does not consider intensity (extreme versus moderate) of the drought imposed. However, we expected that losses in productivity under extreme drought would be magnified over time and most pronounced when drought intensity was consistently extreme over multiple years. We tested this prediction in four ways. First, we examined relationships between productivity responses and drought severity for each year of the drought using multimodel comparisons that also included the previous year's drought severity to account for potential carry-over effects of the severity of drought from one year to the next (*23*). Consistent with simple linear regression analyses (figs. S2 to S5 and table S2), the current year's drought severity was the best predictor of variation in productivity response, regardless of ecosystem type or the previous year's drought severity (Fig. 2 and table S4). However, this analysis does not consider whether drought intensity was extreme or not. Therefore, we tested whether the slope of the relationship between productivity responses and drought severity would change depending on whether drought intensity was extreme versus moderate. This analysis allowed us to consider the magnitude of the drought treatment as both a continuous (i.e., severity) and categorical variable when describing the productivity response to drought over time. We found that, by year 3, the relationship between drought severity and productivity responses differed significantly between moderate versus extreme droughts, with the difference in these relationships most pronounced in year 4 (Fig. 2 and table S5). In other words, the slope of the relationship between drought severity and productivity loss became more negative over time when the intensity of the drought treatment was extreme, whereas the slope of the relationship for moderate intensity droughts did not change significantly over time. Third, we assessed the impact of extreme versus moderate drought intensity in any given year during the 4-year period of precipitation reductions, regardless of the previous year's drought severity. We found that average productivity losses significantly increased over time when drought was extreme, whereas the effects of moderate intensity droughts on productivity were independent of the year in which they occurred (Fig. 3A and table S6). Lastly, we quantified productivity responses of sites that had experienced only extreme drought for 1 to 4 years. For the subset of sites with such consecutive extreme drought years, the strongest duration effects were revealed (Fig. 3B and table S7), with a ~2.5-fold greater loss of productivity as duration increased from 1 to 4 years (a 29 versus 77% reduction, respectively). Collectively, these results support predictions that droughts of extreme intensity cause greater impacts on ecosystem functioning than moderate droughts of similar duration (*10*). However, most notably, we show that increasing drought duration concurrent with consistently extreme drought results in progressive losses in ecosystem functioning that are more profound than previously reported (*11*, *12*).

Conclusions

Our results help to reconcile contrasting patterns of drought duration responses reported previously. IDE results show that, after an initial loss of function in year one, ecosystems subjected to multiple years of moderate (or less severe) drought are likely to maintain this level of limited functioning (i.e., exhibit ecosystem acclimation). By contrast, an increase in severity to historically extreme levels will result in a pattern of cumulative loss of function over time. There are several mechanisms that may result in patterns of ecosystem acclimation versus cumulative effects of drought (*10*, *20*, *21*), including demographic and community shifts resulting from mortality or establishment failure (leading to loss in function) as well as plastic or adaptive responses to drought over time (leading to mitigation of loss over time). Although the IDE was not designed to rigorously test such mechanisms, available data from 49 sites on species gains and losses as well as changes in species richness suggest that demographic and community shifts likely occurred (fig. S6A and tables S8 and S9), and over time, greater species losses were significantly related to increased losses in productivity with drought (fig. S6B and table S10). Although additional research will be required to test mechanisms that may determine acclimation versus cumulative responses to drought, such mechanistic understanding is crucial in a future where extreme droughts become the norm.

The lack of duration effect with moderate drought intensity is not entirely surprising, given that many grassland and shrubland ecosystems occur in a broad range of semiarid to arid climates, as did a majority of IDE sites (table S2). The ability of these water-limited systems to rapidly respond to short-term fluctuations in precipitation (*22*, *36*, *37*) but also maintain functioning for more extended dry periods is consistent with the long-term stability of these ecosystems (*38*). Indeed, it is also worth highlighting that a subset of sites was resistant to multiple years of drought, regardless of severity. It may be that these ecosystems are less water limited (table S2) and therefore less impacted by drought, as has been observed for mesic grasslands [e.g., (*14*,*16*)]. However, it should also be noted that drought experiments may underestimate drought effects (*39*), and although passive rainout shelters alter precipitation inputs and soil moisture in ways that accurately simulate changes in rainfall during natural droughts (*28*), they do not reproduce ancillary drought attributes, such as higher temperatures and vapor pressure deficits that typically accompany drought events (*40*–*42*). Although direct temperature effects are not particularly strong in grasslands (*43*, *44*), an increase in vapor pressure deficits during drought has the potential to reduce photosynthesis and productivity (*45*, *46*), and the lack of a temperature manipulation in this study could partially explain why some IDE sites were unresponsive to drought over time.

The discovery that the resistance to drought duration of grasslands and shrublands rapidly eroded with prolonged drought of extreme intensity portends an uncertain future for these ecosystems, threatening their long-term stability and the ecosystem goods and services they provide. Particularly alarming were the 160%-greater (or 2.5-fold–greater) reductions in productivity observed when extreme drought years occur consecutively. Extreme, consecutive drought years, including megadroughts (*8*), are expected to increase in the future with climate change (*8*,*31*). Although concerns about ecosystem stability in the face of ongoing increases in both drought magnitude and duration have been voiced for decades (*47*, *48*), our results provide experimental evidence in support of recent observations (*5*) that the functioning of these globally important ecosystems are at risk from longer and more intense droughts.

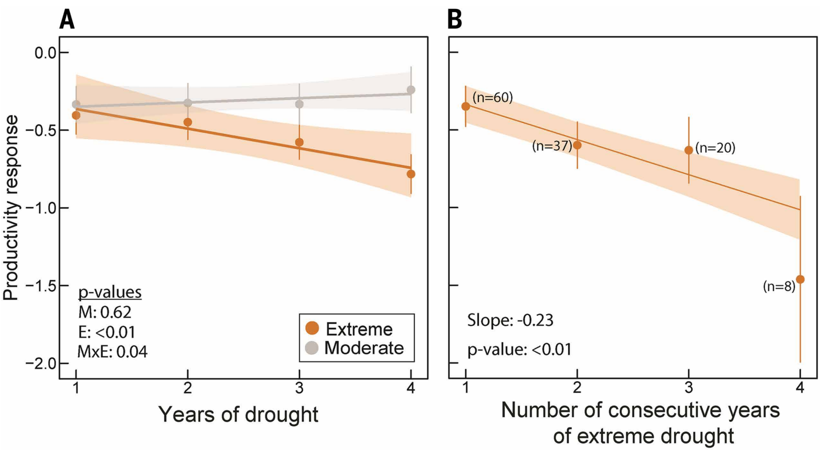

Fig. 3. Effects of drought duration (1 to 4 years) on productivity responses for moderate versus extreme drought intensities. (**A**) Despite an initial loss of productivity in the first year, drought duration had no effect on productivity responses when drought was moderate (gray line), irrespective of whether drought was of extreme or moderate intensity in previous years. By contrast, drought duration increased productivity losses when drought was extreme (orange line), irrespective of whether previous years were extreme or moderate. Thus, an extreme drought in year four reduced productivity more than an extreme drought in year one. *P* values for moderate and extreme regressions are shown in the bottom left corner of each panel (table S5): M, moderate regression; E, extreme regression; MxE, the interaction between moderate and extreme regressions (i.e. whether the slopes differ from each other). (**B**) Drought duration had much greater cumulative impacts on productivity if the years were consecutively extreme. The slope of the relationship between time and productivity response for consecutive extreme drought was twofold greater than in (A). Productivity responses to consecutive moderate droughts could not be assessed owing to an insufficient number of sites experiencing 3 ($n = 7$) and 4 ($n = 3$; see Fig. 1B) consecutive years of moderate drought. In both (A) and (B), productivity response was calculated as the natural log of the ratio of productivity during drought to long-term mean productivity (*23*), error bars represent standard error, and shading represents the 95% confidence interval of the regression. Summary statistics for the linear mixed effects model are shown in the bottom left corner: slope and *P* value of the regression (tables S6 and S7).

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SUPPLEMENTARY MATERIALS

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