



# Resolving the Dust Bowl paradox of grassland responses to extreme drought

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Edited by Sarah E. Hobbie, University of Minnesota, Saint Paul, MN, and approved July 14, 2020 (received for review December 16, 2019)

During the 1930s Dust Bowl drought in the central United States, species with the C<sub>3</sub> photosynthetic pathway expanded throughout C<sub>4</sub>-dominated grasslands. This widespread increase in C<sub>3</sub> grasses during a decade of low rainfall and high temperatures is inconsistent with well-known traits of C<sub>3</sub> vs. C<sub>4</sub> pathways. Indeed, water use efficiency is generally lower, and photosynthesis is more sensitive to high temperatures in C<sub>3</sub> than C<sub>4</sub> species, consistent with the predominant distribution of C<sub>3</sub> grasslands in cooler environments and at higher latitudes globally. We experimentally imposed extreme drought for 4 y in mixed C<sub>3</sub>/C<sub>4</sub> grasslands in Kansas and Wyoming and, similar to Dust Bowl observations, also documented three- to fivefold increases in C<sub>3</sub>/C<sub>4</sub> 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, C<sub>4</sub> grasses dominate where precipitation and air temperature are strongly related (warmest months are wettest months). In contrast, C<sub>3</sub> 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 C<sub>3</sub> 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 C<sub>3</sub> and C<sub>4</sub> species.

climate change | extreme drought | photosynthetic pathway | precipitation seasonality

The iconic “Dust Bowl” drought of the 1930s is widely regarded as one 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 C<sub>3</sub> 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 C<sub>4</sub> grasses. In some cases, this C<sub>3</sub> grass completely displaced the dominant C<sub>4</sub> grasses (11, 12). Because the C<sub>4</sub> photosynthetic pathway had yet to be discovered at this time, and traits associated with C<sub>3</sub> and C<sub>4</sub> pathways were not yet understood, the expansion of this C<sub>3</sub> 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 C<sub>3</sub> vs. C<sub>4</sub> photosynthetic pathways, such a widespread increase in C<sub>3</sub> 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 C<sub>4</sub> grasses (15). These traits are consistent with the broader C<sub>3</sub>/C<sub>4</sub> paradigm of C<sub>4</sub> photosynthesis initially evolving in response to low CO<sub>2</sub> (16–18) but spreading widely in part due to the capacity of C<sub>4</sub> 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 (C<sub>4</sub> grasses) decreased, while those preferring cooler climates (C<sub>3</sub> 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 C<sub>3</sub> 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.

Author contributions: A.K.K., S.L.C., Y.L., and M.D.S. designed research; R.J.G.-N., L.E.B., C.J.W.C., J.E.G., A.M.H., A.K.P., and I.J.S. performed research; A.C., R.J.G.-N., L.E.B., A.M.H., X.L., and I.J.S. analyzed data; and A.K.K. and M.D.S. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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Data deposition: The data reported in this paper are available in Dryad (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.3j9kd51dv>).

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This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1922030117/-DCSupplemental>.

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  $\sim 350,000$  km<sup>2</sup> region from South Dakota to Kansas (6, 7), represents a paradox today.

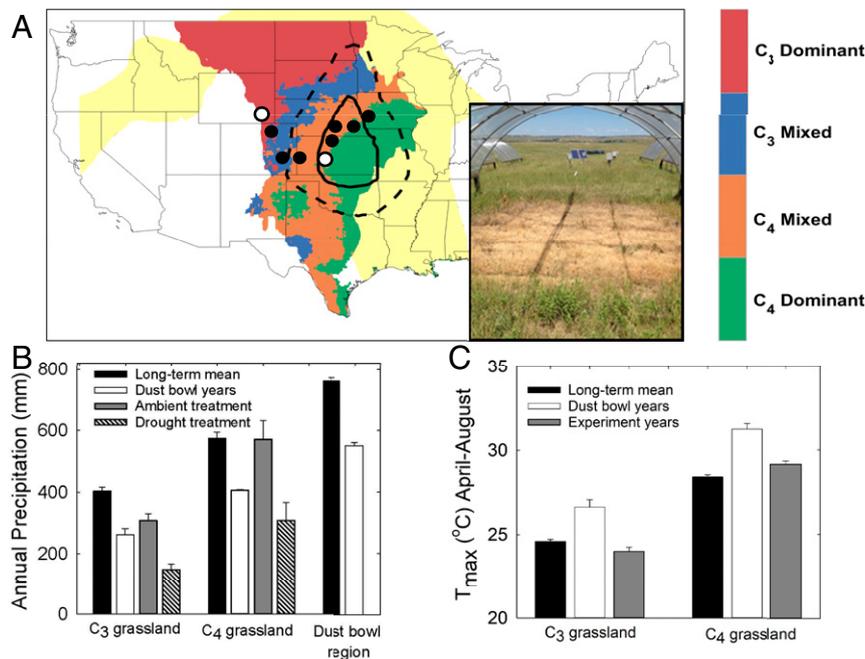
Here, we report results from a 4-y drought experiment (*Methods*) conducted in two native grasslands with a mix of  $C_3$  and  $C_4$  species. These grasslands were selected because their plant communities included *P. smithii*, the  $C_3$  grass that increased most notably during the Dust Bowl drought (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](http://www.ncdc.noaa.gov)). Means and  $\pm 1$  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 C<sub>3</sub> to C<sub>4</sub> grass biomass (C<sub>3</sub>/C<sub>4</sub> ratio) for a C<sub>3</sub>-dominated mixed grassland in Wyoming and a C<sub>4</sub>-dominated mixed grassland in Kansas**

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

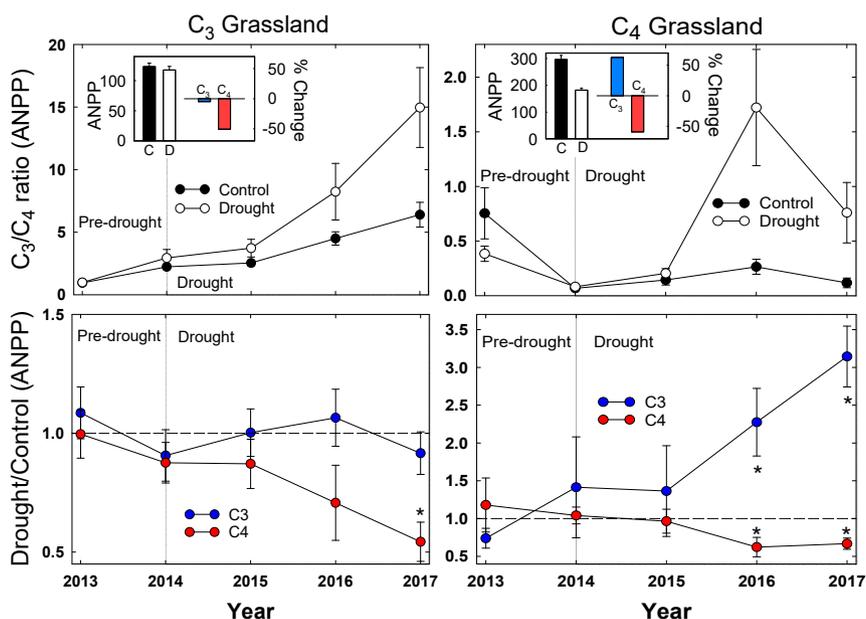
Year was a continuous term. Pretreatment data were not included in this analysis. F, F statistic.

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 C<sub>3</sub> grass that increased the most in the C<sub>4</sub>-dominated grassland (predrought *P. smithii* = 7.9 ± 1.02 g/m<sup>2</sup> [~2% of total ANPP] vs. 40.4 ± 5.21 g/m<sup>2</sup> [~23% of ANPP] in years 3 and 4 of the experimental drought). This represents a fivefold increase in ANPP of this C<sub>3</sub> grass during the experiment. Consequently, experimental drought transformed this Kansas grassland from C<sub>4</sub> dominance to C<sub>3</sub>/C<sub>4</sub> 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 C<sub>3</sub>/C<sub>4</sub> dominance to occur. In fact, the C<sub>3</sub> 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 C<sub>3</sub>-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 C<sub>3</sub> Wyoming grassland; 1,798 vs. 1,614 mm/y in the C<sub>4</sub> 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 C<sub>3</sub> and C<sub>4</sub> 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 C<sub>3</sub> vs. C<sub>4</sub> species in grasslands globally



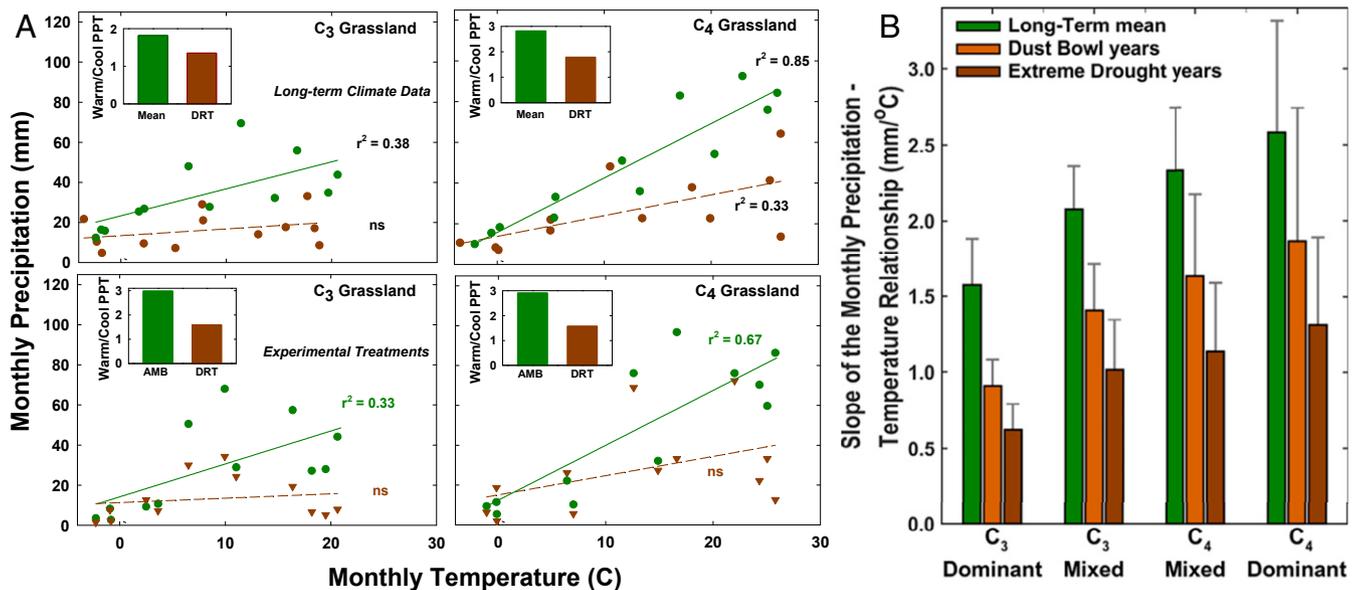
**Fig. 2.** Response of C<sub>3</sub>- and C<sub>4</sub>-dominated grasslands to a 4-y experimental drought (~50% reduction in annual precipitation). Predrought (2013) data shown as well. (*Top, Insets*) Total ANPP was insensitive to drought in the C<sub>3</sub> grassland, but ANPP was significantly reduced ( $P < 0.01$ ) in all years in the C<sub>4</sub> grassland. C = control plots, D = drought plots; values are 4-y means + SE. By year 4 of the experimental drought, productivity from C<sub>4</sub> species (red bars) had decreased by ~50% in both grasslands, but C<sub>3</sub> productivity (blue bars) only increased in the C<sub>4</sub>-dominated site. (*Top, Main*) In both grasslands, the ratio of C<sub>3</sub>/C<sub>4</sub> grass ANPP was increased by drought (year 4 in the C<sub>3</sub>-dominated grassland, years 3–4 in the C<sub>4</sub>-dominated grassland,  $P < 0.01$ ). See Table 1 for additional statistical details. (*Bottom*) Time course of how the proportion of C<sub>3</sub> (blue symbols) or C<sub>4</sub> (red symbols) grass biomass in drought vs. control plots varied. For C<sub>3</sub> grass biomass, this proportion did not vary over the 4 y in the C<sub>3</sub>-dominated grassland, but C<sub>3</sub> biomass increased threefold by year 4 in the C<sub>4</sub> grassland. In contrast, the proportion of C<sub>4</sub> grass biomass in drought vs. control plots decreased ~twofold in both grasslands by year 4 (C<sub>3</sub>) and 3 (C<sub>4</sub>). \* 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 m<sup>2</sup>, 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 C<sub>3</sub> vs. C<sub>4</sub> 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 m<sup>2</sup>) 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 (C<sub>4</sub> grasses, C<sub>3</sub> grasses, and C<sub>3</sub> forbs). Subshrubs and succulents, comprising < 5% of ANPP at both sites, were excluded from calculations due to measurement difficulties, but C<sub>3</sub> sedges, as graminoids, were included in the C<sub>3</sub> 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](http://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 C<sub>3</sub>/C<sub>4</sub> 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 C<sub>3</sub>/C<sub>4</sub> grassland categories in Fig. 1. The number of grid cells in each grassland category were: C<sub>3</sub> Dominated = 43,676, C<sub>3</sub> Mixed = 17,961, C<sub>4</sub> Mixed = 39,112, C<sub>4</sub> 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 C<sub>3</sub> and C<sub>4</sub> 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](http://www.ncdc.noaa.gov)) and the PRISM Climate Data website ([www.prism.oregonstate.edu](http://www.prism.oregonstate.edu)).

**ACKNOWLEDGMENTS.** We thank Songbai Hong and Yue Li for assistance in preparing and analyzing the climate data. N. Lemoine contributed to preliminary analyses of portions of the data. Research support was provided by the NSF: Macrosystems Biology/Emerging Frontiers Programs (EF-1239559, EF-1137378), Drought-Net Research Coordination Network DEB-1354732, and the Konza Prairie Long-Term Ecological Research program (DEB-1440484). Logistical support provided by the Colorado State University Agricultural Experiment Station, the United States Department of Agriculture–Agricultural Research Service High Plains Grasslands Research Station (Cheyenne, WY), and Keith Harmony, Kansas State University Agricultural Research Center (Hays, KS).

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