Received: 7 July 2022 | Accepted: 21 November 2022

DOI: 10.1111/1365-2435.14239

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Interspecific and intraspecific trait variability differentially affect community-weighted trait responses to and recovery from long-term drought

Wentao Luo[1] | **Robert J. Griffin-Nolan**[2] | **Lin Song**[1] | **Niwu Te**[1] | **Jiaqi Chen**[1] | **Yuan Shi**[1] | **Taofeek O. Muraina**[3] | **Zhengwen Wang**[1] | **Melinda D. Smith**[4,5] | **Qiang Yu**[6,7] | **Alan K. Knapp**[4,5] | **Xingguo Han**[1,8] | **Scott L. Collins**[9]

[1]Erguna Forest-Steppe Ecotone Research Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China; [2]Department of Biology, Santa Clara University, Santa Clara, California, USA; [3]Department of Animal Health and Production, Oyo State College of Agriculture and Technology, Igbo-Ora, Igbo-Ora, Nigeria; [4]Department of Biology, Colorado State University, Fort Collins, Colorado, USA; [5]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA; [6]National Hulunber Grassland Ecosystem Observation and Research Station, Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing, China; [7]School of Grassland Science, Beijing Forestry University, Beijing, China; [8]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China and [9]Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA

Correspondence
Wentao Luo
Email: wentaoluo@iae.ac.cn

Funding information
National Natural Science Foundation of China, Grant/Award Number: 31971465 and 32171549; National Key Research and Development Program of China, Grant/Award Number: 2022YFF1300603; Strategic Priority Research Program of Chinese Academic of Sciences, Grant/Award Number: XDA23080401; National Science Foundation, Grant/Award Number: DEB-1856383; Youth Innovation Promotion Association CAS, Grant/Award Number: 2020199

Handling Editor: Laura Yahdjian

Abstract

1. Plant traits are useful proxies of plant strategies and can influence community and ecosystem responses to climate extremes, such as severe drought. Few studies, however, have investigated both the immediate and lagged effects of drought on community-weighted mean (CWM) plant traits, with even less research on the relative roles of interspecific vs. intraspecific trait variability in such responses.
2. We experimentally reduced growing season precipitation by 66% in two cold-semi-arid grassland sites in northern China for four consecutive years to explore the drought resistance of CWM traits as well as their recovery 2 years following the drought. In addition, we isolated the effects of both interspecific and intraspecific trait variability on shifts in CWM traits.
3. At both sites, we observed significant effects of drought on interspecific and intraspecific trait variability which, in some cases, led to significant changes in CWM traits. For example, drought led to reduced CWM plant height and leaf phosphorous content, but increased leaf carbon content at both sites, with responses primarily due to intraspecific trait shifts. Surprisingly, these CWM traits recovered completely 2 years after the extreme drought. Intraspecific trait variability influenced CWM traits via both positive and negative covariation with interspecific trait variability during drought and recovery phases.
4. These findings highlight the important role of interspecific and intraspecific trait variability in driving the response and recovery of CWM traits following extreme, prolonged drought.

KEYWORDS
climate extreme, environmental filtering, leaf economic spectrum, plant functional traits, plant height, semi-arid grassland

1 | INTRODUCTION

Plant traits are valuable predictors of the ecological functions of communities and their resistance and resilience to climate change (de Bello et al., 2021; McGill et al., 2006; Violle et al., 2007). Species responses to environmental changes, as well as their relative influence on ecosystem processes are hypothesized to be mediated by plant traits (i.e. response-effect trait framework; Lavorel & Garnier, 2002, Suding et al., 2008). Plant traits can be linked to ecosystem processes, including net primary productivity, biogeochemical cycling and decomposition in terrestrial ecosystems (Griffin-Nolan et al., 2019; Luo, Griffin-Nolan, Felton, et al., 2022; Reichstein et al., 2014; Wilcox et al., 2021). For example, community-weighted plant height was positivity correlated with above-ground net primary productivity (ANPP) during drought in a semi-arid grassland (Luo, Griffin-Nolan, et al., 2021). Indeed, grassland communities dominated by species with conservative traits, such as those with lower specific leaf area (SLA) and higher leaf dry matter content (LDMC), have been shown to exhibit relatively high temporal stability of ANPP (Kramp et al., 2022; Poorter et al., 2009). Therefore, traits are likely to mediate ecosystem responses to forecast increases in the frequency and magnitude of extreme drought (Dai, 2013; Trenberth et al., 2014), which can inflict significant and long-lasting impacts on plant community composition and plant traits (Jentsch et al., 2007; Knapp et al., 2020). Thus, additional research is need to fully capture the degree to which plant traits drive community response to extreme events.

Ecological communities and their responses to environmental changes can be quantified by various metrics of functional composition. However, community-weighted mean (CWM) traits (i.e. traits weighted by species abundances), which reflect the functional characteristics of dominant species (mass-ratio hypothesis; Grime, 1998), have great potential to predict the functional responses to alterations in resource availability (Griffin-Nolan et al., 2018; He et al., 2019). Community resistance to drought partially depends on the relative abundance of species with competitive and acquisitive traits (e.g. tall stature, high SLA, high leaf nutrient content) vs. those with less competitive and more conservative traits (Reich, 2014; Wright et al., 2004). Furthermore, recovery of community properties is dependent on the traits of the species that survive drought (Hoover et al., 2014; Smith, 2011). Yet, how CWM traits respond to extreme drought (i.e. resistance) or recover following drought (i.e. resilience) is not well understood in semi-arid ecosystems.

Variation in CWM traits can be attributed to both interspecific trait variability (i.e. variations in species composition and/or relative abundance) and intraspecific trait variability (i.e. variations in traits within species due to phenotypic or genotypic diversity) (Albert et al., 2010; Lepš et al., 2011). When trait shifts within and between species are in the same direction (i.e. species produce larger leaves and large-leaved species become more abundant), they can magnify CWM trait responses to environmental changes, whereas opposing shifts can weaken responses (i.e. species that produce larger leaves become less abundant) (Jung et al., 2010). Recent studies have shown that intraspecific trait variability is substantial and contributes strongly to CWM trait responses to environmental changes (Luo et al., 2019; Song et al., 2022). However, many studies have focused solely on changes in CWM traits due to interspecific trait variation, with the implicit assumption that intraspecific trait variability would respond similarly or be less important (Jung et al., 2014; Lepš et al., 2011). Thus, quantifying the relative role of interspecific and intraspecific trait variability is critical for understanding and predicting community-level functional responses to environmental drivers, such as extreme drought.

In this study, we conducted a 4-year drought manipulation experiment in two grassland sites in northern China. We assessed CWM traits during drought and 2 years following drought. We hypothesized that (i) CWM traits would shift to reflect shorter species/individuals and more conservative traits (e.g. low SLA and leaf nutrient content) during drought, but would revert back to ambient trait values after drought and (ii) drought resistance and recovery of CWM traits would be driven by both interspecific and intraspecific shifts in trait expression such that the impact of intraspecific trait variability would be similar to or even stronger than that of interspecific trait variability.

2 | MATERIALS AND METHODS

2.1 | Study sites

We established the experiment in two grassland sites in Hulunbeir, northeastern Inner Mongolia, China. These sites are in a cold-semi-arid natural biome at the eastern extremity of the Eurasian steppe (Figure S1). These sites included the National Hulunbeir Grassland (NHG) Ecosystem Observation and Research Station (49.35°N and 120.01°E) and the Erguna Forest-Steppe (EFS) Ecotone Research Station (50.16°N and 119.39°E). All necessary permits were gained before the beginning of field investigation. These two grassland sites share relatively similar species composition and climatic conditions, but have very different management history. Before our drought experiment, EFS had been fenced since 2014, while the other had been fenced since 1998. Based on long-term (1957–2016) meteorological records, mean annual temperature was approximately −2°C and mean annual precipitation was about 350 mm, with about 75% of this amount falling during the growing season (May–August) (Figure S2). Snow covered the vegetation for approximately 5–6 months (November to April) in each year. The vegetation was characterized by a dominant perennial rhizomatous grass, *Leymus chinensis*. Plant communities of both grasslands reached peak productivity (average

ANPP of about 240 g m^{-2} for NHG and 160 g m^{-2} for EFS) in August. The soil was classified as chestnut according to the China soil taxonomy classification system, equivalent to Calcicorthic Aridisol in the US soil taxonomy classification (Kang et al., 2007).

2.2 | Experimental treatments

At each site, we imposed drought treatments alongside control (ambient rainfall) plots using passive rainout shelters during the 2015–2018 growing seasons (Figure S1). We placed rainout shelters on the drought plots to reduce growing season precipitation by 66% following the methods of Yahdjian and Sala (2002). At each site, we established 12 plots ($n = 6$ control and drought plots) in a topographically uniform area. All plots are 6 m × 6 m in size and are paired spatially into blocks with treatments assigned randomly within a block. We hydrologically isolated the soil within the 36 m^2 footprint of each shelter from the surrounding soil matrix using aluminium flashing and plastic barriers installed to a depth of 1 m. During the recovery year (2019–2020), we imposed no drought treatments and all plots received ambient precipitation in the two grassland sites.

Further details on the experimental design can be found in Luo, Griffin-Nolan, et al. (2021) and Muraina et al. (2021).

2.3 | Data collection

We established a sampling subplot (4 m × 4 m) at the centre of each plot. In early August of 2018 (the fourth year of drought treatment) and 2020 (the second year of post-drought), we harvested all above-ground plant material in two quadrats (0.5 m × 0.5 m) located within each sampling subplot. We sorted all live samples to species, oven-dried them at 65°C for 48 h and weighed them after drying.

In each drought and control plot, we measured traits of three randomly selected individuals of each species in two additional quadrats (0.5 m × 0.5 m) to quantify community trait distributions. The cumulative abundance of these harvested species represented ~90% total biomass in each plot. For each individual sampled, we measured six functional traits related to the global spectrum of plant form and function (Díaz et al., 2016): plant height, SLA, LDMC, leaf carbon content (LCC), leaf nitrogen content (LNC) and leaf phosphorus content (LPC). Plant height was measured as the distance (cm) from the ground to the top of the general canopy of the plant. Several mature, healthy leaves from the upper third of the canopy of each selected individual were collected for leaf trait measurements. We measured leaf area (mm^2) of one side, leaf fresh mass (mg) after full rehydration and leaf dry mass after oven drying at 65°C for 48 h. SLA was calculated as fresh leaf area divided by dry mass, and LDMC was calculated as leaf dry mass divided by leaf fresh mass. We measured LCC (the ratio of leaf total carbon to leaf dry mass, mg g^{-1}) and LNC (the ratio of leaf total nitrogen to leaf dry mass, mg g^{-1}) using an elemental analyser (2400II CHN elemental analyser; Perkin-Elmer, USA). We measured LPC (the ratio of leaf total phosphorus to leaf dry mass, mg g^{-1}) using inductively coupled plasma atomic emission spectrometry (OPTIMA 3000 DV; Perkin Elmer, USA) after acid digestion.

2.4 | Calculation and statistical analysis

For each trait in each plot, CWM traits were calculated as:

$$\text{CWM trait} = \sum_{i=1}^{n} p_i \times \text{trait}_i, \tag{1}$$

where p_i is the relative biomass of species i in each plot, and trait_i is the trait value of species i.

In each plot, we quantified CWM traits as the mean of trait values weighted by the relative biomass of each species in a community for each of the six traits separately. Using this approach, changes in the resulting CWM traits from control to treatment plots can be attributed to either inter- or intraspecific trait changes (Figure 1) Specifically, we partitioned the relative effects of interspecific (C_{Inter}) and intraspecific trait variability (C_{Intra}) on the total variation of CWM traits during the drought and recovery periods following Jung et al. (2014), as:

$$C_{\text{Inter}} = T_{\text{Dr}*} - T_{\text{Ct}} \tag{2}$$

$$C_{\text{Intra}} = T_{\text{Dr}} - T_{\text{Dr}*} \tag{3}$$

where T_{Dr} and T_{Ct} are the observed CWM trait values in treatment and control plots, respectively, calculated from relative biomass and trait values of each species measured in their respective plot. $T_{\text{Dr}*}$ is the CWM trait value recalculated in the treatment plots using species' relative biomass in the treatment plots, but the trait values measured in the control plots. C_{Inter} and C_{Intra} represent the isolated effects of interspecific and intraspecific trait variability, respectively, in driving the response of CWM traits to drought and recovery after drought.

We used a mixed model analysis of variance with treatment (control and drought/post-drought) and site (EFS and NHG) as fixed effects and block as a random effect to analyse CWM trait values as well as CWM trait values due to interspecific or intraspecific trait variability only. When interactive effects of treatment and site were significant, we separately applied the mixed model analysis of variance with block as a random effect to assess the effects of drought and post-drought on CWM trait values between control and drought/post-drought plots (i.e. T_{Dr} vs. T_{Ct} and $T_{\text{Dr}*}$ vs. T_{Ct}), as well as the significance of the effects of drought/post-drought on intraspecific trait variability.

We conducted all statistical analyses using the NLME package in R version 4.1.1 (R Core Team, 2021).

3 | RESULTS

Experimental drought generally altered CWM traits, particularly at EFS, but CWM traits fully recovered after drought at both sites

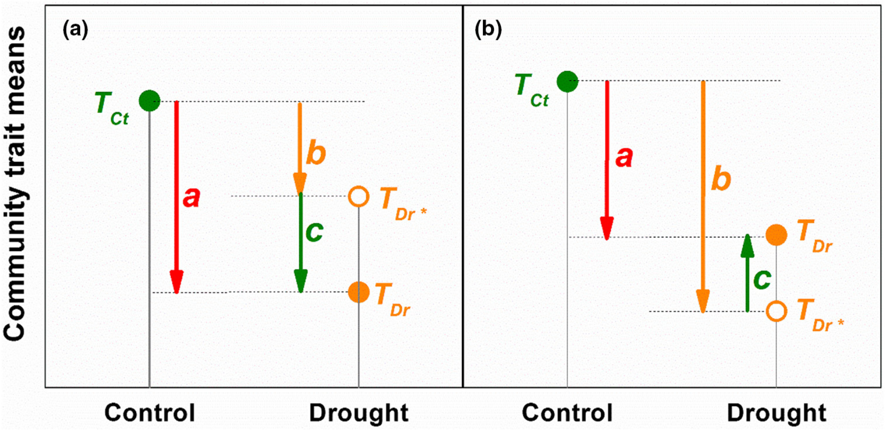

FIGURE 1 Changes in community-weighted mean (CWM) trait values due to both interspecific and intraspecific trait variability (red arrow *a*) and due to interspecific trait variability only (orange arrow *b*). Intraspecific trait variability (olive arrow *c*) corresponds to the difference between the above two measured values (arrow *a* − arrow *b*). T_{Ct} and T_{Dr} correspond to the observed CWM traits in control plots and in drought plots; T_{Dr*} corresponds to the CWM traits in drought plots recalculated from trait values measured in control plots. A parallel direction of shift in interspecific and intraspecific trait variability indicates positive covariation (a), whereas an opposite direction of shift in interspecific and intraspecific trait variability indicates negative covariation (b).

(Figure 2 and Figure S3). The plant community was shorter during drought (CWMs of plant height; both $p < 0.1$) but height increased in drought plots relative to control plots during recovery at both sites (both $p < 0.05$) (Figure 2 and Figure S3). Drought had no main effect on CWMs of SLA, LDMC or LNC during the drought or recovery periods (Figure 2 and Figure S3) in either site. Drought led to increased CWMs of LCC at both sites, and more so at EFS compared with NHG ($p < 0.1$, Table 1), but LCC completely recovered to the control level following drought at both sites (Figure 2 and Figure S3). Drought reduced CWMs of LPC more at EFS than at NHG ($p < 0.001$, Table 1), and CWMs of LPC recovered to the control levels following the drought treatment at both sites (Figure 2 and Figure S3).

3.1 | Interspecific trait responses

Many of the shifts in CWM traits were due to interspecific trait differences. For example, interspecific differences in height led to increased CWM plant height during drought at EFS, but not at NHG ($p < 0.05$; Figure 2 and Figure S3). In addition, higher CWM height in treatment plots post-drought was at least partially driven by interspecific differences (Figure 2 and Figure S3). At both sites, CWMs of SLA declined in response to drought due to interspecific trait variation (both $p < 0.05$), but recovered completely to the control level following drought (Figure 2 and Figure S3). Moreover, interspecific differences were behind the drought-induced increase in CWMs of LDMC at EFS ($p < 0.01$), but not NHG (Figure 2 and Figure S3), and no significant response of LDMC was observed during recovery (Figure 2 and Figure S3). While CWMs of LCC did not shift due to interspecific variation during drought, LCC increased during recovery at both sites due to interspecific variation ($p < 0.05$ and $p < 0.01$ for NHG and EFS, respectively, Figure 2 and Figure S3). Experimental drought had no effect on CWMs of LNC during drought or recovery periods at both sites (Figure 2 and Figure S3). Experimental drought had no effect on CWMs of LPC at NHG but led to decreases in this trait (both $p < 0.05$) at EFS during the drought and recovery period (Figure 2 and Figure S3).

3.2 | Intraspecific trait responses

Intraspecific variability in plant height diminished more with drought at EFS compare with NHG ($p < 0.05$, Table 1), but fully recovered at both sites following drought (Figure 2 and Figure S3). CWMs of SLA and LDMC did not vary during drought or recovery periods at either site based on intraspecific variation (Figure 2 and Figure S3). CWMs of LCC increased with drought at both sites (both $p < 0.001$), yet declined after drought at EFS and did not change at NHG (Figure 2 and Figure S3) based on intraspecific variation. CWMs of LNC did not vary with drought at NHG but marginally increased at EFS ($p < 0.1$, Figure 2 and Figure S3). During recovery, within species CWMs of LNC decreased at NHG and increased at EFS (both $p < 0.05$, Figure 2 and Figure S3). CWMs of LPC decreased with drought at EFS, more so than at NHG ($p < 0.01$, Table 1), but completely recovered following drought at both sites (Figure 2 and Figure S3).

Shifts in CWM traits in response to drought were primarily due to intraspecific trait variability, whereas recovery of CWM traits was driven primarily by interspecific trait variability for both grassland sites (Figure 3). During drought at EFS, the effects of interspecific and intraspecific trait variability were synergistic (i.e. responded in same directions) for CWMs of LNC and LCC but were antagonistic (i.e. responded in opposite directions) for the remaining four traits (Figure 3). At NHG, the effects of interspecific and intraspecific trait variability were synergistic for CWMs of LCC and LPC but were antagonistic for the remaining four traits during drought (Figure 3). During recovery, we observed contrasting effects of interspecific vs. intraspecific trait

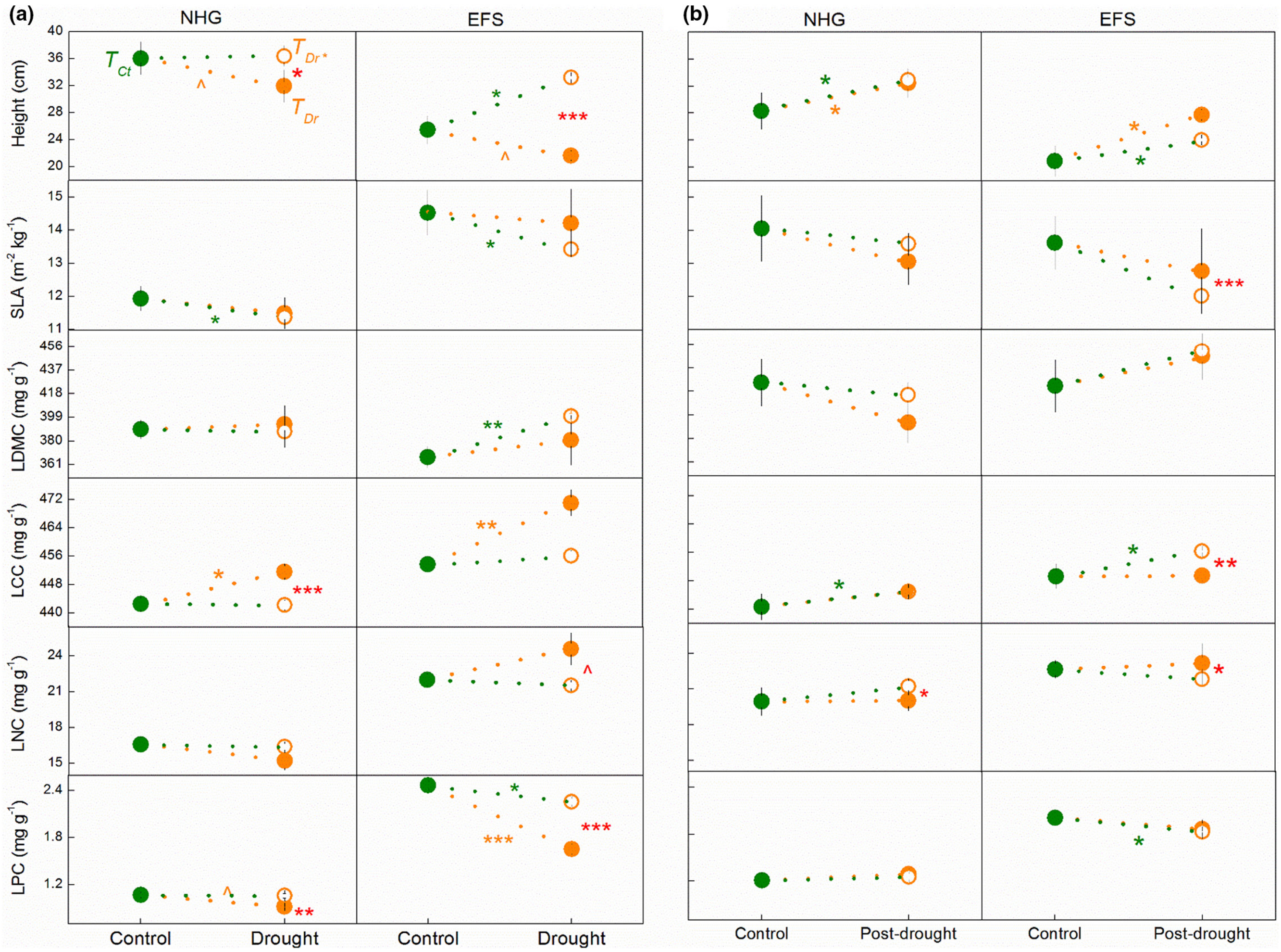

FIGURE 2 Changes in community-weighted mean (CWM) traits in response to (a) drought and (b) post-drought in two grassland sites (EFS and NHG) in northern China. This figure shows the response estimated to be due to both interspecific and intraspecific trait variability and due to interspecific trait variability alone for each grassland. T_{Cr} (solid green circles) and T_{Dr} (solid orange circles) correspond to the observed community traits in control and treatment (drought/post-drought) plots, respectively; $T_{\mathrm{Dr*}}$ (open orange circles) corresponds to the community traits in drought plots recalculated from traits measured in control plots. Statistical significance of treatment effects depicted as ^$p<0.1$, *$p<0.05$, **$p<0.01$ and ***$p<0.001$. Orange, green and red asterisks indicate significant differences in total trait variations, interspecific trait variability and intraspecific trait variability, respectively. EFS, Erguna Forest-steppe ecotone Research Station; LCC, leaf carbon content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SLA, specific leaf area.

variability on CWMs of plant height and LNC, but similar responses for the remaining four traits at EFS (Figure 3). At NHG, we only observed the same directional response for CWMs of plant height, and opposite responses for the other five traits during recovery (Figure 3).

4 | DISCUSSION

In our study, experimental drought altered CWM traits in both grassland sites, with higher drought sensitivity in the more recently grazed site, EFS. Shifts in CWM trait values during drought suggest conservative strategies were more adaptive, and plants were less productive. However, CWM traits were highly resilient, returning to control-level trait values in the 2 years following drought. We found that intraspecific trait variability played a more important role than interspecific trait variability in driving the net responses of CWM traits during drought, suggesting that species-specific responses rather than species turnover are important drivers of drought resistance in these communities. In addition, intraspecific responses either amplified or dampened the CWM trait responses mediated by interspecific variability during drought and recovery. Thus, these two components of trait variability do not always respond to drought in similar ways. Our results demonstrated that certain CWM traits are more sensitive to a multi-year drought than others (e.g. decreased plant height and increased LCC) in cold-semi-arid grasslands (Figure 2 and Figure S3). Environmental filtering can partially explain these results as extreme drought allows only certain species or trait values to persist (e.g. shorter and more resource conservative species) (Niinemets, 2001; Reich, 2014; Wilcox et al., 2021). Plant height and leaf economics traits represent two different axes

TABLE 1 Results of mixed model analysis of variance for community traits as well as for community-weighted mean traits driven by interspecific or intraspecific trait variability. Treatment (control and drought/post-drought) and grassland sites (EFS and NHG) were used as fixed factors and block as a random factor within the drought and recovery stages

	Height	SLA	LDMC	LCC	LNC	LPC
	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$	$F_{1,15}$
Total variability						
Site (S)	31.33***	15.64**	1.65	45.91***	72.20***	489.09***
Drought (D)	4.49^	0.32	0.42	33.77***	0.50	99.42***
S×D	0.01	0.01	0.13	3.35^	5.08*	47.61***
Interspecific variability						
S	20.93***	40.07***	0.35	76.30***	150.45***	1180.35***
D	7.14*	5.11*	3.42^	0.51	0.63	8.53*
S×D	6.06*	0.54	4.27^	0.90	0.12	6.60*
Intraspecific variability						
S	25.57***	16.99***	0.00	52.76***	94.37***	558.57***
D	35.89***	0.61	0.23	27.81***	1.65	81.5***
S×D	7.11*	0.34	0.81	1.47	7.99*	32.96**
Total variability						
S	8.53*	0.15	1.99	5.42*	6.53*	93.99***
Post-drought (PD)	6.98*	0.91	0.04	0.63	0.07	0.19
S×PD	0.43	0.01	2.22	0.53	0.04	2.52
Interspecific variability						
S	20.22***	2.38	1.39	15.90**	4.64*	158.02***
PD	4.56*	2.47	0.39	5.28*	0.08	1.49
S×PD	0.16	0.74	1.65	0.30	1.86	4.30^
Intraspecific variability						
S	31.79***	1.58	11.63**	42.05***	0.01	86.07***
PD	1.81	0.02	0.97	8.30*	4.65*	0.34
S×PD	3.00	0.73	0.44	7.82*	2.14	0.00

Note: $F_{df1,df2}$ values were shown.

Abbreviations: EFS, Erguna Forest-Steppe Ecotone Research Station; LCC, leaf carbon content ($mg\,g^{-1}$); LDMC, leaf dry matter content ($mg\,g^{-1}$); LNC, leaf nitrogen content ($mg\,g^{-1}$); LPC, leaf phosphorus content ($mg\,g^{-1}$); NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SLA, specific leaf area ($m^{-2}\,kg^{-1}$).

^ $p < 0.1$.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

in the global spectrum of plant form and function associated with (1) plant size and competitive ability and (2) plant resource use strategies (e.g. conservative vs. acquisitive) (Díaz et al., 2016; Reich, 2014). Theoretical and empirical evidence suggests that species with more conservative traits should persist during drought compared to acquisitive species (Wright et al., 2004), although this is highly dependent on the timing of drought and phenology of resident species (Griffin-Nolan et al., 2019; Knapp et al., 2020).

Surprisingly, shifts in CWM traits during drought did not preclude their rapid recovery following extreme drought (Figures 2 and 3), indicating that more acquisitive and productive growth strategies are favourable during recovery years, even after multi-year drought (Niinemets, 2001; Reich, 2014). Moreover, although the CWM shifts during drought were different between sites, resilience after drought was similar (Figures 2 and 3). Therefore, multi-year drought had little to no legacy effect on community trait composition in these ecosystems. This is consistent with other studies that found rapid resilience, rather than high resistance, maintained ecosystem productivity in grasslands following extreme drought (Hoover et al., 2014; Stuart-Haëntjens et al., 2018). High functional resilience will be important for the long-term stability of these grasslands under future climate change scenarios.

Consistent with previous findings (Messier et al., 2010; Siefert et al., 2015), intraspecific trait variability, caused by either genetic variation or phenotypic plasticity within the population, contributed more to CWMs than interspecific trait variability during drought (Figure 3). In a grassland fertilization experiment in grasslands, Siefert and Ritchie (2016) found that intraspecific variability was almost entirely responsible for fertilization-induced shifts in plant height, leaf area and SLA at the community level. Similarly, Jung

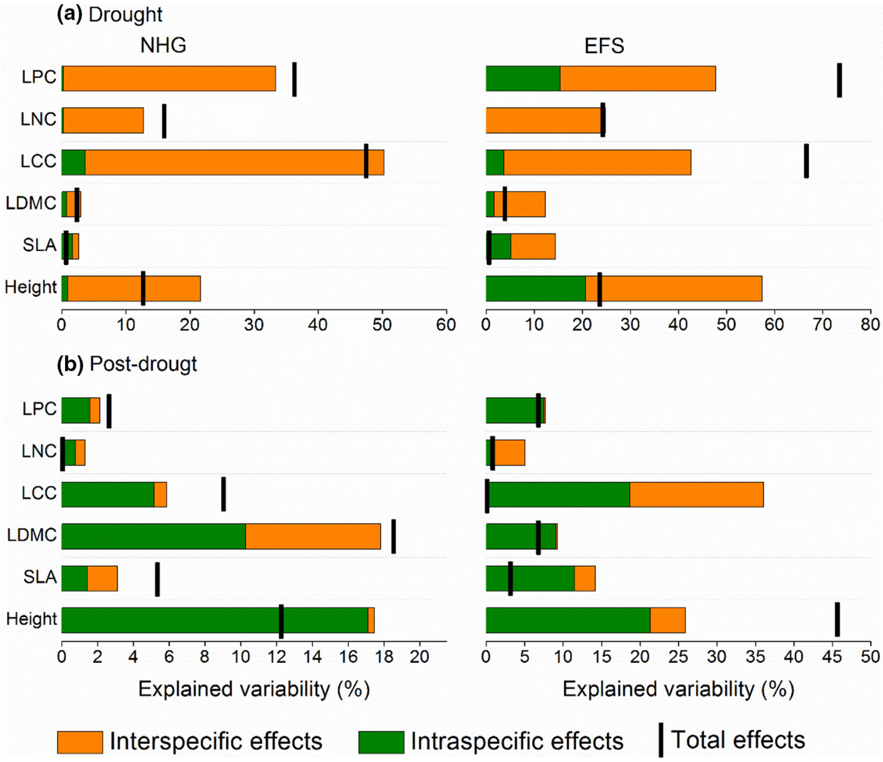

FIGURE 3 Decomposition of the total variability in community-weighted mean (CWM) traits into intraspecific, interspecific and covariation effects with (a) experimental drought and (b) post-drought in two grassland sites in northern China. Covariation strength is represented by the interval between the 'total variability effects' and the sum of interspecific and intraspecific variability effects. A value of total variability effects that is lower than the sum of interspecific and intraspecific variability effects indicates negative covariation, and a value of total variability effects that is higher than the sum of interspecific and intraspecific variability effects indicates positive covariation. See Figure 2 legend for the abbreviation of plant traits and sites.

et al. (2014) demonstrated that intraspecific variability contributed more than interspecific variability to shifts in CWM traits in response to experimental drought in a subalpine meadow. Moreover, recent studies have demonstrated that intraspecific trait shifts were as important as interspecific shifts in determining the overall change in CWM traits in response to multiple drivers of environmental change (Pichon et al., 2021). Overall, these results highlight the importance of accounting for intraspecific trait variability when quantifying and predicting the responses of community trait composition to environmental variability.

Our results are generally consistent with the Hierarchical Response Framework which predicts that initial responses to global environmental change will be phenotypic adjustments within species (Smith et al., 2009). Although intraspecific trait variability was the main driver of CWM shifts during drought, interspecific differences also contributed, sometimes in the opposite direction. For instance, species re-ordering and interspecific differences in trait values led to reductions in CWMs of SLA during drought, which were dampened by intraspecific responses in the opposite direction (Figure 2 and Figure S3). Similarly, opposing responses of interspecific vs. intraspecific trait variation were observed during recovery for CWMs of LNC leading to no difference between control and droughted plots (Figure 2 and Figure S3). Previous studies examining variations in CWM traits in response to drought (Luo et al., 2018; Song et al., 2022) or along a natural aridity gradient (Kichenin et al., 2013; Luo, Wang, et al., 2021) have also shown that trait shifts driven by interspecific and intraspecific variability may either reinforce or oppose each other. Negative covariation between interspecific and intraspecific responses may occur if variations at one level pre-empt variations at the other. For instance, rapid genetic and phenotypic responses of resident species delayed the large responses of species composition to climate variation in grasslands (Grime et al., 2008). In contrast, rapid migration facilitated alien species with functional traits pre-adapted to new habitats to replace resident species before they adapt to local environmental conditions (Donoghue, 2008). These findings suggest that interspecific and intraspecific trait variability and the interaction between these two processes can drive the responses of community trait composition to environmental changes and their relative roles may change across treatments and over time.

5 | CONCLUSIONS

Four years of experimental drought significantly altered community trait composition in two cold-semi-arid grasslands. Nevertheless, these communities exhibited substantial and rapid resilience of community-weighted trait composition following extreme drought mediated by interactions between intraspecific and interspecific trait variability. These results show how functional composition of plant communities can partly drive ecosystem responses to drivers of global environmental change. Therefore, understanding mechanisms of resistance and resilience via community-weighted trait dynamics may improve predictions of ecosystem responses to climate change, such as extreme drought. Furthermore, our results demonstrate that trait variations within and among species are potentially stabilizing processes in plant communities, yet additional research in less extreme environments is needed to fully capture the degree to which trait variation can affect resistance and resilience of plant communities to extreme events.

AUTHOR CONTRIBUTIONS

Wentao Luo, Zhengwen Wang, Qiang Yu, Xingguo Han and Scott L. Collins conceived the research; Wentao Luo, Lin Song, Niwu Te, Jiaqi Chen and Yuan Shi managed the field experiment and collected the data; Wentao Luo and Robert J. Griffin-Nolan analysed the data and wrote the first draft. Taofeek O. Muraina, Melinda D. Smith and Alan K. Knapp revised the manuscript.

ACKNOWLEDGEMENTS

This study was supported by funding from National Natural Science Foundation of China (31971465 and 32171549), National Key Research and Development Program of China (2022YFF1300603), Strategic Priority Research Program of Chinese Academic of Sciences (XDA23080401), National Science Foundation (DEB-1856383), and Youth Innovation Promotion Association CAS (2020199).

CONFLICTS OF INTEREST

Authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data available from https://doi.org/10.6084/m9.figshare.21514644.v1 (Luo, Griffin-Nolan, Muraina, et al., 2022).

ORCID

Wentao Luo https://orcid.org/0000-0002-9543-1123
Robert J. Griffin-Nolan https://orcid.org/0000-0002-9411-3588
Taofeek O. Muraina https://orcid.org/0000-0003-2646-2732
Zhengwen Wang https://orcid.org/0000-0002-4507-2142
Melinda D. Smith https://orcid.org/0000-0003-4920-6985
Qiang Yu https://orcid.org/0000-0002-5480-0623
Alan K. Knapp https://orcid.org/0000-0003-1695-4696
Xingguo Han https://orcid.org/0000-0002-1836-975X
Scott L. Collins https://orcid.org/0000-0002-0193-2892

REFERENCES

Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., & Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra- *vs.* interspecific variability in plant traits. *Functional Ecology*, *24*, 1192–1201.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*, 52–58.

de Bello, F., Lavorel, S., Hallett, L. M., Valencia, E., Garnier, E., Roscher, C., Conti, L., Galland, T., Goberna, M., Májeková, M., Montesinos-Navarro, A., Pausas, J. G., Verdú, M., E-Vojtkó, A., Götzenberger, L., & Lepš, J. (2021). Functional trait effects on ecosystem stability: Assembling the jigsaw puzzle. *Trends in Ecology & Evolution*, *36*, 822–836.

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., & Colin Prentice, I. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167–171. https://doi.org/10.1038/nature16489

Donoghue, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 11549–11555.

Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., Ocheltree, T. W., Smith, M. D., Whitney, K. D., & Knapp, A. K. (2019). Shifts in plant functional composition following long-term drought in grasslands. *Journal of Ecology*, *107*, 2133–2148.

Griffin-Nolan, R. J., Bushey Julie, A., Carroll Charles, J. W., Challis, A., Chieppa, J., Garbowski, M., Hoffman Ava, M., Post Alison, K., Slette Ingrid, J., Spitzer, D., Zambonini, D., Ocheltree Troy, W., Tissue David, T., & Knapp Alan, K. (2018). Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes. *Functional Ecology*, *32*, 1746–1756.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910.

Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., & Bennett, C. R. (2008). Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 10028–10032.

He, N., Liu, C., Piao, S., Sack, L., Xu, L., Luo, Y., He, J., Han, X., Zhou, G., Zhou, X., Lin, Y., Yu, Q., Liu, S., Sun, W., Niu, S., Li, S., Zhang, J., & Yu, G. (2019). Ecosystem traits linking functional traits to macroecology. *Trends in Ecology & Evolution*, *34*, 200–210.

Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, *95*, 2646–2656.

Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: Events, not trends. *Frontiers in Ecology and the Environment*, *5*, 365–374.

Jung, V., Albert, C. H., Violle, C., Kunstler, G., Loucougaray, G., & Spiegelberger, T. (2014). Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, *102*, 45–53.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology*, *98*, 1134–1140.

Kang, L., Han, X., Zhang, Z., & Sun, O. J. (2007). Grassland ecosystems in China: Review of current knowledge and research advancement. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *362*, 997–1008.

Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, *27*, 1254–1261.

Knapp, A. K., Chen, A., Griffin-Nolan, R. J., Baur, L. E., Carroll, C. J. W., Gray, J. E., Hoffman, A. M., Li, X., Post, A. K., Slette, I. J., Collins, S. L., Luo, Y., & Smith, M. D. (2020). Resolving the dust bowl paradox of grassland responses to extreme drought. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 22249–22255.

Kramp, R. E., Liancourt, P., Herberich, M. M., Saul, L., Weides, S., Tielbörger, K., & Májeková, M. (2022). Functional traits and their plasticity shift from tolerant to avoidant under extreme drought. *Ecology*, e3826.

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology*, *16*, 545–556.

Lepš, J., Bello, F. d., Šmilauer, P., & Doležal, J. (2011). Community trait response to environment: Disentangling species turnover *vs* intraspecific trait variability effects. *Ecography*, *34*, 856–863.

Luo, W., Griffin-Nolan, R. J., Ma, W., Liu, B., Zuo, X., Xu, C., Yu, Q., Luo, Y., Mariotte, P., Smith, M. D., Collins, S. L., Knapp, A. K., Wang, Z., & Han, X. (2021). Plant traits and soil fertility mediate productivity losses under extreme drought in C_3 grasslands. *Ecology*, *102*, e03465.

Luo, W., Griffin-Nolan, R. J., Felton, A. J., Yu, Q., Wang, H., Zhang, H., Wang, Z., Han, X., Collins, S. L., & Knapp, A. K. (2022). Drought has inconsistent effects on seed trait composition despite their strong association with ecosystem drought sensitivity. *Functional Ecology*, *36*(11), 2690–2700. https://doi.org/10.1111/1365-2435.14165

Luo, W., Griffin-Nolan, R. J., Muraina, T. O., Song, L., Te, N., Cheng, J., Shi, Y., Wang, Z., Smith, M. D., Yu, Q., Knapp, A. K., Han, X., & Collins, S. L. (2022). Inter- and intraspecific trait variability differentially affect community-weighted trait responses to and recovery from long-term drought. *Figshare*, https://doi.org/10.6084/m9.figshare.21514644.v1

Luo, W., Wang, X., Auerswald, K., Wang, Z., Bird, M. I., Still, C. J., Lü, X. T., & Han, X. (2021). Effects of plant intraspecific variation on the prediction of C_3/C_4 vegetation ratio from carbon isotope composition of topsoil organic matter across grasslands. *Journal of Plant Ecology*, *14*, 628–637.

Luo, W., Zuo, X., Griffin-Nolan, R. J., Xu, C., Ma, W., Song, L., Helsen, K., Lin, Y., Cai, J., Yu, Q., Wang, Z., Smith, M. D., Han, X., & Knapp, A. K. (2019). Long term experimental drought alters community plant trait variation, not trait means, across three semiarid grasslands. *Plant and Soil*, *442*, 343–353.

Luo, W., Zuo, X., Ma, W., Xu, C., Li, A., Yu, Q., Knapp, A. K., Tognetti, R., Dijkstra, F. A., Li, M. H., Han, G., Wang, Z., & Han, X. (2018). Differential responses of canopy nutrients to experimental drought along a natural aridity gradient. *Ecology*, *99*, 2230–2239.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178–185.

Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, *13*, 838–848.

Muraina, T. O., Xu, C., Yu, Q., Yang, Y., Jing, M., Jia, X., Jaman, M. S., Dam, Q., Knapp, A. K., Collins, S. L., Luo, Y., Luo, W., Zuo, X., Xin, X., Han, X., & Smith, M. D. (2021). Species asynchrony stabilises productivity under extreme drought across northern China grasslands. *Journal of Ecology*, *109*, 1665–1675.

Niinemets, Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, *82*, 453–469.

Pichon, N. A., Cappelli, S. L., & Allan, E. (2021). Intraspecific trait changes have large impacts on community functional composition but do not affect ecosystem function. *Journal of Ecology*, *110*, 644–658.

Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*, 565–588.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301.

Reichstein, M., Bahn, M., Mahecha, M. D., Kattge, J., & Baldocchi, D. D. (2014). Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13697–13702.

Siefert, A., & Ritchie, M. E. (2016). Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia*, *181*, 245–255.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., Dantas, V. D., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419.

Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, *99*, 656–663.

Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, *90*, 3279–3289.

Song, L., Luo, W., Griffin-Nolan, R. J., Ma, W., Cai, J., Zuo, X., Yu, Q., Hartmann, H., Li, M. H., Smith, M. D., Collins, S. L., Knapp, A. K., Wang, Z., & Han, X. (2022). Differential responses of grassland community nonstructural carbohydrate to experimental drought along a natural aridity gradient. *Science of the Total Environment*, *822*, 153589.

Stuart-Haëntjens, E., De Boeck, H. J., Lemoine, N. P., Mänd, P., Kröel-Dulay, G., Schmidt, I. K., Jentsch, A., Stampfli, A., Anderegg, W. R. L., Bahn, M., Kreyling, J., Wohlgemuth, T., Lloret, F., Classen, A. T., Gough, C. M., & Smith, M. D. (2018). Mean annual precipitation predicts primary production resistance and resilience to extreme drought. *Science of the Total Environment*, *636*, 360–366.

Suding, K. N., Lavorel, S., Chapin, F. S., III, Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., & Navas, M. L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140.

Trenberth, K. E., Dai, A., Van Der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, *4*, 17–22.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892.

Wilcox, K. R., Blumenthal, D. M., Kray, J. A., Mueller, K. E., Derner, J. D., Ocheltree, T., & Porensky, L. M. (2021). Plant traits related to precipitation sensitivity of species and communities in semiarid shortgrass prairie. *New Phytologist*, *229*, 2007–2019.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827.

Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, *133*, 95–101.

SUPPORTING INFORMATION

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

How to cite this article: Luo, W., Griffin-Nolan, R. J., Song, L., Te, N., Chen, J., Shi, Y., Muraina, T. O., Wang, Z., Smith, M. D., Yu, Q., Knapp, A. K., Han, X., & Collins, S. L. (2023). Interspecific and intraspecific trait variability differentially affect community-weighted trait responses to and recovery from long-term drought. *Functional Ecology*, *37*, 504–512. https://doi.org/10.1111/1365-2435.14239