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RESEARCH ARTICLE

Responses of bud banks and shoot density to experimental drought along an aridity gradient in temperate grasslands

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Abstract

1. Climate change is expected to increase the magnitude and frequency of extreme drought in most grassland ecosystems. Exploring the responses of below-ground bud banks and their relationships with above-ground plant structure and drought is need to explain how climate change will impact grassland ecosystems. However, studies on the response of community-scale bud and shoot densities to experimental drought along an aridity gradient are rare.
2. We experimentally removed 66% of growing season precipitation for 4 years in three temperate grasslands that spanned an aridity gradient in northern China. We quantified the legacy effects of drought on grass, forb and total community below-ground bud density, above-ground shoot density and the ratio of bud to shoot density 1 year following treatment.
3. Below-ground bud density was lowest at the highest aridity site for the entire community, while above-ground shoot density was highest at the medium aridity site. Below-ground bud and above-ground shoot densities were the lowest at the high aridity site for grasses but the highest for forbs at this site. Bud:shoot ratios decreased with increasing aridity for grasses, yet remained constant for forbs along the aridity gradient. Below-ground bud density in drought plots remained lower than controls a year following drought at each site. Experimental drought did not alter the below-ground bud bank for grasses but decreased forb bud banks across sites. Experimental drought had little legacy effects on above-ground shoot density and bud:shoot ratios for grasses, forbs and the total community at each site.

Jianqiang Qian and Zhiming Zhang contributed equally to this work.

4. Our results suggest that grass and forb bud banks can differ in their responses to both multi-year drought along an aridity gradient, and that bud limitation for shoot generation may increase as grasslands get drier. Bud bank responses to climate will impact plant community functioning and resilience. Thus, incorporating bud bank dynamics will improve projections of grassland ecosystems under future climate change.

KEYWORDS
bud bank, clonal trait, community composition, extreme drought, functional trait, population regeneration, shoot density

1 | INTRODUCTION

Contemporary climate change is increasing the frequency and intensity of extreme drought in various regions across the world (Spinoni et al., 2014). Frequent and severe droughts can have large and long-lasting effects on ecosystem structure and function, particularly in water-limited grasslands (Du et al., 2018; Luo et al., 2021, 2022; Maurer et al., 2020; Sankaran & Staver, 2019). The level of resilience of ecosystems (i.e. the degree of recovery from disturbance), which drives ecosystem productivity following droughts, may differ among grasslands (Stuart-Haëntjens et al., 2018). For example, some grasslands exhibit rapid recovery from extreme drought as above-ground net primary productivity (ANPP) fully recovered to pre-drought levels within a year (Griffin-Nolan et al., 2019; Hoover et al., 2014; Wilcox et al., 2020). In other grasslands, drought resulted in a legacy of lower ANPP the following year (Yahdjian & Sala, 2006). However, the underlying mechanisms of differential drought sensitivity among grasslands remain understudied, especially from the perspective of plant population regeneration or recruitment. Additionally, most studies have concentrated on community structure and ecosystem functioning above-ground, while few studies have focused on the response of the below-ground bud bank to drought, especially along natural aridity gradients where drought sensitivity is expected to increase along with aridity (Knapp et al., 2015).

Plant dynamics and primary productivity almost entirely driven by asexual reproduction via below-ground bud banks in perennial grasslands (Benson & Hartnett, 2006; Klimešová & Klimeš, 2007). Below-ground bud banks play a key role in plant population regeneration, community dynamics, and ecosystem functioning following disturbances and environmental change (Ferraro et al., 2022; Ott et al., 2019; Siebert et al., 2019). As a primary resources of above-ground regrowth, the ability of bud banks to withstand drought can drive accelerated or delayed ecosystem resilience once drought ceases (Dalgleish & Hartnett, 2006, 2009; Qian et al., 2022). A recent study showed that a short-term drought reduced below-ground bud density and above-ground stem density in mesic grasslands, but bud density in the drought plots rapidly recovered and surpassed that of the non-drought plots 1 year post-drought (Carter et al., 2012). In contrast, extreme drought had a negative legacy effect on below-ground bud bank and above-ground shoot density in semiarid grasslands (Qian et al., 2022). Although these studies differ in drought duration and intensity, they suggest that ability of below-ground bud banks to recover from drought depends on functional traits and climate conditions. Below-ground bud banks can also affect the sensitivity of ANPP to environmental variation (i.e. meristem limitation hypothesis, Knapp & Smith, 2001; Dalgleish & Hartnett, 2006). If above-ground responses to precipitation are largely determined by below-ground bud banks, there is need for thorough understanding of below-ground bud dynamics to predict the responses of different grasslands to long-term extreme drought.

The vulnerability of below-ground bud banks differs among plant functional groups, with consequences for plant composition and ecosystem function (Mackie et al., 2019; Taylor et al., 2011). For example, functional groups with greater bud density and/or conservative leaf water use traits (e.g. lower specific leaf area and high leaf dry matter content) may have greater recovery ability after drought than other functional groups (Xu et al., 2017). In addition, previous studies have suggested that experimental drought had contrasting effects on grass and forb bud bank production in a restored grassland, mediating the dynamics of population structure and community composition above-ground during drought and recovery (Carter et al., 2012). Thus, understanding the differential effects of drought on below-ground bud banks between grasses and forbs is critical for explaining and predicting the changes in plant community structure, composition and functions in the context of climate change.

In this study, we investigated the legacy effects of a four-year experimental drought (i.e. 66% reduction in growing season precipitation) on below-ground bud banks, above-ground shoot density, and their community and functional group (grasses and forbs) relationships in three temperate grasslands along an aridity gradient in northern China. We hypothesized that (1) drought and increasing aridity would reduce below-ground bud bank and above-ground shoot density, whereas bud:shoot ratios (a measure of meristem limitation) would remain relatively constant, and (2) responses of below-ground bud banks and above-ground shoot density to water limitation would be higher for grasses than forbs due to their different functional strategies.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

In 2014 (pretreatment year), experimental drought infrastructure was established at three sites that represent much of the east–west extent of the temperate grasslands in northern China (Figure S1). The three sites, as part of the Drought-Net Research Coordination Network (http://drought-net.colostate.edu) and the Extreme Drought in Grasslands Experiment, vary in aridity index (AI), species composition and climatic properties (Table 1). The low aridity site (AI = 0.58) located at the National Hulunber Grassland Ecosystem Observation and Research Station (50°10′N, 119°22′E; 750 m a.s.l) receives 354 mm of mean annual precipitation (MAP) and has a mean annual temperature (MAT) of −1.1°C. The medium aridity site (AI = 0.49), located at the Inner Mongolia Grassland Ecosystem Research Station (43°33′N, 116°40′E; 1200 m a.s.l), is drier and hotter than the low aridity site (MAT = 1.9 °C; MAP = 346 mm). The high aridity site (AI = 0.17), located at the Urat Desert-Grassland Research Station (106°58′E, 41°25′N; 1650 m a.s.l), receives an average of 175 mm of precipitation annually and is the warmest of the three sites (MAT = 5.6°C). Growing season precipitation varied at each site during the drought (2015–2018) and recovery (2019) periods (Figure S2). In most years of the experiment, precipitation was lower than MAP at each site (Figure S2). Plant communities at all sites were dominated by perennial species with community productivity declining with increasing aridity. The dominant species were *Leymus chinensis* and *Stipa baicalensis* at the low aridity site, *L. chinensis* and *S. grandis* at the medium aridity site, and *S. breviflora* and *Peganum harmala* at the high aridity site (see Table 1 for more detailed information about each site). All necessary permits were gained before the beginning of field investigation.

The drought experiment employed a completely randomized block design with six blocks, each including one control (ambient precipitation) and one drought treatment (66% reduction in growing season precipitation; Figure S1). The precipitation reduction matches the criteria that define an extreme drought event (Slette et al., 2020). Each plot was 6 × 6 m in size ($n = 6$ control, $n = 6$ drought; 12 plots per site), with at least 2 m spacing between plots. Aluminium flashing was inserted to a depth of 1 m around the plot to hydrologically isolate all plots. To manipulate precipitation, rainout shelters were used covered with strips of transparent polyethylene for each plot. The roofs of rainout shelters were 2.5 m high at the highest point, allowing for the near-surface air exchange and avoiding unwanted greenhouse effects. The effects of rainout shelters on the light environment were small, permitting more than 90% penetration of photosynthetically active radiation. For more detailed information on experimental design, see Luo et al. (2021, 2022) and Muraina et al. (2021).

Rainout shelters were installed on May 1st and removed at the end of August for 4 years (2015–2018), followed by a recovery

TABLE 1 Climate and vegetation properties of the three study sites located within the temperate grasslands of northern China.

	Low aridity site	Medium aridity site	High aridity site
General			
Latitude	49.35°N	43°33′	41°25′N
Longitude	120.01°E	116°40′	106°58′E
Elevation (m)	760	1200	1650
Climate			
MAP (mm)	354	346	175
MAT (°C)	−1.1	1.9	5.6
PET (mm)	610	706	1029
GSP (mm)	263	242	133
AI	0.58	0.49	0.17
Vegetation			
Dominant species	*Leymus chinensis and Stipa baicalensis*	*L. chinensis* and *S. grandis*	*S. glareosa* and *Peganum harmala*
ANPP ($g\,m^{-2}$)	237	158	23
Species richness	11.5	9.5	5.4

Note: The climatic variables are calculated from a 45-year record (1972–2016) for the low aridity site, and a 33-year record (1982–2014) for the other two sites. All vegetation characteristics (e.g. biomass and species richness) were calculated from the control plots of the experiment (2015–2018). MAP, mean annual precipitation; MAT, mean annual temperature. GSP, growing season precipitation; PET, potential evapotranspiration; AI, aridity index, AI was calculated as the ratio of MAP to PET, with values closer to 0—denoting greater aridity. ANPP, above-ground net primary production.

period in 2019 when shelters were removed and all plots received ambient rainfall.

2.2 | Sampling and data collection

In early August of 2019 (the first recovery year following a 4-year experimental drought), below-ground bud bank and above-ground vegetation were investigated within a 0.3 m × 0.3 m quadrat in each experimental plot at each site. Given that most below-ground buds are concentrated in the 0–30 cm soil profile in these grasslands, all below-ground parts were excavated to a depth of 30 cm (Qian et al., 2017, 2022). The connection between below- and above-ground plant parts was kept intact to identify the buds of different species. Below-ground buds were categorized into tiller buds (axillary buds at the shoot base of caespitose and rhizomatous grasses), rhizome buds (axillary buds and apical buds on hypogenous rhizomes), bulb buds (meristems wrapped in the swollen leaf base or scale leaf of bulb species), and dicot buds (buds on below-ground tissues of dicotyledonous herbs) following the procedures in Qian et al. (2021). The number of below-ground buds and above-ground shoots of grasses and forbs was counted within each bud bank sampling quadrat. See Table S1 for more detailed information.

2.3 | Statistical analyses

Before statistical analysis, we regarded the number of below-ground buds and above-ground shoots recorded in each quadrat as the measures of bud and shoot densities (per square meter), respectively. To assess the extent of to which the below-ground bud bank constrained above-ground vegetation, we calculated the ratio between bud density and shoot density in each quadrat (Benson et al., 2004).

To test the interactive effects of drought treatment and study site on below-ground bud density, above-ground shoot density, and bud: shoot ratio separately for each of the two functional groups (grasses and forbs) and the whole community, we used linear mixed effects models including treatment and site as fixed effects and block as a random effect. When the interactive effects of drought treatment and site were significant, the mixed effects model was separately applied for each site with drought treatment as a fixed factor and block as a random factor. We compared bud density, shoot density, and bud: shoot ratio across control and drought plots at three sites using analysis of variance (ANOVA), with Duncan's Test as the post-hoc test for multiple comparisons separately for grasses, forbs and the entire community.

Levene's tests and Shapiro–Wilk were conducted to check the heteroscedasticity and normality of all data before statistical analyses, respectively. Given their homogeneity of variance and normal distribution, untransformed data were used in our statistical analyses. All analyses were conducted in NLME package of R 4.2.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Buds and shoots of the entire community

For the entire community, there was no drought treatment × site interaction for below-ground bud density, above-ground shoot density, and bud: shoot ratios, indicating that the responses of these structural attributes to experiment drought were similar among grassland sites (Table 2). Experimental drought significantly reduced

TABLE 2 Results of a mixed-model analysis of variance on the effects of study site, drought treatment, and their interaction on below-ground bud density, above-ground shoot density, and ratios of buds to shoots separately for grasses, forbs and the whole community in temperate grasslands in northern China.

	Site		Treatment		Site × treatment	
	$F_{1,5}$	p	$F_{1,5}$	p	$F_{1,5}$	p
Community						
Bud density	**4.36**	**0.03**	**4.44**	**0.04**	0.10	0.91
Shoot density	**17.35**	**<0.01**	0.95	0.34	0.49	0.62
Bud: shoot ratios	**3.50**	**0.04**	0.61	0.44	0.31	0.74
Grasses						
Bud density	**29.72**	**<0.01**	1.95	0.17	0.59	0.56
Shoot density	**31.98**	**<0.01**	0.07	0.79	0.48	0.63
Bud: shoot ratios	**30.55**	**<0.01**	1.22	0.28	0.71	0.50
Forbs						
Bud density	**22.74**	**<0.01**	**2.98**	**0.09**	0.43	0.66
Shoot density	**31.98**	**<0.01**	0.07	0.79	0.44	0.65
Bud: shoot ratios	1.15	0.34	0.98	0.33	0.14	0.87

Note: Drought treatment (drought vs. control) and site (low, medium and high aridity sites) were used as fixed factors and block as a random factor. *F*-statistic, degrees of freedom (*df*) and *p*-value were given. The bold values indicate significant differences at $p < 0.05$ level and marginally significant difference at $p < 0.10$ level.

community below-ground bud density ($F = 4.44$, $p < 0.05$, Table 2), corresponding to 22%, 31% and 32% reduction in bud density at the low, medium and high aridity sites, respectively (Figure 1). Experimental drought had little influence on community above-ground shoot density and bud: shoot ratios at each grassland site (Table 2, Figure 1).

Along the aridity gradient, total bud density was significantly higher at the low and medium aridity sites than the high aridity site ($F = 7.46$, $p < 0.05$, Figure 1). Total shoot density was significantly higher at the medium aridity site than the other two sites ($F = 8.31$, $p < 0.05$, Figure 1). The ratio of buds to shoots was lower at the medium vs. low aridity site ($F = 8.04$, $p < 0.05$, Figure 1).

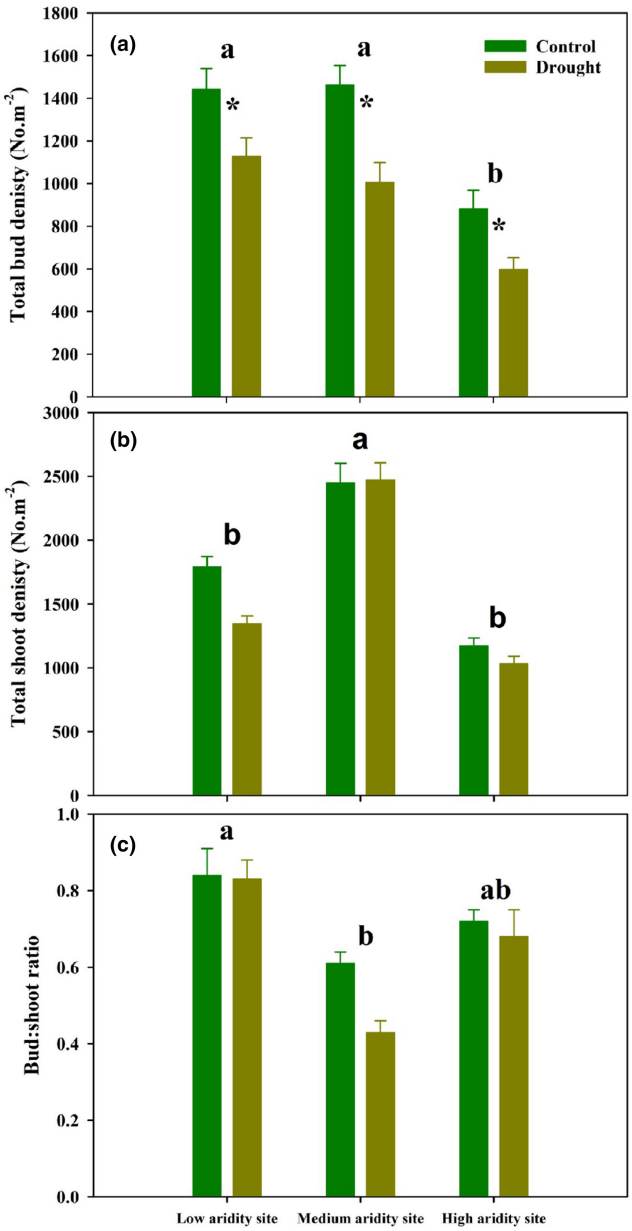

FIGURE 1 Values of (A) total below-ground bud density, (B) total above-ground shoot density and (C) ratios of buds to shoots measured at three sites (low, medium and high aridity site) along an aridity gradient in temperate grasslands in northern China. Values are shown as means ($n = 6$) and standard error (SE). Lowercase letters indicate significant differences ($p < 0.05$) among sites, and stars indicate significant ($p < 0.05$) drought effects at each site.

3.2 | Buds and shoots of grasses and forbs

Experimental drought had little legacy effect on below-ground bud density, above-ground shoot density and their ratios for grasses at each site (Table 2, Figure 2). Drought marginally reduced below-ground bud density of forbs (all $p < 0.10$, Table 2), corresponding to 85%, 68% and 31% relative reduction in bud density at the low, medium and high aridity site, respectively (Figure 2). Experimental drought unaltered above-ground shoot density and bud:shoot ratios for forbs at any site (Table 2, Figure 2).

Along the aridity gradient, bud and shoot densities were significantly higher at the low and medium aridity compared to the high aridity site for grasses ($F = 2.98$, $p < 0.05$, Table 2, Figure 2). In contrast, bud and shoot densities were highest at the high aridity site for forbs ($F = 10.45$, $p < 0.05$, Figure 2). The bud: shoot ratio significantly decreased with increasing aridity for grasses ($F = 30.55$, $p < 0.01$), suggesting greater meristem limitation in drier grasslands, but remained relatively constant for forbs along the aridity gradient (Table 2, Figure 2).

4 | DISCUSSION

In perennial grasslands, below-ground meristems are key determinants of how plant communities and ecosystem processes respond to climate variability (Dalgleish & Hartnett, 2006). These bud banks can differ for populations and communities across climate gradients, and investigating their responses to short- and long-term water availability is important for predicting grassland responses to climate change (Ding et al., 2019; Ott & Hartnett, 2015; Qian et al., 2017). In this study, we imposed a severe multi-year drought in three temperate grasslands along a natural gradient and assessed the legacy effects of manipulative drought and aridity on below-ground bud banks and their relationship with shoot densities in northern China. Below-ground bud density was lowest in the most arid site at the community scale (Figure 1). This was driven by dominant grass species that had extremely low bud bank density, but this was partly compensated by higher bud bank density of forbs (Figure 2). The smaller below-ground bud banks in drier grasslands are consistent with a reduction in below-ground bud banks of plant communities with decreasing precipitation in North American grasslands (Dalgleish & Hartnett, 2006). Additionally, below-ground bud density decreased towards the dry and hot end of the climatic gradient in steppes and alpine meadows in China (Ding et al., 2019; Qian et al., 2017). Together, these results suggest that climate plays a strong role in limiting the potential for grassland plants to store resources, produce above-ground shoots, and recover from drought.

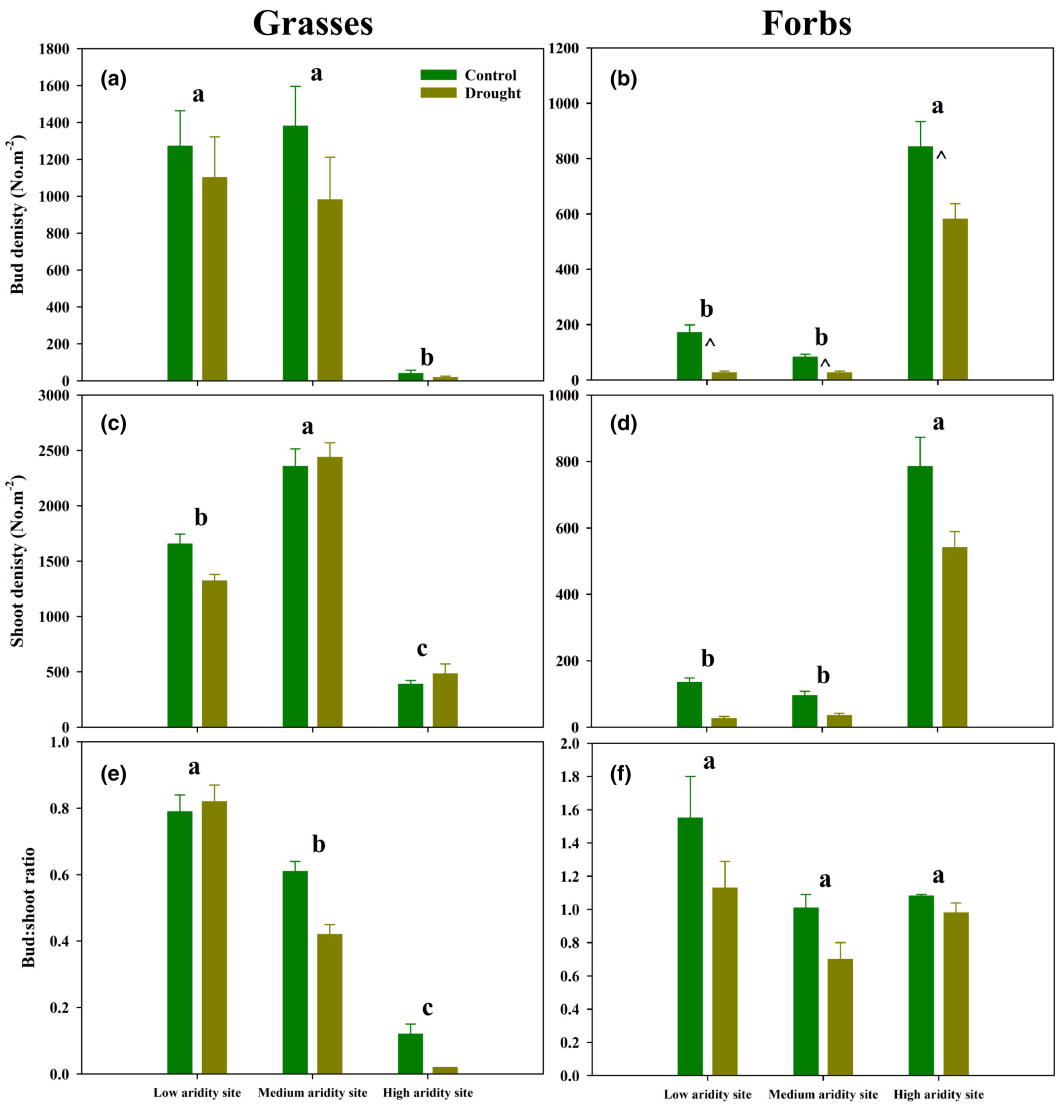

FIGURE 2 Values of (A, B) below-ground bud density, (C, D) above-ground shoot density and (E, F) ratios of buds to shoots measured at three sites (low, medium and high aridity site) along an aridity gradient for grasses and forbs in temperate grasslands in northern China. Values are shown as means ($n = 6$) and standard error (SE). Lowercase letters indicate significant differences ($p < 0.05$) among sites, and the symbol ^ indicates the marginally significant ($p < 0.10$) drought effects at each site. Note differences in *y*-axis scales between grasses and forbs.

Meristem limitation via bud bank dynamics can be an important control on grassland productivity (Hartnett et al., 2006; Reichmann & Sala, 2014), and has been found to be affected by drought and/or chronic water stress (Dalgleish & Hartnett, 2009; Qian et al., 2017; Wang et al., 2019). We hypothesized that, due to concurrent declines in both below-ground bud and above-ground shoot densities, the ratio of buds to shoots would remain relatively constant along the aridity gradient, resulting in no change in meristem limitation. However, the ratio of bud to shoot density (i.e. meristem limitation) varied among the three grassland sites along the aridity gradient, with the highest ratio, and therefore, the lowest meristem limitation at the more mesic sites (Figure 1). This occurred because below-ground bud banks and above-ground shoot densities did not change consistently with increasing aridity. Instead, shoot densities were highest at the medium aridity site while bud density was highest at the most mesic site (Figure 1). These results are consistent with other work describing higher meristem limitation in drier grasslands (Dalgleish & Hartnett, 2009). Studies show that plants can regulate their reproductive strategy in response to water stress, which is manifested by prioritizing sexual reproduction with increased aridity (Wang et al., 2018). Therefore, seed bank may have contributed more than bud bank in supporting shoot density regeneration at the more arid sites (Dalgleish & Hartnett, 2006; Knapp & Smith, 2001). Indeed, the relative dominance of annual species increased at the drier sites; thus, above-ground shoot regeneration of these species reduced the overall plant community dependence on below-ground bud banks (Qian et al., 2017). As grasslands become more arid, perennial plant persistence may be constrained by climate, leading to changes in communities and functioning.

Four years of experimental drought had negative legacy effects on community below-ground bud banks at each site (Figure 1), a

response mostly driven by forbs (Figure 2). The negative legacy effects of experimental drought on community bud banks can affect plant regeneration and recruitment, which likely limited the recovery of above-ground vegetation following drought in these grasslands (Qian et al., 2022). A previous study also found that one-year severe drought reduced below-ground bud bank density at the community scale in a restored grassland (Carter et al., 2012). In contrast, community below-ground bud bank dynamics was insensitive to drought in a short-term (2-year) experiment with a 76% reduction of growing season precipitation in a moist tallgrass prairie (VanderWeide et al., 2014). These differences indicate that the effects of drought on below-ground bud bank composition may vary with ecosystems, drought intensity and duration (Carroll et al., 2021). The drought treatment in our study was longer (4 years), which may have depleted plant resources more and led to larger negative effects on plant bud banks. Further research is needed to assess how below-ground bud bank composition responds to the intensity and duration of drought across ecosystems.

In contrast to the negative impact of experimental drought on community bud banks, we did not find evidence that experimental drought affected community shoot density or bud: shoot ratios at any of the three grassland sites (Figure 1). This challenges previous predictions that below-ground bud banks would be more resistant to extreme drought than above-ground portions of plants (VanderWeide & Hartnett, 2015). For instance, plants may distribute more photosynthate to below-ground organs than above-ground growth to avoid death during drought (Meng et al., 2022; Raven & Griffiths, 2015; VanderWeide et al., 2014). The lower sensitivity of above-ground stem density than below-ground bud banks to drought in our study may indicate that below-ground buds sprouted into above-ground shoots to increase photosynthetic capacity upon recovery after drought (Ott et al., 2019). However, chronic drought may eventually deplete bud bank resources, leading to lower densities similar to what our study documented under experimental drought. These results highlight the important role of below-ground bud bank dynamics in understanding the impacts of long-term drought on grassland community structure and composition.

Our results showed that grass bud banks were less sensitive to experimental drought than forbs in all three grasslands. Differential responses in below-ground bud bank and shoot density to drought were also observed between grasses and forbs along our natural aridity gradient (Figure 2). This is consistent with a previous study that observed differential responses of bud and shoot densities to drought, in which forbs were least resistant to, but had the greatest recovery from, 1 year drought (Carter et al., 2012). Similarly, grass bud banks were more resistant than forbs to severe drought in tallgrass prairie (VanderWeide & Hartnett, 2015). Grass and forb bud banks have also shown distinct responses to other types of global environmental change (e.g. nitrogen deposition and increased precipitation) in a temperate grassland of Inner Mongolia (Qian et al., 2021), as well as to burning and grazing management regimes in mesic grasslands (Benson et al., 2004; Dalgleish & Hartnett, 2009). Perennial forbs tend to reproduce via seeds more than grasses (Rabinowitz & Rapp, 1980; Stampfli & Zeiter, 2004), so under drought stress grasses may invest more in maintaining bud banks than forbs. Indeed, previous work has found that forb bud banks decreased more than grass bud banks under drought, yet above-ground forb stem densities quickly recovered, suggesting that forbs rely more on seed regeneration and less on bud banks for drought resilience (Carter et al., 2012). Our study likewise found no differences in forb shoot densities despite decreased bud bank density with drought. If grass and forb bud banks consistently differ in their responses to drought, bud bank dynamics may play a key role in shaping plant population and community changes under climate change.

The response of below-ground plant demography to four-year drought was not predictable from trends across the precipitation gradient (Figures 1 and 2). The different spatial vs. temporal responses of community traits to water limitation have been reported for other functional traits. For example, the differences in plant community leaf trait distributions (e.g. plant height, specific leaf area, and leaf nutrient content) along a natural aridity gradient did not match those observed in response to experimental drought (Luo et al., 2018, 2019). This likely reflects the short-term nature of drought within a site (Yuan et al., 2017) vs. long-term evolutionary history across the natural aridity gradient. In short-term experiments, plant community composition remains relatively constant, with variability in community traits mostly explained by responses of the extant species to water limitation (Sandel et al., 2010). However, shorter-term responses to drought will differ from longer-term responses, perhaps due to lag effects in species composition over the long-term to resource feedbacks, growth, and competition (Knapp et al., 2018). That is, species re-ordering may contribute more to drought responses on functional composition and dynamics over the long term (Luo et al., 2018, 2019). Therefore, it may be hard to extrapolate the effects of persistent changes in climate like those expected in our study region from short-term manipulations.

Our study was unable to inventory bud banks directly following drought, which precludes assessment of rates of recovery, or whether lack of difference between drought and control treatments are due to lack of response to drought vs. rapid recovery from drought. Nonetheless, our results demonstrated that drought can decrease bud banks for up to a year following drought and that these effects may exacerbate meristem limitation of grassland plants (Dalgleish & Hartnett, 2006; Knapp & Smith, 2001). These legacy effects of drought can constrain above-ground biomass and resource capture, and the decrease in bud bank density with increasing aridity suggests that persistent drought conditions may constrain grassland productivity and resilience.

5 | CONCLUSIONS

We investigated legacy effects of drought on below-ground bud density, above-ground shoot density, and ratios of bud to shoot density, using identical drought experiments at three sites along a natural aridity gradient. At the community scale, below-ground bud density

decreased with experimental drought and along the aridity gradient, but above-ground shoot density showed differential responses to water limitation. Below-ground bud banks of forbs were more sensitive to experimental drought than grasses, and were stronger drivers of community-level bud bank responses in the drier grasslands. This suggests that major plant functional groups differ in their bud bank responses to long-term water availability, and that climate change may impact plant communities through changes in bud bank density. We further observed a non-congruous change between below-ground bud banks and above-ground shoot densities in response to water limitation, indicating that below-ground plant responses to climate change cannot necessarily be inferred from above-ground responses. Additionally, these results suggest that the degree of bud limitation for shoot generation may be affected by extended changes in drought length and/or severity. Predictions of how grassland ecosystems will respond to climate change may be improved by incorporating the demography of below-ground bud banks (Kühn et al., 2021), highlighting the need for more studies on bud bank responses to environmental change.

AUTHOR CONTRIBUTIONS

Jianqiang Qian, Zhiming Zhang, and Wentao Luo conceived the ideas and designed. All authors contributed critically to the draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data available from https://doi.org/10.6084/m9.figshare.21903624.v1 (Qian & 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.

Table S1. Functional groups and bud types at three sites along an aridity gradient in the temperate grasslands in northern China.

Figure S1. A natural aridity gradient in the temperate grasslands of northern China was used in this experiment. Three study sites, with low, medium and high aridity, were selected along this gradient (a). In

each site, we reduced 66% of the growing season precipitation using large rainfall exclusion shelters (b).

Figure S2. Growing season precipitation (from May to August) for control and drought plots during drought (2015-2018) followed by a recovery (2019) for the three grassland sites along the aridity gradient in northern China. Horizontal broken lines indicate the average of long-term growing season precipitation. Growing season precipitation is based on a 33-year mean (1982-2014) for the low aridity site, and 44-year means (1971-2014) for the medium and high aridity sites.

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