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RESEARCH ARTICLE

High below-ground bud abundance increases ecosystem recovery from drought across arid and semiarid grasslands

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Abstract

1. Asexual reproduction plays a fundamental role in the structure, dynamics and persistence of perennial grasslands. Thus, assessing how asexual reproductive traits of plant communities respond to drought may be key for understanding grassland resistance to drought and recovery following drought.
2. Here, we quantified three asexual reproductive traits (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds) during a 4-year severe drought and a 2-year drought recovery period in four grasslands that spanned an aridity gradient in northern China. We also assessed the relationship between these traits and the resistance and recovery of above-ground net primary productivity (ANPP).
3. We found that drought had limited and largely inconsistent effects on asexual reproduction among drought and recovery years and grasslands overall. Drought increased tiller abundance in the first treatment year and reduced bud banks by the fourth treatment year across grasslands. However, neither of the three asexual reproductive traits were correlated with drought resistance of ANPP. Drought legacies differed among the four grasslands with positive, negative and no legacies evident for the three asexual reproductive traits, and no clear relationship with aridity. Bud banks and tiller to bud ratio decreased and increased, respectively, in the first recovery year, but not in the second recovery year. In contrast to drought resistance, community bud abundance was strongly related to recovery, such that communities with higher bud abundance had greater ANPP recovery following drought.
4. *Synthesis*. These results suggest that asexual reproductive traits may be important drivers of ecosystem recovery after drought, but that variable responses of

these asexual reproduction traits during drought complicates predictions of overall grassland responses.

KEYWORDS
above-ground net primary productivity, bud bank, climate change, drought recovery, drought resistance, grasslands, reproductive traits, tiller abundance

1 | INTRODUCTION

Globally, growing season drought is expected to increase in magnitude and frequency in most terrestrial ecosystems due to climate change (Dai, 2013). Grassland biomes, which constitute nearly one-third of the global land area, are important for land–atmosphere interactions and provide a variety of ecosystem services (Bengtsson et al., 2019). Grasslands are often water limited and highly sensitive to inter- and intra-annual precipitation variability (Broderick et al., 2022; Griffin-Nolan et al., 2021; Huxman et al., 2004; Maurer et al., 2020). Droughts are known to affect above-ground net primary productivity (ANPP) of grasslands (Knapp et al., 2015; Luo et al., 2021), plant composition (Cleland et al., 2013), and soil carbon and nutrient cycles (Holguin et al., 2022; Müller & Bahn, 2022) in grasslands. In addition to the concurrent effects of drought on grasslands, these effects can persist after drought has ended and affect grassland responses to future drought events (Luo, Muraina, et al., 2023; Vilonen et al., 2022). Although grasslands often have low capacity to withstand drought, these ecosystems can exhibit high capacity to recover functioning after drought (Hoover et al., 2021; Xu et al., 2021). Therefore, in-depth understanding of the ecological consequences of intensified drought and the mechanisms determining drought resistance and recovery is important for forecasting how climate change will impact grassland ecosystems.

Plant traits are useful proxies for understanding plant ecological strategies for coping with environmental stress (Adler et al., 2014; He et al., 2023; Majekova et al., 2014). Indeed, mechanistic models incorporating plant traits can predict ecosystem resistance to and recovery from climate change (McGill et al., 2006). However, to date, trait-based research on ecological strategies and their links to ecological gradients and ecosystem functioning have focused primarily on vegetative traits such as leaf (Griffin-Nolan et al., 2019; Luo et al., 2019), stem (Avila-Lovera et al., 2017), and root functional traits (Chandregowda et al., 2022; Zhou et al., 2019), with considerably less research on plant reproductive traits (Arend da Silva et al., 2020; Griffin-Nolan, Bushey, et al., 2018; Luo et al., 2022; Stuefer et al., 2002).

Meanwhile, asexual reproductive traits such as tiller abundance and bud banks play fundamental roles in above-ground plant population and community persistence, structure and dynamics in perennial grasslands (Benson et al., 2004; Clarke et al., 2013; Cornelissen et al., 2014; Ott & Hartnett, 2012). In these grassland communities, tiller recruitment largely occurs from buds rather than seeds (Benson & Hartnett, 2006; Klimešová et al., 2016; Klimešová, Ottaviani, et al., 2021; Qian et al., 2017), and in some cases, >99% of all established above-ground tillers originate from buds (Benson & Hartnett, 2006; Qian et al., 2017). Therefore, incorporating plants' asexual reproductive traits in trait-based models could help forecast how plants will respond to climate change, including the increase in extreme drought events (Arend da Silva et al., 2020; Klimešová & Klimeš, 2007; Klimešová, Mudrák, et al., 2021).

During drought, plants adopt ecological strategies associated with avoidance and/or tolerance of low soil water availability (Wellstein et al., 2017). For instance, when drought stress decreases plant net photosynthetic rates and plant growth due to stomatal closure (Chaves et al., 2009), plants may distribute their limited resources to asexual reproductive organs like below-ground buds to avoid death (Raven & Griffiths, 2015; VanderWeide et al., 2014). Plants can alternatively tolerate drought-induced lower tissue water content by reducing their tiller abundance and carbon allocation for growth and undergoing temporary above-ground senescence (Dalgleish & Hartnett, 2006; Meng et al., 2022; Qian et al., 2023; Reichmann et al., 2013). Given that bud banks can withstand the extremes of drought better than above-ground portions of plants (VanderWeide & Hartnett, 2015), the ability of below-ground buds during drought determines the post-drought recovery of perennial (Loydi & Collins, 2021; Luo, Ma, et al., 2023; Vesk & Westoby, 2004). Thus, when adequate soil moisture returns, perennial plants reduce below-ground bud production and increase above-ground tillers to maximize above-ground productivity (Dalgleish & Hartnett, 2006).

These strategies suggest that the proportion of tillers to buds, which determines the degree of impacts of below-ground buds on above-ground population recruitment/regeneration (meristem limitation; Benson et al., 2004; Klimešová et al., 2023; Knapp & Smith, 2001), plays key roles in perennial grasslands' resistance to drought and recovery post-drought (Klimešová, Mudrák, et al., 2021; Reichmann & Sala, 2014). How plant asexual reproductive traits will respond to the immediate or legacies of drought may, however, vary with prolonged droughts (Ogle & Reynolds, 2004; Vandegeer et al., 2020; Xu et al., 2021), as different grasslands possess different plant composition, structure and soil, and/or experience different climatic conditions (Heisler-White et al., 2009; Muraina et al., 2021). Thus, studying the responses of asexual reproductive traits (e.g. tiller abundance, bud abundance, ratio of tillers to buds) to multi-year drought across multiple grasslands may improve our general understanding of the dynamics of plant community structure and function during and following drought.

In this study, we imposed an extreme drought (excluding all precipitation in two middle months of a 4-month growing season) over 4 years in four perennial grasslands in northern China. We then monitored subsequent recovery 2 years post-drought. We assessed the responses of three asexual reproductive traits (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds) to extreme drought during and after the drought periods. We also evaluated the relationship of the three asexual reproductive traits with ANPP resistance and recovery. Overall, we tested the following two hypotheses: (H_1) Drought treatment would alter the three asexual reproductive traits and that the magnitude of the drought effects would vary with drought year and/or site. Specifically, the drought treatment would decrease and increase tiller abundance and bud abundance, respectively, through the drought years; decrease tiller: bud ratios would through drought years; the three traits would recover through the post-drought years; and the magnitude of these drought effects would vary with drought year and/or site. (H_2) Drought resistance of ANPP would be driven by above-ground tiller abundance, while drought recovery of ANPP would be driven by below-ground bud abundance.

2 | MATERIALS AND METHODS

2.1 | Study region

We conducted our study in four grasslands that span an aridity gradient in northern China (see sites and abbreviations in Table 1). Drought was imposed in these perennial grasslands based on the extreme drought in grassland experiment approach (Carroll et al., 2021). The sites varied in plant community composition, climatic and edaphic properties. The dominant plant species in the more mesic grasslands were the perennial grasses *Leymus chinensis* and *Stipa baicalensis*, *L. chinensis* and *S. grandis* dominated the medium aridity grassland, and *S. krylovii* dominated the drier grassland. The climate is temperate continental with warm, humid summers and cold, dry winters. Precipitation and temperature are unimodal, with peaks in summer months (July–August) for each grassland. Mean annual precipitation decreases, temperature increases and the proportion of clay and silt in soils decreases across the mesic to arid gradient (Table 1). We have appropriate permits to carry out our field work.

2.2 | Experimental design

In each of the four grasslands, we imposed a 100% reduction in precipitation for 2 months (June–July) of the growing season (May–August) over 4 years (2015–2018), followed by 2 years (2019–2020) of recovery under ambient precipitation. We established all experimental plots in areas with uniform vegetation to minimize small-scale heterogeneity in each grassland. The experiment used a randomized block design with six blocks, each of which has one drought and one control plot. We removed all precipitation in the drought-treated plots using large rainout shelters, with 100% of the roof surface covered with clear polycarbonate sheet to allow light into the plots. All plots were 6 × 6 m in size, with at least 2 m spacing between plots. We buried 6-mm-thick metallic and plastic flashing vertically to 1 m beneath the soil surface around the perimeter to hydrologically isolate each plot. Drought shelters, which were 0.5 and 2 m above the ground at the lowest and highest point, respectively, allowed air to circulate and minimized microclimatic effects. The drought-treated plots included a 1 m external buffer zone to minimize the edge effects of the shelter. This rainout shelter design has been thoroughly described in previous studies (Luo et al., 2021; Muraina et al., 2021).

2.3 | Data collection

Biomass of each species in two 0.25 m^2 quadrats per plot was clipped at ground level at the end of each growing season (i.e. every August of the drought and recovery years). We used total dry mass of all the clipped plant species averaged over the two quadrats to estimate ANPP in each plot (quadrat = 576; 2 quadrats, 12 plots, 4 grasslands and 6 years).

TABLE 1 Climate, plant and soil community properties of four arid and semiarid grasslands in northern China.

Grasslands	NHG	EFS	IMG	DGS
Location	N49°21′ E120°0.6′	N50°10′ E119°22′	N43°33′ E116°40′	N41°47′ E111°53′
MAP (mm year^{-1})	380	336	331	257
Aridity	0.17	0.25	0.40	0.49
Dominant species	*Leymus chinensis*, *Stipa baicalensis*	*L. chinensis*, *S. baicalensis*	*L. chinensis*, *S. grandis*	*S. krylovii*
ANPP (g m^{-2})	183.49	135.27	114.63	56.36
SOC (g kg^{-1})	43.20	28.12	24.26	16.45
STN (g kg^{-1})	4.10	3.11	3.15	2.83
SAP (g kg^{-1})	5.99	1.13	2.42	2.23
pH	6.98	7.89	7.28	7.68
Clay and silt (%)	73	51	26	13

Note: Aridity (unitless) is defined as 1 − Aridity Index (AI), where AI, the ratio of precipitation to potential evapotranspiration, is the aridity index.
Abbreviations: ANPP, above-ground net primary production; DGS, Damaoqi Grassland Station; EFS, Erguna Forest-Steppe Ecotone Research Station; IMG, Inner Mongolia Grassland Ecosystem Research Station; MAP, mean annual precipitation; NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SAP, soil available phosphorus; SOC, soil organic carbon; STN, soil total nitrogen.

Asexual reproductive traits per site were not measured in drought plots to avoid destructive measurements. At the four grassland sites, the asexual reproductive traits (i.e. above-ground tillers, below-ground buds and the ratios of tillers to buds) were measured only in control areas (i.e. under ambient conditions), as has been done in similar studies (e.g. Griffin-Nolan et al., 2019; Klimešová, Mudrák, et al., 2021; Luo et al., 2022; Sandel et al., 2010). This method was used to prevent destructive measurements, which could hinder the regeneration of plants in drought plots. However, the asexual reproductive trait values in the drought plots were mathematically inferred from traits' data obtained in the control plots (see details in metrics and data analysis section below).

Briefly, above-ground tillers and below-ground buds were measured within a 0.3 m × 0.3 m quadrat in each control plot in each grassland site. Given that previous studies have reported that most roots and buds occurred in the top 30 cm of soil in grasslands of northern China (Qian et al., 2017), surface soil (at 30 cm depth) was carefully excavated in each plot to obtain intact root systems. The connections between below- and above-ground plant parts were kept intact to accurately identify the buds of different species. We carefully removed soils adhering to the roots and recorded the number of above-ground tillers and below-ground buds (expressed as number m^{-2}) of each species within each quadrat per grassland.

2.4 | Metrics and data analysis

Tiller or bud abundance of each species was calculated as ratio of number of tillers or buds to above-ground biomass. The tiller to bud abundance ratio of each species is an estimate of meristem limitation (Benson et al., 2004; Knapp & Smith, 2001). For each species, we averaged these reproductive trait metrics across the plots.

For each plot, community-weighed means for each of the three asexual reproductive traits (i.e. above-ground tillers, below-ground buds and the ratio of tillers to buds) were quantified as the overall means across all species weighted by the relative biomass of each individual species ($n = 288$; 12 plots, 4 grasslands and 6 years). Here, we used the relative biomass of species from each experimental plot in each of the six experimental years and asexual reproductive trait values of the species from control plots in 1 year (Griffin-Nolan et al., 2019; Sandel et al., 2010). Therefore, any shift in community-weighted traits indicates variation in species composition and/or relative abundance rather than intraspecific trait variability (i.e. variation in traits within species due to phenotypic or genotypic diversity) (Klimešová, Mudrák, et al., 2021; Klimešová, Ottaviani, et al., 2021; Luo et al., 2022).

The following models were built to address the first hypothesis (H_1). First, we tested the interactive effects of drought treatment, year and site on each of the three asexual reproductive traits (i.e. tiller abundance, bud abundance and the ratio of tillers to buds) during the drought or recovery period across the four grasslands. We used linear mixed-effects models including drought treatment, year and site as fixed factors, and block as a random factor (model 1).

$$Y \sim \text{treatment} \times \text{year} \times \text{site}, \text{random} = \text{block}. \qquad \text{(model 1)}$$

Next, to examine the annual responses of each of the three asexual reproductive traits to drought and their post-drought recovery across the four grasslands, we used linear mixed-effects models with drought treatment as a fixed factor and block nested within site as a random factor (model 2).

$$Y \sim \text{treatment}, \text{random} = \text{site} / \text{block}. \qquad \text{(model 2)}$$

Finally, to examine the drought and post-drought effects on asexual reproductive traits for each grassland, we used linear mixed-effects models including drought treatment as a fixed factor and block nested within year as a random factor (model 3).

$$Y \sim \text{treatment}, \text{random} = \text{year} / \text{block}. \qquad \text{(model 3)}$$

To address the second hypothesis (H_2), we first calculated ANPP resistance to drought and recovery post-drought. For each of the six blocks in each grassland, ANPP in the control plots was paired with ANPP in the drought-treated plots in each of the six experimental years. Resistance of ANPP to drought was calculated as the relative change in the drought-treated plots compared with the control plots during the drought period, which is as follows (Hsu et al., 2012):

$$\text{Resistance} = \left(\text{ANPP}_{\text{drought}} - \text{ANPP}_{\text{control}}\right) / \text{ANPP}_{\text{control}},$$

where $\text{ANPP}_{\text{control}}$ is ANPP in the control plots each year from 2015 to 2018 and $\text{ANPP}_{\text{drought}}$ is ANPP in the drought-treated plots in each of those years.

Recovery of ANPP from drought was estimated as the relative change in the drought-treated plots compared with the control plots during the recovery period, which is as follows (Ru et al., 2023):

$$\text{Recovery} = \left(\text{ANPP}_{\text{drought}} - \text{ANPP}_{\text{control}}\right) / \text{ANPP}_{\text{control}},$$

where $\text{ANPP}_{\text{control}}$ is ANPP in the control plots of 2019 and 2020 and $\text{ANPP}_{\text{drought}}$ is ANPP in the drought-treated plots in each of those years.

Resistance and recovery indicate a relative change in ANPP induced by the same percent reduction in precipitation for each site.

Next, to determine whether the asexual reproductive traits determine ANPP resistance and recovery (H_2), linear mixed-effects models were used to assess the relationships of community asexual reproductive traits in control plots with annual ANPP drought resistance ($n = 96$; six blocks, four grasslands and 4 years) and recovery ($n = 48$; six blocks and four grasslands and 2 years). In each of these models, the random effect was block nested within site and year (model 4).

$$Y \sim X, \text{random} = \text{year} / \text{site} / \text{block}. \qquad \text{(model 4)}$$

Additionally, we investigated the correlation among the three asexual reproductive traits during drought and recovery using cor.test function in base R. Linear mixed-effects models were performed using ‘NLME’ and ‘MuMIn’ package in R software.

3 | RESULTS

Across the four sites, the responses of community asexual reproductive traits (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds) to extreme drought and their recovery were not simultaneously influenced by the drought year and site (nonsignificant treatment × site × year interactions; Table 2; Figure S1). However, we found some significant interactive effects of drought and site, as well as drought and year on the asexual reproductive traits during the drought and recovery periods (Table 2). Specifically, during the drought years, we found significant drought and year as well as drought and site interactive effects on tiller abundance and bud abundance. During the recovery years, we observed significant drought and site interactive effects on tiller abundance and tiller: bud ratio, and significant drought effect, which did not interact with year or site, on bud abundance. Below, we first report on trait responses across all sites combined. Next, we present trait differences within sites averaged over time. Finally, we relate trait responses to post-drought recovery.

Across the four sites (NHG, EFS, IMG and DGS), tiller abundance marginally increased in the first drought year, but did not change in the remaining three drought years (Figure 1a). Drought had no effect on community tiller abundance in each of the recovery years across grasslands (Figure 1a). Experimental drought did not alter community bud abundance during the first 3 years but increased in the fourth year across grasslands (Figure 1b). During the recovery period, community bud abundance marginally decreased in the first year but did not change in the second year across grasslands (Figure 1b). Experimental drought had no effect on community tiller: bud ratio throughout the four drought years, but had positive legacy effect in the first recovery year and no legacy effect in the second year (Figure 1c).

Within sites across the four drought years (2015–2018), community tiller abundance declined at EFS, and did not change at NHG, IMG and DGS (Figure 2a). Across the two recovery years (2019–2020), community tiller abundance decreased at EFS, increased at DGS, and did not change at the other two grasslands (Figure 2b). Community bud abundance declined at IMG and DGS but did not change at the other two grasslands in response to drought (Figure 2c). During the recovery period, community bud abundance declined at both EFS and IMG, but did not change at NHG or DGS (Figure 2d). Across years, community tiller: bud ratio declined at EFS but did not change at the other three grasslands during drought (Figure 2e). During recovery, community tiller: bud ratio declined at EFS and increased at DGS across years (Figure 2f).

Drought resistance of ANPP was not related to bud abundance, tiller abundance or tiller: bud ratio (Table 3). We observed a positive relationship between community bud abundance and ANPP drought recovery across the four grasslands ($R^2_c = 0.46$, $R^2_m = 0.24$, $p < 0.01$; Figure 3; Table 3), whereas recovery was not correlated with either tiller abundance or tiller: bud ratio of plant communities (Table 3). We observed strong positive correlations among above-ground tiller abundance, below-ground bud abundance and tiller: bud ratio during the drought and recovery periods (Table S1).

TABLE 2 Results of mixed model analysis of variance for community asexual reproductive traits (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds) during drought (2015–2018) and recovery (2019–2020) periods. Drought treatment, year and site were used as fixed factors and block as a random factor. The value of *F* and *p* are shown. Bold text indicates significance at $p < 0.1$.

	Tiller abundance		Bud abundance		Tiller:bud ratio	
	F	*p*	*F*	*p*	*F*	*p*
Drought period						
Drought (D)	0.00	0.967	**7.48**	**0.007**	0.49	0.49
Year (Y)	**6.43**	**<0.001**	**6.34**	**<0.001**	1.33	0.27
Site (S)	**40.82**	**<0.001**	**51.09**	**<0.001**	**105.87**	**<0.001**
D × Y	**2.18**	**0.093**	**2.29**	**0.081**	0.85	0.467
D × S	**2.70**	**0.048**	**3.42**	**0.019**	1.09	0.356
S × Y	**1.91**	**0.054**	**7.90**	**<0.001**	**1.74**	**0.083**
D × S × Y	0.73	0.678	0.49	0.877	0.84	0.581
Recovery period						
Drought (D)	2.11	0.151	**5.18**	**0.026**	**8.04**	**0.006**
Year (Y)	0.12	0.733	0.80	0.375	0.04	0.851
Site (S)	**84.96**	**<0.001**	**31.89**	**<0.001**	**81.12**	**<0.001**
D × Y	0.24	0.628	0.01	0.919	0.01	0.919
D × S	**5.53**	**0.002**	1.27	0.293	**7.31**	**<0.001**
S × Y	0.62	0.605	0.60	0.617	0.02	0.997
D × S × Y	0.77	0.517	0.697	0.557	0.02	0.997

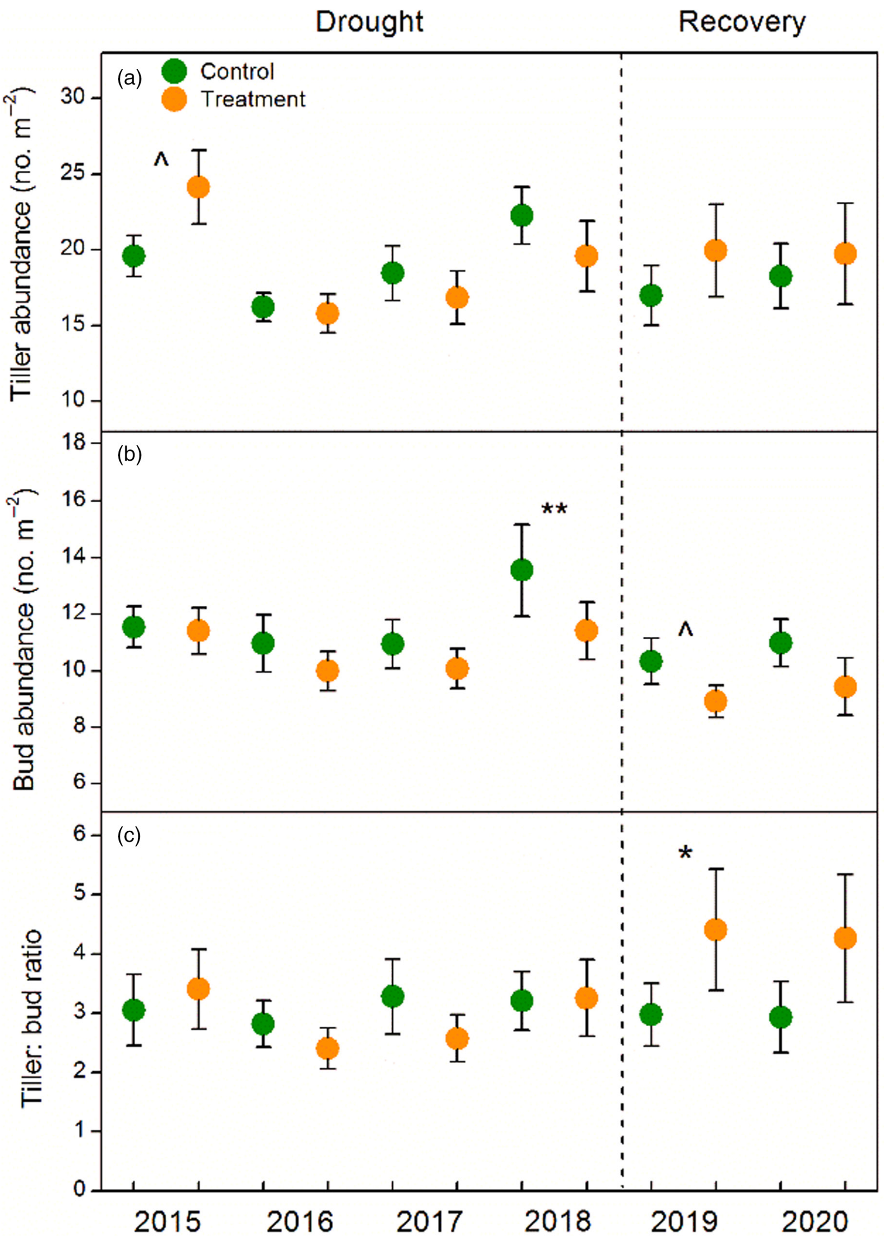

FIGURE 1 Annual responses of community asexual reproductive traits to experimental drought and recovery across four grasslands combined in northern China. Asexual reproductive traits include tiller and bud abundance as well as their ratios. Each point represents the trait means with error bars indicating standard errors for each treatment. Years with significant drought treatment effects are depicted as $^{**}p<0.01$, $^{*}p<0.05$ and $^{\wedge}p<0.1$. See Table S2 for the linear mixed model results.

4 | DISCUSSION

4.1 | Responses of asexual reproductive traits to drought and recovery

We imposed a severe multi-year drought (excluding all rainfall in 2 months of the growing season over 4 years) in four perennial grasslands in northern China. We estimated above-ground tiller abundance, below-ground bud abundance as well as their ratios in the four perennial grasslands over 4 years of drought and 2 years of recovery (ambient precipitation). Contrary to our first hypothesis, tiller abundance initially increased slightly but otherwise did not differ from controls during the last three treatment years. Furthermore, the below-ground bud bank only responded in the fourth year of drought but not earlier (Figure 1). The lack of sensitivity of tillers and buds to a 100% precipitation exclusion for 2 months is consistent with previous study that noted high tiller and bud resistance to extreme drought (VanderWeide & Hartnett, 2015). It is possible, however, that the perennial plants in these grasslands may have rapidly replaced below-ground stem bases and/or recruited above-ground tillers in the early spring period prior to rainout shelter installation (Dalgleish & Hartnett, 2006; Ott et al., 2019).

The declines in bud abundance in the fourth drought year and first recovery year likely indicate that the threshold of below-ground buds' resistance to drought may not exceed three consecutive drought years. These bud declines also imply that the negative effects of prolonged drought on bud banks in perennial grasslands can be accumulative over time (Dreesen et al., 2014; Xu et al., 2021) and extend to the early post-drought years (Griffin-Nolan, Carroll, et al., 2018). While below-ground bud banks can limit the recruitment and recovery of above-ground tillers during and after disturbances, respectively (meristem limitation; Benson et al., 2004;

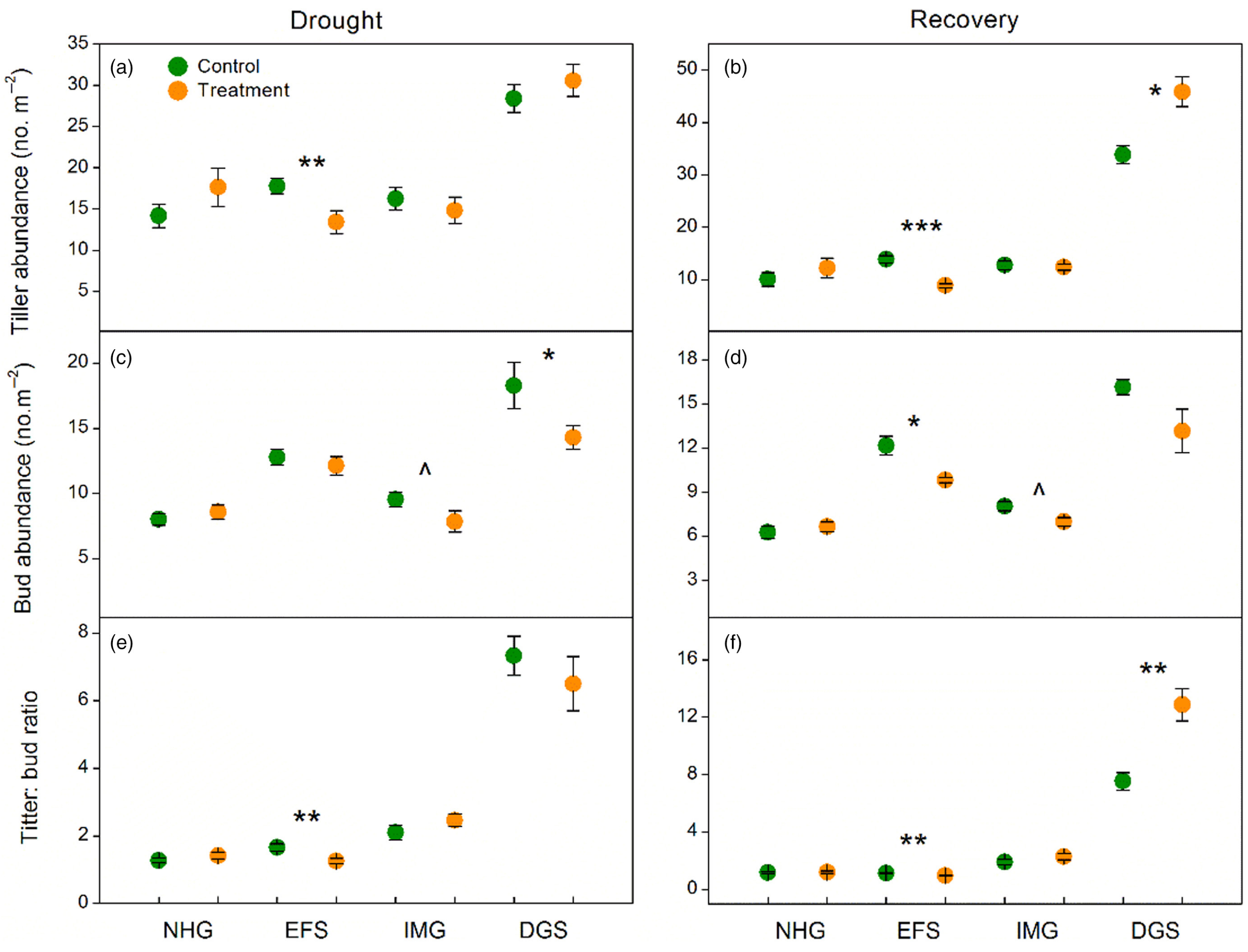

FIGURE 2 Responses of community asexual reproductive traits to experimental drought and recovery averaged across years for each of the four grasslands in northern China. Asexual reproductive traits include tiller and bud abundance as well as their ratios. Each point represents the trait means with error bars indicating standard errors for each treatment. Sites with significant drought treatment effects are depicted as $^{***}p<0.001$, $^{**}p<0.01$, $^{*}p<0.05$ and $^{\wedge}p<0.1$. See Table S3 for the linear mixed model results. See Table 1 for site abbreviation.

Klimešová & Klimeš, 2007; Klimešová et al., 2023), the decreases in bud abundance during the final drought and first recovery years in our study could not impose similar accumulative drought effects on tiller abundance and tiller: bud ratio during and after drought. Hence, this result suggests that when and how the decline in bud abundance limit tiller abundance during and after drought is most likely a function of the level of negative sensitivity of below-ground buds to drought.

Our results revealed that the impacts of multi-year extreme drought and post-drought on asexual reproductive traits (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds) of plant communities differed among grasslands (Figure 2). Most of the instances where drought or its legacy negatively or positively impacted the traits, the impact either varied with drought year or site (Table 2). This pattern of findings contradicts our expectations of concurrent variations in the three reproductive traits during and after drought. However, this dissimilarity is not surprising, as similar differential drought impacts have been reported for other ecosystem properties such as leaf economic traits (Luo et al., 2019), primary productivity (Knapp et al., 2015), species richness and stability of productivity (Muraina et al., 2021) among multiple grasslands. Importantly, the sensitivity of tillers, buds and their ratios to extreme drought and post-drought was lowest for the least arid grassland, NHG (Figure 2). The insensitivity of tiller and bud abundance to drought and post-drought can possibly promote the temporal stability of ANPP during drought and recovery. The lower drought sensitivity in mesic grasslands is consistent with previous studies that have demonstrated a higher sensitivity of ANPP in response to drought in more arid grasslands (Knapp et al., 2015; Luo et al., 2021).

Legacy effects of drought on ecosystem functions (i.e. drought-driven changes in ecosystems function after drought) have been reported in many grassland ecosystems, based on multiple mechanisms (Qian et al., 2022, 2023; Sala et al., 2012; Wei et al., 2022). We observed negative, positive and a lack of drought legacy effects on reproductive traits across the four grasslands (Figure 2). These inconsistent responses are contrary to our first hypothesis that plant tiller and bud abundance and their ratios would recover completely

TABLE 3 Bivariate relationships between drought resistance (i.e. % variation in ANPP in drought plots relative to control in a given year, 2015–2018) and each asexual reproductive trait (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds), and between drought recovery (i.e. % variation in ANPP in drought plots relative to control in a given year, 2019–2020) and each asexual reproductive trait across four perennial grasslands of northern China. The marginal (m) and conditional (c) R^2, F, and p values for the model are shown. Bold text indicates significance at $p < 0.05$.

	F	*p*	R^2m	R^2c
Drought resistance				
Above-ground tiller abundance	1.91	0.172	0.01	0.65
Below-ground bud abundance	0.70	0.404	0.00	0.62
Tiller:bud ratio	0.00	0.951	0.00	0.60
Drought recovery				
Above-ground tiller abundance	2.25	0.147	0.08	0.47
Below-ground bud abundance	**8.03**	**0.007**	**0.24**	**0.46**
Tiller:bud ratio	0.00	0.958	0.00	0.38

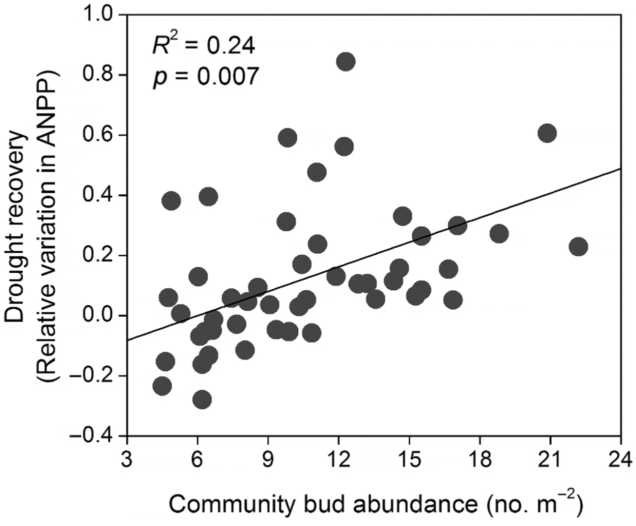

FIGURE 3 Bivariate relationships between drought recovery (i.e. % variation in ANPP in drought plots relative to control in a given year, 2019–2020) and community bud abundance across four perennial grasslands in northern China. More details on the relationships between drought resistance and recovery and asexual reproductive traits (i.e. above-ground tiller abundance, below-ground bud abundance and the ratio of tillers to buds) are shown in Table 3.

the year following drought. Similar mixed legacies have been reported for ANPP across six central US grasslands (Griffin-Nolan, Carroll, et al., 2018). These results together suggest that responses of grasslands to drought and recovery are context dependent, exhibiting diverse strategies for resistance and recovery. The different responses of plant reproductive traits during and after drought were largely inconsistent with the report of a strong correlation between ecosystem sensitivity during drought and legacy effect after drought (Griffin-Nolan, Carroll, et al., 2018; Smith, 2011). Thus, extreme drought effects may extend beyond the drought periods in some grasslands (Griffin-Nolan, Carroll, et al., 2018), and ecosystem responses under drought may not predict the pattern of ecosystem recovery following drought.

4.2 | Effects of asexual reproductive traits on ecosystem resistance and recovery

Plant communities with higher tiller abundance have greater niche complementarity among multiple tillers (Cardinale et al., 2013), which can increase their resistance to environmental change. Tiller diversity can also promote stability (resistance) via tiller asynchrony, which results from dissimilar responses of different tillers to drought such that tillers compensate for each other within and/or among species (Muraina et al., 2021). Thus, a plant community with more tillers would be less sensitive to environmental change factors. For example, Dalgleish and Hartnett (2006) found that most of the variation in community biomass in grasslands was explained by differences in tiller abundance. However, our results demonstrated that community above-ground tiller abundance was not correlated with resistance of ANPP to long-term extreme drought (Table 3). This suggests that community asexual regenerative traits related to tiller number would not provide valuable indicators of grassland resistance to extreme drought.

We found that below-ground bud abundance promoted drought recovery across the four grasslands (Figure 3), which supported our hypothesis. In other words, grassland communities with higher bud abundance experienced higher post-drought recovery of ANPP. This positive role of bud abundance on ecosystem recovery is consistent with our linear mixed model results, which showed that bud abundance remained unchanged or fully recovered in drought-treated plant communities by the second recovery year (Figure 1). These results collectively suggest that the recovery of growth post-drought was largely determined by rapid re-sprouting from below-ground buds (Dalgleish & Hartnett, 2006; Zeppel et al., 2015). This is not surprising, as nearly all plants in perennial grasslands regenerate from below-ground bud-bearing organs (Benson et al., 2004; Benson & Hartnett, 2006), with or without disturbance (Ott et al., 2019). Given that buds constitute a very small fraction of total plant biomass (Dalgleish & Hartnett, 2006), plant communities that have a large population of below-ground buds throughout the growing season can utilize their bud bank to respond more rapidly post-drought when abundant precipitation is available (Dalgleish &

Hartnett, 2006; Zeppel et al., 2015). These results imply that plant asexual reproductive traits related to below-ground population of meristems can predict how drought legacies will impact the functioning and services of grassland ecosystems.

5 | CONCLUSIONS

We explored one of the less studied areas in trait-based community ecology by examining the role of asexual reproductive traits as indicators of ecosystem resistance and recovery in grasslands across a precipitation gradient in northern China. Four years of experimental growing season drought had inconsistent effects on vegetation tiller and bud traits across four grasslands, and none of these asexual reproductive traits was related to ANPP resistance to drought. However, post-drought legacy effects on asexual reproductive traits of plant communities were observed in 1 of 2 years in three of the four grasslands. In these cases, below-ground buds promoted the post-drought recovery of ecosystem functioning. Despite the well-known role that asexual reproductive traits play in grasslands, our results highlight that drought—even a 4-year extreme drought—had little consistent impact on resistance in these grasslands, although our study did not consider intraspecific responses. However, the strong influence of asexual reproductive traits on grassland community recovery after drought suggests that below-ground meristem density confers recovery potential and thus their role in ecosystem recovery from global environmental change warrants further study.

AUTHOR CONTRIBUTIONS

Wentao Luo, Zhengwen Wang, Qiang Yu, Xingguo Han and Scott Collins conceived the research; Wentao Luo, Jianqiang Qian, Niwu Te and Xiaoan Zuo managed the field experiment and collected the data; Wentao Luo, Taofeek Muraina and Robert J. Griffin-Nolan analysed the data and wrote the first draft. Scott Collins, Melinda Smith and Alan K. Knapp revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interests. Wentao Luo and Taofeek Muraina are Associate Editors for *Journal of Ecology*, but took no part in the peer-review or decision-making process for this article.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from Figshare https://doi.org/10.6084/m9.figshare.22807088.v2 (Luo & Qian, 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: Correlations among plant community asexual reproductive traits (aboveground tiller abundance, belowground bud abundance, and the ratios of tillers to buds) during drought (2015–2018) and recovery (2019–2020) periods. The value of *R* and *p* are shown.

Table S2: Annual responses of community asexual reproductive traits to experimental drought and recovery across four grasslands in northern China. Asexual reproductive traits include tiller and bud abundance as well as their ratios. In this model, drought treatment was used as a fixed factor and block nested within site as a random factor. The value of *F* and *p* are shown.

Table S3: Responses of community asexual reproductive traits to experimental drought and recovery across years for each of the four grasslands in northern China. Asexual reproductive traits include tiller and bud abundance as well as their ratios. In this model, drought treatment was used as a fixed factor and year nested within site as a random factor. The value of *F* and *p* are shown.

Figure S1: Resistance and recovery of community asexual reproductive traits to experimental drought at each grassland for each year in northern China. Asexual reproductive traits include tiller and bud abundance as well as their ratios. Each point represents the trait means with error bars indicating standard errors calculated from replicate plots for each treatment. NHG, National Hulunber Grassland Ecosystem Observation and Research Station; EFS, Erguna Forest-Steppe Ecotone Research Station; IMG, Inner Mongolia Grassland Ecosystem Research Station; DGS, Damaoqi Grassland Station.

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