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Demographic and Growth Dynamics Jointly Shape Grassland Productivity Under Extreme Drought

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ABSTRACT

Understanding how plant communities maintain productivity in arid environments remains a key ecological question. Using two independent 4-year drought experiments with a 66% reduction in growing season precipitation in a semi-arid grassland, we found that reductions in plant density and individual size jointly contributed to drought-induced declines in aboveground net primary productivity (ANPP), and that their relative importance depends on drought duration, intensity, and plant functional group. For graminoids, ANPP decline was primarily driven by reduced individual size, whereas for forbs it was driven by reduced plant density. There was a trade-off between the contributions of plant density and individual size to productivity, which was mediated by leaf functional traits, including leaf carbon content and leaf nitrogen. Our findings highlight the role of the trade-off between demographic and growth-related processes in regulating productivity under climate change.

1 | Introduction

Climate models predict an increase in frequency and severity of droughts across most terrestrial ecosystems. Understanding the impact of these changes is particularly critical for the management of grasslands, which cover approximately 40% of the earth's surface and provide a wide range of ecosystem services (Gibson 2009; Bengtsson et al. 2019). Drought strongly reduces grassland productivity by reducing plant density (the number of individuals per unit area) and/or diminishing individual size (the biomass per plant) (Hoover et al. 2014; Zhang et al. 2020; Sun et al. 2022). Plant density is directly tied to changes in demographic processes, reflecting the net effect of survival, mortality, and recruitment (Connell et al. 1984). Individual size mirrors shifts in growth-related processes, like photosynthesis or nutrient uptake, determining individual plant biomass (Schroeder-Georgi et al. 2015; Tatsumi and Loreau 2023). Although many studies have elucidated the ecological mechanisms governing productivity responses to drought (Mariotte et al. 2013; Byrne et al. 2017; Luo et al. 2021; Meng et al. 2021), the relative roles of plant demographic and growth-related processes remain poorly understood. Clarifying the relative contributions of these two processes is crucial for elucidating the mechanisms governing grassland productivity's response to drought and for improving process-based predictions of future community dynamics.

According to the hierarchical-response framework (Smith et al. 2009), drought first limits individual growth and later increases mortality as stress accumulates. Therefore, productivity loss should initially be driven more by individual size reduction, while plant density is expected to play a larger

role as drought continues for a certain period. Plants can acclimate to drought through physiological and morphological adjustments, thus alleviating the adverse impacts of persistent drought on their survival (McDowell et al. 2008; Künzi et al. 2025; Ploughe et al. 2019; Smith 2011). For instance, some recent work conducted in forests and grasslands suggests that plants can adjust functional traits (e.g., higher leaf dry matter content [LDMC]) to slow down individual growth but improve survival rate (Zhang et al. 2020; Umaña et al. 2023). By facilitating plant survival in water-deficient environments, these adjustments could sustain plant density despite the decrease of individual plant size (Zuo et al. 2022). Considering how plant growth and survival change over time under drought is essential for understanding plant drought responses (Volaire et al. 2026). However, studies concerning ecological consequences of drought have rarely probed into the relative roles of collective survival versus individual growth, impeding our understanding of the mechanisms underlying the links between individual growth, demographic processes, and community productivity.

The pervasive negative correlation between individual plant size and plant density reflects a fundamental trade-off in resource allocation, governing how plants balance growth against survival (Nee et al. 1991; Blackburn et al. 1993; White et al. 2007; Chu et al. 2008; Tatsumi and Loreau 2023). Droughts are likely to reduce both plant size and density (Zhang et al. 2020), yet the relationship between these declines has received little attention. Under drought conditions, the growth-survival trade-off could be manifested as a primary specialization axis: investing in drought resistance and tolerance versus maximizing resource acquisition capacity (Volaire 2018; Griffin-Nolan et al. 2019; Zhang et al. 2024; Russo et al. 2021). Consequently, resource allocation to drought resistance confers a survival advantage to plants at the cost of growth (Rose et al. 2009; Russo et al. 2021; Luong et al. 2021; Volaire et al. 2026). This trade-off could induce a pronounced reduction in individual size coupled with a more moderate decline in density (Luo et al. 2021; Zuo et al. 2022). Although the growth-survival trade-off is widespread across species, its validation at the community level and its consequent impacts on productivity are still lacking.

The pattern of such growth-survival trade-off may differ within and across plant lifeforms (Volaire et al. 2026). Graminoids and forbs are the two dominant functional groups in temperate grasslands and they differ greatly in drought sensitivity (Lü et al. 2018; Hallett et al. 2019). Although species from both functional groups consistently experience size reduction under drought (Zhang et al. 2020; Ma et al. 2020), their densities respond differently. Forbs tend to undergo greater drought-induced reductions in density, while graminoids exhibit higher resistance and maintain more stable densities (Qian et al. 2023). This difference may stem from contrasting regenerative strategies (e.g., bud bank) or divergence among plant functional groups in trait-survival relationships (Funk et al. 2021; Luo et al. 2023; Künzi et al. 2025). For example, a conservative resource-use strategy (e.g., lower SLA) could alleviate drought impacts on graminoid survival while exacerbating them in forbs (Künzi et al. 2025). Consequently, different functional groups could exhibit distinct density-size-productivity relationships, as evidenced by a biodiversity experiment demonstrating that graminoids enhanced productivity by producing more smaller individuals, while forbs did so by retaining fewer but larger modules (Marquard et al. 2009).

Here, we report two independent 4-year drought experiments initiated in different years in a semi-arid grassland of northern China. In each experiment, we exposed half plots to extreme drought by intercepting 66% of growing-season precipitation, while leaving the other half plots intact. We tracked aboveground net primary productivity (ANPP) at both the community and functional group levels of all the plots over time. We specifically asked: (i) Does the negative impact of drought on ANPP intensify with drought duration, and is such intensification driven by progressive declines in plant density? (ii) Do graminoids and forbs differ in the relative contributions of individual size and density to productivity loss? and (iii) Does adopting resource-conservative strategies (e.g., lower SLA, higher LDMC) help plants survive and maintain density under drought, thereby buffering the decline in ANPP caused by growth limitation? By running two independent but comparable 4-year experiments, we were able to test the generality of density and size responses to drought across time and strengthen our inference by verifying whether growth-demography-productivity linkages behave consistently across experiments.

2 | Materials and Methods

2.1 | Study Area

The experiments were conducted in a temperate steppe near Erguna Forest-Steppe Ecotone Ecosystem Research Station, Institute of Applied Ecology, Chinese Academy of Sciences (50.16° N, 119.39° E, 530 m a.s.l.). The experimental field was an intact, native grassland that had not been grazed by large ungulates since 2013. This region is characterized by a semiarid temperate continental climate. Long-term (1972–2018) mean annual precipitation is 362 mm, 80% of which falls from May to August, and the mean annual temperature is −2.4°C. The dominant and common plant species in the ecosystem are *Leymus chinensis*, *Stipa baicalensis*, *Carex duriuscula*, *Pulsatilla turczaninovi*, and *Artemisia tanacetifolia*. According to the FAO classification system, the soil is chernozem, with topsoil (0–10 cm) pH ranging from 6.8 to 7.0.

2.2 | Experimental Design

We conducted two independent extreme drought experiments at locations very close to each other within the same grassland site (Figure S1). One drought experiment ran from 2015 to 2018 (hereafter referred to as the **EARLY experiment**), while the other ran from 2018 to 2021 (hereafter referred to as the **LATE experiment**) (Detailed basic information is provided in Tables S1 and S2). Both experiments used a randomized block design, consisting of six blocks, with two plots in each block randomly assigned to the two treatments: control (ambient precipitation) and drought treatment (intercepting 66% of rainfall amount from May to August). Thus, each experiment included

12 plots. Each plot was 36 m^2 (6 m × 6 m) in size, including a central zone (4 m × 4 m) and a 1 m wide buffer belt at the periphery of the central zone to minimize the edge effect. Every two adjacent plots were located 2 m apart.

Precipitation reduction was achieved passively by installing the rainout shelters following Yahdjian and Sala (2002), with 66% of the roof area covered with polypropylene stripes from May to August each year. High light-transmittance polypropylene stripes were arrayed at controlled densities to reduce the rainfall, while minimally affecting microclimatic conditions. In order to ensure unhindered air circulation and to avoid the concomitant warming effect, the shelter roofs are supported by an arch stainless-steel frame up to 2.5 m and 1 m above the ground at the highest and lowest points, respectively. To prevent external subsurface water from permeating into the experimental plots, we hydrologically isolated all plots by trenching to a depth of 1 m and lining the trench with watertight aluminum plates and thick plastic films around the plots.

2.3 | Measurements of ANPPs

At the start of the experiment, a 2 m × 2 m subplot at the central zone of each plot was selected and further divided into four quadrats (1 m × 1 m). We sampled different quadrats in different years to avoid sampling the same location between years. In mid-August of each experimental year, we sampled one quadrat, which was divided into four sub-quadrats (50 cm × 50 cm each in size). Two diagonal sub-quadrats were used to survey community composition and productivity, and the other two sub-quadrats were used for functional trait measurements.

For the investigation of community composition and productivity, all aboveground live plant material in two sub-quadrats was harvested and the individuals for each species were counted. The harvested plant material was sorted into species and then oven-dried at 75°C for 48 h and weighed to the nearest 0.1 g for biomass. The total ANPP was calculated as the sum of aboveground dry weight of all the species from the quadrats. We classified all the species into two functional groups, that is, graminoids and forbs. The individual size of each species was calculated as the total biomass of that species divided by its total number of individuals. Species richness was determined as the total number of plant species recorded in two sub-quadrats where productivity was measured, and Simpson's diversity index was calculated as: $1-\sum p_i^2$, where p_i is the relative biomass of species i in the quadrat.

2.4 | Measurements of Plant Functional Traits

In each year, the remaining two sub-quadrats (50 cm × 50 cm) were designated for measuring plant traits of the most abundant species, including plant height (Height, cm), specific leaf area (SLA, $m^2\ kg^{-1}$), leaf dry mass content (LDMC, g kg^{-1}), leaf carbon content (LCC, mg g^{-1}), and leaf nitrogen content (LNC, mg g^{-1}). Height of each species was determined in the field as the mean value of distance (cm) from the ground to the uppermost boundary of the main photosynthetic tissues of 5–10 randomly selected individuals. Then, three normal, fully expanded leaves without obvious symptoms of damage were collected from each of the five randomly selected individuals. After full rehydration, these leaves were first measured for leaf area (mm^2) and leaf fresh mass (mg), and then for leaf dry mass after being oven-dried at 65°C for 48 h. SLA was calculated as the ratio of fresh leaf area to leaf dry mass and LDMC as the ratio of leaf dry mass to leaf fresh mass. We measured LCC and LNC using a Vario MICRO Cube elemental analyzer (Elementar, Hanau, Germany). All traits were measured following standard protocols (Pérez-Harguindeguy et al. 2013).

Community-weighted mean (CWM) for each trait in a community (or the functional group, graminoids or forbs) was quantified as the mean of trait values weighted by the relative biomass of all the species recorded within the community (Garnier et al. 2004).

2.5 | Data Analysis

The biomass of each species is equal to plant density (the number of individuals per unit area, d) multiplied by individual size (the mean biomass per individual, w) (Tatsumi and Loreau 2023). Thus, ANPP can be calculated as (Equation 1):

$$\mathrm{ANPP} = \sum_{i=1}^{S} d_i w_i \tag{1}$$

where d_i and w_i are plant density and individual size of species i in each plot, respectively, and S is species richness.

Drought-induced changes in ANPP are driven by alterations in plant density and/or individual size. To differentiate the contributions of these two components at the species, functional group and community level, we adopted the method described by Jung et al. (2014). We calculated ANPP under three scenarios (Figure S1): (1) ANPP_{Ct}: ANPP in control plots, calculated using plant density and mean individual size measured within control plots (Equation 2); (2) ANPP_{Dr}: ANPP in drought-treatment plots, calculated using plant density and mean individual size measured within drought-treatment plots (Equation 3); (3) ANPP_{Dr^*}: hypothetical ANPP in drought-treatment plots, estimated using the observed plant density in the drought plot combined with mean individual size from control plots within the same year (Equation 4).

$$\mathrm{ANPP}_{Ct} = \sum_{i=1}^{S} d_{Ct\_i} w_{Ct\_i} \tag{2}$$

$$\mathrm{ANPP}_{Dr} = \sum_{i=1}^{S} d_{Dr\_i} w_{Dr\_i} \tag{3}$$

$$\mathrm{ANPP}_{Dr*} = \sum_{i=1}^{S} d_{Dr\_i} w_{Ct\_i} \tag{4}$$

Here, d_{Ct_i} and w_{Ct_i} are the plant density and mean individual size of species i in the control plots, and d_{Dr_i} and w_{Dr_i} are

the plant density and mean individual size of species *i* in the drought plots.

Based on the above results, we can quantify the absolute ANPP changes that are solely driven by the density change ($\Delta ANPP_{Density} = ANPP_{Dr*} - ANPP_{Ct}$) and driven by the individual size change under drought ($\Delta ANPP_{Size} = ANPP_{Dr} - ANPP_{Dr*}$). We further calculated the relative change in ANPP to remove interannual variation, where each ΔANPP was divided by the mean control ANPP of the corresponding year and drought experiment.

To examine the effects of drought treatment, year, and experiment identity (i.e., EARLY and LATE) on total ANPP and that of each functional type (i.e., graminoids and forbs), we used repeated measures linear mixed-effect models with treatment, year, and experiment identity and their interaction as fixed factors, and plot nested within block as a random factor (*lme* function, *nlme* package). Next, to examine the effects of drought treatment and year on ANPP for each experiment, we used linear mixed-effect models with treatment, year and their interaction as fixed factors, and plot nested within block and block nested within year as random factors. Pairwise comparisons between treatments were performed using the *emmeans* function (*emmeans* package) with Tukey adjustment (adjusted *p*-values reported). Mixed-effect models were also performed across the 4 years and for each year separately to test the significance of the effects of individual size and density alone, that is, $ANPP_{Dr}$ versus $ANPP_{Dr*}$ and $ANPP_{Ct}$ versus $ANPP_{Dr*}$, respectively. Similar mixed models were run to test for significant differences in CWM traits. To assess the impact of precipitation difference among experimental years on ANPP responses to drought, we fitted mixed-effects models including annual precipitation or growing season precipitation as a fixed factor, and experiment identity and plot as random factors.

Standardized major axis regressions were performed to estimate the line of best fit between the change in ANPP mediated by plant density and by individual size, without any constraints on the axes (Warton et al. 2012). Meanwhile, we used linear mixed-effect models to examine bivariate relationships between relative change in ANPP and CWM of each trait in each experiment, with plot nested within year as a random factor. All statistical analyses were performed in R 3.4.2.

3 | Results

3.1 | Annual Precipitation During the Experimental Years

During the experimental years (2015–2021), the drought treatment reduced annual precipitation to the level below the 5th percentile of historical precipitation probability distribution according to long-term records of annual precipitation, except for 2021 when such probability was at the 8.5th percentile (Figure 1). For the control treatment, annual precipitation was normal from 2015 to 2020, but was exceptionally high in 2021, ranking among the highest 10% on record (Figure 1).

3.2 | Drought Effect on Productivity via Changes in Plant Density and Individual Size

Across the 4 years, no significant difference in drought effect between the two experiments was observed (no interactions of treatment × experiment identity, Table S3). Across the two experiments, droughts reduced total ANPP and that of graminoids and forbs by 44%, 35.1%, and 66.9%, respectively (Figures 2 and S2). In **EARLY experiment**, reductions in total ANPP and that of forbs were driven by decreases in both plant density and individual size, whereas reduction in graminoid ANPP was driven mainly by individual size decline (Figures 2, S3 and Table S4). In **LATE experiment**, reduction in total ANPP and that of graminoids were driven by reduced individual size, while that of forbs was driven by decreases in plant density (Figures 2, S4 and Table S4).

Drought-induced reduction in ANPP in the two experiments showed different temporal dynamic patterns (Significant interaction of treatment × experiment identity × treatment duration, Table S3). In **EARLY experiment**, reduction in total ANPP escalated from 31.9% in the first year to 61.6% in the fourth year, with main driver shifting from individual size decline alone to the decrease of both individual size and plant

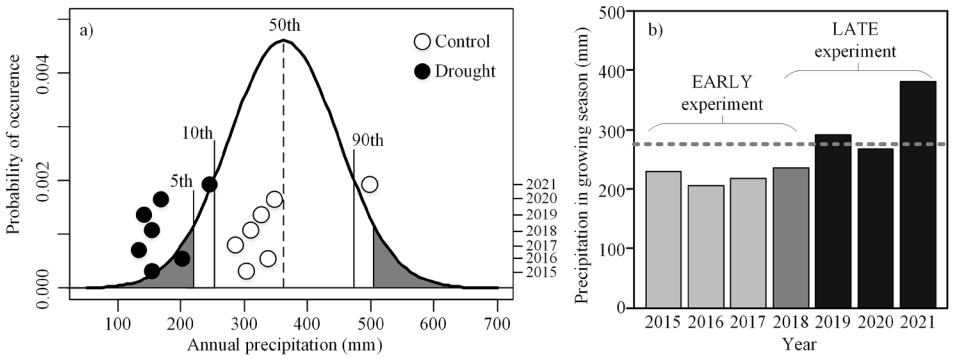

FIGURE 1 | The annual precipitation actually received in the control and drought plots from 2015 to 2021 (*x*-axis), and their probability of occurrence (*y*-axis) calculated based on 52 years (1970–2021) of precipitation data (a); the growing season precipitation patterns from 2015 to 2021 (b), where grey dotted line represents the historical average growing season precipitation. The **EARLY experiment** was conducted from 2015 to 2018, and the **LATE experiment** from 2018 to 2021.

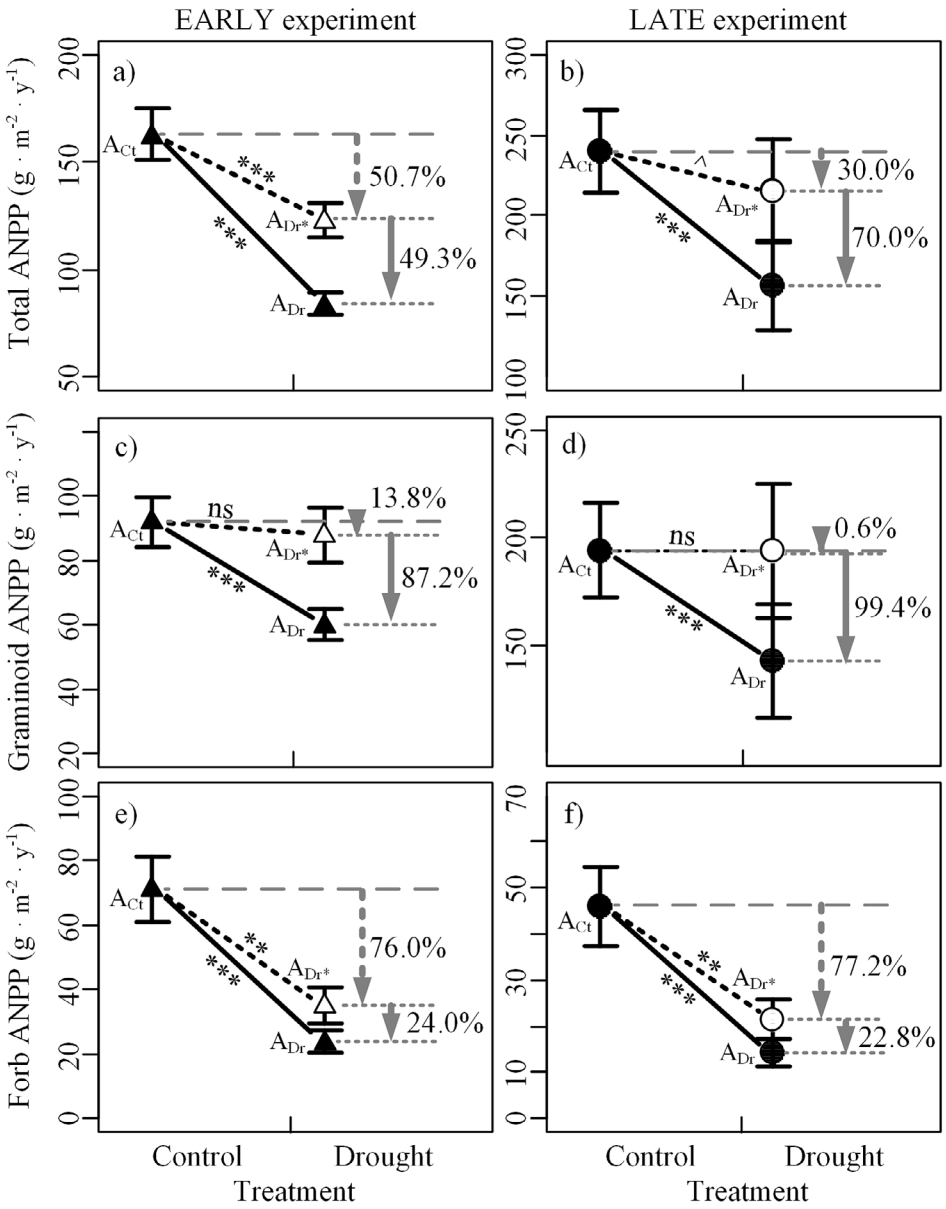

FIGURE 2 | Four-year average changes in aboveground net primary productivity (ANPP) due to changes in both density and individual size (dark solid line) and due to changes in density only (dark dashed line) for two experiments at the community (a, b), graminoid (c, d), and forb (e, f) levels. A_{Ct} and A_{Dr} correspond to the observed ANPP in control plots and in drought plots, respectively; A_{Dr*} correspond to the hypothetical ANPP in drought plots calculated using individual size measured in control plots. Arrow with percentage indicate the respective contributions of plant density alone and size alone to the changes in ANPP. Data represent the means and standard errors of ANPP. Significance levels: ns, no significant difference; *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***$p < 0.001$.

density (Figure 3 and Table S5); Concurrently, substantial species loss occurred in the third and fourth years (Figure S5 and Table S5). In contrast, in **LATE experiment**, drought decreased total ANPP by 45.5%, 43.7% and 66.5% in the first 3 years, mainly due to the decrease of both individual size and plant density (Figure 3 and Table S5). In the fourth year it was decreased only by 13.8% due to the decrease of individual size, without change in plant density (Figure 3 and Table S5). Moreover, drought in the **LATE experiment** caused earlier and more pronounced species loss, with reduced species richness observed from the first year onward (Figure S5 and Table S5). A combined analysis of both experiments revealed that as natural rainfall increased, the drought-induced decline in both total ANPP and its density-mediated component were gradually mitigated, whereas the size-mediated component remained constant (Figure S6).

3.3 | Relationship Between ANPP Components and Functional Traits

Both drought experiments demonstrated a consistent trade-off between size- and density-mediated changes in ANPP. This negative correlation was observed for both absolute and relative changes within graminoids, forbs, and dominant species in **both experiments**, but only for absolute changes at the community level in the **LATE experiment** (Figures 4, S7, and S8).

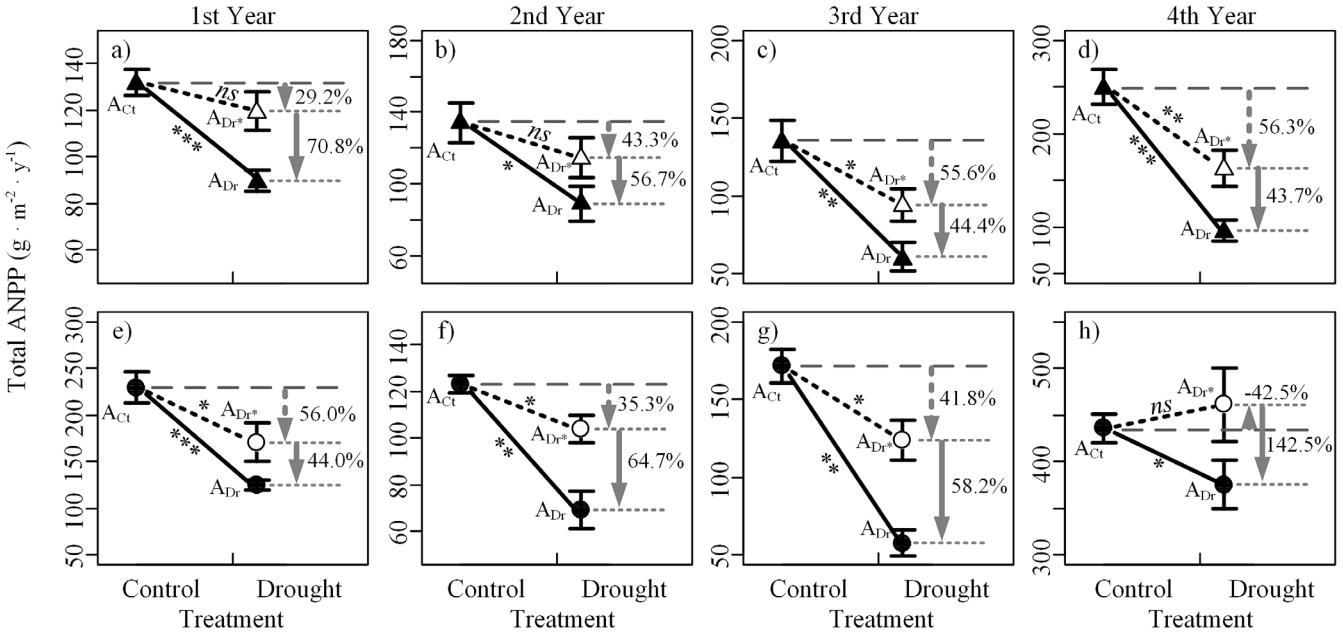

FIGURE 3 | Annual changes in aboveground net primary productivity (ANPP) of community due to changes in both density and individual size (dark solid line) and due to changes in density only (dark dashed line) in EARLY experiment (a–d) and LATE experiment (e–g). A_{Ct} and A_{Dr} correspond to the observed ANPP in control plots and in drought plots, respectively; A_{Dr*} correspond to the hypothetical ANPP in drought plots calculated using individual size measured in control plots. Arrow with percentage indicate the respective contributions of plant density alone and size alone to the changes in ANPP. Data are means and standard errors of ANPP. 1st–4th Year refers to the consecutive years of sustained drought treatment during the experiment. Significance levels: ns, no significant difference; *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***$p < 0.001$.

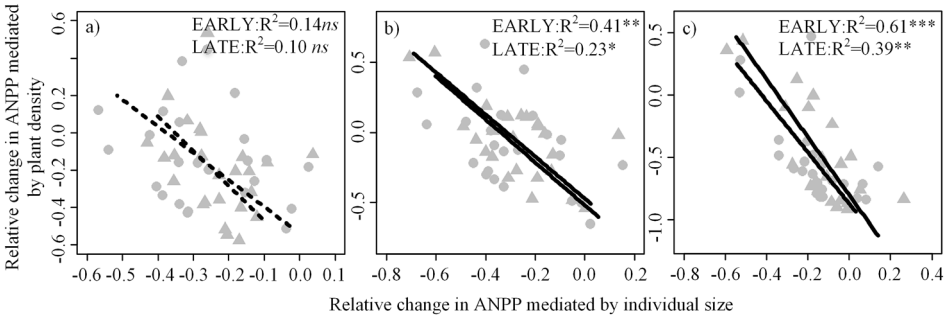

FIGURE 4 | The relationship between size- and density-mediated ANPP changes in two drought experiments at the community (a), graminoid (b), and forb (c) levels. The solid line represents a statistically significant relationship, whereas the dashed line denotes a non-significant relationship. Triangular symbols denote the **EARLY experiment**, and circular dots denote the **LATE experiment**. Significance levels: ns, no significant difference; *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***$p < 0.001$.

Experimental drought also altered community-weighted means (CWMs) of several functional traits (Figure S9). Specifically, in the **EARLY experiment**, drought increased community-level LDMC and LCC, decreased Height, and increased LNC in forbs, and increased LCC in graminoids. In **LATE experiment**, drought decreased Height of community, graminoids and forbs, and increased community-level LCC (Figures S9 and S10). Across experiments, reductions in total ANPP were positively correlated with the decreases in Height (Figure 5 and Table S6). Other traits—including LNC, LCC, and SLA—better explained variation in ANPP changes when the density-mediated and individual size-mediated components were analyzed separately (Figure 5 and Table S6–S9).

Importantly, these trait-ANPP relationships varied with functional group and experiment identity (Figure 5 and Table S6). In **EARLY experiment**, changes in density-mediated ANPP at the community level were best explained by variation in LNC, while those in size-mediated ANPP were not correlated with any traits (Figure 5 and Table S7). For graminoids, the changes in size-mediated and density-mediated ANPP were negatively and positively correlated with variation in LCC, respectively (Figure 5 and Table S8). For forbs, the changes in size-mediated and density-mediated ANPP were positively and negatively correlated with variation in SLA and LNC, respectively (Figure 5 and Table S9). In **LATE experiment**, changes in size-mediated ANPP of both community and graminoids were best explained by SLA variation, exhibiting a consistently negative relationship (Figure 5 and Tables S7 and S8). Changes in density-mediated ANPP of community and both functional groups were positively correlated with variation in plant Height (Figure 5 and

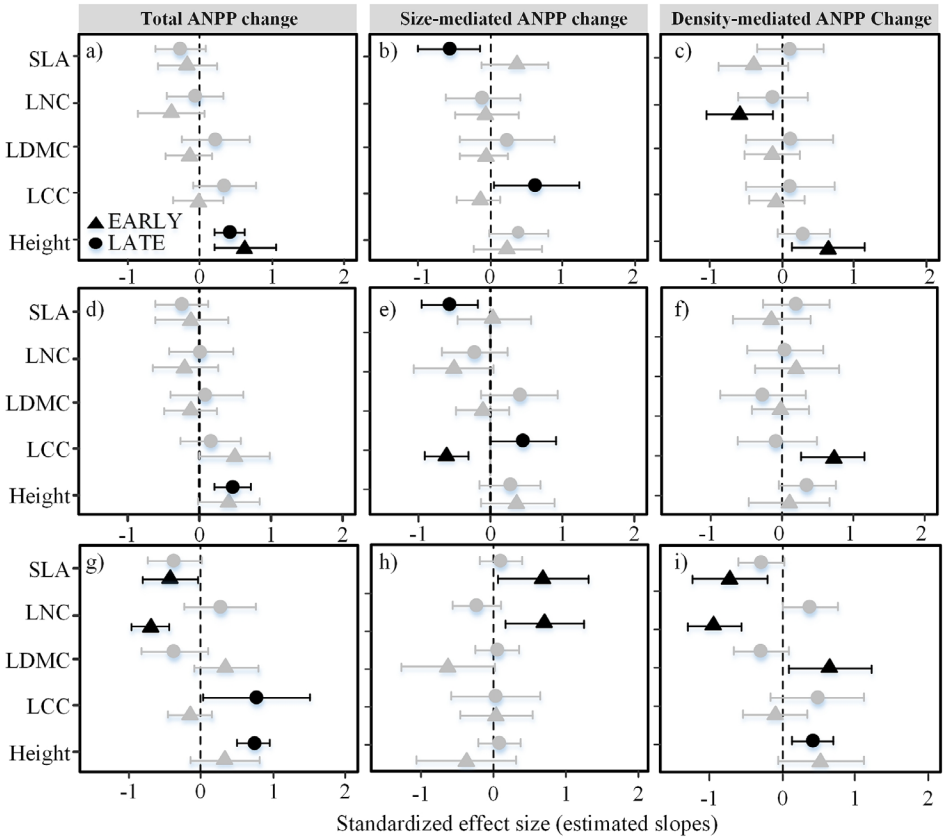

FIGURE 5 | Standardized effect size (95% confidence intervals) of changes in functional traits on corresponding change in ANPP mediated by size, density and both. Results are shown for the community (a–c), graminoids (d–f), and forbs (g–i). Trait effect is considered significant when its 95% error bar does not cross zero line in the middle of each panel. Significant effects are shown in dark; non-significant effects are shown in gray. The circle and the triangle represent **LATE and EARLY** drought experiments, respectively. Height, plant height; LCC, leaf carbon concentration; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area.

Tables S7–S9). However, changes in size-mediated ANPP of forbs were not correlated with any trait (Figure 5 and Table S9).

4 | Discussion

Using two independent drought experiments in a semi-arid steppe, we demonstrate how drought duration and plant functional group identity jointly shape grassland productivity and elucidate its underlying mechanisms. By explicitly separating the contributions of changes in plant density and individual size, we uncovered a trade-off between survival rate and individual growth that coordinatively governed ANPP responses to drought. This approach goes beyond traditional community-level measures of biomass per unit area, revealing how demographic and growth-related processes interact over time. Moreover, we show that these dynamics are mediated by functional traits depending on plant functional groups, highlighting the importance of linking trait variation to both population and individual-level processes when predicting ecosystem responses to increasing drought stress.

4.1 | Temporal Dynamics of the Drought Impact on ANPP Response

Our results provide experimental evidence for time-dependent drought-adaptive strategies in plant communities (Smith 2011; Volaire 2018), whereby growth-related regulation gradually gives way to demographic regulation with continued drought. This supports our first hypothesis that drought-driven declines in plant density exacerbate the negative effects on ANPP as drought persists. In **EARLY experiment**, ANPP initially declined due to suppressed individual size (first and second years) (Figure 3a–d). As drought persisted, density losses became increasingly important, and in the third and fourth years they exceeded the contribution of growth suppression (Figure 3a–d). This temporal shift highlights a transition from growth–related to demographic regulation on productivity. The density-mediated effects likely reflect reduced recruitment and/or shoot survival in this perennial-dominated grassland (Luo et al. 2023; Qian et al. 2023). Both processes can trigger long-lasting legacy effects on ecosystem structure and functioning (Hu et al. 2018). Therefore, quantifying their relative contribution to population persistence will be critical to understanding how ecosystem functions are maintained under recurrent drought.

In contrast, the **LATE experiment** showed no clear temporal shift: ANPP declined from the outset due to simultaneous reductions in both plant density and individual size. This pattern does not contradict the time-dependent mechanism, but likely reflects fundamental differences in community structure between the two experiments. Specifically, the community in the **LATE experiment** was characterized by greater species dominance (e.g., *Leymus chinensis*: ~60% community biomass in

the **LATE experiment** vs. ~30% in the **EARLY experiment**) and lower species diversity (e.g., Simpson's diversity index) than those in the **EARLY experiment** (Tables S1 and S2). Under drought stress, communities in the **LATE experiment** experienced rapid and substantial species loss starting in the first year of treatment, which accounted for approximately 83% of the plant density-mediated reduction in ANPP (Figures S5 and S11). Such biomass declines were not compensated by species gain or species-specific density changes (Figure S11), partly due to low initial species diversity. This resulted in a persistent and strong contribution of density reduction to ANPP decline from the very beginning of the experiment. Consequently, ANPP reduction in the **LATE experiment** was driven jointly by declines in both plant size and density from drought initiation, with no discernible temporal shift between the two components.

Interestingly, an anomalous rainfall event in the final year of **the LATE experiment** alleviated productivity loss (Figure S2). While this is often explained by the nonlinear productivity-rainfall relationship (Knapp and Smith 2001; Hoover et al. 2018; Zhang et al. 2019; López-Rubio et al. 2022), our results suggest an alternative mechanism: demographically-mediated compensation partly offset growth-related declines. This compensation involved a shift toward smaller individual size, along with increased plant density in spite of the lack of statistical significance for this increase (Figure 3). Similar patterns were also observed in subtropical forests where mortality-recruitment imbalances between large and small individuals drive community responses to drought (Zhou et al. 2013).

4.2 | Divergent Growth-Survival Strategies Among Plant Functional Groups

Consistent with previous studies, our results suggest that forbs are more sensitive to drought than graminoids (Figure 2c–f; Hoover et al. 2014; Ma et al. 2020). Further, our results clearly show that drought exerted a greater inhibitory effect on growth than on survival in graminoids but posed a greater threat to survival than to growth in forbs. This differential response reflects contrasting drought-adaptive strategies between the two functional types in terms of population subsistence: graminoids tend to maintain more but smaller individuals while forbs are inclined to promote growth of fewer individuals (Figure 2c–f). These findings were consolidated by the consistency of the two experiments. Moreover, a recent common-garden experiment conducted in temperate grassland also declared that forbs experienced greater post-drought reductions in abundance than graminoids (Künzi et al. 2025). Importantly, both drought-adaptive strategies could arise from a fundamental growth-survival trade-off under drought (Figure 4). While such trade-offs have been documented at interspecific and intraspecific levels (Martin et al. 2010; Iida et al. 2023; Zhang et al. 2024), our results show that this strategy operates not only at the species level but also at the plant functional group level under extreme drought (Figures 4 and S8). Notably, the trade-off exhibited a steeper slope in forbs than in graminoids (Figure 4), suggesting that forbs allocate resources more aggressively to growth at the cost of survival under water stress. Such contrast in drought-adaptive strategies between the two functional groups may have weakened the apparent trade-off at the community level.

4.3 | Resource Use Strategies Regulate Plant Growth and Survival

Consistent with previous studies, Height was the best predictor of total ANPP (Figure 5; Moles et al. 2009; Quan et al. 2024). Our analysis also reveals that species tended to increase LCC and LNC under drought, and this change was predominantly linked to changes in density- and/or size-mediated components of ANPP at functional group level (Figure 5). For graminoids in **EARLY experiment**, as LCC increases, the reduction in plant density-mediated ANPP gradually diminished, whereas the reduction in individual size-mediated ANPP gradually intensifies. These results imply that in **EARLY experiment**, graminoids favored a resource-conservative strategy that would enhance population survival at the cost of individual growth. Conversely, forbs in **EARLY experiment** increased LNC, an indicator of a resource acquisition strategy, which supported individual size maintenance but resulted in reduced plant density. Similar effect of conservative-acquisitive trade-off on plant performance has also been reported in forest ecosystems (Umaña et al. 2023). Furthermore, for the graminoids in **EARLY experiment**, increased LCC exerts a negative effect on individual growth but a positive effect on their survival rate, thereby limiting its utility as a predictor of total ANPP of graminoids. Such opposite effects of traits on survival versus on growth complicate identification of mechanisms driving productivity under climate change and reduce the reliability of trait-based predictions for ecosystem functions (Chacón-Labella et al. 2023; He et al. 2023).

We further observed that relationships between trait and ANPP differed between the two experiments. Specifically, higher SLA was linked to stronger size-mediated reduction in ANPP in **LATE experiment**, but to more pronounced density-mediated reduction in **EARLY experiment** (Table S7). This pattern suggests that the effect of traits on growth and survival is context-dependent. Probably, soil fertility drove this discrepancy (Table S1), as demonstrated by Laughlin et al. (2018), who found that low SLA herbaceous perennial species in pine forests exhibited high survival in fertile soil but low survival in infertile soil. Collectively, these results emphasize the complex and context-dependent role of plant traits in regulating productivity responses to drought.

While passive field-based simulations are the predominant methodological approach in drought research (Evans et al. 2011; Tielbörger et al. 2014; Byrne et al. 2013; Slette et al. 2019), they inherently fail to control for natural precipitation variability and species composition, hindering the identification of generalizable ecological mechanisms. Unlike single passive drought experiments which are susceptible to environmental stochasticity, a temporally replicated design offers a more effective means of isolating drought effects from concurrent environmental variability. This approach is especially valuable in light of recent findings highlighting aridity-dependent biases in estimating precipitation effects on ANPP (Xiao et al. 2025). Moreover, comparing outcomes across temporally replicated experiments could enhance the predictability of community-level responses to drought (Estiarte et al. 2016). Consistent results across multiple experiments are more likely to reflect a generalizable mechanism underpinning drought response, whereas discrepancies

reveal how drought effects are modulated by other factors that must be accounted for in ecological assessments. Although caution should still be taken when extrapolating to future climate scenarios, temporally replicated experiments provide a more rigorous framework for identifying consistent ecological responses to drought, thereby improving the reliability of conclusions about drought impacts on terrestrial ecosystems.

5 | Conclusion

By explicitly separating the contributions of changes in plant density and in individual size over two consecutive four-year periods, we uncovered a survival-growth trade-off that consistently governed ANPP responses to drought. This approach goes beyond traditional community-level measures of biomass, revealing how demographic and growth dynamics jointly shape grassland productivity under extreme drought over time. Moreover, these dynamics were modulated by plant functional groups, with graminoids prioritizing survival rate and forbs allocating more resources to individual growth. These findings are of great significance in predicting the dynamics of plant community composition under the context of climate change and in restoring the degraded grasslands.

Author Contributions

Shinichi Tatsumi: writing – review and editing. **Xingguo Han:** conceptualization, methodology, writing – review and editing, supervision, resources. **Qiang Yu:** methodology, conceptualization, supervision, resources. **Jiaxin Hu:** investigation, writing – review and editing. **Bingchuan Zhang:** writing – review and editing, investigation. **Wentao Luo:** writing – review and editing, investigation. **Xiaotao Lü:** writing – review and editing. **Wang Ma:** conceptualization, writing – review and editing, writing – original draft, formal analysis, investigation, visualization, software, data curation, validation. **Zhengwen Wang:** conceptualization, methodology, writing – original draft, writing – review and editing, project administration, funding acquisition, supervision, data curation, validation. **Xiaosa Liang:** writing – review and editing, investigation. **Yann Hautier:** writing – review and editing, conceptualization.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Science Data Bank https://doi.org/10.57760/sciencedb.34885. Additional supporting information can be found online in the Supporting Information section.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Experimental plots and schematic diagram of drought effects on ANPP. (a) Aerial and on-site photographs of the two drought experiments with the distance between them shown. (b) Schematic diagram illustrating the process through which drought leads to the decline of ANPP by decreasing density and individual size. As schematically illustrated, total ANPP was decreased by 190 g (Path ①) under drought, of which, 68% (130 g) was driven by reduced plant population density (Path ②), while 32% (60 g) was driven by decreased individual plant size (Path ③). **Figure S2:** Response of aboveground net primary productivity (ANPP) and plant abundance to experimental drought in EARLY (a) and LATE (b) experiment respectively, and drought-induced relative changes in ANPP (c) and abundance (d) across the four experimental years in both experiments. The different lowercase letters indicate significant differences between treatments in each year. The asterisk indicates the significant difference in drought effects between the two experiments in each year. Significance levels: ns, no significant difference; ^, $0.05 < p < 0.1$; **, $0.001 < p < 0.01$; ***$p < 0.001$. **Figure S3:** Changes in aboveground net primary productivity (ANPP) of graminoids and forbs due to changes in both density and individual size (dark solid line) and due to changes in density only (dark dashed line) in the EARLY experiment. ACt and ADr correspond to the observed ANPP in control plots and in drought plots, respectively; ADr* is the hypothetical ANPP in drought plots calculated using individual sizes measured in control plots. Arrow with percentage indicate the respective contributions of plant density alone and size alone to the changes in ANPP. 1st–4th Year refers to the consecutive years of sustained drought treatment during the experiment. Significance levels: $0.05 < ^ < 0.1$, *$0.01 < p < 0.05$, **$0.001 < p < 0.01$, ***$p < 0.001$, ns, non-significant. **Figure S4:** Changes in aboveground net primary productivity (ANPP) of graminoids and forbs due to changes in both density and individual size (dark solid line) and due to changes in density only (dark dashed line) in the LATE experiment. ACt and ADr correspond to the observed ANPP in control plots and in drought plots; ADr* correspond to the hypothetical ANPP in drought plots calculated using individual size measured in control plots. Arrow with percentage indicate the respective contributions of plant density alone and size alone to the changes in ANPP. Data are means and standard errors of ANPP. 1st–4th Year refers to the consecutive years of sustained drought treatment during the experiment. Significance levels: $0.05 < ^ < 0.1$, *$0.01 < p < 0.05$, **$0.001 < p < 0.01$, ***$p < 0.001$, ns, non-significant. **Figure S5:** Effects of drought on community species composition, species richness, and species turnover in the two experiments. Panels (a) and (b) show the mean relative biomass of the top 10 species (ranked by their relative abundance in the control treatment) under control and drought treatments; Panels (c) and (d) illustrate inter-annual differences in species richness between control and drought treatment across the 4 years; Panels (e) and (f) present the number of species lost and gained under drought over time, determined by comparing the species pool of all plots within each treatment (i.e., all control plots vs. all drought plots per site and year). Abbreviations of species name are as follows: Af, Artemisia frigida; Cda, Cymbaria dahurica; Cdu, Carex duriuscula; Cs, Cleistogenes squarrosa; Ha, Heteropappus altaicus; Kcr, Koeleria cristata; Lc, Leymus chinensis; Pta, Potentilla tanacetifolia; Ptu, Pulsatilla turczaninovii; Sb, Stipa baicalensis; Tl, Thermopsis lanceolata; Sc, Serratula centauroides. **Figure S6:** The relationship between precipitation and ANPP change mediated by individual size (a, b), plant density (c, d), and their combination (e, f) for the whole community, using pooled data from both experiments. The solid line represents a statistically significant relationship, whereas the dashed line denotes a non-significant relationship. **Figure S7:** Standardized major axis regression between absolute changes in ANPP mediated by individual size and by plant density for the whole community (a), graminoids (b), and forbs (c) in **EARLY and LATE** experiments. $\Delta ANPP_{Density}$ and $\Delta ANPP_{Size}$ represent drought-induced absolute changes in ANPP attributable to changes in plant density and individual size, respectively. The solid line represents a statistically significant relationship, whereas the dashed line denotes a non-significant relationship. Triangular symbols denote the EARLY experiment, and circular dots denote the LATE experiment. Significance levels: *ns* $p > 0.01$, *$0.01 < p < 0.05$, **$0.001 < p < 0.01$, ***$p < 0.001$. **Figure S8:** Standardized major axis regression between changes in ANPP mediated by individual size and by plant density for the dominant species (*Leymus chinensis*). Regression results based on absolute (a) and relative changes (b) in ANPP, respectively. Triangular symbols denote **the EARLY experiment**, and circular dots denote **the LATE experiment**. Significance levels: $0.05 < ^ < 0.1$, *$0.01 < p < 0.05$, **$0.001 < p < 0.01$, ***$p < 0.001$. **Figure S9:** Effect of experimental drought on functional traits, calculated as the community-weighted mean (CWM) across plots and 4 years in the two experiments. Different capital letters indicate significant difference between EARLY and LATE experiment while the different lowercase letters indicate significant difference between the control and drought treatments. Height, plant height; LCC, leaf carbon concentration; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; SLA,

specific leaf area. **Figure S10:** Effects of experimental drought on functional trait values of the two major functional groups as averaged across plots and 4 years in the two experiments. The different lowercase letters indicate significant differences between the control and drought treatments. Height, plant height; LCC, leaf carbon concentration; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area. **Figure S11:** Density-mediated ANPP change attribute to total density effect, species loss, and other components in the first year of EARLY (2015) and LATE (2018) experiments. The other components included species gain and species-specific density changes. **Table S1:** Basic information on location, natural precipitation, soil and vegetation (mean ± SE) during the experimental treatment in the two drought experiments. **Table S2:** Basic information of the common species presented in the two drought experiments. **Table S3:** Results of three–way repeated measure ANOVA for species richness (SR), aboveground net primary productivity (ANPP) of whole community (total) and the two functional groups (graminoid and forb) based on linear mixed models during drought periods. Treatment (control and drought), experiment identity (EARLY and LATE experiment), year (1st year, 2nd year, 3rd year and 4th year) and their interactions were used as fixed factors and the plot nested within the block as a random factor. The values of F and p are displayed. Bold text indicates significance at $p < 0.05$. **Table S4:** Results of two-way repeated measure ANOVA for species richness (SR), net primary productivity (ANPP) components, abundance, community biomass-weighted mean traits of whole community (total) and the two functional groups (graminoid and forb) in the two experiments. Treatment (control and drought), year (1st year, 2nd year, 3rd year, and 4th year) and their interaction were used as fixed factors, and plot nested within the block as a random factor. The values of F and p are displayed. Bold text indicates significance at $p < 0.05$. Height, plant height; LCC, leaf carbon concentration; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area. **Table S5:** Effects of drought on species richness (SR), net primary productivity (ANPP) components, abundance, community biomass–weighted mean traits of whole community (total) and the two functional groups (graminoid and forb) in the two experiments for each experimental year. Treatment (control and drought) were used as a fixed factor and the block as a random factor. The values of F and p are displayed. Bold text indicates significance at $p < 0.05$. Height, plant height; LCC, leaf carbon concentration; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area. **Table S6:** The effect of functional traits, experiment identity (EI: EARLY and LATE experiment) and their interaction on community, graminoid, and forb ANPP changes mediated by plant density, individual size, and their combination. The values of F and p are displayed. Bold text indicates significance at $p < 0.05$. **Table S7:** Bivariate relationships between trait change and ANPP change mediated by plant density, individual size, and their combination at community levels. The estimate value (mean ± SE), p values and R^2 for the model are shown. Bold text indicates significance at $p < 0.05$. **Table S8:** Bivariate relationships between trait change and ANPP change mediated by plant density, individual size, and their combination for Graminoids. The estimate value (mean ± SE), p values and R^2 for the model are shown. Bold text indicates significance at $p < 0.05$. **Table S9:** Bivariate relationships between trait change and ANPP change mediated by plant density, individual size, and their combination for forbs. The estimate value (mean ± SE), p values and R^2 for the model are shown. Bold text indicates significance at $p < 0.05$.