Received: 18 November 2022 | Accepted: 2 March 2023

DOI: 10.1111/1365-2745.14096

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Compensatory dynamics drive grassland recovery from drought

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Funding information
Strategic Priority Research Program of Chinese Academic of Sciences, Grant/Award Number: XDA23080401; National Natural Science Foundation of China, Grant/Award Number: 41877542, 32171549 and 31971465; Youth Innovation Promotion Association CAS, Grant/Award Number: 2020199; National Science Foundation, Grant/Award Number: DEB-1856383

Handling Editor: Pierre Mariotte

Abstract

1. Grasslands are expected to experience droughts of unprecedented frequency and magnitude in the future. Characterizing grassland responses and recovery from drought is therefore critical to predict the vulnerability of grassland ecosystems to climate change. Most previous studies have focused on ecosystem responses during drought while investigations of post-drought recovery are rare. Few studies have used functional traits, and in particular bud or clonal traits, to explore the mechanisms underlying grassland responses to and recovery from drought.
2. To address this issue, we experimentally imposed a four-year drought in a C_3-dominated grassland in northeastern China and monitored recovery for 3 years post-drought. We investigated the immediate and legacy effects of drought on total above-ground net primary productivity (ANPP), ANPP of functional groups (rhizomatous grasses, bunch grasses and forbs), and how the legacy effects were driven by plant species diversity, clonal traits and vegetative traits.
3. We found that drought progressively reduced total ANPP over the 4-year period. The reductions in total ANPP in the first and third drought years were caused by the decrease in ANPP of bunch grasses only, while that of the second year was caused by declines in ANPP of bunch grasses and forbs, and the fourth year decline was linked to all three functional groups. The post-drought recovery of ANPP, which occurred despite the continued loss of plant species diversity, was mainly driven by rapid recovery of rhizomatous and bunch grasses, which compensated for the slow response by forbs. The rapid post-drought recovery of

these grasses can be attributed to their relatively large, intact bud and shoot densities post-drought, as well as the recovery of plant height and specific leaf area. The rapid recovery of grasses possibly restricted the growth and distribution of forbs, resulting in reduced forb ANPP and, consequently, lower species diversity during the recovery period.

4. *Synthesis*. These results highlight the potential for positive legacy effects of drought on ANPP as well as the important and complementary roles of plant reproductive and vegetative traits in mediating ecosystem recovery from drought in a C_3-dominated grassland.

KEYWORDS
bud bank, clonal traits, diversity, drought, grasslands, productivity, recovery, vegetative traits

1 | INTRODUCTION

Grasslands occupy 40% of the earth's land surface and provide critical ecosystem services, such as water and nutrient cycling, biodiversity and forage production (Bai & Cotrufo, 2022). Grasslands are expected to experience severe drought of unprecedented frequency and magnitude with climate change (Hessl et al., 2018; Huang et al., 2016), threatening their ability to provide these ecosystem functions and services (Gremer et al., 2015; Yao et al., 2020). Given the high sensitivity of grassland productivity to interannual variability in precipitation, the negative effects of drought on ecosystem function and structure are expected to be particularly strong in these water-limited systems (Bondaruk et al., 2022; Huxman et al., 2004; Maurer et al., 2020). Identifying the mechanisms governing variations in ecosystem function and structure under drought conditions is therefore critical to predict the vulnerability of grasslands to extreme climate events.

Grassland function and structure can be shaped by current drought conditions (Luo et al., 2021; Ma et al., 2022) and the legacy of past drought (Griffin-Nolan et al., 2018; Luo et al., 2023; Sala et al., 2012; Sun et al., 2022). The magnitude and direction of grassland responses to drought are governed by the capacity of a grassland to either withstand drought or rapidly recover after drought (Albertson & Weaver, 1944; Isbell et al., 2015). To date, most studies have assessed grassland responses to drought (Gao et al., 2019; Luo et al., 2021), while studies investigating how grassland ecosystems recover from drought are less common (Griffin-Nolan et al., 2018; Ingrisch & Bahn, 2018; Müller & Bahn, 2022; Sun et al., 2022; Zhou et al., 2022). However, drought legacies can influence grassland processes and functions for many years following severe drought (Broderick et al., 2022; De Boeck et al., 2018; Smith & Boers, 2023). Therefore, quantifying drought recovery and factors determining legacy effects of drought on grassland function and structure remains a major knowledge gap.

Natural grasslands are generally composed of three plant functional groups based on their functional traits—rhizomatous grasses, bunch grasses and forbs (Kang et al., 2007; Qian et al., 2017). These three functional groups could exhibit different responses to drought and/or during the post-drought recovery period (Jones et al., 2016; Mackie et al., 2019; Wellstein et al., 2017). The degree of compensatory dynamics—maintenance of ecosystem function by some productive plant species or functional groups that compensate for the reduced, slow or no contribution of others at a particular time of and/or after an event (Valerio et al., 2022)—may drive the recovery of productivity after a drought spell (Zhou et al., 2022). For example, above-ground net primary productivity (ANPP) drastically declined in a grassland via biomass losses of grasses and forbs during a 2-year experimental drought, but completely recovered 1-year post-drought (Hoover et al., 2014). During the recovery period, however, productivity of forbs remained stunted due to limited shoot densities, but the productivity of the dominant rhizomatous grasses increased via increases in tiller densities (Hoover et al., 2014). Therefore, understanding the compensatory dynamics between different plant functional groups is critical for unveiling how grassland ecosystems recover from drought.

Recently, plant trait-based approaches have been widely adopted to explain and predict ecosystem responses to and recovery from climate anomalies, such as extreme drought (Chandregowda et al., 2022; Griffin-Nolan et al., 2019; Jung et al., 2014; Ru et al., 2023). Traits reflect many aspects of plant performance and fitness, including growth, survival and reproduction (Adler et al., 2014; He et al., 2019). Clonal traits (e.g. the bud bank and shoot density) are particularly important for regulating population persistence and community structure and dynamics (Benson et al., 2004; Benson & Hartnett, 2006); Indeed, clonal traits could largely determine the rate of recovery of grasslands following drought (Meng et al., 2021; Reichmann et al., 2013; Reichmann & Sala, 2014). Furthermore, water availability after drought may drive grassland recovery via rapid growth of resource-acquisitive plants (e.g. plants with high specific leaf area, SLA) which can compensate for the slow recovery of more conservative resource-capturing species (e.g. plants with low SLA; Grady et al., 2013; Wellstein et al., 2017). In contrast, plants with conservative resource-capture traits, such as low plant height (Luo et al., 2021) and low SLA (Griffin-Nolan et al., 2019) that experience minimal productivity loss during drought,

may promote the rapid recovery of productivity after drought. Thus, an in-depth understanding of mechanisms underlying compensatory dynamics is needed to predict how grasslands will respond to extreme climatic events in the future.

To explore how plant functional groups and traits contribute to post-drought recovery, we imposed an extreme 4-year drought followed by a 3-year recovery period in a C_3-dominated perennial grassland in northeastern China. We investigated the immediate and legacy effects of drought on total ANPP, ANPP of each functional group (rhizomatous grasses, bunch grasses and forbs), and whether legacy effects were driven by species diversity, clonal traits (bud and shoot densities and shoot: bud ratio), and vegetative traits (plant height and SLA). We hypothesized that drought would progressively reduce grassland ANPP with increasing duration due to the loss of each functional group (rhizomatous grass, bunch grass and forbs), while ANPP would rapidly recover from drought via compensatory dynamics between the three functional groups. We also tested the hypothesis that large bud banks and community traits (i.e. high plant height and SLA) would confer a higher recovery rate of ANPP following drought.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted our drought experiment in a grassland dominated by C_3 species at the Erguna Forest-Steppe Ecotone Research Station of the Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, located in Inner Mongolia Autonomous Region, northeastern China (50°10′46″ N, 119°22′56″ E). These experimental plots are part of the global Drought-Net research network (https://drought-net.colostate.edu/). This site was modestly grazed by domestic livestock until 2013. The region is characterized by a temperate continental monsoon climate. Based on long-term meteorological data (1970–2021), mean annual temperature of the site is −1.9°C and mean annual precipitation is ~354 mm. About 75% of the total precipitation falls during the growing season (May–August) when peak temperatures also occur. This grassland site is a representative of the regional grassland biome, based on the perennial C_3 species that dominate grasslands in northeastern China (Kang et al., 2007), such as *Leymus chinensis* (rhizomatous grass), *Carex duriuscula* (rhizomatous sedge), *Stipa baicalensis* (bunch grass), *Pulsatilla turczaninovii* (deep-rooted forb) and *Artemisia frigida* (deep-rooted forb). The soil is classified as chestnut under the China soil taxonomy classification system, equivalent to calcicorthic aridisol soils in the United States (Kang et al., 2007). We have appropriate permits to carry out our field work.

2.2 | Experimental treatments

In 2015, we established drought and control plots in a relatively homogeneous grassland with similar soils, vegetation and climate. We imposed drought with rainout shelters designed to exclude 100% of precipitation in mid-growing season (June and July) each year (2015–2018; Figure S1). This is equivalent to a 50% reduction in annual precipitation amounts and events, because ~75% of annual precipitation falls during the growing season at this site. This precipitation reduction treatment meets the definition of an extreme drought event (Slette et al., 2020; Figure S2). We removed the rainout shelters to assess recovery from 2019 to 2021. During this recovery period, both drought and control plots received ambient precipitation throughout the growing season.

The experimental design was a randomized complete block design with six replications of each treatment, 12 plots of 6 m × 6 m within 6 blocks. The rainout shelters were constructed with light scaffolding and covered by strips of transparent polyethylene (Beijing Plastics Research Institute, Beijing, China; Yahdjian & Sala, 2002). The shelters had minimal shading effects (<10% reduction in photosynthetically active radiation; wavelength range: 250–700 nm) and exerted little impact on air and soil temperature (automatically gathered with sensors). The roofs of these shelters were 2.5 m high at the highest point, allowing for near surface air exchange while avoiding unwanted greenhouse effects. We hydrologically isolated all plots from the surrounding soil by trenching the perimeter to a depth of 1 m and lining the trench with 6-mm-thick plastic and metal flashing. Further details on the experimental design can be found in Luo et al. (2021) and Muraina et al. (2021).

2.3 | Field sampling and measurements

To assess drought and post-drought effects on total ANPP and the ANPP of rhizomatous grasses, bunch grasses and forbs in each plot, we sampled plant biomass within two 50 cm × 50 cm vegetation quadrats at the end of each growing season (mid-August) of each drought (2015–2018) and recovery (2019–2021) year. We harvested above-ground biomass of all plants by clipping them at the ground level (excluding the dead materials from previous year). For each plot, we sorted the total above-ground biomass into different functional groups and species before oven-drying at 65°C for 48 h. Total ANPP ($g\,m^{-2}$) for each plot per year was estimated as the sum of the dry biomass weight of all plants averaged across the two quadrats. The functional group or individual species biomass in each plot was recorded as the average of each functional group biomass or individual species biomass across the two quadrats in each plot (Luo et al., 2021).

To measure clonal traits (i.e. bud and shoot densities and shoot:bud ratio), a soil block (30 cm × 30 cm × 30 cm) attached to the above-ground shoots was excavated near one of the two quadrats where biomass was sampled in each plot in the first recovery year (2019). The connections between above-ground shoots and below-ground organs were kept intact for species and bud type identification. Then, below-ground buds were categorized into four types: (1) tiller buds (axillary buds at the shoot base of caespitose and rhizomatous grasses); (2) rhizome buds (axillary and apical buds on hypogeogenous rhizomes); (3)

bulb buds (meristems wrapped in the swollen leaf base or scale leaf of a bulb); and (4) dicot buds (buds on below-ground parts of dicotyledonous herbs; Qian et al., 2017). Shoot and bulb bases were dissected to count tiller and bulb buds, while rhizome and dicot buds were counted without dissection (Qian et al., 2017).

We measured plant height (the distance from the ground level to the top of a plant, cm) from more than five sun-exposed individuals of each species near one of the two vegetation quadrats in each plot. Then, three newly emerged and fully expanded leaves were clipped from the same individuals at the base of the petiole and placed in plastic bags containing a moist paper towel. Leaves were scanned after being completely rehydrated, and leaf area was estimated using ImageJ software (https://imagej.nih.gov/ij/). Leaf dry weight was then measured after drying of leaves at 65°C for 48 h to calculate SLA (the ratio of leaf area to leaf dry mass, $m^2\ kg^{-1}$) following standardized protocols (Garnier et al., 2001). The species that we measured vegetative traits of cumulatively represented at least 90% of the total ANPP in each plot. Measurements of plant height and SLA were repeated during two recovery years (2020 and 2021).

2.4 | Statistical analyses

Growing season precipitation patterns (i.e. rainfall amounts, event number, event size and the length of dry period intervals) for the control and drought treatments were compared to the estimated probability density functions of long-term (1970–2021) growing season precipitation every year (2015–2021).

Plant species were sorted into rhizomatous grasses with rhizome buds, bunch grasses with tillers and rhizome buds, and forbs with bulb and dicot buds (Figure S3).

Species diversity was calculated using the relative biomass of each species by means of two diversity indices: Simpson's diversity index (D) calculated as:

$$D = 1 - \sum_{i=1}^{S} p_i^2, \quad (1)$$

and Shannon's diversity (H) index calculated as:

$$H = -\sum_{i=1}^{S} p_i \times \ln(p_i), \quad (2)$$

where p_i is the relative biomass of species i and S is the number of species.

Community-weighted means (CWM) of plant height or SLA (total, rhizomatous grasses, bunch grasses and forbs) were quantified as:

$$\text{CWM traits} = \sum_{i=1}^{S} p_i x_i, \quad (3)$$

where p_i is the relative biomass of species i, x_i is the trait values of species i and S is the species number.

Mixed-model analysis of variance (mixed-model ANOVA, *lme* function in NLME package) was used to explore the impact of drought on ANPP (total, rhizomatous grasses, bunch grasses and forbs) and species diversity (i.e. Simpson's and Shannon's diversity indices) in both drought and recovery years. With this model, we explored the interaction of drought treatment and year (fixed effects) on ANPP and diversity while block was set as a random effect. When interactions between treatment and year were significant, we used a mixed-model ANOVA with block as a random effect to analyse the treatment effect in each year.

To identify which species contributed to ANPP (total, rhizomatous grasses, bunch grasses and forbs) during drought and recovery, we estimated the effect of drought and recovery on each species in our study site by calculating the difference in biomass between drought and control plots in each drought (2015–2018) and recovery (2019–2021) year. We conducted linear mixed-effect models using *lme* function in NLME package, with year and block set as random effects, to explore the relationships between total ANPP and species diversity during the 4 years of drought and 3 years of recovery. Next, we investigated the correlation between grass and forb ANPP during the 4 years of drought and 3 years of recovery using *cor.test* function in base R.

We calculated the legacy effects of drought on clonal traits (i.e. bud and shoot densities, and shoot:bud ratio) and vegetative traits (i.e. CWM of plant height and SLA) for the whole community (total) and each functional group (rhizomatous grasses, bunch grasses and forbs). In each model, drought treatment was used as a fixed factor with block and year as random factors.

We performed Shapiro–Wilk's Test to test for normality of all data before statistical analyses using the *shapiro.test* function in base R. For all analyses, non-normal data were transformed prior to analyses. We conducted all analyses using R software (R i386 3.4.0).

3 | RESULTS

3.1 | Drought effects on precipitation

Growing season precipitation amount was close to the 50th percentile of historic amounts and similar across the first 6 years of the experiment (2015–2020), but higher in the final year of drought and recovery (2021; Figure S2). Mean daily temperature was similar throughout the experiment (2015–2021; Figure S4).

3.2 | Effects of drought and recovery on productivity

Drought reduced ANPP and that of forbs and grasses differently over time (significant treatment × year interactions; Table 1, Figure 1). Drought decreased total ANPP in each drought year (Table 1, Figure 1a), with drought more than doubling the loss of ANPP by the fourth year (74% decline) compared to the first year (34% decline),

TABLE 1 Results of mixed-models analysis of variance for above-ground net primary productivity (ANPP) (total, rhizomatous grasses, bunch grasses and forbs) and species diversity (Simpson's and Shannon's diversity) in a C_3-dominated grassland.

			ANPP				Species diversity	
Effect	numDF	denDF	Total	Rhizomatous	Bunch	Forb	Simpson	Shannon
Drought								
Treatment (T)	1	39	90.30***	13.38***	56.94***	26.01***	23.77***	51.68***
Year (Y)	1	39	12.16**	12.22**	0.39	0.89	5.34*	6.50*
T×Y	1	39	24.90***	8.72**	1.47	6.86*	3.96	4.94*
Recovery								
T	1	27	12.17**	37.99***	0.03	21.96***	131.46***	118.15***
Y	1	27	10.90**	3.69	3.29	1.45	4.89*	2.21
T×Y	1	27	0.09	1.95	0.05	3.01	0.06	0.05

Note: Treatment (drought vs. control) and year were used as fixed factors with block as a random factor. *F*-values and degree of freedom are shown. Statistical significance is represented by asterisks (***$p<0.001$, **$p<0.01$, and *$p<0.05$).

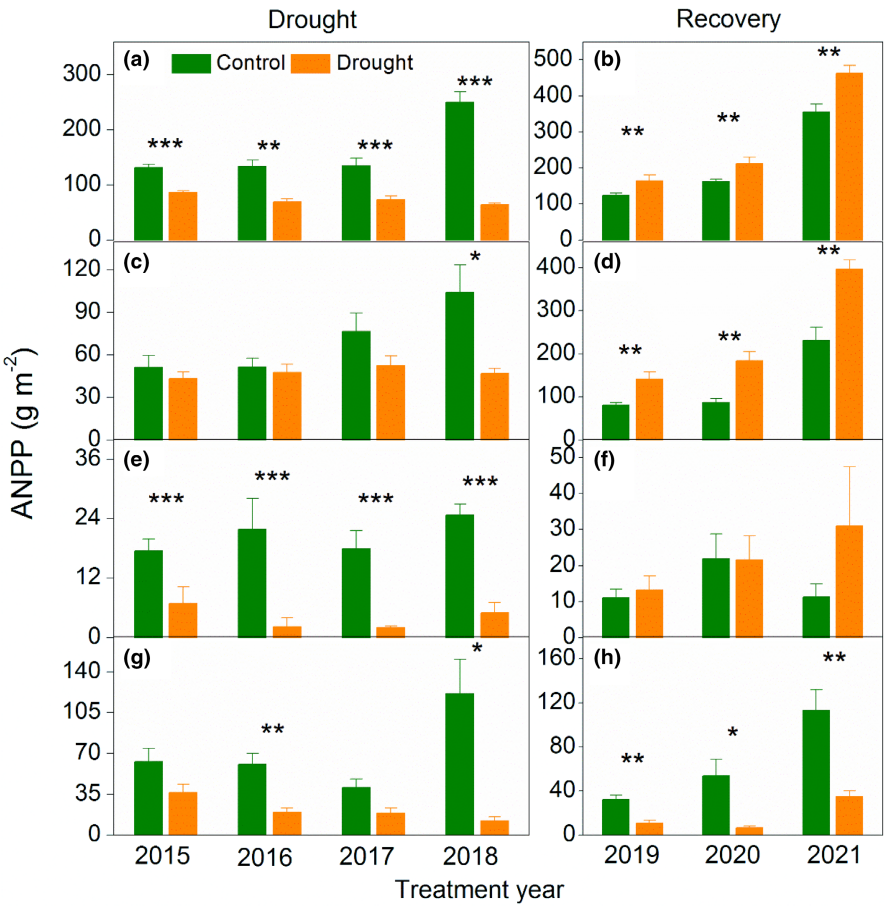

FIGURE 1 Responses of above-ground net primary productivity (ANPP) to 4 years of experimental drought as well as recovery over 3 years. Responses of ANPP are divided into (a, b) total, (c, d) rhizomatous grasses, (e, f) bunchgrasses and (g, h) forbs. Statistical significance of treatment effect is depicted as ***$p<0.001$, **$p<0.01$ and *$p<0.05$. Note the differences in y-axis scales between drought and recovery.

although this relative reduction depended on the productivity in ambient plots (i.e. 2018 being very productive). The reduction in total ANPP during drought was driven by reductions in rhizomatous grasses (i.e. *L. chinensis* and *C. duriuscula*), bunch grasses (e.g. *S. baicalensis*) and forbs (e.g. *P. turczaninovii* and *A. frigida*; Figure S3). ANPP of rhizomatous grasses did not change in the first three drought years (2015–2017), but was 55% lower than in control plots in the fourth year of drought ($F = 9.67$, $p<0.05$; Figure 1b), although this was likely due to a very wet a productive ambient year (Figure S2). Drought reduced ANPP of forbs in the second ($F = 29.25$, $p<0.01$) and fourth ($F = 13.50$, $p<0.05$) treatment years by 68% and 90%, respectively, but not in the other years (Figure 1d). Drought significantly decreased the ANPP of bunch grasses regardless of year (non-significant treatment×year interactions; Table 1, Figure 1c).

The legacy effects of drought did not vary for total ANPP and ANPP of each functional group (rhizomatous grasses, bunch grasses

and forbs) across the three recovery years (Table 1). As precipitation amount was higher in the final year of our study (2021; Figure S2), total ANPP in control plots was relatively higher in this recovery year than the previous 6 years (2015–2020; Figure 1).

During the recovery period, total ANPP was ~30% higher in drought vs. control plots regardless of year (nonsignificant treatment × year interactions; Table 1, Figure 1a). The recovery of total ANPP after drought was driven by the increased growth of the rhizomatous grass, *L. chinensis*, and bunch grass, *S. baicalensis*, which compensated for the continued stunted growth of forbs, such as *P. turczaninovii*, *Thermopsis lanceolate* and *A. frigida* (Figure S3). The ANPP of rhizomatous grasses in droughted plots was significantly higher than that of control plots in 2019 ($F = 19.61$, $p < 0.01$), 2020 ($F = 29.48$, $p < 0.01$) and 2021 ($F = 27.35$, $p < 0.01$), respectively (Figure 1b), but ANPP of bunch grasses did not differ between control and drought plots (Table 1, Figure 1c). In contrast, negative drought legacy effects on forb ANPP were observed in each recovery year (Figure 1d), as ANPP of forbs was significantly lower in drought vs. control plots in 2019 ($F = 36.07$, $p < 0.01$), 2020 ($F = 9.85$, $p < 0.05$) and 2021 ($F = 24.84$, $p < 0.01$), respectively (Figure 1d).

No correlation was observed between grass and forb ANPP during the 4 years of drought (Figure S5a). However, a strong negative correlation was observed between grass and forb ANPP during the recovery period (Figure S5b).

3.3 | Immediate and legacy effects of drought on species diversity

Drought decreased Simpson's diversity regardless of year (2015–2018; nonsignificant treatment × year interactions; Table 1, Figure 2). Drought did not alter Shannon's diversity in 2015, but significantly decreased it in 2016 ($F = 11.14$, $p < 0.05$), 2017 ($F = 11.56$, $p < 0.05$) and 2018 ($F = 39.59$, $p < 0.01$; Figure 2). The legacy effects of drought on species diversity did not vary across the three post-drought years (Table 1). Both diversity indices were significantly lower in drought vs. control plots in each recovery year (nonsignificant treatment × year interactions; Table 1, Figure 2).

A positive relationship was observed between total ANPP and each index of species diversity during the 4 years of drought (Figure S6). However, a negative relationship was observed between total ANPP and species diversity during the recovery period (Figure S6).

3.4 | Drought legacy effects on plant traits

No legacy effects of drought were observed on below-ground bud density of all plants in the community, bunch grasses or rhizomatous grasses (Figure 3a), and on above-ground shoot density of all plants or each functional group (Figure 3a). However, a negative drought legacy effect was observed on below-ground bud density of forbs ($F = 9.84$, $p < 0.05$), as well as their shoot: bud ratio ($F = 18.45$, $p < 0.01$; Figure 3a).

Plant height of the whole community significantly increased by 28% in drought vs. control plots during the recovery period ($F = 15.88$, $p < 0.01$), but SLA did not vary (Figure 3b). Plant height of rhizomatous and bunch grasses in drought plots was 19% ($F = 7.07$, $p < 0.05$) and 125% ($F = 22.14$, $p < 0.001$) higher than in control plots during the recovery period, respectively (Figure 3b). We did not observe drought legacy effects on SLA of rhizomatous grasses, bunch grasses or forbs (Figure 3b).

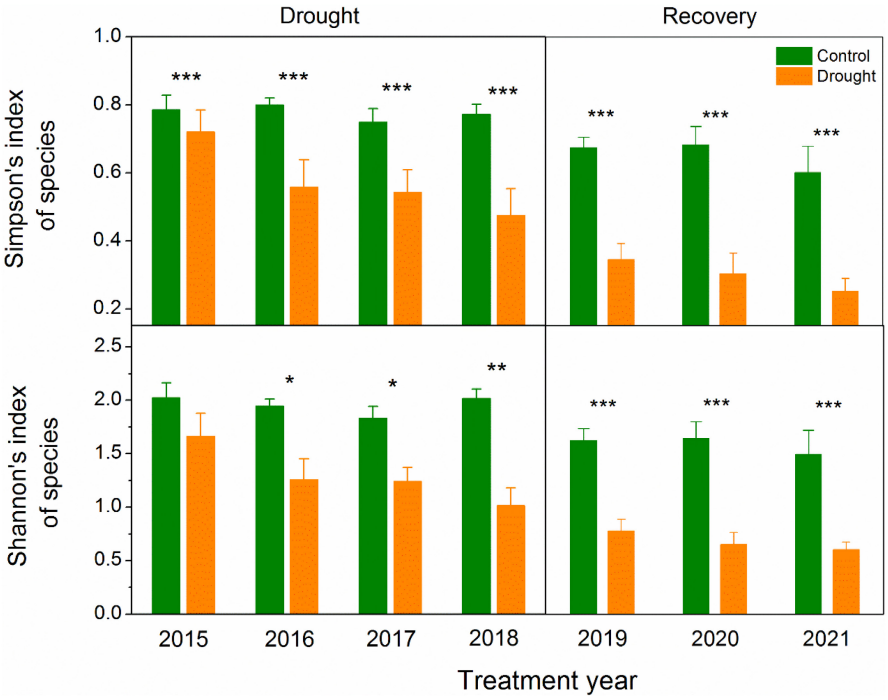

FIGURE 2 Responses of plant species diversity to 4 years of experimental drought as well as recovery over 3 years. Focal diversity included Simpson's and Shannon's diversity indices. Significance of treatment effect is depicted as ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$.

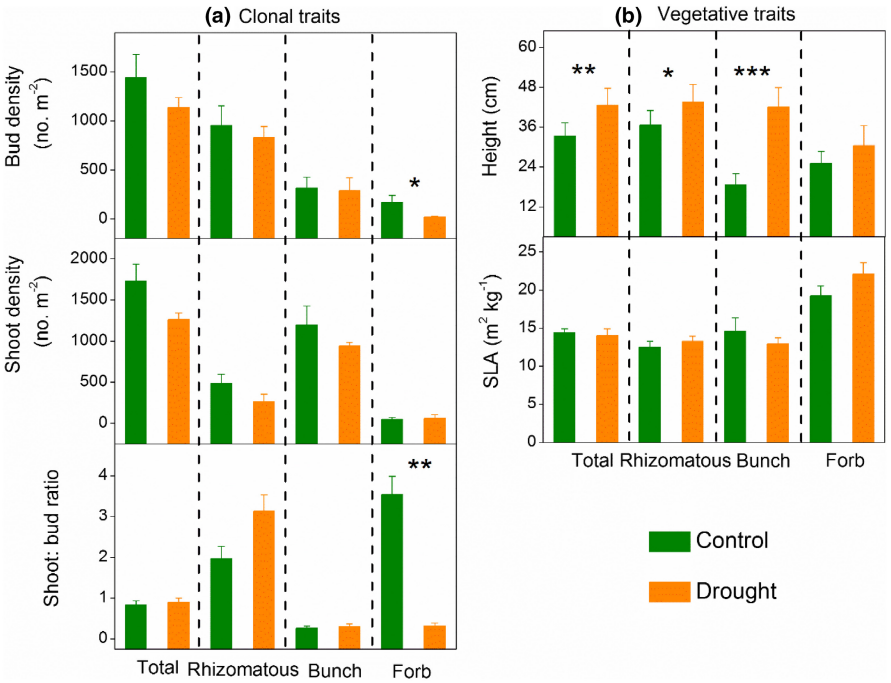

FIGURE 3 Legacy effects of drought on (a) clonal traits (below-ground bud density, above-ground shoot density and shoot:bud ratio) and (b) vegetative traits (plant height and specific leaf area, SLA) of the whole community (total) and the functional groups (rhizomatous grasses, bunch grasses and forbs). Different letters indicate significant differences between functional groups at $p < 0.05$. Statistical significance of drought legacy effect is depicted as $^{***}p < 0.001$, $^{**}p < 0.01$ and $^{*}p < 0.05$.

4 | DISCUSSION

4.1 | Ecosystem response to drought

Grassland productivity in any given year can be affected by antecedent conditions from previous years (Müller & Bahn, 2022); yet, our understanding of the recovery pattern of grassland productivity after multi-year extreme drought events is limited. Here, we showed the immediate and legacy effects of extreme drought (i.e. 100% precipitation exclusion in two growing season months for 4 years followed by 3 years of recovery) on productivity of a C_3-dominated grassland. We anticipated a progressive reduction in the total productivity over time during drought. Consistent with our expectation, our experimental drought substantially reduced grassland ANPP (Figure 1) and the reduction increased over time as predicted, which may be due to differences in variation in ambient precipitation (Figure S2). Similar drought-induced reductions in ANPP have been reported in C_4-dominated grasslands (Carroll et al., 2021; Hoover et al., 2014). Unlike the larger productivity losses observed in our C_3-dominated grassland in China, Carroll et al. (2021) observed minimal loss of ANPP (i.e. 6%) in the first year of a similar type of 4-year drought in a C_3-dominated grassland in the United States. These contrasting responses further substantiate the possibility of variations in the magnitude and direction of responses of different ecosystems to climate perturbations (Knapp et al., 2020; Muraina et al., 2021).

Experimental drought led to variable impacts on rhizomatous grasses, bunch grasses and forbs over time. Specifically, ANPP of rhizomatous grasses only declined in the fourth year of drought, while bunch grasses and forbs experienced declines throughout the 4-year drought period (Figure 1). This suggests that rhizomatous grasses, which represent the bulk of total ANPP in this grassland and regionally (Kang et al., 2007), were resistant to multi-year drought. The rhizomatous grasses (e.g. *L. chinensis*) possibly succeeded in avoiding the negative drought effects during the first 3 years by using their large network of rhizomes to access water and nutrients from a larger volume of soil (Chaves et al., 2003; Volaire et al., 2009; Zhou et al., 2014). The rhizomatous grasses could have also maintained growth via the carbohydrate, nutrients and water stored in their rhizomes (Bai et al., 2010; Meng et al., 2021; Wang et al., 2008). On the other hand, the consistent susceptibility of the bunch grasses (e.g. *S. baicalensis*) could be traced to their tufted growth habit, which lacks a network of rhizomes for accessing water from larger volumes of soil during drought or stored adequate nutrients for use during water deficit (Chen et al., 2005).

4.2 | Ecosystem recovery from drought

We expected that grassland productivity would fully recover from drought through compensatory dynamics between rhizomatous grasses, bunch grasses and forbs. Despite substantial declines in grassland productivity during the 4-year drought, productivity recovered completely in the first year after drought, and even exceeded productivity of control plots (Figure 1). These observations are consistent with the studies that suggest grassland ecosystems have low capability to withstand drought, but high capability to recover from experimental drought (Hoover et al., 2014; Stampfli et al., 2018; Vogel et al., 2012).

The rate of recovery after drought in our ecosystem was mainly due to the rapid regrowth of rhizomatous grasses (e.g. *L. chinensis*) and bunch grasses (e.g. *S. baicalensis*; Figure 1 and Figure S3). Rhizomatous grasses in particular rapidly recruit new individuals and restore growth after drought, which has been shown to contribute

to the high recovery of total ANPP (Hoover et al., 2014). This rapid post-drought recovery of ANPP occurred, even though species diversity declined during drought and remained low during the recovery period (Figure 2 and Figure S6). This result is consistent with other grassland research that found full recovery of ecosystem function but not functional diversity after only 1 year of drought (Hoover et al., 2014; Ru et al., 2023; Vogel et al., 2012). In contrast, while grasses promoted recovery in our grassland ecosystem, Ratajczak et al. (2019) and Wilcox et al. (2020) found forbs were responsible for recovery of ecosystem function in grasslands in North America and South Africa. Notably, the third recovery year (2021) was a relatively wet year with higher ANPP, yet we still observed large differences between previously droughted and control plots.

Below-ground buds account for more than 99% of above-ground shoot variations in temperate grassland ecosystems (Benson & Hartnett, 2006). Thus, the demography of buds and shoots is an important ecological mechanism for understanding post-drought recovery (Qian et al., 2022; Stampfli et al., 2018). In our study, both rhizomatous and bunch grasses had relatively higher bud and shoot densities, allowing them to quickly re-sprout post-drought. Moreover, the lack of drought legacy effects on bud and shoot density of grasses (Figure 3a) aided the high recovery rate, and subsequent dominance, of grasses following drought. The observed higher recovery rate of rhizomatous grasses than bunch grasses could be attributed to their rhizome buds, which allow them to rapidly take advantage of available resources, recruit new individuals and populate the surrounding habitat following drought (Dalgleish & Hartnett, 2006).

In contrast to grasses, we observed negative legacy effects of drought on the productivity of deeper-rooted forbs, such as *P. turczaninovii*, *T. lanceolate* and *A. frigida* (Figure S3). The potential explanations for this legacy effect on forbs include a lack of below-ground buds for regeneration (Klimešová & Herben, 2015) and dependence on deeper soil moisture (Schwinning et al., 2005). The observed negative legacy effects of drought on forb bud densities and shoot:bud ratios indicates that the bud limitation for tiller growth may have impeded forb productivity following drought. Because sampling bud banks is highly destructive we only measured bud banks in the first year following drought to assess potential for recovery. This precluded longer-term assessment of the relationship between clonal traits and post-drought recovery in this grassland.

Plant vegetative traits, such as plant height and SLA, have been associated with community resource-use strategies during drought events and recovery periods (Jung et al., 2014; Luo et al., 2021). Therefore, these two traits are expected to be predictive of ecosystem recovery potential after drought. As expected, we observed a positive drought legacy effect on community plant height, and height of rhizomatous and bunch grasses. However, we did not observe legacy effects for community-level SLA or for each functional group (Figure 3b). When environmental conditions permit rapid acquisition of resources after drought, grasses take advantage of water availability and re-sprouted from basal meristems, restricting the growth and distribution of forbs (Stampfli et al., 2018). The higher plant height of the grasses, especially *L. chinensis*, possibly gave them competitive advantage over forbs to efficiently acquire light and water, which led to their strong recovery after drought. Indeed, we found a negative correlation between grass and forb productivity during the post-drought period (Figure S5), which suggests high competition between grasses and forbs following drought but not during drought. The rapid recovery of grasses, which may be due to their taller stature, possibly restricted the growth and distribution of forbs, resulting in reduced forb productivity and lower species diversity during the recovery period. These results highlight the important roles of plant traits in mediating ANPP recovery from drought in the studied grasslands.

5 | CONCLUSIONS

In this study, we assessed how plant functional groups and their traits determine productivity response to and recovery from long-term drought in a C_3-dominated perennial grassland. We found a reduction in ecosystem productivity due to reduced ANPP of grasses and forbs in response to drought. Despite this loss of ANPP, full recovery of this important ecosystem function occurred in one growing season after drought. The presence of tall grasses with drought-resistant clonal traits, which favoured rapid plant regeneration and resource acquisition, likely promoted rapid ecosystem recovery. These findings have important implications for evaluating the interactive roles of plant reproductive and vegetative traits in mediating the impacts of future drought on ecosystem structure and functions in C_3-dominated perennial grasslands.

AUTHOR CONTRIBUTIONS

Wentao Luo, Xingguo Han and Scott L. Collins planned and designed the research. Wentao Luo, Wang Ma, Lin Song, Niwu Te, Jiaqi Chen, Jianqiang Qian, Chong Xu, Qiang Yu and Zhengwen Wang performed the experiments, conducted the field and laboratory work, and managed the research site. Wentao Luo, Kate Wilkins, Robert J. Griffin-Nolan and Taofeek O. Muraina wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

This study was supported by funding from Strategic Priority Research Program of Chinese Academic of Sciences (XDA23080401), National Natural Science Foundation of China (31971465, 32171549 and 41877542), Youth Innovation Promotion Association CAS (2020199) and National Science Foundation (DEB-1856383).

CONFLICT OF INTEREST STATEMENT

The authors have no competing interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14096.

DATA AVAILABILITY STATEMENT

Data available from https://doi.org/10.6084/m9.figshare.22126157.v1 (Luo, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. General view of the drought experiment.

Figure S2. Effects of experimental drought on (a) total precipitation amount (mm), (b) the number of precipitation events, (c) precipitation

event size (mm) and (d) the length of dry period intervals (# of days) during the growing season from 2015 to 2021. These precipitation characteristics were the same between control and treatment plots during the recovery period (2019–2021). These precipitation characters were recorded by a meteorological station near the experimental site. The effects of experimental drought were mapped on the estimated probability density curve based on 52-year historical precipitation data (1970–2021).

Figure S3. Difference in the biomass of each species in drought vs. control plots across four drought years (2015–2018) and three recovery years (2019–2021). Plant species were divided into rhizomatous grasses, bunch grasses and forbs. Orange and green circles indicate the observed biomass differences between control and drought plots during drought and recovery, respectively. All species except *Chenopodium* spp. are perennials.

Figure S4. The mean daily temperature under ambient conditions across the 7 years of the drought experiment (2015–2021). The temperature character was recorded in the meteorological station near experimental site.

Figure S5. Correlation between above-ground net primary productivity (ANPP) of grasses and forbs during years of experimental growing season drought and the recovery years after drought under ambient precipitation.

Figure S6. Bivariate relationships between total above-ground net primary productivity (ANPP) and species diversity (Simpson's and Shannon's diversity indices) during 4 years of experimental growing season and the three recovery years after drought under ambient precipitation.

How to cite this article: Luo, W., Ma, W., Song, L., Te, N., Chen, J., Muraina, T. O., Wilkins, K., Griffin-Nolan, R. J., Ma, T., Qian, J., Xu, C., Yu, Q., Wang, Z., Han, X., & Collins, S. L. (2023). Compensatory dynamics drive grassland recovery from drought. *Journal of Ecology*, *111*, 1281–1291. https://doi.org/10.1111/1365-2745.14096