



Resolving the Dust Bowl paradox of grassland responses to extreme drought

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During the 1930s Dust Bowl drought in the central United States, species with the C₃ photosynthetic pathway expanded throughout C₄-dominated grasslands. This widespread increase in C₃ grasses during a decade of low rainfall and high temperatures is inconsistent with well-known traits of C₃ vs. C₄ pathways. Indeed, water use efficiency is generally lower, and photosynthesis is more sensitive to high temperatures in C₃ than C₄ species, consistent with the predominant distribution of C₃ grasslands in cooler environments and at higher latitudes globally. We experimentally imposed extreme drought for 4 y in mixed C₃/C₄ grasslands in Kansas and Wyoming and, similar to Dust Bowl observations, also documented three- to fivefold increases in C₃/C₄ biomass ratios. To explain these paradoxical responses, we first analyzed long-term climate records to show that under nominal conditions in the central United States, C₄ grasses dominate where precipitation and air temperature are strongly related (warmest months are wettest months). In contrast, C₃ grasses flourish where precipitation inputs are less strongly coupled to warm temperatures. We then show that during extreme drought years, precipitation–temperature relationships weaken, and the proportion of precipitation falling during cooler months increases. This shift in precipitation seasonality provides a mechanism for C₃ grasses to respond positively to multiyear drought, resolving the Dust Bowl paradox. Grasslands are globally important biomes and increasingly vulnerable to direct effects of climate extremes. Our findings highlight how extreme drought can indirectly alter precipitation seasonality and shift ecosystem phenology, affecting function in ways not predictable from key traits of C₃ and C₄ species.

climate change | extreme drought | photosynthetic pathway | precipitation seasonality

The iconic “Dust Bowl” drought of the 1930s is widely regarded as one of the most important environmental, economic, and social disasters to befall the United States in the 20th century (1–4). While the climatic causes, human toll, and resulting changes in agricultural practices have received much attention (2, 3, 5), this extended period of drought also led to widespread ecological degradation of native grasslands throughout the central United States (6, 7). Severe reductions in ecosystem function and alterations in grassland structure were variously attributed to the direct effects of the drought’s extreme high temperatures and sustained rainfall deficits, as well as to livestock overgrazing and burial by wind-blown soil from poorly managed agricultural lands (6, 7). Because contemporary climate models forecast an increase in drought extremity and a greater likelihood for more frequent “Dust Bowl type” pancontinental droughts to occur in the future (8–10), there is renewed interest in understanding the causes and consequences of the Dust Bowl and the lessons that can be learned from this period of extreme drought (4).

Ecologists in the 1930s provided a richly detailed account of how native North American grasslands responded to the Dust Bowl drought (11–13). While many of their observations were

unsurprising (i.e., rapid reductions in plant cover and biomass, 13), a striking transformation of central Great Plains grasslands was documented as the drought progressed. By the third year of drought, a number of C₃ species, most notably *Pascopyron smithii*, a grass species more abundant in northern, cooler regions of the Great Plains (14), increased dramatically in many grasslands formerly dominated by C₄ grasses. In some cases, this C₃ grass completely displaced the dominant C₄ grasses (11, 12). Because the C₄ photosynthetic pathway had yet to be discovered at this time, and traits associated with C₃ and C₄ pathways were not yet understood, the expansion of this C₃ grass during drought was assumed to be due to its superior drought tolerance relative to the formerly dominant species (11, 14). Today, with our contemporary understanding of the evolution and ecology of C₃ vs. C₄ photosynthetic pathways, such a widespread increase in C₃ grasses during hot, dry periods is a challenge to reconcile. Indeed, research conducted subsequent to the Dust Bowl has shown that *P. smithii* grows best at cool temperatures, has lower water use efficiency, and has higher soil moisture requirements than cooccurring C₄ grasses (15). These traits are consistent with the broader C₃/C₄ paradigm of C₄ photosynthesis initially evolving in response to low CO₂ (16–18) but spreading widely in part due to the capacity of C₄ plants, particularly grasses, to

Significance

During the Dust Bowl drought, central US grasslands responded unexpectedly to a decade of hot, dry conditions. Grass species adapted to high temperatures with higher water use efficiency (C₄ grasses) decreased, while those preferring cooler climates (C₃ grasses) increased. We reproduced this surprising response by experimentally imposing extreme drought in two native grasslands. Analysis of historical climate records revealed that during extreme drought years, the proportion of annual precipitation that occurs during cooler months increases. This previously unidentified shift in seasonal precipitation patterns during extreme drought years provides a mechanism for C₃ grasses to increase despite overall hot, dry conditions. Thus, alterations in precipitation seasonality may be as important as reduced precipitation amount when forecasting ecosystem responses to extreme drought.

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better cope with high temperatures and water deficits relative to most C_3 species (19–22). Although C_3 grasses do occur in warm, arid climates, it is well-established that C_4 plants have inherently higher water use efficiency than C_3 plants and that net carbon gain is reduced more at high temperatures in C_3 than C_4 plants (23, 24). Consistent with these traits and their phylogenetic history, C_4 species generally dominate low-latitude, warmer grasslands, while C_3 grasses increase in abundance and dominance at higher latitudes and elevation in North America and globally (20, 25–27). Thus, the widespread increase in C_3 grass abundance and the decline in C_4 grasses during this historically hot and dry North American drought would not be predicted based upon today's understanding of the traits of these species. As a result, what was initially documented almost a century ago as an extensive shift in species abundances, encompassing an $\sim 350,000$ km² region from South Dakota to Kansas (6, 7), represents a paradox today.

Here, we report results from a 4-y drought experiment (*Methods*) conducted in two native grasslands with a mix of C_3 and C_4 species. These grasslands were selected because their plant communities included *P. smithii*, the C_3 grass that increased most notably during the Dust Bowl drought (11, 12). Further, they differed in C_3/C_4 dominance with the more C_3 -dominated grassland ($\sim 70\%$ C_3 biomass near Cheyenne, WY) located at the edge of the most severe extent of the Dust Bowl drought, and a more C_4 -dominated grassland ($\sim 70\%$ C_4 biomass near Hays, KS) located centrally within the Dust Bowl footprint (Fig. 1A). The experimental droughts, imposed by decreasing annual precipitation amounts by $\sim 50\%$ over 4 y (Fig. 1B and *SI Appendix, Fig. S1*), allowed us to replicate a key aspect of the Dust Bowl drought—sustained multi-year rainfall deficits—and independently corroborate responses observed during the 1930s. We resolve this paradoxical shift in C_3

vs. C_4 abundance in response to extended extreme drought by integrating our experimental results with analyses of long-term climate records from across the central United States, focusing on those years with the greatest (most extreme) precipitation anomalies. This has allowed us to identify a mechanism that can explain the expansion of C_3 grasses into C_4 grasslands during multiyear extreme droughts and provide insight into how these globally important biomes might respond in the future.

Results and Discussion

Soil moisture levels were consistently reduced in both grasslands during the 4-y experimental drought (*SI Appendix, Fig. S2*). In response, total aboveground net primary production (ANPP) for the C_4 grassland was reduced by $>40\%$ (Table 1 and Fig. 2). In contrast, the C_3 grassland was much less sensitive to reduced growing season precipitation, consistent with previous studies (29–32). In both grasslands, however, drought significantly increased the ratio of C_3 to C_4 grass biomass (Table 1 and Fig. 2), as observed during the Dust Bowl. In the C_3 -dominated grassland, the increase in C_3/C_4 ratio was driven primarily by a 40% reduction in the contribution of C_4 grasses to ANPP in droughted plots (Fig. 2). However, in the C_4 grassland, significant reductions in the proportion of C_4 biomass were accompanied by equivalent increases in C_3 grass biomass (Fig. 2). Thus, as observed during the Dust Bowl in Kansas, Nebraska, and Iowa (11, 12), C_3 grasses increased from being a minor proportion of ANPP initially to equaling or even exceeding C_4 ANPP.

There are many aspects of the Dust Bowl drought that our experiment did not replicate (see below), but the drought treatments we imposed did approximate the seasonal pattern of precipitation anomalies during the Dust Bowl. In our experiment, the

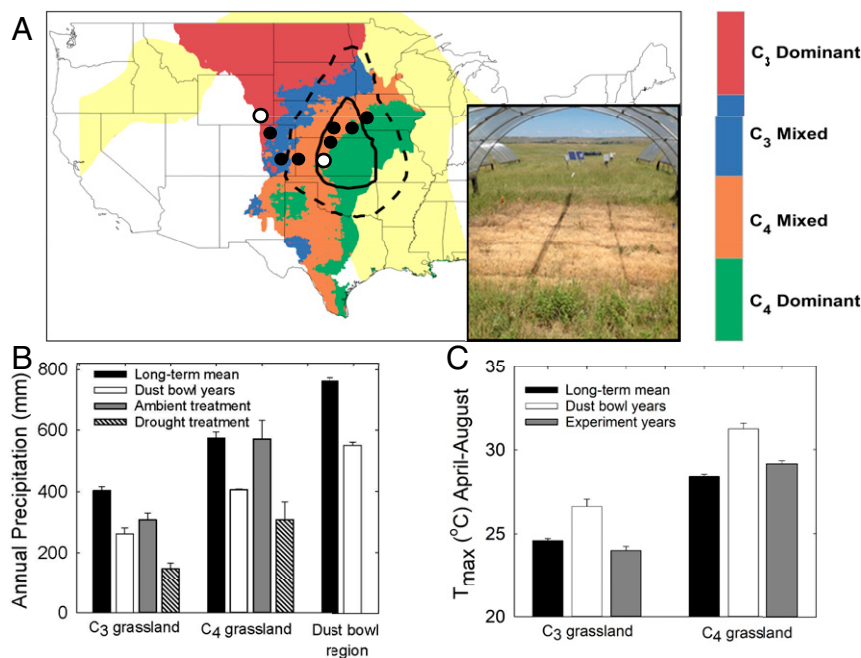


Fig. 1. (A) Extent of the Dust Bowl drought of the 1930s. Data from ref. 1. Black solid line encloses the region with greatest daily precipitation anomalies (>3 mm/day), dashed line denotes anomalies > 2 mm/day, and yellow shaded area denotes >1 mm/day (values averaged from 1932 to 1938). White dots denote approximate locations of experimental droughts imposed near Hays, KS, and Cheyenne, WY. Black dots indicate native grassland sites observed to undergo decreases in C_4 grasses during the 1930s (sites west of Hays) or increases in C_3 and decreases in C_4 grasses (east of Hays, 6–7, 11–12). Also shown on this map is the proportional distribution of C_3 vs. C_4 biomass based on empirical data and statistical models for North America (28). C_3 Dominant = $>60\%$ C_3 biomass; C_3 Mixed = 50–60% C_3 biomass; C_4 Mixed = 50–60% C_4 biomass; C_4 Dominant = $>60\%$ C_4 biomass. (*Inset photo*) Experimental drought plot, Hays, KS, July 2015, during the second year of experimental drought. (B) Mean annual precipitation for the C_3 (Cheyenne) and C_4 (Hays) grassland sites for 1900–2015 (long-term mean), the four driest Dust Bowl years, and the ambient and 4-y drought treatments imposed from 2014 to 2017 (*SI Appendix, Fig. S1*). Long-term mean annual precipitation and Dust bowl precipitation are also shown for the region enclosed by the solid line (= Dust bowl region). (C) Mean daily maximum air temperature during April–August for the same time periods and locations as in B. Note that ambient and drought treatments in the experiment experienced identical air temperatures. Climatic data are from NOAA (www.ncdc.noaa.gov). Means and ± 1 SEs are reported in B and C.

Table 1. Summary of repeated measures analysis of variance of year and drought effects on ANPP and the ratio of C₃ to C₄ grass biomass (C₃/C₄ ratio) for a C₃-dominated mixed grassland in Wyoming and a C₄-dominated mixed grassland in Kansas

	Year	Drought	Year × drought
	F, P > F	F, P > F	F, P > F
<i>C₃ grassland</i>			
ANPP	57.3, <0.01	0.52, 0.48	0.68, 0.57
C ₃ /C ₄	14.8, <0.01	4.30, 0.05	2.98, 0.04
<i>C₄ grassland</i>			
ANPP	5.14, <0.01	38.36, <0.01	1.25, 0.30
C ₃ /C ₄	8.22, <0.01	7.37, <0.01	5.57, 0.02

Year was a continuous term. Pretreatment data were not included in this analysis. F, F statistic.

largest reductions in precipitation occurred during the summer (June–July–August), with spring (March–April–May) precipitation much less reduced (*SI Appendix, Fig. S1*). This is consistent with patterns observed during the 1930s drought (1). Also consistent with the Dust Bowl, *P. smithii* was the C₃ grass that increased the most in the C₄-dominated grassland (predrought *P. smithii* = 7.9 ± 1.02 g/m² [~2% of total ANPP] vs. 40.4 ± 5.21 g/m² [~23% of ANPP] in years 3 and 4 of the experimental drought). This represents a fivefold increase in ANPP of this C₃ grass during the experiment. Consequently, experimental drought transformed this Kansas grassland from C₄ dominance to C₃/C₄ codominance within 3 y (Fig. 2).

The Primacy of Water Stress during Extreme Drought. The extreme drought we imposed did not include high air temperatures, which typically occur during extreme drought (33), overgrazing, or dust

deposition; all notable attributes of the Dust Bowl drought (Fig. 1C and 6, 7). Of these, burial of plant communities by dust was most often invoked by ecologists in the 1930s as a key mortality mechanism that allowed other species to increase (11–13). However, while dust burial may have facilitated species turnover, our experiment shows that neither burial nor high temperatures were necessary for shifts in C₃/C₄ dominance to occur. In fact, the C₃ species that increased most in response to both the Dust Bowl and our experimental drought, *P. smithii*, dominates grasslands in the cooler regions of the northern Great Plains and is from the temperature-sensitive C₃-BEP *Poaceae* clade (26). This species would not be expected to increase in abundance with increased temperatures. While our results suggest that high temperatures did not play a direct role in these drought responses, consistent with previous experiments that manipulated temperature and precipitation independently (34), increased air temperatures during drought may affect grasslands indirectly, by exacerbating water stress via increased evaporative demand. We estimated potential evapotranspiration (PET) during the four driest Dust Bowl years (*Methods*), and, as expected, PET was higher in the 1930s than during our experiment (1,274 vs. 1,195 mm/y, respectively, in the C₃ Wyoming grassland; 1,798 vs. 1,614 mm/y in the C₄ Kansas grassland). However, by experimentally reducing precipitation (P) inputs to a greater extent than occurred during the Dust Bowl (Fig. 1), we were able to impose potential water deficits (PET-P) more similar to those during the Dust Bowl (PET-P for experimental drought = 1,046 and 1,311 mm/y in the C₃ and C₄ grassland, respectively, vs. Dust Bowl PET-P = 1,012 and 1,390 mm/y, respectively).

The Importance of Precipitation Seasonality. Temperature is most often invoked as the primary environmental determinant of the relative abundance of C₃ vs. C₄ species in grasslands globally

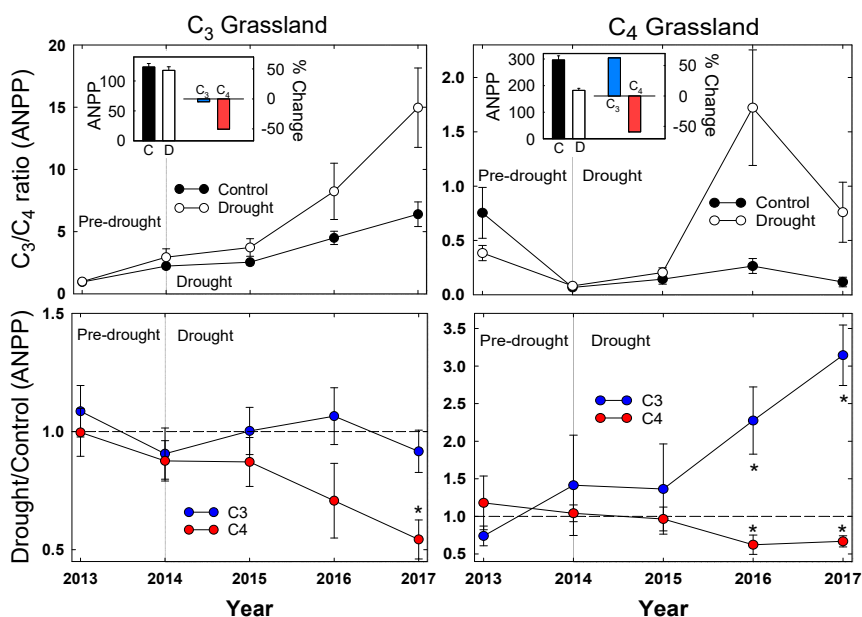


Fig. 2. Response of C₃- and C₄-dominated grasslands to a 4-y experimental drought (~50% reduction in annual precipitation). Predrought (2013) data shown as well. (*Top, Insets*) Total ANPP was insensitive to drought in the C₃ grassland, but ANPP was significantly reduced ($P < 0.01$) in all years in the C₄ grassland. C = control plots, D = drought plots; values are 4-y means + SE. By year 4 of the experimental drought, productivity from C₄ species (red bars) had decreased by ~50% in both grasslands, but C₃ productivity (blue bars) only increased in the C₄-dominated site. (*Top, Main*) In both grasslands, the ratio of C₃/C₄ grass ANPP was increased by drought (year 4 in the C₃-dominated grassland, years 3–4 in the C₄-dominated grassland, $P < 0.01$). See Table 1 for additional statistical details. (*Bottom*) Time course of how the proportion of C₃ (blue symbols) or C₄ (red symbols) grass biomass in drought vs. control plots varied. For C₃ grass biomass, this proportion did not vary over the 4 y in the C₃-dominated grassland, but C₃ biomass increased threefold by year 4 in the C₄ grassland. In contrast, the proportion of C₄ grass biomass in drought vs. control plots decreased ~twofold in both grasslands by year 4 (C₃) and 3 (C₄). * indicates when the ratio of Drought/Control ANPP differed from unity ($P < 0.05$).

(19). But metrics describing the seasonal distribution of precipitation (e.g., warm vs. cool season precipitation) are often included in statistical and process-based models to more successfully predict regional and global distributions of these photosynthetic pathways (26, 28, 35). Simply put, these models constrain C_4 grasses to regions where precipitation inputs occur predominately during warm months, while C_3 grasses increase in dominance as the proportion of cool season precipitation increases. Winter-rainfall Mediterranean grasslands exemplify the relationship between cool season precipitation regimes and C_3 dominance (27, 36, 37). We evaluated relationships between mean monthly air temperature (T) and precipitation (P) using PRISM historical climate data from 1895 to 2017 (Methods) for central US grasslands differing in C_3/C_4 abundance. We used the slope of this relationship (P-T, mm/°C) as an indicator of precipitation seasonality. A strong positive slope indicates a large proportion of precipitation falling in the warmer months (expected to favor C_4 grasses, 26, 28), and a less positive slope reflects a more equitable distribution of precipitation seasonally, with a greater proportion falling in cooler months (favoring C_3 species, 28). The value of this metric is evident from the twofold greater P-T slope for the C_4 -dominated grassland relative to the C_3 -dominated site (Fig. 3).

Precipitation Seasonality and Extreme Drought. Many precipitation attributes, besides total amount, differ markedly between extreme dry and average years (38–40). Because our experimental drought primarily impacted rainfall inputs during the warmest months, reducing summer rainfall dominance (SI Appendix, Fig. S1 and Methods), we tested the hypothesis that during extreme drought years, the seasonal distribution of precipitation in the central United States would also shift from strong summer dominance to a pattern more favorable for C_3 grasses. We first tested this hypothesis in the C_4 and C_3 grassland sites in Kansas

and Wyoming where experimental drought was imposed. In both grasslands, the P-T slope was reduced during years with extreme negative precipitation anomalies compared to average years (Fig. 3A). As a result, warm season dominance of precipitation was reduced, and the proportion of precipitation falling during cooler months increased (Fig. 3A, Insets). As expected, a shift in seasonality was also evident when we compared the P-T slope for the ambient vs. extreme drought treatments during the 4-y experimental period (Fig. 3A). This confirms that during our experimental drought, and in years with extreme precipitation anomalies, seasonal patterns of precipitation inputs were altered similarly; in both cases the proportion of precipitation during the cooler months increased. Finally, we compared relationships between temperature and precipitation for central US grasslands more broadly for 1) all years in the historical PRISM database, 2) the driest Dust Bowl years, and 3) the years with the most extreme precipitation anomalies (Fig. 3B). In all cases, extreme drought reduced the slope of the P-T relationship, decreasing summer rainfall dominance and increasing the equitability of monthly precipitation inputs across these grasslands (Fig. 3B).

We posit that a shift in precipitation seasonality during extreme drought provides the most plausible mechanism for the unexpected increase in abundance of C_3 grasses under conditions expected to be better suited for C_4 species. This was observed in our 4-y experiment, during the decadal-scale Dust Bowl drought, and during extended periods of drought during the middle Holocene (41). This increase in C_3 abundance (primarily *P. smithii* in our experiment but including other C_3 species during the Dust Bowl, 6, 7) occurred even though there was a slight decrease in precipitation during the spring months (SI Appendix, Fig. S1 and see also ref. 1). This suggests that the negative impact of summer precipitation deficits on the C_4 grasses, which included substantial mortality during the Dust Bowl (11, 13), may benefit C_3 species by providing access to key resources (soil moisture and

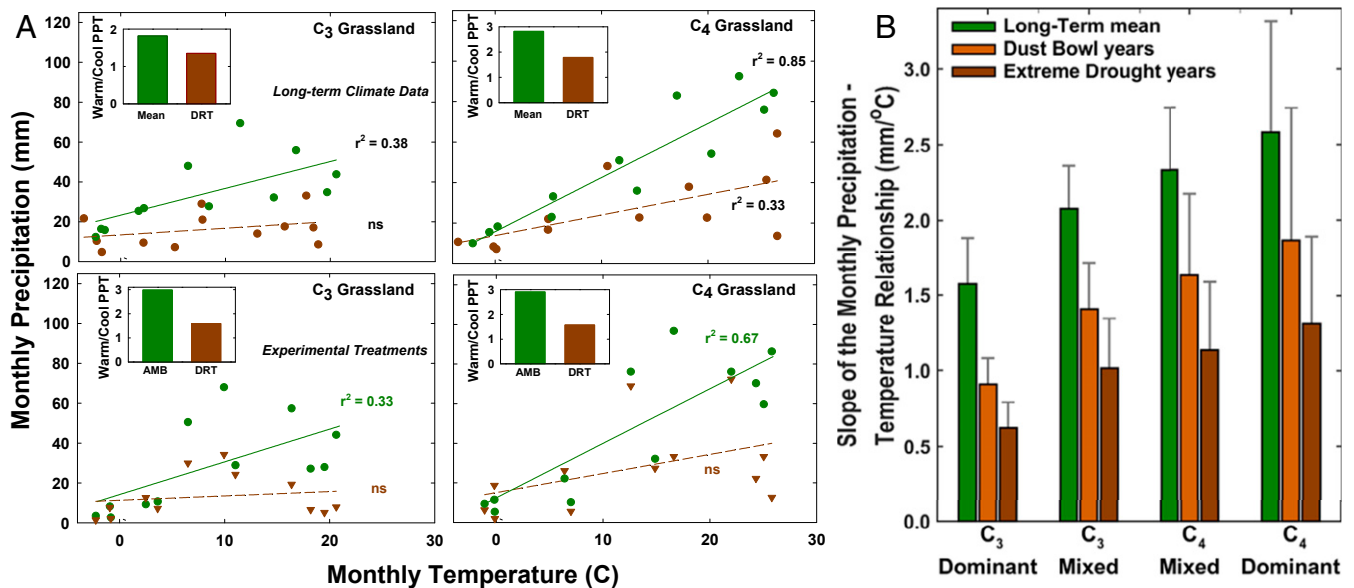


Fig. 3. (A) Upper Relationship between mean monthly temperature (T) and precipitation (P) for all years (green symbols, 1900–2015, NOAA database, see Methods) vs. the four driest years (= extreme drought years, brown symbols) during this time period in C_3 (WY) and C_4 grassland (KS) sites. Similar relationships (Bottom) for the ambient (green) vs. drought (brown) treatments are shown for the experimental time period (2014–2017). (Insets) Ratio of precipitation amount for the six warmest vs. the six coolest months for each P-T relationship. Note that the long-term P-T slope was twofold greater for the C_4 -dominated grassland ($2.7 \text{ mm/}^\circ\text{C} \pm 0.34$) compared to the C_3 -dominated site ($1.3 \text{ mm/}^\circ\text{C} \pm 0.48$). As a result, the ratio of precipitation in the six warmest vs. the six coolest months was 2.8 for the C_4 grassland and 1.8 for the C_3 grassland. (B) Mean slopes of the P-T relationship (PRISM Climate Data) for all four grassland types in Fig. 1 for the 1895–2017 period (long-term mean), the four driest Dust Bowl years, and the four most extreme drought years. N varied from 17,961 grid cells for C_3 mixed grasslands to 43,676 grid cells for the more extensive C_3 -dominated grasslands for this analysis (+1 SD above each bar). All P-T slopes within a grassland type differed ($P < 0.001$) among mean, Dust Bowl, and extreme drought years.

nutrients) not consumed by the C_4 grasses. Consistent with this scenario, note that the C_3/C_4 ratio at the C_3 -dominated site also increased moderately in control plots exposed to ambient precipitation during our experiment (Fig. 2). At this site, there was a 4-y drying trend driven by a significant reduction in summer precipitation from year 1 to 4 (*SI Appendix, Fig. S3*). This response is also consistent with a shift in precipitation seasonality negatively affecting C_4 species and subsequently increasing the dominance of the C_3 grasses. However, in the C_4 -dominated grassland, a prominent increase in the C_3/C_4 ratio in year 3 of the experiment occurred in an anomalously wet year ($\sim 30\%$ above Mean Annual Precipitation, MAP) when April and May rainfall was >120 mm greater than in any other year of the experiment. This indicates that these C_3 species can respond directly to increases in cool season precipitation, as well as indirectly to reductions in C_4 grasses caused by summer drought.

A Shifting C_3 - C_4 Paradigm. In the past decades, much research has challenged generalizations regarding how photosynthetic type has influenced the past and present distribution and ecology of C_3 and C_4 grasses, leading to a more nuanced understanding of the key roles of, for example, disturbance regime, phylogenetic history, and other traits not specific to photosynthetic type (42, 43). For example, tolerance of water stress can in some cases be greater in C_3 than C_4 species (44). Indeed, when comparing traits of the North American C_3 vs. C_4 grasses in the present study, some differences are consistent with past generalizations (lower leaf N in the C_4 grasses), while traits associated with drought tolerance (leaf turgor loss point) did not differ (*SI Appendix, Fig. S4 and Table S1* and 45). This latter result, in particular, is consistent with the importance of precipitation seasonality driving shifts in species abundances during extreme drought, not differences in drought tolerance as previously assumed (11, 14). Similarly, recent analyses suggest that increases in warm-season precipitation, not warming or CO_2 levels, may have driven the late Neogene expansion of C_4 grasses in North America (46). Finally, although results from the 4-y experiment were consistent with responses to a decadal drought, time scales of responses for ecosystems with both C_3 and C_4 grasses can require more than a decade (47). Indeed, our results add to previous short- and long-term global change experiments reporting unexpected responses of grasslands, including one positing that the combined effects of elevated CO_2 and warming may increase productivity of C_4 grasses more than C_3 grasses, due to reduced summer water limitations (48). Whether elevated CO_2 levels can offset the effects of more frequent and extreme droughts forecasted for grasslands remains to be evaluated.

Implications. Extreme, multiyear droughts are expected to increase in frequency in the 21st century (9, 10), and our results suggest that these droughts have the potential to decrease C_4 grassland cover and initiate widespread increases in C_3 grass abundance across the central United States. Sea surface temperature anomalies have been linked to land surface drought in general (10, 49), and, specific to the Dust Bowl, these anomalies can disproportionately reduce summer precipitation, with lesser effects on spring precipitation and even slight increases in winter precipitation (1). Thus, predicted increases in sea surface temperature anomalies will result in both precipitation reductions and changes in seasonality that differentially impact C_4 grasses.

After the Dust Bowl, 20 y were required for the C_3 grasses that expanded into C_4 -dominated grasslands to return to predrought abundances (7, 50). This prolonged postdrought recovery is consistent with the importance of strong priority effects evident in grasslands once dominance is achieved (43). It is not possible to know if future drought-induced shifts in C_3 - C_4 abundances will be transient or more permanent (41). But based on differences in how C_3 vs. C_4 species respond to light, temperature,

CO_2 , and nitrogen (37, 47), combined with differences in phenology (green-up to senescence occurs earlier in C_3 grasslands), important alterations in land-atmosphere exchanges of carbon, water, and energy can be expected when C_3 species replace C_4 grasses (51). Of particular importance, C_3 plant canopies generally partition more net radiation to latent heat than C_4 grasslands, increasing early season evapotranspiration and potentially depleting soil water that would otherwise be available for use by C_4 grasses in the summer (52). In this way, drought-induced expansion of C_3 grasses may exacerbate summer soil water stress, negatively impacting C_4 grasses and further reinforcing C_3 dominance. Limited observations of soil moisture dynamics during the Dust Bowl drought support this scenario (53). Moreover, an increase in sensible heat in the warmest months due to senescence of C_3 canopies (and loss of C_4 plant cover) can amplify surface temperatures, resulting in heat waves and further reducing precipitation (2). Compound climate extremes, those that include multiple stressors such as heat waves and drought, often have disproportionate impacts on humans and ecosystems (33).

In summary, we have experimentally corroborated and resolved the Dust Bowl paradox by showing that extreme drought leads to a more equitable seasonal distribution of precipitation, aligning this limiting resource more closely with the seasonal growth period of C_3 grasses. This previously unrecognized shift in seasonal precipitation patterns provides a mechanism for C_3 species to increase during multiyear extreme drought and replace C_4 species as dominants in grasslands. Such a transformation will have significant impacts on ecosystem phenology. Changes in land surface phenology, particularly earlier spring greening, are considered fingerprints of climate warming for terrestrial ecosystems (54–56). Drought-induced shifts to dominance by earlier-growing C_3 species may advance spring green-up independent of warming. Indeed, spring green-up and peak greenness can differ by 30 d between cooccurring C_3 - vs. C_4 -dominated grasslands (57). This far exceeds the magnitude of warming-driven advances in phenology for much of the world (58). More broadly, C_4 grass-dominated ecosystems house substantial biodiversity, C_4 grass species account for almost 25% of terrestrial net primary productivity, and because C_4 grasslands are among the most sensitive ecosystems to precipitation change (59), they interact strongly with the land carbon sink (19, 60–62). Thus, predicting how the distribution and abundance of C_4 grasses and grasslands may be altered by global change drivers has economic and ecological value of global importance (63, 64). While altered precipitation seasonality during extreme drought may reduce C_4 grass dominance, there is also emerging evidence that, independent of drought, seasonal precipitation patterns are being altered with climate change, including a dampening of seasonality (65–67). The net effect that these and other global change drivers will have on the extent of C_3 and C_4 grasslands over the next century remains to be resolved.

Methods

Field Sites and Experiments. Field experiments were conducted concurrently in two grasslands chosen for their contrasting mixtures of C_3 and C_4 grasses. The mixed-grass prairie near Hays, KS, is a C_4 -dominated native grassland (73.1% C_4 based on ANPP measurements from control plots during the pretreatment and four experimental years) located within the epicenter of the 1930s Dust Bowl drought and where drought-induced increases in C_3 grasses were documented historically (Fig. 1 and (11, 12)). The grassland near Cheyenne, WY, is a C_3 -dominated grassland (69.8% C_3), located at the periphery of the most severe extent of the Dust Bowl drought. In addition to their geographic locations at the edge and center of Dust Bowl drought, these sites were chosen because *P. smithii* (the C_3 grass that increased extensively during the Dust Bowl (11, 12)) was present at both sites; as a dominant species at the C_3 site and as a widespread, moderately abundant member of the plant community in the C_4 grassland. Both grasslands were lightly grazed prior to a pretreatment sampling year (2013) and were protected from domestic grazers during the subsequent 4-y experimental

period. Although most grasslands are naturally grazed by native or domesticated large herbivores, including their activities as part of this experiment was not feasible.

Drought was experimentally imposed at each site for 4 y using large rainfall exclusion shelters (Fig. 1A and 68). At each site, 30 plots, each 36 m², were established across a topographically uniform area. Each plot was hydrologically isolated from the surrounding soil using aluminum flashing to a depth of 20 cm and 6-mil plastic barriers installed to a depth of 50 cm. Drought was imposed in 20 plots per site by installing large shelters (10 × 10 m) that were used to block 66% of incoming rainfall during each growing season—this is roughly equivalent to a 50% reduction in annual precipitation given that 60–75% of MAP falls during the growing season in these ecosystems. The remaining 10 plots per site were trenched and hydrologically isolated as well, serving as controls that received ambient rainfall. Drought was imposed by reducing the same quantity of growing season rainfall inputs in two different ways. We removed a portion (66%) of each rain event (68) during the entire growing season (April–August; chronic drought treatment, *n* = 10 plots/site) or we fully excluded all rain events for a shorter portion of the growing season (May through mid-August, intense drought treatment, *n* = 10 plots/site). Soil moisture was measured in the center of each plot at a depth of 0–15 cm and 0–30 cm with 30-cm time-domain reflectometry probes (Model CS616, Campbell Scientific, Logan, UT) inserted at a 45° angle or perpendicular to the soil surface. Responses in soil moisture and ratios of C₃ vs. C₄ ANPP to each type of drought were consistent (SI Appendix, Figs. S5 and S6), thus results were combined into a single drought treatment. Treatment infrastructure was installed in the spring of 2012, but drought treatments did not begin until 2014 because 2012 was a natural extreme drought year and not appropriate as a pretreatment year. Rain gauges were established in a subset of control and treatment plots to confirm the efficacy of the infrastructure in removing rainfall inputs to experimental plots. Infrastructure effects on the microclimate were also monitored, particularly photosynthetically active radiation and soil temperature, and these effects were similar to those documented for many other studies of rainfall exclusion infrastructure effects (10–20% reductions in photosynthetically active radiation, depending on the time of day; minimal differences in air, soil, and leaf temperatures; no differences in leaf-to-air vapor pressure differences under the infrastructure compared with controls; 68–70).

At the end of each growing season, all aboveground biomass was harvested in three quadrats (0.1 m²) placed randomly in new locations each year in two 2 × 2 m subplots designated for destructive measurements. A different subplot was harvested each year. Biomass was sorted to remove the previous year's growth, dried for 48 h at 60 °C, and weighed to estimate total ANPP, as well as ANPP of dominant plant growth forms (C₄ grasses, C₃ grasses, and C₃ forbs). Subshrubs and succulents, comprising < 5% of ANPP at both sites, were excluded from calculations due to measurement difficulties, but C₃ sedges, as graminoids, were included in the C₃ grass category.

Analyses of Long-Term Climate Data. For the two grassland sites where drought experiments were located, we retrieved precipitation and temperature data (1900–2015) from the National Oceanic and Atmospheric Administration (NOAA) National Climate Data Center (www.ncdc.noaa.gov): NOAA station COOP ID numbers 481675 for Cheyenne, WY, and 143527 for Hays, KS. These weather stations were within 5 and 25 km, respectively, of the experimental

sites. To assess the relationships between monthly temperature and precipitation at regional scales, and for grasslands that differed in C₃/C₄ composition, we downloaded PRISM Climate Data (<https://prism.oregonstate.edu>) with a 4 × 4 km spatial resolution for the period 1895–2017 (123 y). We used simple linear regression to calculate the slope of monthly temperature and precipitation relationship for each grid cell (total = 132,541) and mapped those grid cells to the C₃/C₄ grassland categories in Fig. 1. The number of grid cells in each grassland category were: C₃ Dominated = 43,676, C₃ Mixed = 17,961, C₄ Mixed = 39,112, C₄ Dominated = 31,792. We confirmed that reduced P-T slopes also corresponded to reduced ratios of warm/cool season precipitation (see *Insets* in Fig. 3A and SI Appendix, Fig. S1). PRISM Climate Data were also used to calculate potential evapotranspiration based on the Hamon method (71).

To compare the 4-y experimental drought period with equivalent durations of Dust Bowl drought and the most extreme drought years in the historical record, we first calculated the annual precipitation for each of the 123 y for all grid cells. We then chose the 4 y with lowest average annual precipitation during this period—these were 1910, 1934, 1936, and 1956. Similarly, the four driest years during the Dust Bowl decade (1930–1940) were 1933, 1934, 1936, and 1939. Our goal was to document how precipitation seasonality is altered in the most extreme dry years on record, defined statistically as below the fifth percentile for all years. These 4 y met that criterion, but we also assessed seasonality for the 10 driest years and observed similar patterns (SI Appendix, Fig. S7). We compared these temperature–precipitation relationships to those calculated from all years (long-term mean) as well as for only those years with annual precipitation within 20% of mean annual precipitation. These latter two relationships did not differ (SI Appendix, Fig. S7).

Statistical Analyses. Responses to experimental treatments were assessed with repeated measures analysis of variance with year and drought as main effects. One-sample *t* tests were used to detect divergence of control/drought plot ratios from unity for C₃ and C₄ ANPP. Simple linear regression analyses were used to calculate the slope of monthly temperature and precipitation for each grid cell, with monthly precipitation amount as the dependent variable and monthly mean temperature as the independent variable.

Data Availability. Data from the field experiments are available via Dryad (<https://datadryad.org/stash>, doi:10.5061/dryad.3j9kd51dv). All climate data are publicly available at NOAA's National Climate Data Center (www.ncdc.noaa.gov) and the PRISM Climate Data website (www.prism.oregonstate.edu).

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1. S. D. Schubert, M. J. Suarez, P. J. Pegion, R. D. Koster, J. T. Bacmeister, On the cause of the 1930s Dust Bowl. *Science* **303**, 1855–1859 (2004).
2. B. I. Cook, R. L. Miller, R. Seager, Amplification of the North American “Dust Bowl” drought through human-induced land degradation. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 4997–5001 (2009).
3. R. Hornbeck, The enduring impact of the American Dust Bowl: Short and long-run adjustments to environmental catastrophe. *Am. Econ. Rev.* **102**, 1477–1507 (2012).
4. R. A. McLeaman *et al.*, What we learned from the Dust Bowl: Lessons in science, policy, and adaptation. *Popul. Environ.* **35**, 417–440 (2014).
5. Z. K. Hansen, G. D. Libecap, Small farms, externalities, and the Dust Bowl of the 1930s. *J. Polit. Econ.* **112**, 665–694 (2004).
6. J. E. Weaver, *North American Prairie*, (Johnson Publishing Company, Lincoln, NE, 1954).
7. J. E. Weaver, *Prairie Plants and their Environment*, (University of Nebraska Press, Lincoln, NE, 1968).
8. B. I. Cook, J. E. Smerdon, R. Seager, E. R. Cook, Pan-continental droughts in North America over the last millennium. *J. Clim.* **27**, 383–397 (2014).
9. B. I. Cook, T. R. Ault, J. E. Smerdon, Unprecedented 21st century drought risk in the American Southwest and central plains. *Sci. Adv.* **1**, e1400082 (2015).
10. A. Dai, Increasing drought under global warming in observations and models. *Nat. Clim. Chang.* **3**, 52–58 (2013).
11. J. E. Weaver, F. W. Albertson, Effects on the great drought on the prairies of Iowa, Nebraska, and Kansas. *Ecology* **17**, 567–639 (1936).
12. J. E. Weaver, Replacement of true prairie by mixed prairie in eastern Nebraska and Kansas. *Ecology* **24**, 421–434 (1943).
13. J. E. Weaver, F. W. Albertson, Deterioration of Midwestern ranges. *Ecology* **21**, 216–236 (1940).
14. J. E. Weaver, Competition of western wheat grass with relict vegetation of prairie. *Am. J. Bot.* **29**, 366–372 (1942).
15. R. K. Monson, M. R. Sackschewsky, G. J. Williams 3rd, Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄) in the Colorado shortgrass steppe. *Oecologia* **68**, 400–409 (1986).
16. T. E. Cerling, J. R. Ehleringer, J. M. Harris, Carbon dioxide starvation, the development of C₄ ecosystems, and mammalian evolution. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **353**, 159–171, 10.1098/rstb.1998.0198 (1998).
17. T. E. Cerling *et al.*, Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**, 153–158 (1997).
18. J. R. Ehleringer, T. E. Cerling, B. R. Helliker, C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* **112**, 285–299 (1997).
19. E. J. Edwards *et al.*, C₄ Grasses Consortium, The origins of C₄ grasslands: Integrating evolutionary and ecosystem science. *Science* **328**, 587–591 (2010).
20. E. J. Edwards, C. J. Still, Climate, phylogeny and the ecological distribution of C₄ grasses. *Ecol. Lett.* **11**, 266–276 (2008).

21. H. Zhou, B. R. Helliker, M. Huber, A. Dicks, E. Akçay, C₄ photosynthesis and climate through the lens of optimality. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 12057–12062 (2018).
22. G. J. Collatz, J. A. Berry, J. S. Clark, Effects of climate and atmospheric CO₂ partial pressure on the global distribution of C₄ grasses: Present, past, and future. *Oecologia* **114**, 441–454 (1998).
23. R. W. Pearcy, J. Ehleringer, Comparative ecophysiology of C₃ and C₄ plants. *Plant Cell Environ.* **7**, 1–13 (1984).
24. C. P. Osborne, L. Sack, Evolution of C₄ plants: A new hypothesis for an interaction of CO₂ and water relations mediated by plant hydraulics. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**, 583–600 (2012).
25. J. A. Teeri, L. G. Stowe, Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* **23**, 1–12 (1976).
26. S. Pau, E. J. Edwards, C. J. Still, Improving our understanding of environmental controls on the distribution of C₃ and C₄ grasses. *Glob. Change Biol.* **19**, 184–196 (2013).
27. R. F. Sage, R. K. Monson, *C₄ Plant Biology*, (Academic Press, San Diego, CA, 1998).
28. J. M. Paruelo, W. K. Lauenroth, Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecol. Appl.* **6**, 1212–1224 (1996).
29. D. A. Frank, Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. *Oecologia* **152**, 131–139 (2007).
30. A. K. Knapp *et al.*, Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* **177**, 949–957 (2015).
31. K. R. Wilcox, J. C. von Fischer, J. M. Muscha, M. K. Petersen, A. K. Knapp, Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. *Glob. Change Biol.* **21**, 335–344 (2015).
32. R. Heitschmidt, M. Haferkamp, M. Karl, A. Hild, Drought and grazing: I. Effects on quantity of forage produced. *J. Range Manage.* **52**, 440–446 (1999).
33. J. Zscheischler, S. I. Seneviratne, Dependence of drivers affects risks associated with compound events. *Sci. Adv.* **3**, e1700263 (2017).
34. D. L. Hoover, A. K. Knapp, M. D. Smith, Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**, 2646–2656 (2014).
35. J. C. Winslow, E. R. Hunt Jr., S. C. Piper, The influence of seasonal water availability on global C₃ versus C₄ grassland biomass and its implications for climate change research. *Ecol. Modell.* **163**, 153–173 (2003).
36. H. A. Mooney, E. L. Dunn, Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. *Evolution* **24**, 292–303 (1970).
37. C. J. Still, J. A. Berry, G. J. Collatz, R. S. DeFries, Global distribution of C₃ and C₄ vegetation: Carbon cycle implications. *Global Biogeochem. Cycles* **17**, 1006 (2003).
38. D. A. Wilhite, *Drought: A Global Assessment*, (Routledge Publ., London, 2000).
39. L. D. Anderegg, W. R. Anderegg, J. A. Berry, Not all droughts are created equal: Translating meteorological drought into woody plant mortality. *Tree Physiol.* **33**, 701–712 (2013).
40. A. K. Knapp *et al.*, Characterizing differences in precipitation regimes of extreme wet and dry years: Implications for climate change experiments. *Glob. Change Biol.* **21**, 2624–2633 (2015).
41. J. S. Clark *et al.*, Drought cycles and landscape responses to past aridity on prairies of the northern Great Plains, USA. *Ecology* **83**, 595–601 (2002).
42. H. Liu, E. J. Edwards, R. P. Freckleton, C. P. Osborne, Phylogenetic niche conservatism in C₄ grasses. *Oecologia* **170**, 835–845 (2012).
43. D. M. Griffith *et al.*, Biogeographically distinct controls on C₃ and C₄ grass distributions: Merging community and physiological ecology. *Glob. Ecol. Biogeogr.* **24**, 304–313 (2015).
44. S. H. Taylor, B. S. Ripley, F. I. Woodward, C. P. Osborne, Drought limitation of photosynthesis differs between C₃ and C₄ grass species in a comparative experiment. *Plant Cell Environ.* **34**, 65–75 (2011).
45. R. J. Griffin-Nolan *et al.*, Extending the osmometer method for assessing drought tolerance in herbaceous species. *Oecologia* **189**, 353–363 (2019).
46. J. M. Cotton, T. E. Cerling, K. A. Hoppe, T. M. Mosier, C. J. Still, Climate, CO₂, and the history of North American grasses since the Last Glacial Maximum. *Sci. Adv.* **2**, e1501346 (2016).
47. P. B. Reich, S. E. Hobbie, T. D. Lee, M. A. Pastore, Unexpected reversal of C₃ versus C₄ grass response to elevated CO₂ during a 20-year field experiment. *Science* **360**, 317–320 (2018).
48. J. A. Morgan *et al.*, C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* **476**, 202–205 (2011).
49. B. Pu, R. Fu, R. E. Dickinson, D. N. Fernando, Why do summer droughts in the southern Great Plains occur in some La Niña years but not others? *J. Geophys. Res. Atmos.* **121**, 1120–1137 (2016).
50. F. W. Albertson, J. E. Weaver, Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecol. Monogr.* **14**, 393–479 (1944).
51. J. Xia *et al.*, Joint control of terrestrial gross primary productivity by plant phenology and physiology. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2788–2793 (2015).
52. X. Lian *et al.*, Summer soil drying exacerbated by earlier spring greening of northern vegetation. *Sci. Adv.* **6**, eaax0255 (2020).
53. J. E. Weaver, F. W. Albertson, Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. *Ecol. Monogr.* **13**, 63–117 (1943).
54. C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
55. E. E. Cleland, I. Chuine, A. Menzel, H. A. Mooney, M. D. Schwartz, Shifting plant phenology in response to global change. *Trends Ecol. Evol.* **22**, 357–365 (2007).
56. J. T. Morissette *et al.*, Tracking the rhythm of the seasons in the face of global change: Phenological research in the 21st century. *Front. Ecol. Environ.* **7**, 253–260 (2009).
57. D. G. Goodin, G. M. Henebry, A technique for monitoring ecological disturbance in tallgrass prairie using seasonal NDVI trajectories and a discriminant function mixture model. *Remote Sens. Environ.* **61**, 270–278 (1997).
58. X. Wang *et al.*, Has the advancing onset of spring vegetation green-up slowed down or changed abruptly over the last three decades? *Glob. Ecol. Biogeogr.* **24**, 621–631 (2015).
59. G. E. Maurer, A. J. Hallmark, R. F. Brown, O. E. Sala, S. L. Collins, Sensitivity of primary production to precipitation across the United States. *Ecol. Lett.* **23**, 527–536 (2020).
60. C. J. Still, J. M. Cotton, D. M. Griffith, Assessing earth system model predictions of C₄ grass cover in North America: From the glacial era to the end of this century. *Glob. Ecol. Biogeogr.* **28**, 145–157 (2019).
61. W. J. Bond, Ancient grasslands at risk. *Science* **351**, 120–122 (2016).
62. D. L. Fox *et al.*, Climatic controls on C₄ grassland distributions during the Neogene: A model-data comparison. *Front. Ecol. Evol.*, 10.3389/fevo.2018.00147 (2018).
63. X. Ma, A. Huete, S. Moran, G. Ponce-Campos, D. Eamus, Abrupt shifts in phenology and vegetation productivity under climate extremes. *J. Geophys. Res. Biogeosci.* **120**, 2036–2052 (2015).
64. B. A. Hungate *et al.*, The economic value of grassland species for carbon storage. *Sci. Adv.* **3**, e1601880 (2017).
65. G. Murray-Tortarolo, V. J. Jaramillo, M. Maass, P. Friedlingstein, S. Sitch, The decreasing range between dry- and wet- season precipitation over land and its effect on vegetation primary productivity. *PLoS One* **12**, e0190304 (2017).
66. D. Polson, G. C. Hegerl, X. Zhang, T. J. Osborn, Causes of robust seasonal land precipitation changes. *J. Clim.* **26**, 6679–6697 (2013).
67. C. Chou *et al.*, Increase in the range between wet and dry season precipitation. *Nat. Geosci.* **6**, 263 (2013).
68. L. Yahdjian, O. E. Sala, A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* **133**, 95–101 (2002).
69. L. A. Gherardi, O. E. Sala, Automated rainfall manipulation system: A reliable and inexpensive tool for ecologists. *Ecosphere* **4**, 1–10 (2013).
70. M. E. Loik, J. C. Lesage, T. M. Brown, D. O. Hastings, Drought-Net rainfall shelters did not cause nondrought effects on photosynthesis for California central coast plants. *Ecohydrology* **12**, e2138 (2019).
71. L. Peng, D. Li, J. Sheffield, Drivers of variability in atmospheric evaporative demand: Multiscale spectral analysis based on observations and physically based modeling. *Water Resour. Res.* **54**, 3510–3529 (2018).