






RESEARCH ARTICLE

Plant traits modulate grassland stability during drought and post-drought periods

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Abstract

1. Grasslands are subject to climate change, such as severe drought, and an important aspect of their functioning is temporal stability in response to extreme climate events. Previous research has explored the impacts of extreme drought and post-drought periods on grassland stability, yet the mechanistic pathways behind these changes have rarely been studied.
2. Here, we implemented an experiment with 4 years of drought and 3 years of recovery to assess the effects of drought and post-drought on the temporal stability of above-ground net primary productivity (ANPP) and its underlying mechanisms. To do so, we measured community-weighted mean (CWM) of six plant growth and nine seed traits, functional diversity, population stability and species asynchrony across two cold, semiarid grasslands in northern China. We also performed piecewise structural equation models (SEMs) to assess the relationships between ANPP stability and its underlying mechanisms and how drought and post-drought periods alter the relative contribution of these mechanisms to ANPP stability.
3. We found that temporal stability of ANPP was not reduced during drought due to grasses maintaining productivity, which compensated for increased variation of forb productivity. Moreover, ANPP recovered rapidly after drought, and both grasses and forbs contributed to community stability during the post-drought period. Overall, ANPP stability decreased during the combined drought and post-drought periods because of rapid changes in ANPP from drought to post-drought. SEMs revealed that the temporal stability of ANPP during drought and post-drought periods was modulated by functional diversity and community-weighted mean traits directly and indirectly by altering species asynchrony and population stability. Specifically, the temporal stability of ANPP was positively correlated with functional divergence of plant communities. CWMs of seed traits (e.g. seed

width and thickness), rather than plant growth traits (e.g. specific leaf area and leaf nutrient content), stabilized grassland ANPP. Productivity of plant communities with large and thick seeds was less sensitive to precipitation changes over time.

4. These results emphasize the importance of considering both the functional trait distribution among species and seed traits of dominant species since their combined effects can stabilize ecosystem functions under global climate change scenarios.

KEYWORDS

community-weighted mean traits, ecosystem stability, experimental drought, functional diversity, plant traits, post-drought recovery, seed traits

1 | INTRODUCTION

The temporal stability of an ecosystem is the degree to which certain functions, such as primary productivity, are maintained over time in response to environmental variability and disturbance (Grman et al., 2010; Isbell et al., 2015). Ecosystem stability is important for the reliability of ecosystem services that affect human well-being (Oliver et al., 2015). The expected rise in atmospheric greenhouse gases and associated warming trends in the coming decades will lead to increases in drought frequency and duration in many regions (Bradford et al., 2020). This predicted intensification of drought has the potential to decrease primary production and biodiversity, and alter community composition, with immediate and potentially long-lasting post-drought impacts on ecosystem function and stability at regional and global scales (He et al., 2022; Knapp et al., 2008; Luo et al., 2023; Xu, Yang, et al., 2022). Indeed, several broad-scale analyses have found that water-limited ecosystems such as grasslands are especially vulnerable to drought both during and after these events end (Knapp et al., 2015; Maurer et al., 2020). Determining how and why ecosystem stability is altered by both drought and post-drought effects may improve our ability to predict how future changes in precipitation will impact ecosystem structure and functions (Broderick et al., 2022; Xu, Yang, et al., 2022). Yet, most studies that model the influence of climate change have focused on ecosystem function and stability during drought periods, whereas ecosystem stability during post-drought periods has received much less attention (de Bello et al., 2021; He et al., 2022; Matos et al., 2020), with even less research on the mechanistic pathways behind these responses.

Several biotic mechanisms could contribute to the maintenance of temporal ecosystem stability during drought and post-drought conditions (Grman et al., 2010; Wang et al., 2020). Decreased soil moisture may cause plant species to experience more severe water limitation, making biomass production more responsive to precipitation variation over time (i.e. reduced temporal stability) (He et al., 2022). Decreased stability of ecosystems during drought can be linked to a loss of diversity, in particular functional diversity

(Loreau et al., 2001) that corresponds to a loss of species interactions (i.e., niche differentiation or complementarity) within a community (Loreau et al., 2001; Wang et al., 2020; Xu, Yang, et al., 2021). Trait-based approaches offer a pathway to decipher species coexistence mechanisms and predict ecosystem function and stability (Adler et al., 2013; Brotherton & Joyce, 2015; de Bello et al., 2021; Polley et al., 2013). Species with different functional traits that respond differently to environmental variability will drive species asynchrony and enhance population and community stability (de Bello et al., 2021; Díaz et al., 2007). Previous studies have shown that greater multi-trait similarity among species is associated with lower asynchrony and community stability (de Bello et al., 2021). For example, Hallett et al. (2017) detected an increase in asynchrony and community stability with increasing community functional diversity under dry and wet conditions in manipulated grassland communities.

Additionally, the traits of the most abundant species in a community (represented as community-weighted mean [CWM] traits) can influence stability response to environmental change, such as drought, both during and after events (i.e. the selection effect) (Majekova et al., 2014; Mokany et al., 2008; Luo et al., 2021). There is increasing empirical evidence that species with conservative traits (e.g. higher leaf dry matter content [LDMC], lower specific leaf area [SLA] and larger and thicker seeds) tend to be more stable than exploitative species in response to environmental change (Valerio et al., 2022; Wright et al., 2001). For example, high CWMs of SLA modulated the temporal stability of above-ground net primary production (ANPP) by promoting species asynchrony and population stability under increased water and nitrogen availability in a semi-arid grassland (Xu, Li, et al., 2022). Hou et al. (2022) also reported that the ANPP stability of alpine grassland communities over a 20-year period was positively associated with high LDMC, given the role this trait plays in species resistance to adverse conditions. Likewise, CWMs of seed mass had an indirect effect on year-to-year and long-term community stability through asynchrony during fertilization in a seminatural Mediterranean grassland (Valerio et al., 2022). These findings suggest that drought and post-drought periods can influence ecosystem stability through altering the traits of dominant species, functional diversity, population stability and asynchronous

dynamics among species (Hautier et al., 2014). However, the relative importance of these drivers to ecosystem stability remains unclear, especially in the context of extreme climatic events, such as prolonged drought.

To quantify how temporal reduction in precipitation affected stability of ecosystem productivity through different underlying mechanisms (i.e. CWM of traits, functional diversity, population stability and species asynchrony), we reduced growing season precipitation for 4 years followed by 3 years of natural recovery in cold-semiarid grasslands of northern China. This ecosystem constitutes an important component of the largest remaining contiguous Eurasian grasslands, and can be sensitive to inter- and intra-annual precipitation variability (Bai et al., 2004; Kang et al., 2007). We tested two hypotheses: (1) temporal stability of ANPP would be reduced during experimental drought and post-drought periods, and (2) both high functional diversity and dominance by species with conservative traits would confer higher ANPP stability directly or indirectly via increasing species asynchrony and population stability during and following drought.

2 | MATERIALS AND METHODS

2.1 | Study descriptions and experimental design

We experimentally manipulated growing season precipitation regimes in two sites in a semiarid grassland region of northern China that represents the typical vegetation of the largest grassland biome across the Eurasian continent (Kang et al., 2007). The study area is characterized by a temperate continental monsoon climate with a 4-month growing season (May–August) and is experiencing intensified climatic warming and drying. The two sites are located at the Erguna Forest-Steppe Ecotone Research Station (EFS) and National Hulunber Grassland Ecosystem Observation and Research Station (NHG). Each site receives about 350 mm of mean annual precipitation and is classified as cold-semiarid grassland (mean annual temperature = -2°C). Both experiments are part of the Drought-Net Research Coordination Network (<https://droughtnet.weebly.com/>) and the Extreme Drought in Grasslands Experiment (Carroll et al., 2021). Plant communities are dominated by *Leymus chinensis* and *Pulsatilla turczaninowii*. Dominant soils are characterized as chestnut according to the Chinese classification and Haplic Calcisols according to the Food and Agriculture Organization classification system. We have appropriate permits to carry out our field work.

Experimental plots were established in relatively flat areas with vegetation composition representative of the larger ecosystem. Drought treatments (100% reduction from June to July during the growing season) were started in 2015 using large rainfall exclusion shelters and lasted until 2018. All the plots received ambient precipitation during the following 3 years (2019–2021). The experimental design was a randomized complete block design with two plots (drought and ambient rainfall) randomly assigned in each block. We had six replicates at each site, totalling twelve $6\text{ m} \times 6\text{ m}$ plots, which

were at least 2 m apart (see replication statement in Table S1). Plots were hydrologically isolated from each other and the surrounding soil by trenching the perimeter to a depth of 1 m and lining the trench with 6-mm-thick plastic and metal flashing (Luo et al., 2019). Rainfall shelters were constructed with light scaffolding and covered in strips of transparent polyethylene plastic (Beijing Plastics Research Institute), which only exerts minimal impacts on the microclimatic conditions (Luo et al., 2018; Yahdjian & Sala, 2002). Shelter roofs were installed at a height of 2.5 m above-ground at the highest point and 0.5 m at the lowest point, allowing for near surface air exchange (see Knapp et al., 2015; Luo et al., 2018 for further details on the rainout shelter and experimental design).

2.2 | Data collection

A 1-m wide buffer was established along the shelter edge to avoid sampling in areas experiencing edge effects; accordingly, 16 m^2 ($4 \times 4\text{ m}$) sampling plots were established in the centre of each plot. In each sampling plot of each site, a $1\text{ m} \times 1\text{ m}$ plot was established and split into four $50\text{ cm} \times 50\text{ cm}$ quadrats, two of which were sampled for above-ground biomass of each species in each year (2015–2021). Plant biomass was measured at peak biomass (10–15 August) by harvesting all above-ground plant material of each species. Biomass was oven-dried at 60°C to constant mass and weighed to the nearest 0.01 g. Total ANPP was estimated as the sum of all species biomass.

The other two quadrats were designated for measurements of plant traits. Plant height (cm) was measured from three sun-exposed individuals of each species per subplot. Leaf area was measured using Image J (<https://imagej.nih.gov/ij/>). Then, leaf dry weight was measured after oven-drying leaves at 65°C for 48 h to calculate both SLA (area/dry weight, $\text{m}^2\text{ kg}^{-1}$) and leaf dry matter content (LDMC, dry weight/fresh weight, mg g^{-1}) following standardized protocols. These same leaves were ground for measurements of leaf nitrogen (LNC, mg g^{-1}) concentration using an elemental analyzer (2400II CHN elemental analyzer; Perkin-Elmer) and P concentration (LPC, mg g^{-1}) using inductively coupled plasma atomic emission spectrometry (OPTIMA 3000 DV; Perkin-Elmer) after H_2SO_4 – H_2O_2 digestion. These traits were measured each year at both sites.

In addition, seeds of these species per site were collected in the ambient areas nearby our experiment during 2016–2020 (see Luo et al., 2022 for further details on seed sampling and trait measurement). Collected seeds were air-dried and stored in the laboratory at ambient conditions until their traits were measured. For each species, 20 seeds were randomly selected to measure seed length (mm), width (mm) and thickness (mm) using digital vernier callipers. To estimate seed mass per 100 seeds (mg), the mass of 100 dry seeds (oven-dried at 65°C for 48 h to constant weight) per species was determined with a precision balance (0.1 mg accuracy). Some seeds were exposed to X-rays (Faxitron MX-20 cabinet X-ray system) at a radiation intensity to optimize visualization of the seed coat (nm). Seed-coat thickness was measured individually on X-ray images using Image J (<https://imagej.nih.gov/ij/>). We then used the same

approach as leaves to measure seed C (SCC, mg g^{-1}), N (SNC, mg g^{-1}) and P (SPC, mg g^{-1}) concentrations. For each species, we averaged seed trait values across years. All harvested species cumulatively represented at least 90% of the total community biomass in each plot at each site.

2.3 | Statistical analyses

Temporal stability of ANPP was calculated as the ratio of the inter-annual mean of community biomass to its standard deviation over the four drought years, over the three post-drought years or over the 7 years combined respectively (Tilman et al., 2006). Next, total ANPP was sorted into grass and forb productivity, and the temporal stability of grass and forb productivity was calculated using the same equation. Similarly, the temporal stability of individual species in each plot was also calculated. Population stability was then calculated as the biomass-weighted mean value of the temporal stability across all species within a plot.

Following the approach in Hautier et al. (2020), species asynchrony was calculated for each plot as $1 - \varphi_b = 1 - \frac{\sigma^2}{(\sum_{i=1}^n \sigma_i^2)^2}$, where φ_b is species synchrony, σ^2 is the temporal variance in ANPP and σ_i is the temporal standard deviation in the biomass of species i in a plot with n species over the four drought years, over the three post-drought years or over the 7 years combined respectively. The degree of species asynchrony ranges from one (when species fluctuations are perfectly asynchronous) to zero (when species fluctuations are perfectly synchronous).

CWMs for each of the measured traits (six growth traits and nine seed traits) were quantified as $\text{CWM} = \sum_{i=1}^S p_i x_i$, where p_i is the relative abundance (per cent biomass) of species i , x_i is the trait value of species i and S is the species number in the plant community per plot (Díaz et al., 2007). Additionally, community functional diversity for all the measured traits together was calculated using a flexible distance-based framework and principal component analysis (Laliberté & Legendre, 2010). The functional diversity indices included 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 multivariate trait space) and functional richness (FRic, the convex hull volume of the individual species in multidimensional trait space). We calculated CWM trait values as well as functional diversity indices in each plot.

The temporal stability of ANPP (total, grass and forb) was analysed using linear mixed-effects models with treatment and site as fixed factors and block as a random factor. When interactive effects of treatment and site were statistically significant ($p < 0.05$), the linear mixed-effects model was separately applied for each site with treatment as a fixed factor and block as a random factor. These models were applied to drought, post-drought or combined periods respectively.

Next, we constructed linear mixed-effects models to explore the bivariate relationships between the temporal stability of ANPP and its potential underlying mechanisms (CWM traits, functional diversity, population stability and species asynchrony). In this model, block nested within site was used as a random factor.

Finally, we performed piecewise structural equation models (SEMs) to further understand the contributions of the four mechanisms (CWM traits, functional diversity, population stability and species asynchrony) to temporal stability of ANPP during the drought and post-drought periods. We used knowledge from previous theoretical and empirical findings to develop a priori SEMs that included all plausible pathways (Figure S1). We obtained the final SEMs by sequentially eliminating nonsignificant pathways when the initial model did not produce an adequate fit. Model adequacy was evaluated using Shipley's test of directed separation on Fisher's C statistic (if $p > 0.05$, then no paths are missing and the model is a good fit; Shipley, 2013) and Akaike's information criterion corrected for sample size (AICc). In these models, block nested within site was used as a random factor. Given that we had multiple candidate variables for CWM traits, one or two CWM traits were included in the initial model, which resulted in many possible models (van der Sande et al., 2018). The best-fitting model ($p > 0.05$) with the highest explained variation of ANPP stability was selected in our study. All data processing and statistical analyses were performed in R software (R version 4.1.1; R Core Team, 2021). The 'nlme' package was used for conducting linear mixed-effects models and the 'piecewiseSEM' package for constructing SEMs (Lefcheck, 2016).

3 | RESULTS

The temporal stability of ANPP significantly increased at EFS ($p < 0.05$) but remained unchanged at NHG during drought (Figure 1a). Temporal stability of ANPP was similar between control and treatment plots during post-drought periods at both EFS and NHG (Figure 1b), but ANPP stability was significantly higher in control versus treatment plots over the combined drought and post-drought periods at both sites (both $p < 0.001$; Figure 1c).

The temporal stability of grass productivity did not change during the drought (Figure 1d) or post-drought period (Figure 1e), but was significantly lower in the treatment plots when drought and post-drought periods were combined at each site (both $p < 0.05$; Figure 1f). The stability of forb productivity decreased during drought ($p < 0.05$; Figure 1g) but stayed constant during the post-drought period at both sites (Figure 1h). The temporal stability of forb productivity did not vary when drought and post-drought periods were combined (Figure 1i).

Bivariate relationship results revealed that temporal stability of ANPP was positively correlated with species asynchrony ($r^2_m = 0.54$, $p < 0.001$) and population stability ($r^2_m = 0.27$, $p < 0.001$) during drought, the post-drought period and over the 7 years combined (Table 1). Temporal stability of ANPP was positively correlated with

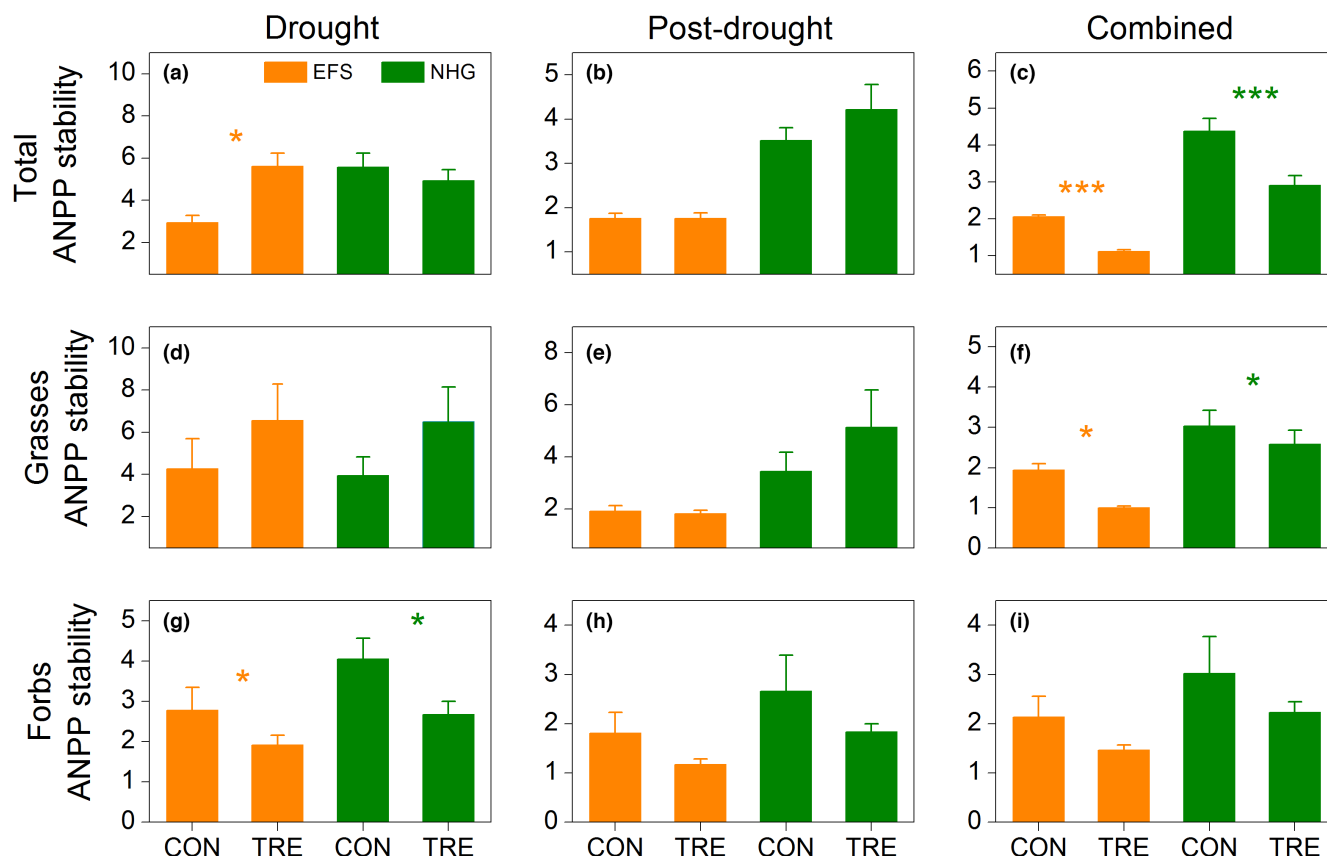


FIGURE 1 The temporal stability of above-ground net primary productivity (ANPP) during drought, post-drought and over drought and post-drought periods combined across two sites in a cold-semiarid grassland region of northern China. Responses of ANPP stability are shown for total (a–c), grass (d–f) and forb productivity (g–i). CON, control, TRE, drought treatment; EFS, Erguna Forest-Steppe Ecotone Research Station, NHG, National Hulunber Grassland Ecosystem Observation and Research Station; Statistical significance of treatment effect is depicted as * $p < 0.05$ and *** $p < 0.001$.

community functional divergence ($r^2_m = 0.16$, $p = 0.002$) and dispersion ($r^2_m = 0.07$, $p = 0.011$), but was not linked with functional richness and evenness during drought, post-drought or over drought and post-drought periods combined (Table 1). The temporal stability of ANPP during drought, post-drought or over all years was not related to any CWMs of growth traits including plant height, SLA, LDMC, LNC and LPC (Table 1).

Rather, temporal stability of ANPP was better explained by CWMs of some seed traits during drought, post-drought and the combined drought and post-drought periods. Specifically, ANPP stability was positively correlated with CWMs of seed width ($r^2_m = 0.15$, $p < 0.001$), seed thickness ($r^2_m = 0.09$, $p < 0.001$), seed volume ($r^2_m = 0.07$, $p = 0.003$), seed mass ($r^2_m = 0.08$, $p < 0.001$) and seed-coat thickness ($r^2_m = 0.31$, $p < 0.001$), but not with other seed traits (Table 1).

When considering multivariate causal relationships with piecewise SEM, we confirmed that community trait composition (i.e. CWM traits and functional diversity) altered temporal stability of ANPP directly or indirectly via species asynchrony and population stability during drought, post-drought and their combined periods at both sites (Figure 2). Specifically, seed width directly reduced ANPP stability (path = -0.31), but indirectly increased ANPP stability by

increasing species asynchrony (path = $0.57 \times 0.83 = 0.47$), leading to a total net effect (path = 0.16) on ANPP stability (Figure 2). Seed thickness directly enhanced ANPP stability (path = 0.38), but indirectly reduced ANPP stability by increasing species asynchrony (path = $-0.26 \times 0.83 = -0.22$), leading to a total net effect (path = 0.17) on ANPP stability (Figure 2). Functional dispersion (FDis) directly reduced ANPP stability (path = -0.32), but indirectly increased ANPP stability by increasing species asynchrony (path = $0.37 \times 0.83 = 0.31$), leading to little overall effect (path = -0.01) on ANPP stability (Figure 2). Functional divergence (FDiv) did not directly affect ANPP stability, but increased ANPP stability indirectly via increasing population stability (path = $0.40 \times 0.41 = 0.16$) (Figure 2). Overall, we observed a total effect of community trait composition on ANPP stability (path = 0.48), including direct (path = -0.24) and indirect effects (path = 0.73) (Figure 2).

4 | DISCUSSION

In this study, we assessed the effects of a 4-year drought and a 3-year post-drought recovery period on the temporal stability of ANPP as well as underlying mechanisms of responses (i.e. CWMs of

	df	<i>f</i>	<i>p</i>	r^2_m	r^2_c	Direction
Functional richness	59	3.49	0.067	0.04	0.34	
Functional evenness	59	3.69	0.060	0.04	0.31	
Functional divergence	59	10.84	0.002	0.16	0.29	Positive
Functional dispersion	59	6.90	0.011	0.07	0.34	Positive
Plant height	59	1.10	0.299	0.04	0.63	
Specific leaf area	59	0.10	0.753	0.01	0.44	
Leaf dry matter	59	0.95	0.333	0.01	0.50	
Leaf nitrogen	59	0.19	0.663	0.03	0.73	
Leaf phosphorus	59	3.43	0.069	0.15	0.89	
Seed length	59	1.11	0.297	0.01	0.36	
Seed width	59	12.44	<0.001	0.15	0.32	Positive
Seed thickness	59	13.23	<0.001	0.09	0.56	Positive
Seed volume	59	9.41	0.003	0.07	0.58	Positive
Seed mass	59	12.40	<0.001	0.08	0.56	Positive
Seed carbon	59	1.43	0.236	0.01	0.36	
Seed nitrogen	59	1.32	0.255	0.04	0.61	
Seed phosphorus	59	1.26	0.267	0.02	0.31	
Seed-coat thickness	59	31.62	<0.001	0.31	0.31	Positive
Species asynchrony	59	73.55	<0.001	0.54	0.57	Positive
Population stability	59	37.08	<0.001	0.27	0.51	Positive

Statistical significance is represented by bold values ($p < 0.05$).

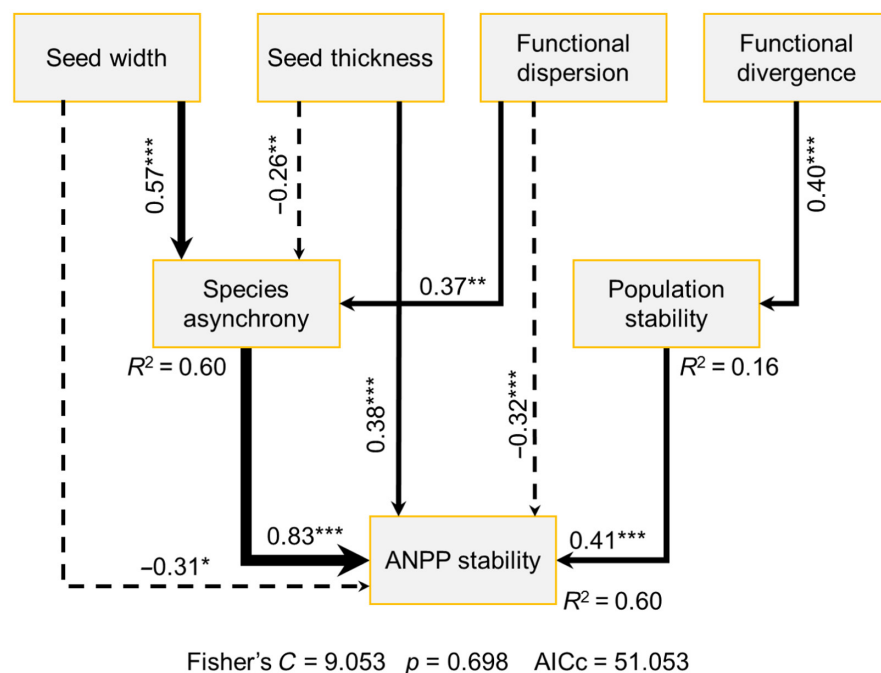


FIGURE 2 The final piecewise structural equation model showing the direct and indirect effects of community-weighted mean (CWM) traits, functional diversity, population stability and species asynchrony on temporal stability of above-ground net primary productivity (ANPP) during drought, post-drought and over drought and post-drought periods combined across two sites in a cold-semiarid grassland region of northern China. Solid and dash arrows indicate positive and negative pathways respectively (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Numbers along the arrows indicate standardized path coefficients. Arrow width is proportional to the strength of the relationship. The proportion of variance explained (R^2) appears alongside response variables in the model.

six growth traits and nine seed traits, functional diversity, population stability and species asynchrony) across two sites in a cold-semiarid grassland of northern China. Contrary to our expectations, our results showed that the temporal stability of ANPP did not decrease during the drought period due to the stability of grass productivity,

which compensated for the instability of forb productivity. In line with this result, plant communities in grasslands of the United Kingdom (Grime et al., 2000) and Israel (Tielbörger et al., 2014) also maintained stable biomass production after long-term precipitation reduction. This result contradicts previous studies classifying

water-limited grasslands as the most vulnerable ecosystems to global climate change, such as summer drought (Knapp et al., 2015; Maurer et al., 2020). We attribute this stabilized vegetation productivity under experimental drought to the dominant species that often exhibit lower responsiveness to reductions and/or variations in water availability (i.e. vegetational constraints hypothesis; Luo et al., 2018; Tielbörger et al., 2014). Plant species in water-limited systems may be adapted to lower soil water levels, making community biomass less responsive to further decreases in water availability (Tielbörger et al., 2014). This stabilized vegetation productivity may also occur because the dominant species can respond to early season moisture, which may be available prior to when the roofs are mounted on the shelters in C₃ grasslands (Knapp et al., 2020).

We observed that ANPP was relatively stable during the 3 years after drought due to the stability in productivity of both grasses and forbs over time. To date, more than 80% of rainfall manipulation experiments have only monitored grassland resistance, not assessing grassland recovery and resilience (Matos et al., 2020). Our experiment fills this literature gap and improves our understanding of grassland stability under extreme precipitation fluctuations. Stability of community biomass during post-drought in these grasslands is due to the complete recovery of total ANPP 1-year post-drought and lower variability in ANPP over time (Xu, Ke, et al., 2021). However, the non-decreasing stability of ANPP during drought and constant stability during post-drought reduced ANPP stability during combined drought plus post-drought periods. This is likely due to the large increases in ANPP from drought to post-drought (Figure S2), which is consistent with previous studies that showed complete recovery of productivity just 1 year after experiencing rapid declines due to drought in a semiarid grassland (Xu, Ke, et al., 2021), African savanna (Wilcox et al., 2020) and tallgrass prairie (Hoover et al., 2014).

Functional diversity has been well recognized as an important driver of ecosystem stability under changing environment conditions (Craven et al., 2018; de Bello et al., 2021; Hallett et al., 2017). We tested this hypothesis by investigating relationships between several functional diversity indices and the temporal stability of ANPP during drought, post-drought and their combined time frames in two cold-semiarid grasslands in northern China. SEMs demonstrated an indirect pathway in which functional trait divergence influenced ANPP stability by altering population stability, providing support for this hypothesis. The SEMs also revealed a direct effect of functional trait dispersion on the temporal stability of ANPP. Strikingly, this effect on ANPP stability through this direct pathway was negative and compensated by the positive indirect effect of functional trait dispersion on ANPP stability via species asynchrony.

Furthermore, CWM traits also contributed significantly to ANPP stability during the drought and post-drought periods. The dependence of community stability on CWM traits provides strong support for the mass ratio and dominance hypotheses, which together state that variations in functional traits of the dominant species in a community can determine the temporal stability of ANPP (Sasaki & Lauenroth, 2011). These results highlight the important role of both

aspects of functional composition (i.e. CWM traits and functional diversity) in either stabilizing or enhancing ecosystem stability under climate extremes.

Interestingly, we observed that seed traits of dominant species, rather than growth traits, were the strongest predictor of ANPP stability both during and after drought. Specifically, the SEM showed that CWMs of both seed width and thickness altered ANPP stability directly or indirectly through altering species asynchrony, leading to a net positive effect of these two seed traits on ANPP stability. The CWM of other seed traits (e.g. seed volume, seed mass and seed-coat thickness) also showed positive relationships with plant community stability in bivariate regressions, but were eliminated from the final SEM because they tended to be closely associated with seed width and thickness. These significant positive relationships for seed traits observed in this study suggest that plant communities with more species exhibiting conservative resource strategies (e.g. larger seeds with higher thickness) are more likely to experience higher ANPP stability under drought and post-drought conditions. Evidence suggests that plant communities dominated by species with slower growth rates and a greater capability to store resources will be more stable over time and can better withstand climate extremes and stressful periods (Chollet et al., 2014; Polley et al., 2013). For example, plant communities characterized by species with higher SLA and LDMC have been shown to be more stable through time in terms of both ecosystem structure and function (Chollet et al., 2014). In addition, increased abundance of species with acquisitive economic traits have been shown to destabilize primary productivity through time in seeding experiments (Craven et al., 2018). However, trait-stability research has mostly focused on growth economic traits (e.g. leaf and root traits), whereas few studies have investigated the links between seed production traits and ANPP stability (de Bello et al., 2021; Saatkamp et al., 2019). Indeed, plant seeds provide the basis of genetic diversity in grasslands and their traits may influence ecosystem stability under extreme drought conditions (Larson et al., 2015; Moles et al., 2007; Saatkamp et al., 2019; Whitney et al., 2019). Therefore, our results help to address this knowledge gap by investigating the relationship between community-level growth, seed traits and temporal stability of grassland primary productivity.

In our study, plant seed samples were not collected in control or drought plots to avoid destructive measurements, and to assess how traits in ambient conditions predict community response to perturbation. Given this was a collaborative project, other aspects of the experiment required seeds to remain in the plots. Therefore, all seed traits were estimated in an ambient area adjacent to experimental plots (Luo et al., 2022), as has been done in similar studies (Griffin-Nolan et al., 2019; Valerio et al., 2022). Therefore, intraspecific seed trait variability and seed trait plasticity were not assessed in our study. Intraspecific seed trait variation is predicted to contribute substantially to community functional response to environmental change and stability, with most evidence based on other functional traits, such as leaf (Jung et al., 2014) and root traits (Zhou et al., 2019). Nevertheless, our findings suggest that plant seed traits under ambient conditions are needed to better

predict if and how grassland stability will respond to future climate change.

5 | CONCLUSIONS

The cold-semiarid grasslands at the northeastern extent of China provide a range of essential ecosystem services, such as forage production, carbon storage and wildlife habitat (Bengtsson et al., 2019; Kang et al., 2007). The unprecedented increase in the frequency, duration and intensity of drought predicted for this region threatens the stability of ecosystem functioning (Ploughe et al., 2019). Unravelling the biotic mechanisms underpinning grassland stability is important to assess the potential ecological impacts of extreme weather events on grassland function and services.

Our study provides novel empirical evidence that drought and post-drought periods decreased the stability of primary productivity. These effects were largely driven by functional dispersion and divergence directly or indirectly via increasing species asynchrony and population stability. Our study also suggests the importance of seed size and thickness of dominant species in modulating community stability both during and after drought. To our knowledge, this is the first study to link both growth and seed traits to grassland stability, emphasizing that plant communities with dominant plant species that have larger and thicker seeds may be less sensitive to precipitation changes over time under future scenarios of global environmental change.

AUTHOR CONTRIBUTIONS

Wentao Luo, Qiang Yu and Xingguo Han conceived and designed the experiments. Wentao Luo analysed the data. Wentao Luo, Kate Wilkins and Scott Collins wrote the manuscript. All conducted the field experiment.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are from Luo (2023) Plant traits modulate grassland stability during drought and post-drought periods, Figshare, <http://doi.org/10.6084/m9.figshare.23598684>.

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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: Replication statement.

Figure S1: *A priori* piecewise SEM.

Figure S2: The aboveground net primary productivity (ANPP) in the control and drought plots during drought (2015–2018) and post-drought (2019–2021) periods. The asterisk indicates the significant difference in ANPP between the control and treatment plots.

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