






## RESEARCH ARTICLE

# Drought has inconsistent effects on seed trait composition despite their strong association with ecosystem drought sensitivity

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## Abstract

1. Seeds provide the basis of genetic diversity in perennial grassland communities and their traits may influence ecosystem resistance to extreme drought. However, we know little about how drought effects the community functional composition of seed traits and the corresponding implications for ecosystem resistance to drought.
2. We experimentally removed 66% of growing season precipitation for 4 years across five arid and semi-arid grasslands in northern China and assessed how this multi-year drought impacted community-weighted means (CWMs) of seed traits, seed trait functional diversity and above-ground net primary productivity (ANPP).
3. Experimental drought had limited effects on CWM traits and the few effects that did occur varied by site and year. For three separate sites, and in different years, drought reduced seed length and phosphorus content but increased both seed and seed-coat thickness. Additionally, drought led to increased seed functional evenness, divergence, dispersion and richness, but only in some sites, and mostly in later years following cumulative effects of water limitation. However, we observed a strong negative relationship between drought-induced reductions in ANPP and CWMs of seed-coat thickness, indicating that a high abundance of dominant species with thick seeds may increase ecosystem resistance to drought. Seed trait functional diversity was not significantly predictive of ANPP, providing little evidence for a diversity effect.

4. Our results suggest that monitoring community composition with a focus on seed traits may provide a valuable indicator of ecosystem resistance to future droughts despite inconsistent responses of seed trait composition overall. This highlights the importance of developing a comprehensive seed and reproductive traits database for arid and semi-arid grassland biomes.

#### KEYWORDS

climate resistance, community-weighted traits, drought sensitivity, functional diversity, grasslands, net primary productivity, seed trait

## 1 | INTRODUCTION

Plant persistence in extant habitats and migration to new habitats both depend on successful reproduction by seeds (Fernández-Pascual et al., 2019). The traits that describe seed form and function are important for understanding the reproductive potential of individual plant species (Jimenez-Alfaro et al., 2016; Saatkamp et al., 2019; Walck et al., 2011) and may influence community resistance and resilience (i.e. regeneration promoting stable population growth) in light of global change (Ma et al., 2021; Prieto et al., 2015). Previous studies have used seed traits to understand dispersal processes germination viability, and seedling establishment (Jimenez-Alfaro et al., 2016). According to the seed ecological spectrum, plant species have evolved to produce seeds with acquisitive/germination trait syndromes that include greater seed size, smaller seed-coat thickness and higher seed nutrient content. These syndromes are prevalent within high-resource environments and help to maximize plant resource acquisition and growth (Saatkamp et al., 2019). In contrast, seeds with conservative/persistence trait syndromes have smaller seed size, greater seed-coat thickness and lower seed nutrient content to ensure seed vigour under low-resource conditions (Saatkamp et al., 2019). Indeed, smaller seeds have been shown to be better at tolerating environmental stress and thus have greater persistence in soils than larger seeds (Lv et al., 2019). Additionally, greater seed-coat thickness can protect seeds from herbivory and lower seed mortality rates for some weedy species (Davis et al., 2008; Gardarin et al., 2010).

With the exception of seed mass and size, trait-based studies that aim to explore ecological strategies and forecast ecosystem functioning have rarely included seed functional traits (Adler et al., 2014; Fernández-Pascual et al., 2019). Compared to other trait spectrums, such as the leaf (Wright et al., 2004) and root economic spectrums (Roumet et al., 2016), seed functional traits are under-represented in trait-based ecology and are infrequently included in community-scale plant trait surveys, particularly in the context of climate change (Griffin-Nolan et al., 2018; Saatkamp et al., 2019). Consequently, little is known about how community-level seed trait composition influences ecosystem functions, such as above-ground net primary productivity (ANPP).

Climate change is projected to increase the magnitude and frequency of extreme droughts in arid and semi-arid grasslands (Spinoni

et al., 2014). Grassland responses to drought are well-documented, and their sensitivity can vary depending on local climate and/or species composition with more arid (lower ANPP) sites being more sensitive (Knapp et al., 2015; Luo et al., 2021). Additionally, the magnitude of drought impacts on grassland functioning generally increases as drought progresses (Xu et al., 2021). Understanding how grasslands will respond to ongoing intensification of droughts is a fundamental component of predicting the effects of climate change on the functioning and services of these expansive ecosystems. Within this context, community-scale measurements of functional traits and new metrics for quantifying functional diversity have improved our understanding of how such environmental changes influence plant community dynamics (Arend da Silva et al., 2020; Gross et al., 2021; Luo et al., 2021; Wilcox et al., 2020).

Most studies of seed traits, however, have focused on trait measurements on individuals. For example, Bladé and Vallejo (2008) found a positive effect of seed mass on seedling height, diameter and relative growth rate at the population level. More broadly, the strategies of plants with shorter generation times and higher seed production rates are generally separated from those with slower reproduction and reliance on fewer, larger seeds (Jakobsson & Eriksson, 2000; Wright et al., 2004). This underscores the differential priorities of energy investment among reproduction, survival and growth in plants (Fridley, 2017). Therefore, the quantification of both community-weighted means (CWMs) of seed traits (i.e. community mean traits weighted by the species abundances) and functional diversity of seed traits (i.e. the distribution of trait values within the community) is expected to provide valuable insights into community assembly processes in response to forecast increases in drought frequency (Saatkamp et al., 2019).

Given that drought is a common occurrence in grasslands and is expected to intensify, it also represents a strong abiotic filter for grassland vegetation whereby certain seed trait combinations confer survival and fitness that are reflected in seed trait means and diversity at the community level (Cornwell & Ackerly, 2009; Luo et al., 2021). The regulation of water loss through seeds can be expressed by several key seed functional traits. For example, summer drought decreased seed size and increased coat thickness, as smaller seeds with higher coat thickness can endure water stress and have a lower mortality rate during drought (Leishman, 2001). Plants

TABLE 1 Climate, soil and vegetative characteristics of the five study sites in arid and semi-arid grasslands of northern China

	NHG	EFS	IMG-1	IMG-2	DGS
Grassland type	Meadow steppe	Meadow steppe	Typical steppe	Typical steppe	Desert steppe
Aridity	0.17	0.25	0.40	0.42	0.49
Location	N49°21' E120°06'	N50°10' E119°22'	N43°33' E116°40'	N43°32' E116°33'	N41°47' E111°53'
MAP (mm)	400	336	331	331	257
MAT (°C)	-2.4	-2.0	0.3	0.3	3.4
Dominant Species	<i>Stipa baicalensis</i>	<i>S. baicalensis</i>	<i>Leymus chinensis</i>	<i>S. grandis</i>	<i>L. chinensis</i>
ANPP (g/m <sup>2</sup> )	183.49	135.27	114.63	111.08	56.36
SOC (g/kg)	43.20	28.12	24.26	21.35	16.45
TN (g/kg)	4.10	3.11	3.15	2.94	2.83
AP (g/kg)	5.99	1.13	2.42	2.56	2.23
pH	6.98	7.89	7.28	8.06	7.68

Abbreviations: ANPP, above-ground net primary productivity; AP, soil available phosphorus; Aridity (unitless) is defined as  $1 - AI$ , where  $AI$ , the ratio of precipitation to potential evapotranspiration, is the aridity index; DGS, Damaoqi Grassland Station; EFS, Erguna Forest-Steppe Ecotone Research Station; IMG-1, Inner Mongolia Grassland Ecosystem Research Station, Site 1; IMG-2, Inner Mongolia Grassland Ecosystem Research Station, Site 2; MAP, the mean annual precipitation; MAT, the mean annual temperature; NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SOC, soil organic carbon; TN, soil total nitrogen.

generally accelerate seed production and consequently decrease seed nutrient content to enhance resource-use efficiency under water-deficient stress (Lv et al., 2019; Sehgal et al., 2018). Therefore, variation in community seed trait composition can provide a mechanistic understanding of ecosystem responses to drought (Violle et al., 2007).

Experiments and observations suggest two primary hypotheses to explain how plant seed trait composition may impact ecosystem resistance and resilience to drought (Fontana et al., 2021; Loreau et al., 2001). The mass ratio hypothesis states that the seed traits of dominant, that is, highly abundant, species in a community determine the dynamics of ecosystem functioning. Thus, ecosystem responses to drought will be mediated by the CWMs of seed traits, suggesting a potential advantage related to particular seed trait values (Fontana et al., 2021; Pakeman, 2014). The diversity hypothesis proposes that seed trait diversity enhances ecosystem resistance to drought via biotic mechanisms such as complementary resource-use among species (Díaz et al., 2007). However, responses of both seed trait means and functional diversity to extreme drought, and the corresponding links with ecosystem functioning, are still unclear.

The objective of this study was to explore the effects of a multi-year extreme drought on the functional composition of seed traits and the corresponding implications for ecosystem resistance across arid and semi-arid grasslands. To this end, we imposed a 4-year experimental growing season drought in five grassland sites across northern China and assessed the impacts of multi-year extreme drought on seed trait composition and the corresponding links with ANPP. We focus on nine key functional seed traits known to be related to species ecological strategies (e.g. acquisitive/germination vs. conservative/persistence resource

economies and drought tolerance vs. avoidance): seed length, seed width, seed thickness, seed size, seed mass, seed-coat thickness, seed carbon content, seed nitrogen content and seed phosphorus content (Saatkamp et al., 2019). We tested the following hypotheses: (a) extreme drought acts as a strong environmental filter that alters functional composition of seed traits, with the shift in mean seed trait values corresponding with increased abundance of tolerant species and reduced functional diversity of seed traits; (b) drought effects on CWMs and functional diversity of seed traits will increase through time and vary across sites with more arid sites being more sensitive; and (c) higher abundance of conservative seed traits and functional diversity of seed traits would be associated with greater ecosystem resistance to drought, assessed as relative reductions in ANPP.

## 2 | MATERIALS AND METHODS

### 2.1 | Site descriptions

We conducted this study as part of the Extreme Drought in Grasslands Experiment (EDGE; <http://edge.biology.colostate.edu/china>), which spanned five native grassland sites encompassing a 130mm gradient in mean annual precipitation (MAP) and a 3.5°C gradient in mean annual temperature (Table 1). These sites are dominated by  $C_3$  grasses and are representative of the major grassland types in northern China, including desert steppe, typical steppe and meadow steppe. Soil textures vary across grasslands from sandy to clay loam. For more detailed information on site characteristics, see Luo et al. (2018, 2021) and Muraina et al. (2021). We have appropriate permits to carry out our field work.

## 2.2 | Experimental drought treatments

We experimentally imposed drought at each site using rainfall exclusion shelters designed to passively intercept 66% of incoming ambient precipitation during the growing season (May to August) for 4 years (2015–2018). We established 12 plots ( $n = 6$  control;  $n = 6$  drought) in a topographically uniform area at each site and arranged plots in a randomized complete block design to control for possible differences in soil and vegetation properties. Each plot was 6 × 6 m in size, with at least 2 m spacing between plots. To minimize the edge effect associated with the rainout shelters, we marked off a 1-m perimeter to act as a buffer. We constructed these shelters using a frame which had removable polycarbonate roof panels that were spaced to block 66% of rainfall. We installed roofs in late April and removed them at the end of August. To allow for adequate air flow under shelters, we raised the roofs to 2 m above-ground at the highest point and 0.5 m above-ground at the lowest point. We installed aluminium flashing vertically around the plot to a depth of 1-m (to prevent below-ground flow into plots), with 10-cm remaining above-ground (to prevent overland flow into plots) to hydrologically isolate all plots (Luo et al., 2018, 2019).

## 2.3 | Sampling and measurement

In early August of each year, we estimated ANPP by harvesting all above-ground biomass from two 0.5 × 0.5 m quadrats in each plot. We sorted plant biomass by species and dried the samples at 65°C for 48 hr before weighing. For each plot, we averaged biomass values across the quadrats.

Seed traits of the most abundant species per site were not measured in control or drought plots to avoid destructive measurements. Thus, all seed traits were estimated in an ambient area adjacent to experimental plots. Briefly, five 10 m × 10 m sampling plots were randomly established with a mean interval of 50 m between them in the spring of 2016. In each plot, seeds were randomly sampled from more than 20 individuals of each species belonging to the recorded species during 2016–2020 (Table S1). For consistency, we collected seeds at maturity (i.e. at seed drop); however, the seed drop date varied greatly among species, ranging from early spring to late autumn. Seeds were air-dried and stored in the laboratory at ambient conditions until traits were measured. For each species, we averaged seed trait values across the plots, sites and years. The final seed trait dataset included trait values for 45 species collectively representing at least 90% of total biomass in each plot.

Here, we focused on nine key functional seed traits (seed length, seed width, seed thickness, seed size, seed mass, seed-coat thickness, seed carbon content, seed nitrogen content and seed phosphorus content) to describe the 45 species that were recorded (Table S1). Trait selection was based on the known importance of various traits in environmental filtering and niche differentiation. Seed length, width and thickness are related to persistence, with low seed length, width and thickness indicating a higher persistence in soils

(Saatkamp et al., 2019). Seed-coat thickness can reflect resource-use strategies, with high seed-coat thickness values indicating a conservative strategy (Davis et al., 2008; Gardarin et al., 2010). Seed mass and size affect seedling survival and colonization capacity of species. That is, species with larger seeds having less seed output but with higher seedling survival (Lv et al., 2019; Westoby et al., 2002). Seed carbon, nitrogen and phosphorus content are useful traits related to nutrient use strategies, with low carbon, nitrogen and phosphorus content indicating higher nutrient use efficiency (Sehgal et al., 2018).

For each species, we randomly selected 20 seeds to measure seed length (mm), width (mm) and thickness (mm) using digital vernier callipers. To estimate seed mass (mg) per 100 seeds, we determined the mass of 100 dry seeds (oven dried at 65°C for 48 hr to constant weight) per species with a precision balance. A subset of these seeds was then fixed in formalin-acetic acid-alcohol, progressively dehydrated in an ethanol series and infiltrated with warm paraffin. Seed transverse sections (10- $\mu$ m thickness) were cut and photographed under a light microscope (Leica DM2500, Germany). The thickness of the seed-coat ( $\mu$ m) was then measured individually using electronic image analysis equipment (MIPS software; Optical Instrument Co., Ltd.). To estimate seed carbon and nitrogen concentrations (mg/g), we ground dried seed samples to a fine powder and used an elemental analyser (2400II CHN elemental analyser; Perkin-Elmer, USA). Finally, we measured seed phosphorus concentrations (mg/g) using Continuous-Flow Analysis (SKALAR SAN<sub>++</sub>, USA) after H<sub>2</sub>SO<sub>4</sub>-H<sub>2</sub>O<sub>2</sub> digestion.

In each field plot, we randomly collected one composite soil core (0–10 cm depth) after removing the litter layer in each of the two quadrats using a soil auger (2.5 cm diameter). We used subsamples of each soil sample to quantify soil water content. We air-dried, ground and filtered subsamples through a 1 mm sieve (NM200; Retsch). We measured soil organic carbon (SOC) and total nitrogen content (TN) using an elemental analyser (2400II CHN elemental analyser; Perkin-Elmer, USA). Soil carbon/nitrogen (C/N) ratios were calculated and used to assess the indirect effects of soil water content on functional composition of seed traits via changes in soil fertility.

## 2.4 | Data analysis

We quantified CWMs for each of the nine seed traits as:  $CWM = \sum p_i \times \text{trait}_i$  (Laliberté & Legendre, 2010), where  $p_i$  is the relative biomass of species  $i$  in the community of the experiment, and  $\text{trait}_i$  is the seed trait value of species  $i$  from outside the experiments. We also calculated four separate indices of functional diversity based on dissimilarity distance across all seed traits (Laliberté & Legendre, 2010). Specifically, we used the *dbFD* function ('*FD*' package) which uses a flexible distance-based framework and principal component analyses to estimate functional dispersion (FDis; the multivariate equivalent of mean absolute deviation in trait space), functional divergence (FDiv, the deviance from the mean distance to the centre of gravity within multidimensional trait space), functional evenness (FEve; the regularity of spacing between species within

TABLE 2 ANOVA table for mixed effects models for community-weighted trait means and multivariate functional diversity

	Community-weighted trait means										Functional diversity			
	Length	Width	Thickness	Size	Mass	Coat thickness	Carbon	Nitrogen	Phosphorus	FDIs	FDiv	FEve	FRic	
Drought (D)	0.01	2.99	1.80	1.94	1.91	15.95***	0.79	0.60	3.84	0.16	9.69**	0.90	0.92	
Site (S)	21.15***	0.00	35.68***	17.54***	31.75***	34.17***	20.62***	6.42***	14.03***	3.59**	18.54***	5.22***	25.26***	
Year (Y)	2.67	0.23	19.31***	3.80	12.37***	5.12*	4.41*	2.08	4.32*	0.20	10.68**	1.61	10.78**	
D×S	5.37***	1.33	5.48***	3.81**	2.67*	3.73**	12.78***	5.73***	2.76*	8.17***	1.88	2.07	0.49	
D×Y	0.66	0.02	3.04	0.08	0.47	0.75	0.38	1.40	0.05	0.77	0.21	1.52	3.34	
S×Y	5.50***	1.89	7.12***	4.84***	6.30***	7.43***	8.03***	8.57***	1.26	8.44***	2.07	0.10	11.77***	
D×S×Y	1.68	0.27	0.76	0.85	0.90	0.04	2.52*	0.57	0.49	1.69	0.33	0.28	1.07	

Notes: F-values are shown for fixed effects and all interactions. Statistical significance is represented by asterisks: \* $p < 0.05$ , \*\* $p < 0.01$  and \*\*\* $p < 0.001$ . Refer to Table S2 for more details of these models. Abbreviations: FDIs, functional dispersion; FDiv, functional divergence; FEve, functional evenness; FRic, functional richness.

multivariate trait space) and functional richness (FRic, the convex hull volume of the individual species in multidimensional trait space). Thus, the responses of CWMs and functional diversity to drought as well as among years and sites represented species turnover and interspecific seed trait differences. Intraspecific seed trait variability and seed trait plasticity were not assessed. These intraspecific seed trait variations were predicted to contribute substantially to the community functional responses to environmental changes, yet only based on previous studies on other functional traits, such as leaf (Jung et al., 2014; Luo et al., 2019; Song et al., 2022) and root traits (Zhou et al., 2019).

To test the interactive effects of drought treatment, year and site on seed trait composition, we used linear mixed effects models including site, treatment and year as fixed effects and block as a random effect ('LME4' package). We ran a separate model for each CWM (i.e. seed length, seed width, seed thickness, seed size, seed mass, seed-coat thickness, seed carbon content, seed nitrogen content and seed phosphorus content) as well as functional diversity (i.e. FDIs, FRic, FDiv and FEve). We conducted pairwise comparisons between drought and control plots within each year and for each site (Tukey-adjusted  $p$ -values are presented).

We conducted path analysis to assess the direct and indirect relationships of soil water and fertility with each index of seed trait composition (CWMs and functional diversity) at each site ( $n = 24$ , six blocks and 4 years; Wilcox et al., 2020). In this model, year and block were included as random factors.

We calculated the sensitivity of ANPP to drought as the % reduction in ANPP in droughted plots each year for each site as follows:

$$\text{Drought sensitivity} = \text{abs} \left( 100 \times \frac{\text{ANPP}_{\text{drought}} - \text{ANPP}_{\text{control}}}{\text{ANPP}_{\text{control}}} \right),$$

where ANPP is the average across all plots of that treatment for each year. We represented drought sensitivity as an absolute value (abs); thus, large positive values indicate greater sensitivity (i.e. greater relative reduction in ANPP) (Griffin-Nolan et al., 2019).

We performed linear mixed effects models to explore the correlations between annual ANPP drought sensitivity ( $n = 20$ ; five sites and 4 years) and functional composition (CWMs and functional diversity) of seed traits whereby site was included as a random effect. Then, to avoid pseudo-replication, we compared these mixed effects models to null models based on the Akaike information criterion (AIC). For the null models, we only considered the random effect of site. The linear models were accepted as valid if  $\text{AIC}_{\text{model}}$  was lower than  $\text{AIC}_{\text{null}}$  (see Griffin-Nolan et al., 2019). Additionally, we calculated both marginal and conditional  $R^2$  values for each mixed effects model using the 'rsquared' function ('PIECEWISESEM' package) to determine the relative importance of random and fixed effects in determining the proportion of data variance explained by our model.

We used Shapiro-Wilk and Levene's Tests to test the normality and heteroscedasticity, respectively, of all data before statistical analyses. Given that the data were normally distributed and

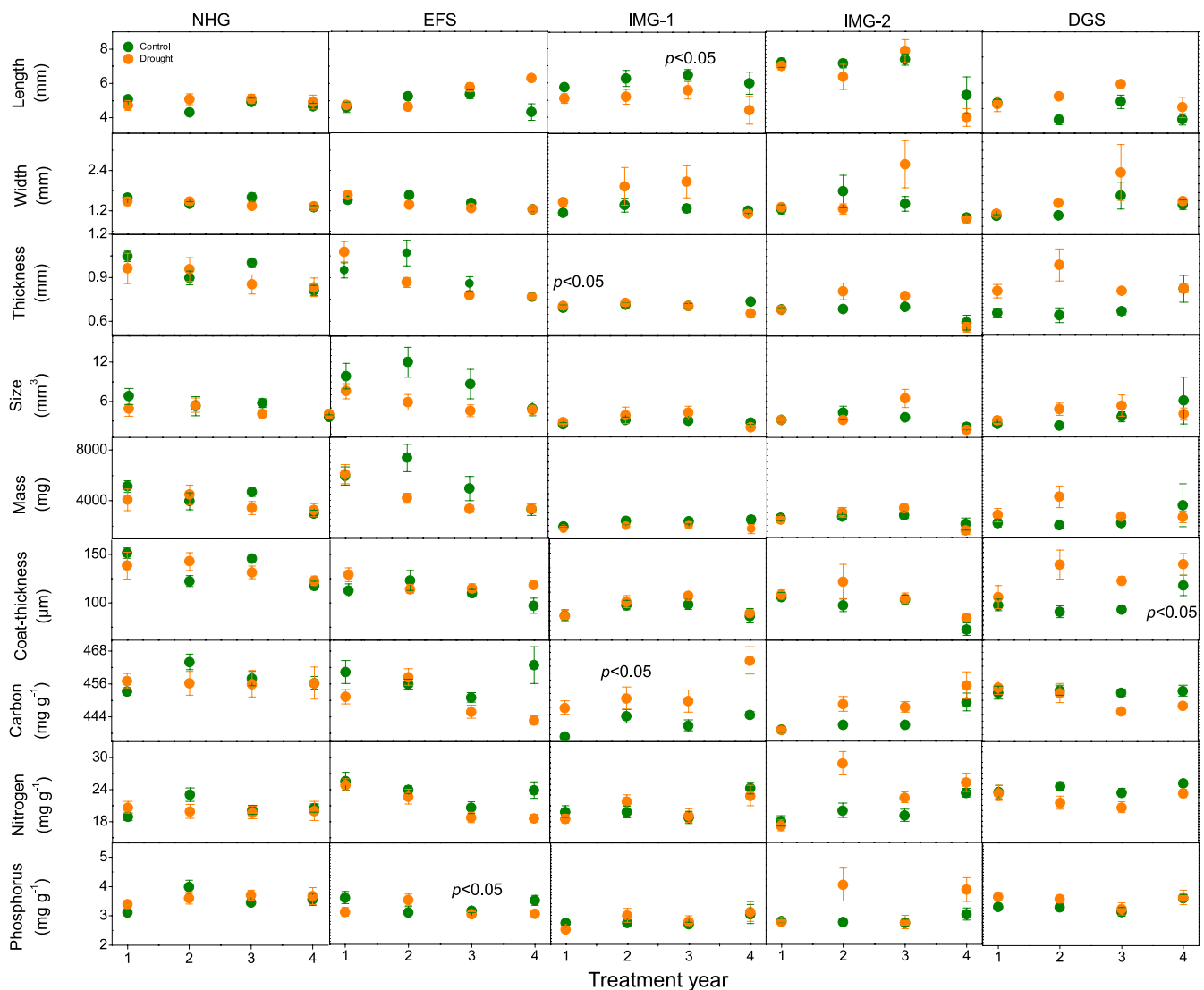
displayed homogeneity of variance, we used the original data in all statistical analyses without transformation. We conducted all analyses using R software.

### 3 | RESULTS

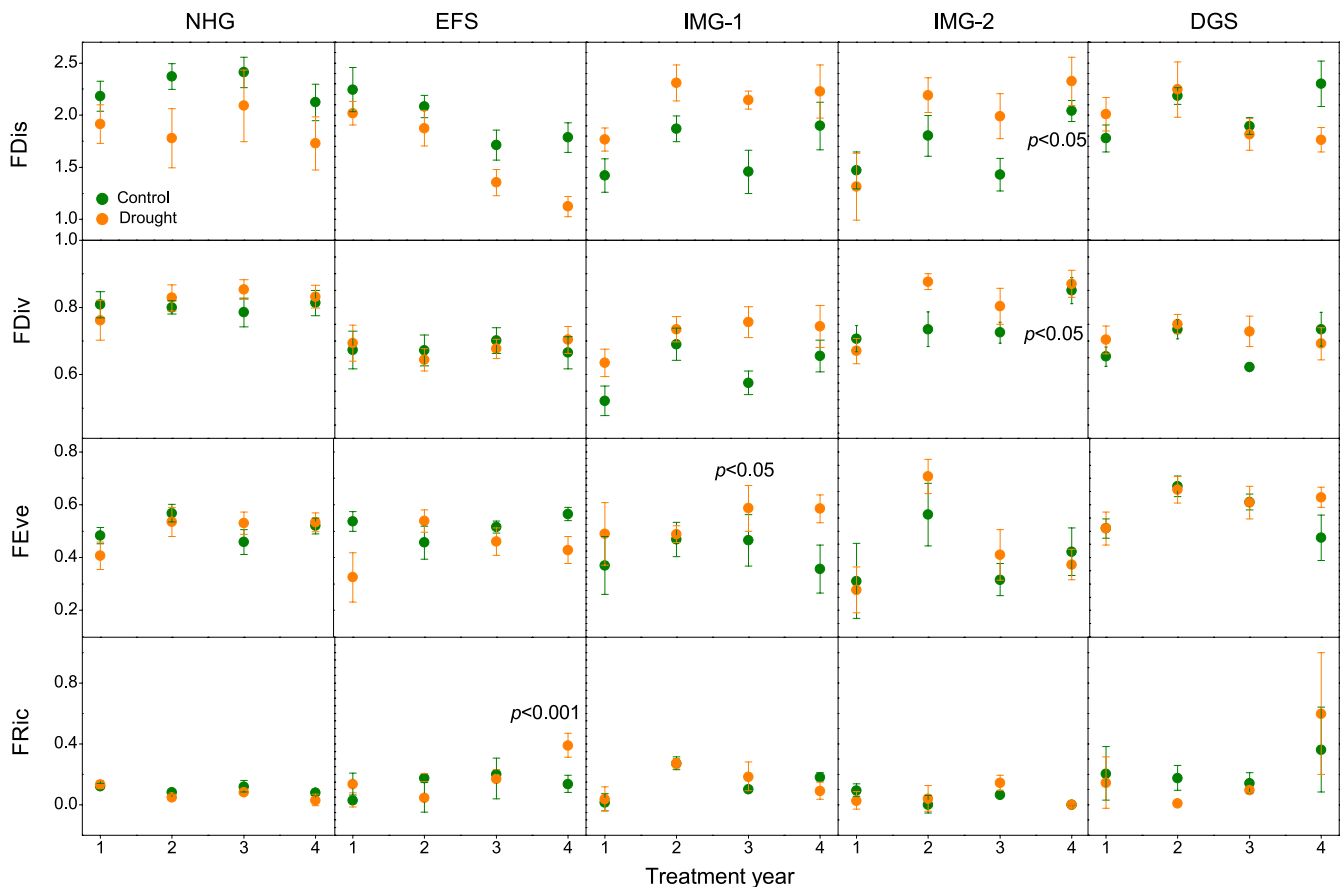
There were significant treatment  $\times$  site interactions for CWMs of eight of the nine seed traits as well as FDis, indicating that the responses of CWM seed traits and one measure of functional biodiversity to extreme drought differed among grassland sites (Table 2). The responses of trait means and diversity to extreme drought through time did not vary across sites (nonsignificant treatment  $\times$  year interactions; Table 2) or by site (nonsignificant treatment  $\times$  year  $\times$  site interactions; Table 2). There was evidence for site-specific temporal dynamics (significant site  $\times$  year interactions), with few exceptions (Table 2).

Of the nine CWM seed traits measured, many were unaltered by drought treatments across the 4 years (Table 2; Figure 1). Notable changes to CWMs at the typical steppe (IMG-1) included increased seed thickness in the first year of drought (2015,  $p < 0.05$ ), decreased seed length in the third year of drought (2017,  $p < 0.05$ ) and increased seed carbon content in the second year of drought (2016,  $p < 0.05$ ) (Figure 1). CWMs of seed-coat thickness significantly increased in the final year of drought treatment (2018,  $p < 0.05$ ) at the desert steppe (DGS) (Figure 1). Finally, we observed reduced seed phosphorus content at the meadow steppe (EFS) in the third year of the drought treatment (2017,  $p < 0.05$ ) (Figure 1). Overall, the observed changes to CWM seed traits in response to drought were inconsistent across sites and years (Figure 1).

Alterations to community-level seed trait composition depended on site and year (Table 2). For example, functional diversity of seeds was not significantly altered by drought until the final 2 years of the experiment and only for certain sites (Figure 2). Specifically, FDis



**FIGURE 1** Responses of community-weighted means of seed traits to 4-year experimental drought. Years with significant treatment effects are noted by  $p$ -values over the points. Refer to Table 1 for site abbreviations.



**FIGURE 2** Responses of community seed trait diversity to a 4-year experimental drought. Seed trait diversity metrics include functional dispersion (FDis), functional divergence (FDiv), functional evenness (FEve) and functional richness (FRic). Years with significant treatment effects are represented. Refer to [Table 1](#) for site abbreviations.

and FDiv both significantly increased at the typical steppe (IMG-2) in the final year of drought (2018) ([Figure 2](#)). Moreover, FEve significantly increased in droughted plots at the other typical steppe (IMG-1) in the third treatment year (2017,  $p < 0.05$ ), and FRic significantly increased at the meadow steppe (EFS) in the final treatment year (2018,  $p < 0.05$ ) ([Figure 2](#)). We observed no significant effects of drought on seed trait diversity at any other site in any other year ([Figure 2](#)).

Path analysis showed that soil water content had limited direct effects on many CWM traits across plots and years, although this was site dependent ([Figure S1](#)). For example, soil water content had direct negative effects on seed width (path =  $-0.48$ ,  $p < 0.05$ ), thickness (path =  $-0.58$ ,  $p < 0.05$ ), mass (path =  $-0.37$ ,  $p < 0.05$ ) and coat thickness (path =  $-0.71$ ,  $p < 0.001$ ), and positive effects on seed carbon content (path =  $0.52$ ,  $p < 0.05$ ) at the meadow steppe (EFS) ([Figure S1](#)). Soil water content directly reduced seed length (path =  $-0.42$ ,  $p < 0.05$ ) and thickness (path =  $-0.46$ ,  $p < 0.05$ ) at the desert steppe (DGS) ([Figure S1](#)). Soil water content also directly reduced seed carbon content at the typical steppe (IMG-1 and the desert steppe (DGS); path =  $-0.45$  and  $-0.41$ , respectively, both  $p < 0.05$ ; [Figure S1](#)).

Soil water content had limited indirect effects on many CWM traits through soil fertility, although this was also site

dependent ([Figure S1](#)). For example, soil water content had positive indirect effects on seed length (path =  $-0.77 \times -0.50 = 0.39$ ) and coat thickness (path =  $-0.77 \times -0.57 = 0.44$ ) and negative indirect effects on seed carbon (path =  $-0.77 \times 0.79 = -0.61$ ), nitrogen (path =  $-0.77 \times 0.57 = -0.44$ ) and phosphorus content (path =  $-0.77 \times 0.50 = -0.39$ ) via negative effects on soil fertility at the EFS site ([Figure S1](#)). Soil water content had positive indirect effects on seed-coat thickness (path =  $-0.46 \times -0.34 = 0.16$ ) and carbon content (path =  $-0.46 \times -0.67 = 0.31$ ) via negative effects on soil fertility at the IMG-1 site ([Figure S1](#)). Soil water content had positive indirect effects on seed-coat thickness (path =  $-0.46 \times -0.41 = 0.19$ ) and mass (path =  $-0.46 \times -0.40 = 0.18$ ) at the DGS site ([Figure S1](#)).

Path analysis also showed that soil water content did not have any direct relationships with any of the indices of functional diversity (i.e. FDis, FDiv, FEve and FRic) across plots and years at any site ([Figure S2](#)). Soil water content had positive indirect effects on FDis via negative effects on soil fertility at EFS (path =  $-0.77 \times -0.54 = 0.42$ ) and IMG-1 sites (path =  $-0.46 \times -0.39 = 0.18$ ), and positive indirect effects on FDiv (path =  $-0.46 \times -0.52 = 0.24$ ) at IMG-1 site ([Figure S2](#)).

Across 12 linear models, the only metrics of community-level seed trait composition that were significant predictors of the sensitivity of ANPP to drought were seed thickness and seed-coat

thickness (Table S3). These predictors were included as fixed effects in separate mixed effects models each with site as a random effect. Based on null model comparisons, we rejected the model with seed thickness but kept the model with seed-coat thickness (Table S3). Following null model comparison (see Section 2), we observed a strong negative relationship between seed-coat thickness and ANPP sensitivity to drought (Figure 3). In other words, grassland communities with a high abundance of species with thicker seed-coats experienced less drought-induced declines in ANPP (Figure 3).

## 4 | DISCUSSION

### 4.1 | Responses of community seed trait composition to water limitation

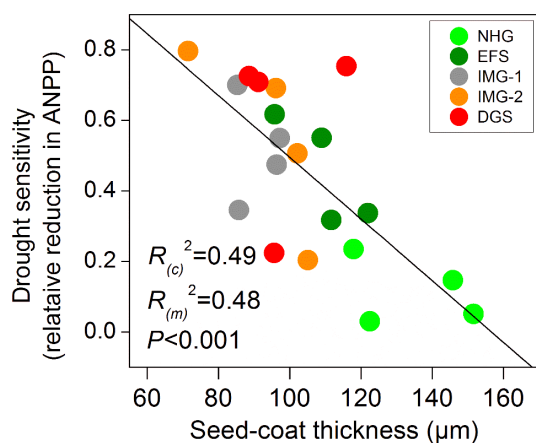
We assessed the impact of a 4-year experimental drought (66% reduction of growing season precipitation) on seed functional traits of five grassland communities in northern China. Our results indicate that reduced soil water content had limited direct effects on CWMs of seed reproductive traits during the drought treatment. The lack of drought effects on CWMs of seed traits suggests high resistance to periods of water limitation in functional aspects of the seed bank in these communities. However, we did find that CWMs of seed traits related to drought tolerance significantly changed in response to drought in some sites. For example, CWMs of seed length were reduced but CWMs of seed thickness and coat thickness increased following drought, which suggests a potential shift away from species with conservative resource-use strategies and towards a community with greater prevalence of drought avoidance and escape strategies.

Moreover, the response of functional diversity to extreme drought did not emerge until the third and fourth years of drought. Previous studies in arid and semi-arid grasslands have reported

similar results. For example, a multi-year drought experiment in the central United States did not reveal shifts in community trait composition until the third year of drought (Griffin-Nolan et al., 2019). Likewise, richness, diversity and evenness were not altered after a 2 years of drought in the semi-arid Patagonian steppe (Yahdjian & Sala, 2002), and 5 years of severe drought had little impact on seed bank diversity and composition in two semi-arid Chihuahuan Desert grasslands (Loydi & Collins, 2021). The increase in functional diversity of seed traits, which maximize trait dissimilarity in multiple dimensions, could possibly minimize competition and/or increase complementarity among seedlings of the same community and allow for successful recruitment under drought (Poschlod et al., 2013; Wagg et al., 2017).

Previous studies have shown that spatial differences in soil fertility resulting from drought likely played a critical role in mediating the changes in functional composition with experimental drought (He & Dijkstra, 2014). Here, we found that experimental drought indirectly altered the functional diversity of seed traits through changes in soil fertility, but only for one or two indices of functional diversity in only two sites. In most cases, experimental drought had limited indirect effects on CWM traits and functional diversity of seed traits through altered soil fertility. It appears that a ~66% reduction in growing season precipitation did not alter soil resources (e.g. water and fertility) enough to immediately impact plant community functional composition of seed traits in the short term (Collins et al., 2014; Smith et al., 2009). It is possible that intraspecific shifts in seed trait composition did occur, yet intraspecific trait variation was not accounted for in this study. Nevertheless, our findings suggest that long-term climate change experiments are needed to better predict if and how community functional composition will respond to future climate change.

The effects of water limitation on seed functional trait means and diversity were rarely consistent over space or time. Similarly, previous studies demonstrated that experimental drought effects on community leaf trait composition varied spatially and temporally across grasslands of North China (Luo et al., 2019) and North America (Griffin-Nolan et al., 2019). These results together suggest that climate change effects on grassland community functional composition will be complex and variable over space and time, which will likely contribute to population stability and/or adaptation to changing climates. Understanding and accounting for the complexity of grassland community functional responses to water limitation are necessary to properly parameterize global models that predict the influences of future changing climate on grassland community structure and functions.



**FIGURE 3** Bivariate relationship between drought sensitivity (i.e. % reduction in ANPP in drought plots relative to control in a given year) and community-weighted means of seed-coat thickness across five grasslands of northern China. The marginal (m) and conditional (c)  $R^2$  values for the model are shown. Refer to Table 1 for site abbreviations.

### 4.2 | Effects of community seed traits on ecosystem sensitivity

Previous studies have revealed that responses of ecosystem functions to climate extremes are partially mediated by the functional structure and composition of plant communities (McGill et al., 2006;



Suding et al., 2008). Therefore, understanding the drought sensitivity of community-scale plant traits as well as their relationships with ecosystem functions may improve predictions of ecosystem responses to climate extremes (Jakobsson & Eriksson, 2000; Suding et al., 2008). Biodiversity, and functional diversity more specifically, is now well-recognized as an important driver of ecosystem resistance to extreme climate events (Schellenberger Costa et al., 2017). We tested this hypothesis across five grasslands by investigating relationships between several functional diversity indices and the sensitivity of ANPP to drought (i.e. drought sensitivity). Our results (no relationship between functional diversity indices and drought sensitivity) do not support this hypothesis.

In contrast, we observed a significant negative correlation between a single CWM traits (seed-coat thickness) and the sensitivity of ANPP to drought, supporting the hypothesis proposed that the traits of dominant species are important proximate determinants of ecosystem structure and function and their responses to environmental change (Avolio et al., 2019). Thus, the mass ratio hypothesis, rather than the diversity hypothesis, is the more appropriate framework to link seed traits to near-term responses to extreme drought, at least in these grasslands. This result is consistent with previous studies that demonstrated the ability of trait means to explain variation in ecosystem structure and functions (Griffin-Nolan et al., 2019; Mokany et al., 2008).

The strongest predictor of drought sensitivity was CWMs of seed-coat thickness. A thicker seed-coat is an example of a 'slow' or conservative trait often associated with stress tolerance strategies (Davis et al., 2008; Gardarin et al., 2010). The significant negative relationship observed in this study suggests that plant communities with a greater abundance of species with high seed-coat thickness (i.e. resource conservative strategies) are less sensitive to drought. These findings suggest the importance of developing a more comprehensive traits dataset, one that goes beyond leaf and root traits and that considers at least some seed traits (Laughlin, 2014).

## 5 | CONCLUSIONS

Our study focused on one of the less studied areas in trait-based ecology by assessing the role of seed traits as indicators of plant community response to an extreme experimental drought across five arid and semi-arid grasslands of northern China. Our results highlight the complexity of drought effects on community functional composition of seed traits over space and time, which will likely contribute to plant community stability and/or adaptation to changing climates. While 4 years of extreme experimental drought exerted minor effects on CWM traits generally in any given year, their effects on functional diversity were cumulative and thus emerged after 3–4 years of treatment. The lack of any significant shift in community seed trait composition in response to extreme drought indicates a high prevalence of conservative strategies in these communities. The sensitivity of ANPP to experimental drought was more strongly related to CWMs of seed-traits and thus dominant species, rather than functional diversity. Seed traits related to coat

thickness, together with other vegetative and reproductive traits should be incorporated into trait-based frameworks to better predict how drought will impact the functioning and services of grassland ecosystems.

## AUTHOR CONTRIBUTIONS

Wentao Luo conceived and designed the experiments; Hongxiang Zhang, Hongyi Wang, Zhengwen Wang, Xingguo Han and Qiang Yu performed the experiments; Wentao Luo and Robert J. Griffin-Nolan analysed the data; Wentao Luo, Robert J. Griffin-Nolan, Alan K. Knapp, Scott L. Collins and Andrew J. Felton wrote the manuscript.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data available from <https://doi.org/10.6084/m9.figshare.20486541.v1> (Luo et al., 2022).

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