



Responses of grassland productivity to mowing intensity and precipitation variability in a temperate steppe

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Abstract

Mowing for hay is an important land use in grasslands that is affected by precipitation variability, due to the water-limited nature of these ecosystems. Past land use and precipitation conditions can have legacy effects on ecosystem functions, potentially altering responses to both mowing and precipitation. Nonetheless, it is still unclear how natural variation in precipitation will affect plant responses to changes in mowing intensity. We conducted a seven-year field experiment with three mowing intensity treatments compared to the traditional mowing intensity (5 cm stubble height) as a control: increased mowing (2 cm stubble), decreased mowing (8 cm stubble) and ceased mowing. Decreased mowing increased both plant aboveground net primary productivity [ANPP] and forage yield across the whole community, driven by increases in graminoids, mainly owing to the positive response of plants to precipitation. Both mowing disturbance and precipitation variability had legacy effects on plant ANPP; however, these responses differed among the whole community, graminoid, and forb levels. Current-year community-wide ANPP [ANPP_n] was positively associated with current-year precipitation [PPT_n] in all mowing treatments, driven by positive precipitation responses of the dominant graminoids. For forbs, however, ANPP_n was negatively associated with prior-year growing season precipitation [PPT_{n-1}] across mowing treatments, potentially due to lagged competition with the dominant graminoids. Our results suggest that the response of the dominant graminoids is the primary factor determining the response of ANPP to mowing and precipitation variability in these grassland ecosystems, and highlight that decreasing mowing intensity may maximize both herder's income and grassland sustainability.

Keywords Mowing · Precipitation · Graminoids · Forbs · Legacies

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Introduction

Anthropogenic disturbances, such as grazing by domestic livestock or mowing for hay, play a critical role in the formation of grassland ecosystems (Maire et al. 2012), and have a prominent impact on biodiversity and ecosystem functions (Maskell et al. 2010). These disturbances may have positive or negative effects on ecosystem functions (e.g., aboveground net primary productivity, ANPP), largely depending on the disturbance intensity (e.g., mowing frequency or height) (Meuriot et al. 2018). Highly intensive disturbance can cause prominent degradation due to loss of sensitive species, removal of nutrients, and other mechanisms (Socher et al. 2012; Li et al. 2018). Conversely, low intensity disturbance or no disturbance may cause the accumulation of litter and the competitive exclusion of less competitive species by dominant species when disturbance is lacking or minimal (Grime 1998; Hautier et al. 2009). Beyond disturbance, grasslands are often water-limited, and chronic or episodic

water shortages can limit their productivity (Wu et al. 2011; Hoover and Rogers 2016). As both extreme weather events and rainfall variability may increase due to global climate change (IPCC 2013; Huang et al. 20; Williams et al. 2020), adverse effects on plant growth and development are expected (Xu et al. 2010). It is unclear how different disturbance intensities will affect the structure and function of grassland plant communities with increasing fluctuation in precipitation, and a better understanding is needed to appropriately manage grassland ecosystems.

Past land use may have long-lasting effects on ecosystem function in subsequent years (i.e., legacies; Bürgi et al. 2017) via changes in the existing plant community and recruitment of new plants into those communities (Grime 1998; Hautier et al. 2009; Zhang et al. 2017; Song et al. 2020). Likewise, past climatic conditions may have similar effects on ecosystem function and the response of these functions to future climate change (e.g., precipitation variability) (Hawkes and Keitt 2015; Nguyen et al. 2018; Leizeaga et al. 2021). These climate legacies are typically mediated through direct and indirect effects on plant communities via the differential sensitivity of plant functional groups (i.e., grass and forb) (Broderick et al. 2022), changes in below-ground bud banks (Qian et al. 2022), and changes in soil biota (Meisner et al. 2018; Leizeaga et al. 2021; Hawkes et al. 2017, 2020), although changes in resource availability can also be important, especially when it coincides with changes in the plant community (Han et al. 2014). Appropriate management of grasslands thus also requires understanding how previous-year disturbances or precipitation conditions will affect current-year ecosystem functions.

Biomass harvesting (mowing for hay) is a widely-practiced disturbance (Han et al. 2012; Shao et al. 2012) and can have positive or negative effects on grassland ecosystem functions and services including forage yield. Plant species differ in their response to mowing due to differences in morphology and physiology, including plant height, below-ground investment, as well as tillering and photosynthetic responses to defoliation (Wang et al. 2020). Compensatory growth is a positive growth response following defoliation (Belsky 1986; Yuan et al. 2015), through physiological and ecological mechanisms (Buhl et al. 2019). For example, plants may reallocate carbohydrates from belowground biomass or the remaining leaves to increase growth after mowing (Wang et al. 2020). The efficacy of these mechanisms, however, is largely driven by mowing intensity, timing, and frequency (Meuriot et al. 2018). Early and frequent mowing may destroy above-ground plant organs and reduce regenerative ability by reducing seed production and recruitment of new individuals, resulting in the loss of sensitive species (Gross et al. 2009; Socher et al. 2012, 2013). In Inner Mongolia steppe, where this study occurred, mowing once per year at mid-August is traditional and may ensure seed set

and plant recruitment, and thus reduce the negative impact on these grassland ecosystems. Further such mowing may increase light availability for subdominant plant species, helping maintain species richness and associated ecosystem functions (Hautier et al. 2009).

Mowing annually may positively or negatively affect biomass production through multiple mechanisms. Mowing can increase plant ANPP by increasing species richness through increased light availability (Zhang et al. 2017). Conversely, mowing may decrease plant ANPP if mowing becomes too intense, due to the loss of intolerant species (Song et al. 2020). Ceasing mowing (or no mowing) also may increase plant ANPP by allowing the dominant species to flourish but may also reduce plant ANPP by decreasing species richness through litter accumulation and the exclusion of less competitive species (Beck et al. 2015). This suggests that mowing can increase or decrease plant ANPP by affecting either the dominant species or species richness. In livestock production systems, there is considerable pressure to maximize forage utilization to increase the income of the herders using a greater proportion of available forage. Increasing mowing intensity has the potential to increase or decrease forage yield. Higher mowing intensity may increase forage yield by improving overall utilization of plant biomass if this increase in intensity does not negatively impact ANPP. Conversely, higher mowing intensity may increase utilization but decrease forage yield due to the reduction in plant biomass through depletion of plant reserves (Zhang and Romo 1994). Reducing mowing intensity may similarly increase or decrease forage yields, although the mechanisms are opposite. Reducing mowing would reduce forage yields assuming if ANPP remains the same or decreases but could increase yield if ANPP increases.

Plant growth is highly climate-dependent and vulnerable to climate change (Herrero et al. 2013; Sloat et al. 2018) and even small climate changes can have a strong effect on spatiotemporal grassland functioning (Petrie et al. 2018). Mowing may alter the response of vegetation to changes in precipitation (Veron and Paruelo 2010); however, the joint effect is dependent on the intensity of those disturbances (Ma et al. 2020). The direction and intensity of the interactive effects between mowing disturbance and precipitation on plant ANPP are unknown. The legacy effects of these interactions may be largely dependent on plant community composition and the traits of those plants (Qian et al. 2022), such as whether they reproduce sexually via seed or asexually by belowground meristems (Ott et al. 2019). To test the responses of plant ANPP to mowing intensity and precipitation variability, we conducted a 7-year mowing experiment comparing traditional mowing with more intense mowing, less intense mowing, and no mowing in an Inner Mongolian steppe. This critical ecosystem covers 300 million hectares and accounts for approximately 10.5% of the total grassland

area in China (Yang et al. 2020). Biomass harvest (or mowing for hay) is a traditional land use as it provides forage for livestock in winter when forage grasses are dormant, and may be more easily managed compared with grazing (Zhang et al. 2022). We tested how these different mowing intensities affected plant ANPP and forage yield and how plant ANPP responds to current and previous year precipitation variability at both the community and plant functional group level (e.g., graminoids and forbs). By comparing how these effects changed over time, we tested for legacy effects of mowing intensity and precipitation variability on plant ANPP.

Methods

Study site

The long-term mowing experiment was located in a typical steppe in Inner Mongolia Autonomous Region, China (116°14'E and 44°12'N, 1100 m a. s. l.). The site has a semi-arid continental monsoon climate. During the experiment period (from 2014 to 2020), mean annual temperature was 4.1 °C and annual precipitation was 300 mm ranged from 169 to 413 mm (Fig. S1). The soil at the study site is a typical calcic chestnut soil (Zhang et al. 2022). This typical steppe is dominated by three graminoid species, including *Stipa grandis*, *Cleistogenes squarrosa* and *Leymus chinensis*, and a forb species, e.g., *Anemarrhena asphodeloides*, which together account for approximately 91% of aboveground net primary productivity [ANPP: g m^{-2}]. All species that were present in the study site from 2014 to 2020 are shown in Table S1. This area had been fenced in 1956 and managed by mowing annually at 5 cm stubble height for decades (Zhang et al. 2016). In 2014, vegetation cover was 26–30% and average plant height was 16 cm before mowing at the beginning of our study (Zhang et al. 2022).

In May 2014, we established a 7.5-hectare (300 × 250 m) experimental site with relatively homogenous vegetation in a state-owned farm with a total area of 640 thousand acres. Four annual mowing treatments were applied, i.e., normal mowing intensity historically (control) involving mowing annually with 5 cm stubble, increased mowing intensity (IM) to 2 cm stubble, decreased mowing intensity (DM) to 8 cm stubble, and ceased mowing (CM) involving no mowing. Within the experimental area, nine replicates of each treatment were set up in a randomized complete block design. In total, our experiment included 36 plots (5 × 3 m), which were separated by a 1.5 m buffer belt. For the IM, DM and control treatments, mowing was done in mid-August in every year after the grasses had gone to seed, while for CM, there was no mowing.

Vegetation sampling

We assessed species composition, plant ANPP and forage yield in every plot during the 7-year sampling period (2014–2020). Field investigations and sampling were conducted in mid-August about 5 days before mowing. Plant community ANPP and forage yield were harvested by clipping a 1 × 1 m quadrat. To avoid repeated clipping effects, each year we chose a new location for the quadrat in each plot. After counting species number and measuring height, we clipped all tissue just above the soil surface, separating it into two parts (forage yield and stubble), with stubble height varying according to the experimental design. For control, IM and DM treatments, we clipped all living tissues with 5, 2 and 8 cm stubble for measuring forage yield and then clipped the stubble, which we summed with forage yield to estimate plant ANPP. For CM treatment, all living tissues were clipped just above the soil surface to measure plant ANPP due to the absence of forage yield. Samples were sorted by species and oven-dried at 65 °C for 48 h to estimate forage yield and plant ANPP. We classified the plants recorded in the all quadrats into two groups, graminoids and forbs, which accounted for 78.3 and 21.7% of total community ANPP, respectively (Table S1).

Precipitation data

Precipitation data included complete monthly precipitation during the experimental years (January 2014 to December 2020) from the local weather bureau (Xilinhot, Inner Mongolia, People's Republic of China). Annual precipitation ($\text{PPT}_{\text{annual}}$) was the total of monthly precipitation from January to December in each year, and growing season precipitation (PPT_{GS}) was the total of monthly precipitation from May to September in each year. PPT_{GS} accounted for 79% of $\text{PPT}_{\text{annual}}$, ranging from 70 to 85% among years (Fig. S1), and was a better predictor of plant ANPP for our study (not shown).

Data analysis

Effects of changed mowing intensity on plant ANPP and forage yield

To assess the effects of changed mowing intensity, year, and their interactions on plant ANPP and forage yield at both community and plant groups (i.e., graminoids and forbs) levels, we ran a repeated-measure mixed model ANOVA with treatment as the fixed effect and year as a repeated-measures factor (for plant ANPP, treatment had 4 levels, year 7 levels, and replicate 9 levels; whereas for forage yield, treatment only had 3 levels).

Legacy effects of changed mowing intensity and precipitation variability on the response of plant ANPP

To assess plant ANPP responses to changed mowing intensity and precipitation variability over time at both community and plant group (i.e., graminoids and forbs) levels, we estimated the mowing response of ANPP using the log response ratio (LRR). The mowing LRR was calculated as $\log(\text{ANPP}_{\text{Mi}} / \text{ANPP}_{\text{IV}})$, where ANPP_{Mi} are the values of ANPP in each plot of each mowing treatment each year, and ANPP_{IV} are the initial values of ANPP for that plot. In our study, the ANPP of initial year (in 2014) were set as the initial values. A positive LRR ($\text{LRR} > 0$) indicates an increase in plant ANPP in a given year compared to the initial year when considering the effects of mowing history with 5 cm stubble, and a negative LRR ($\text{LRR} < 0$) is opposite. We then tested for significant differences in LRR between the IM, DM and CM treatments and the LRR in the normal history mowing intensity (control treatment). If these differences were small and non-significant, we considered this is an indication that the traditional mowing regime had legacy effects on plant ANPP. Conversely, if the differences in LRR were significant compared with the traditional mowing regime, the effects of current mowing intensities on plant ANPP are more pronounced than traditional mowing regime (control), and we considered traditional mowing regime has weak or no legacy effects on plant ANPP. Similar patterns are the legacy effects of precipitation variability. Additionally, we tested the effects of changed mowing intensity, year, and their interactions on the LRR_{ANPP} for the whole community, graminoids and forbs using repeated-measures mixed model ANOVAs with treatment as the fixed effect and year as a repeated-measures factor (4 treatments, 6 years, 9 replicates).

We used a mixed model regression to test the legacy effects of changed mowing intensity and precipitation variability on ANPP for the whole community, graminoids and forbs, using separate models. These included the LRR of current-year ANPP [LRR_{ANPP}] as the dependent variable, current-year growing season precipitation [PPT_n], prior-year growing season precipitation [PPT_{n-1}], or the LRR of prior-year ANPP [$\text{LRR}_{\text{ANPP}(n-1)}$] as independent variables. Finally, we used a stepwise regression modeling to filter the main driving factors affecting the current-year ANPP, with LRR_{ANPP} as the dependent variable, and PPT_n , PPT_{n-1} , and $\text{LRR}_{\text{ANPP}(n-1)}$ as the independent variable. Data analysis was conducted using SPSS 19.0 (IBM Corp., Armonk NY) and all figures were made in SigmaPlot 12.0 (Systat Software Inc., San Jose, CA).

Results

Effects of changed mowing intensity on plant ANPP and forage yield

ANPP of both the whole community and graminoids differed among mowing treatments ($F = 6.35$, $P < 0.01$, $F = 6.00$, $P < 0.01$, respectively), with decreased and ceased mowing having higher ANPP than either the control or increased mowing (Fig. 1a, b). For forbs, conversely, there were no significant differences in ANPP among all mowing treatments ($F = 0.12$, $P = 0.95$; Fig. 1c). There were significant differences in ANPP among years for the whole community, graminoids or forbs; however, there was only a significant interaction between mowing and year when considering the graminoids (Table S2). Treatment effects on forage production were similar. Decreased mowing had significantly positive effects on forage yield [g m^{-2}] of the whole community and of graminoids ($F = 6.09$, $P = 0.01$, $F = 5.58$, $P = 0.02$, respectively; Fig. 2a, b), whereas there was no effect on forage yield of forbs ($F = 1.02$, $P = 0.38$; Fig. 2c). There were also significant differences in forage yield among years for the whole community, graminoids or forbs; however, there were no significant interactions between mowing and year when considering forage production (Table S3).

Legacy effects of changed mowing intensity and precipitation variability on the response of plant ANPP

There were no significant differences in the response ratio of ANPP [LRR_{ANPP}] between the IM, DM and CM treatments and the LRR_{ANPP} in the control treatment across experimental years (2014–2020) nor were there significant cumulative effects of the mowing treatments on the LRR_{ANPP} for the whole community, graminoids or forbs ($P = 0.19$, $P = 0.59$, $P = 0.15$, respectively; Fig. 3). There were significant differences in LRR_{ANPP} among years for the whole community, graminoids, and forbs (all $P < 0.01$; Fig. 3), but there were no significant interactions between mowing treatment and year for the whole community, graminoids, or forbs ($P = 0.59$, $P = 0.09$, $P = 0.38$, respectively; Fig. 3).

The response ratio of plant ANPP [LRR_{ANPP}] was positively correlated to current-year growing season precipitation [PPT_n ; mm] both for the whole community and graminoids in all mowing treatments (for whole community, $R^2 = 0.25$, $P < 0.01$, $R^2 = 0.24$, $P < 0.01$, $R^2 = 0.34$, $P < 0.01$, $R^2 = 0.33$, $P < 0.01$ in the control, IM, DM and CM treatments, respectively; for graminoids, $R^2 = 0.31$,

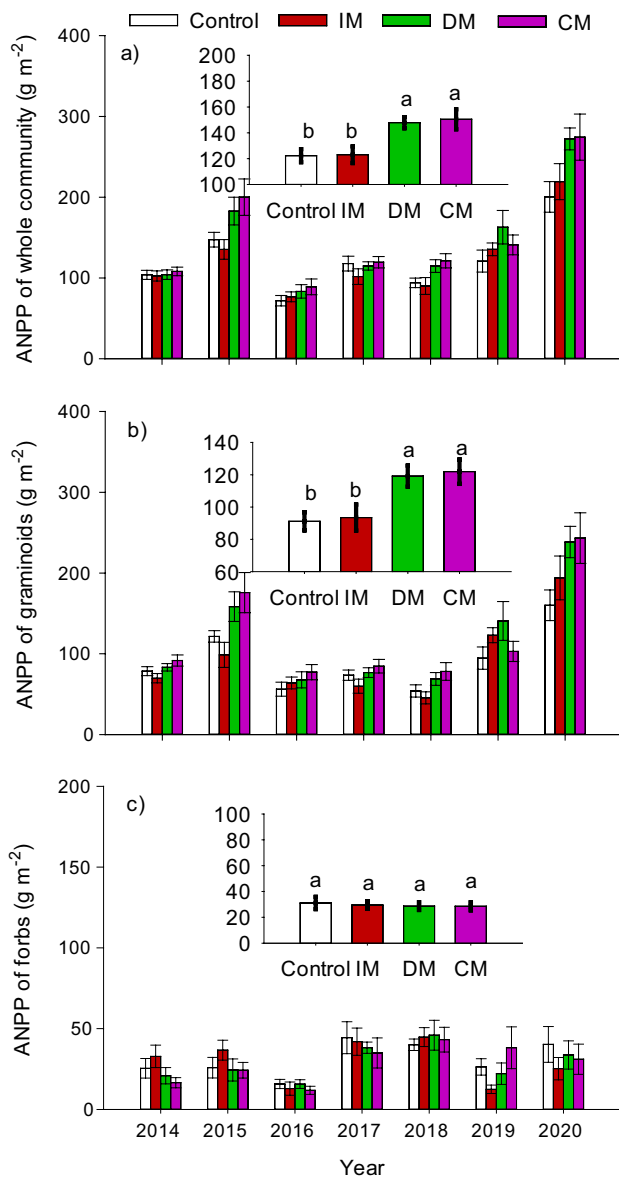


Fig. 1 Effects of changed mowing intensity on annual net primary production (ANPP: g m^{-2}) of **a** whole community, **b** graminoids, and **c** forbs, from 2014 to 2020 in a typical steppe in China, based on a repeated measures ANOVA. Shown are means \pm SE. Different lowercase letters indicate significant differences among treatments, and the significance level was $P < 0.05$. Treatment codes are: Control: normal mowing intensity, mowing annually at 5 cm stubble height; IM: increased mowing intensity, mowing annually at 2 cm stubble height; DM: decreased mowing intensity, mowing annually at 8 cm stubble height; CM: ceased mowing

$P < 0.01$, $R^2 = 0.23$, $P < 0.01$, $R^2 = 0.40$, $P < 0.01$, $R^2 = 0.31$, $P < 0.01$; Fig. 4a, b), indicating that ANPP of both whole community and graminoids tended to increase with increasing precipitation of growing season, and precipitation can stimulate plant ANPP. There were no significant relationships between LRR_{ANPP} and prior-year growing season precipitation [PPT_{n-1} : mm] for either the

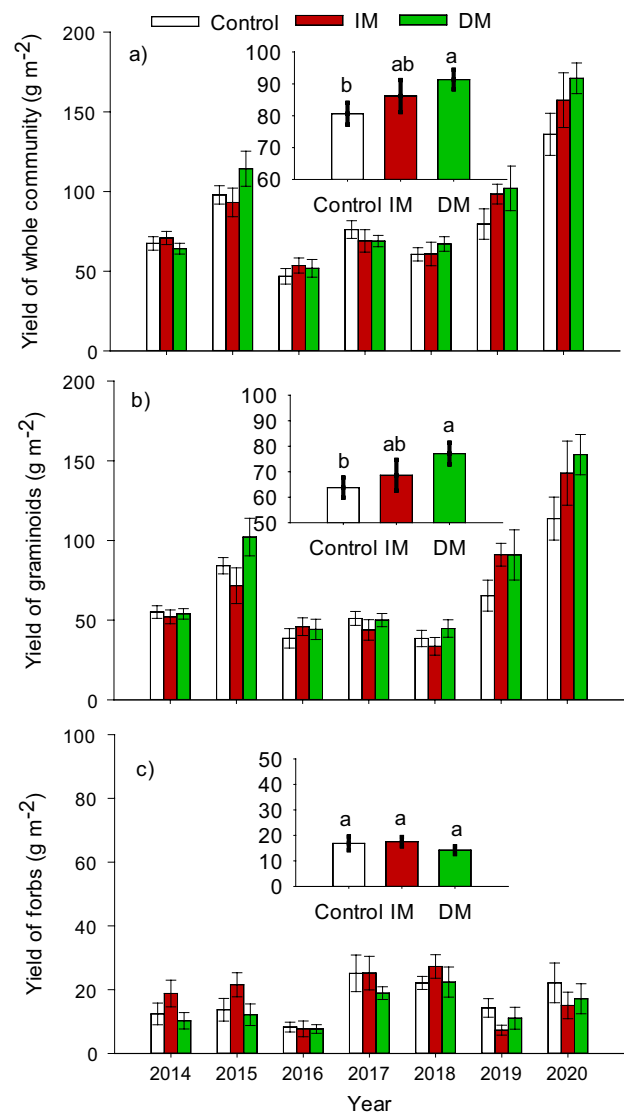


Fig. 2 Effects of changed mowing intensity on forage yield (g m^{-2}) of **a** whole community, **b** graminoids, and **c** forbs, from 2014 to 2020 in a typical steppe in China, based on a repeated measures ANOVA. Shown are means \pm SE. Different lowercase letters indicate significant differences among treatments, and the significance level was $P < 0.05$. Treatment codes are: Control: normal mowing intensity, mowing annually at 5 cm stubble height; IM: increased mowing intensity, mowing annually at 2 cm stubble height; DM: decreased mowing intensity, mowing annually at 8 cm stubble height; CM: ceased mowing

whole community or graminoids (all $P > 0.05$; Fig. 4d, e). For forbs, however, there were no significant relationships between LRR_{ANPP} and PPT_n in any mowing treatment ($R^2 = 0.01$, $P = 0.40$, $R^2 < 0.01$, $P = 0.76$, $R^2 = 0.02$, $P = 0.32$, $R^2 < 0.01$, $P = 0.63$ in the control, IM, DM and CM, respectively; Fig. 4c), but LRR_{ANPP} of forbs was negatively correlated with PPT_{n-1} in all mowing treatments ($R^2 = 0.19$, $P < 0.01$, $R^2 = 0.19$, $P < 0.01$, $R^2 = 0.14$, $P = 0.01$, $R^2 = 0.14$, $P = 0.01$ in the control, IM, DM and

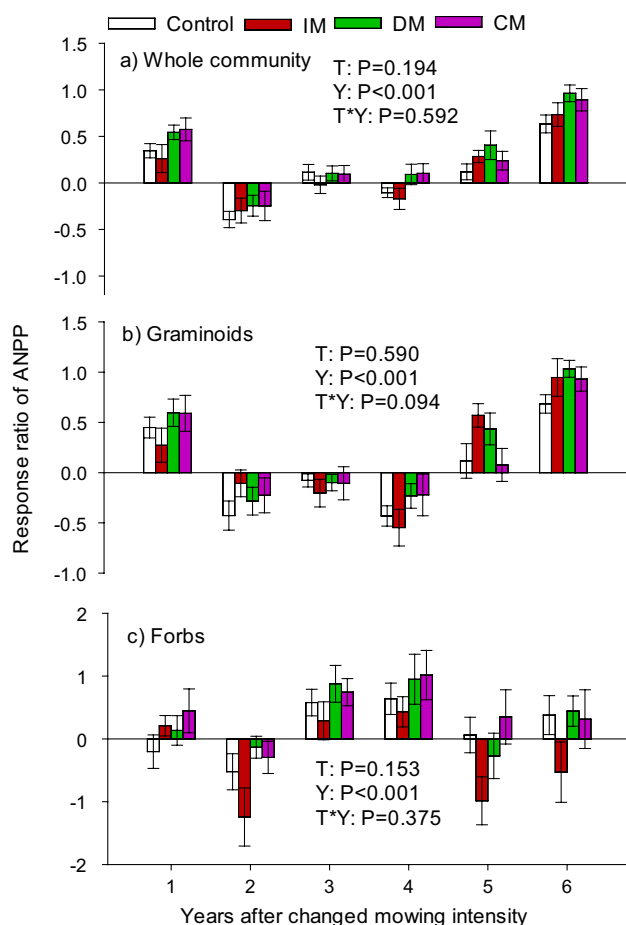


Fig. 3 Effects of changed mowing intensity on response ratio of annual net primary production (LRR of ANPP) of **a** whole community, **b** graminoids, and **c** forbs, from 2014 to 2020 in a typical steppe in China, based on a repeated measures ANOVA. Shown are means \pm SE. Treatment codes are: Control: normal mowing intensity, mowing annually at 5 cm stubble height; IM: increased mowing intensity, mowing annually at 2 cm stubble height; DM: decreased mowing intensity, mowing annually at 8 cm stubble height; CM: ceased mowing

CM treatments, respectively; Fig. 4f), manifesting that forb ANPP was less affected by current-year precipitation and tended to be negatively driven by prior-year precipitation. LRR_{ANPP} was correlated with the response ratio of prior-year ANPP [$LRR_{ANPP(n-1)}$] for the whole community in the IM and DM treatments ($R^2 = 0.14$, $P = 0.01$, $R^2 = 0.11$, $P = 0.03$, respectively; Fig. 4g), whereas LRR_{ANPP} was correlated to the response ratio of prior-year ANPP [$LRR_{ANPP(n-1)}$] for graminoids in the IM and CM treatments ($R^2 = 0.13$, $P = 0.02$, $R^2 = 0.09$, $P = 0.046$, respectively; Fig. 4h). For forbs, however, the positive relationships between LRR_{ANPP} and $LRR_{ANPP(n-1)}$ were only significant in the control treatment ($R^2 = 0.18$, $P < 0.01$; Fig. 4i).

Finally, stepwise regression showed that LRR_{ANPP} was mainly positively driven by PPT_n both for whole community and graminoids in all mowing treatments (Table 1). For the whole community, there was also a significant negative effect of $LRR_{ANPP(n-1)}$ on LRR_{ANPP} , but only in the control treatment (Table 1). For forbs, LRR_{ANPP} was mainly negatively driven by PPT_{n-1} in all mowing treatments, with $LRR_{ANPP(n-1)}$ also having a positive effect, but only in the control treatment (Table 1).

Discussion

Our continuous seven-year mowing experiment demonstrated that decreased mowing intensity both increased plant ANPP and forage yield [$g\ m^{-2}$], which was driven by increases in graminoids in this temperate grassland. These findings highlight the importance of graminoids in regulating the ecosystem functions and hay production of grassland plant communities. Both mowing disturbance and precipitation variability had legacy effects on plant ANPP; however, these responses differed among the whole community, graminoid, and forb levels. Our results suggest that decreasing mowing intensity may be an appropriate management strategy in Mongolian steppes to improve both ANPP and herder incomes, although ceasing mowing can also increase ANPP.

Effects of changed mowing intensity on plant ANPP and forage yield

Mowing has clear effects on the properties and processes of grassland ecosystems (Hsu et al. 2012; Maurer et al. 2020) and can also alter vegetation responses to precipitation (Veron and Paruelo 2010), which is the primary limiting resource in grasslands (Bai et al. 2004). Our seven-year mowing experiment showed that both ceased mowing and decreased mowing intensity increased plant whole community and graminoid ANPP, mainly owing to the positive response of plants to precipitation. Both ceased and decreased mowing treatments had stronger positive responses to precipitation (as evidenced by more positive slopes) than in the control and increased mowing intensity treatments. This was especially apparent when comparing wetter and drier years (e.g., in 2015 and 2020). Compared with the initial year (in 2014, PPT_{GS} : 204.8 mm, ANPP: $104.69\ g\ m^{-2}$), community ANPP increased by 58.97% in 2015 (PPT_{GS} : 322.3 mm, ANPP: $166.42\ g\ m^{-2}$) and 130.73% in 2020 (PPT_{GS} : 332.9 mm, ANPP: $241.55\ g\ m^{-2}$) across all mowing treatments. Likewise, plant ANPP responded more strongly to decreased mowing in wet than dry years (e.g., in 2015 and 2020), likely due to increases in water or nutrient availability (Shen et al. 2016; Han et al. 2021).

Fig. 4 Relationships between response ratio of current-year aboveground net primary productivity (LRR_n) with current-year precipitation of growing season (PPT_n , growing season: mm), prior-year precipitation of growing season (PPT_{n-1} , growing season: mm, prior-year), and response ratio of prior-year aboveground net primary productivity (LRR_{n-1}), for whole community, graminoids, and forbs, respectively, based on a linear regression ($n = 63$). Treatment codes are: Control: normal mowing intensity, mowing annually at 5 cm stubble height; IM: increased mowing intensity, mowing annually at 2 cm stubble height; DM: decreased mowing intensity, mowing annually at 8 cm stubble height; CM: ceased mowing. Statistical results in detail are shown in Table S4

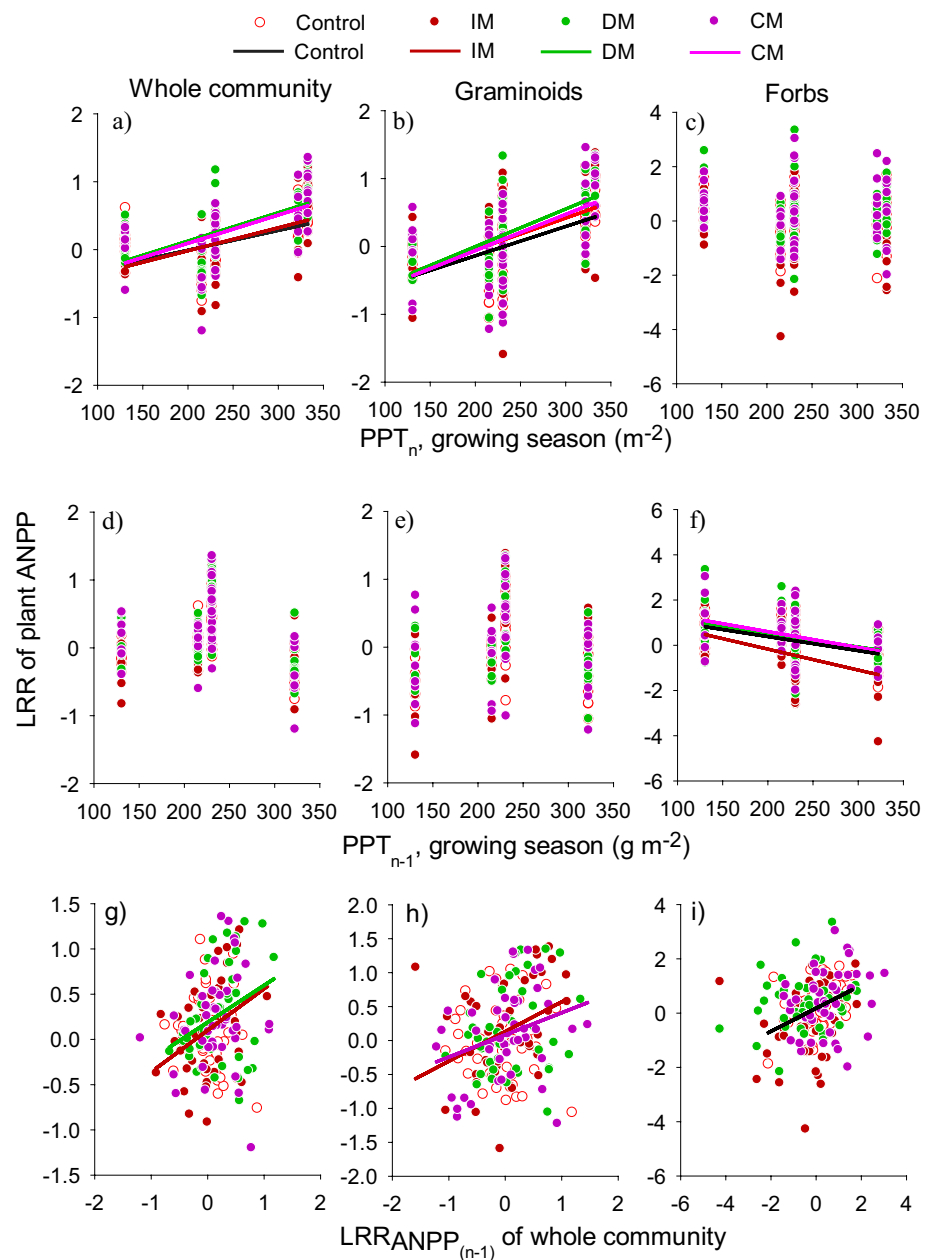


Table 1 Stepwise regression modeling of relationships between response ratio of current-year aboveground net primary productivity [LRR_n] and its driving factors, with LRR_n as the dependent variable, and current-year precipitation [PPT_n ; mm, growing season], prior-

year precipitation [PPT_{n-1} ; mm, growing season] and response ratio of prior-year aboveground net primary productivity [LRR_{n-1}] as the independent variable

Treatment	Community			Graminoids			Forbs		
	R^2	P	Equation	R^2	P	Equation	R^2	P	Equation
Control	0.387	<0.001	$LRR_n = 0.660 PPT_n - 0.468 LRR_{n-1}$	0.235	<0.001	$LRR_n = 0.485 PPT_n$	0.290	0.001	$LRR_n = -0.349 PPT_{n-1} + 0.332 LRR_{n-1}$
IM	0.287	<0.001	$LRR_n = 0.536 PPT_n$	0.287	<0.001	$LRR_n = 0.536 PPT_n$	0.194	0.002	$LRR_n = -0.441 PPT_{n-1}$
DM	0.331	<0.001	$LRR_n = 0.660 PPT_n$	0.391	<0.001	$LRR_n = 0.825 PPT_n$	0.136	0.013	$LRR_n = -0.368 PPT_{n-1}$
CM	0.303	<0.001	$LRR_n = 0.560 PPT_n$	0.284	<0.001	$LRR_n = 0.533 PPT_n$	0.143	0.002	$LRR_n = -0.378 PPT_{n-1}$

Treatment codes are: Control: normal mowing intensity, mowing annually at 5 cm stubble height; IM: increased mowing intensity, mowing annually at 2 cm stubble height; DM: decreased mowing intensity, mowing annually at 8 cm stubble height; CM: ceased mowing

Compared with control, community ANPP increased in the decreased mowing treatment by 24.04% in 2015 and 35.82% in 2020 and by 35.72% and 36.93% in the ceased mowing treatment in 2015 and 2020, respectively. These increases in community ANPP were driven by graminoids, not forbs. We speculate that mowing once per year at mid-August when all seeds have been released may allow plant recruitment (Socher et al. 2013) and maintain grassland productivity, provided that mowing intensity remains low. Interestingly, only the dominant graminoid species (*Stipa grandis*), which accounted for approximately 60% of community ANPP (Table. S1), increased in the decreased and ceased mowing treatments (Fig. S2). This suggests that the response of the dominant species to mowing is the primary factor determining the response of ANPP to mowing in these grassland ecosystems.

Compensatory growth following defoliation can maintain or increase ANPP (Belsky 1986; Yuan et al. 2015). Previous studies reported that moderate mowing (40% clipping) may cause overcompensation and positively affect plant ANPP (Wang et al. 2020). Mowing may increase lateral branching after removal of the apical meristem (Wan and Sosebee 2002) or increase tillering by stimulating photosynthesis in the remaining leaves or by redistributing carbohydrates among plant organs (Wang et al. 2020). We found more leaves of *S. grandis* were retained in the decreased mowing treatment (8 cm stubble) compared with the control (5 cm stubble) or increased mowing intensity treatments (2 cm stubble). We speculate that the greater amount of remaining leaf area likely allowed *S. grandis* to continue photosynthesizing and to maximize regrowth and its response to available moisture while minimizing drains on belowground stores, especially in wet years (e.g., in 2015 and 2020). This increase in growth also explains the increase in whole-community and graminoid forage yield in the decreased mowing treatments, despite a reduction in the utilization rate (from 70 to 65%).

Legacy effects of changed mowing intensity and precipitation variability on the response of plant ANPP

Prolonged precipitation changes can have prominent legacy effects on ecosystem function (Hawkes and Keitt 2015; Nguyen et al. 2018; Leizeaga et al. 2021) that emerge slowly over time (Broderick et al. 2022), especially in water-limited ecosystems (e.g., grasslands) (Hoover et al. 2014; Luo et al. 2021; Zhang et al. 2021). Previous studies revealed that drought effects on grasslands may last for more than a year, altering the composition of plant communities through differences in plant water use and hydraulic responses among functional groups (Wu et al. 2018). Our results show that current-year ANPP of both the whole community and

graminoids were positively driven by current-year precipitation [PPT_n], whereas forbs were negatively affected by prior-year PPT [PPT_{n-1}]. Community ANPP was largely driven by graminoids due to their dominance within the community (78% of total biomass), consistent with the mass ratio hypothesis (Grime 1998). With their expansive fibrous root systems, grasses are well adapted to responding to pulsed belowground resources, as occurs with the intermittent rainfalls that are common in grassland ecosystems (Bennett and Cahill 2013). This increase in grass abundance could also explain the negative response of forbs to prior-year precipitation, if increased reserves or increased litter biomass from in the previous year allowed grasses to suppress forb growth the following year (Dudney et al. 2017). Despite increases in ANPP in the decreased or ceased mowing treatments, there were no significant differences in ANPP in individual years at either the whole community, graminoid, or forb level. This suggests that short-term studies of altered mowing regimes may not be capable of identifying treatment effects and that longer-term studies, such as ours, are required.

Conclusions

Both ceased mowing and decreased mowing intensity increased graminoid, and thus community productivity; however, ceasing mowing would have negative economic effects on herders. Consequently, we suggest decreased disturbance to be the most appropriate management regime in this typical grassland to maximize both sustainability and herder income. Considering that large areas of semi-arid grassland in China are used for hay harvesting (11–17%), this change may have significant ecological and economic impacts. Although we explored the joint effects of mowing intensity and precipitation variability, longer-term effects may not have been captured given the modest duration (7 years) of our experiment, and future directional climate change could alter our conclusions.

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Author contribution statement FZ, KB, MZ and GH conceived and designed the experiments; FZ, TZ performed the experiments and analyzed the data, FZ, JAB and BZ wrote the manuscript. All authors critically contributed to drafts as well as giving the final approval for publication.

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Availability of data and material The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Bai Y, Han X, Wu J, Chen Z, Li L (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431:181–184. <https://doi.org/10.1038/nature02850>
- Beck JJ, Hernández DL, Pasari JR, Zavaleta ES (2015) Grazing maintains native plant diversity and promotes community stability in an annual grassland. *Ecol Appl* 25:1259–1270. <https://doi.org/10.1890/14-1093.1>
- Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. *Am Nat* 127:870–892. <https://doi.org/10.1086/284531>
- Bennett JA, Cahill JF Jr (2013) Conservatism of responses to environmental change is rare under natural conditions in a native grassland. *Perspect Plant Ecol Evol Syst* 15:328–337. <https://doi.org/10.1016/j.ppees.2013.10.001>
- Broderick CM, Wilkins K, Smith MD, Blair JM (2022) Climate legacies determine grassland responses to future rainfall regimes. *Glob Chang Biol*. <https://doi.org/10.1111/gcb.16084>
- Buhl C, Strauss SH, Lindroth RL (2019) Genetic down-regulation of gibberellin results in semi-dwarf poplar but few non-target effects on chemical resistance and tolerance to defoliation. *J Plant Ecol* 12:124–136. <https://doi.org/10.1093/jpe/rty003>
- Bürgi M, Östlund L, Mladenoff DJ (2017) Legacy effects of human land use: ecosystems as time-lagged systems. *Ecosystems* 20, 94–103. <https://doi.org/10.1007/s10021-016-0051-6>
- Dudney J, Hallett LM, Larios L, Farrer EC, Spotswood EN, Stein C et al (2017) Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands? *J Ecol* 105:484–495. <https://doi.org/10.1111/1365-2745.12671>
- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* 86:902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Gross N, Bloor JM, Louault F, Maire V, Soussana JF (2009) Effects of land-use change on productivity depend on small-scale plant species diversity. *Basic Appl Ecol* 10:687–696. <https://doi.org/10.1016/j.baae.2009.09.001>
- Han Y, Zhang Z, Wang C, Jiang F, Xia J (2012) Effects of mowing and nitrogen addition on soil respiration in three patches in an oldfield grassland in Inner Mongolia. *J Plant Ecol* 5:219–228. <https://doi.org/10.1093/jpe/rtr015>
- Han J, Chen J, Han G, Shao C, Sun H, Li L (2014) Legacy effects from historical grazing enhanced carbon sequestration in a desert steppe. *J Arid Environ* 107:1–9. <https://doi.org/10.1016/j.jaridenv.2014.03.007>
- Han J, Chen J, Shi W, Song J, Hui D, Ru J et al (2021) Asymmetric responses of resource use efficiency to previous-year precipitation in a semi-arid grassland. *Funct Ecol* 35:807–814. <https://doi.org/10.1111/1365-2435.13750>
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638. <https://doi.org/10.1126/science.1169640>
- Hawkes CV, Keitt TH (2015) Resilience vs. historical contingency in microbial responses to environmental change. *Ecol Lett* 18:612–625. <https://doi.org/10.1111/ele.12451>
- Hawkes CV, Waring BG, Rocca JD, Kivlin SN (2017) Historical climate controls soil respiration responses to current soil moisture. *Proc Nati Acad Sci* 114:6322–6327. <https://doi.org/10.1073/pnas.1620811114>
- Hawkes CV, Shinada M, Kivlin SN (2020) Historical climate legacies on soil respiration persist despite extreme changes in rainfall. *Soil Biol Biochem* 143:107752. <https://doi.org/10.1016/j.soilbio.2020.107752>
- Herrero M, Havlík P, Valin H, Notenbaert A, Rufino MC, Thornton PK et al (2013) Biomass use, production, feed efficiencies, and greenhouse gas emissions from global livestock systems. *Proc Nati Acad Sci* 110:20888–20893. <https://doi.org/10.1073/pnas.1308149110>
- Hoover DL, Rogers BM (2016) Not all droughts are created equal: The impacts of interannual drought pattern and magnitude on grassland carbon cycling. *Glob Chang Biol* 22:1809–1820. <https://doi.org/10.1111/gcb.13161>
- Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* 95:2646–2656. <https://doi.org/10.1890/13-2186.1>
- Hsu JS, Powell J, Adler PB (2012) Sensitivity of mean annual primary production to precipitation. *Glob Chang Biol* 18:2246–2255. <https://doi.org/10.1111/j.1365-2486.2012.02687.x>
- IPCC 2013 Climate change 2013: The physical science basis. Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change, Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.
- Leizeaga A, Hicks LC, Manoharan L, Hawkes CV, Rousk J (2021) Drought legacy affects microbial community trait distributions related to moisture along a savannah grassland precipitation gradient. *J Ecol* 109:3195–3210. <https://doi.org/10.1111/1365-2745.13550>
- Li P, Liu L, Wang J, Wang Z, Wang X, Bai Y, et al. (2018) Wind erosion enhanced by land use changes significantly reduces ecosystem carbon storage and carbon sequestration potentials in semiarid grasslands. *Land Degrad Dev* 29. <https://doi.org/10.1002/ldr.3118>
- Luo W, Griffin-Nolan RJ, Ma W, Liu B, Zuo X, Xu C, et al. (2021) Plant traits and soil fertility mediate productivity losses under extreme drought in C3 grasslands. *Ecology* 102, e03465. <https://doi.org/10.1002/ecy.3465>
- Ma Z, Chen HY, Li Y, Chang SX (2020) Interactive effects of global change factors on terrestrial net primary productivity are treatment length and intensity dependent. *J Ecol* 108:2083–2094. <https://doi.org/10.1111/1365-2745.13379>
- Maire V, Gross N, Borger L, Raphae Proulx R, Christian Wirth C, da Silveira PL et al (2012) Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytol* 196:497–509. <https://doi.org/10.1111/j.1469-8137.2012.04287.x>
- Maskell LC, Smart SM, Bullock JM, Thompson KEN, Stevens CJ (2010) Nitrogen deposition causes widespread loss of species richness in British habitats. *Glob Chang Biol* 16:671–679. <https://doi.org/10.1111/j.1365-2486.2009.02022.x>
- Maurer GE, Hallmark AJ, Brown RF, Sala OE, Collins SL (2020) Sensitivity of primary production to precipitation across the United States. *Ecol Lett* 23:527–536. <https://doi.org/10.1111/ele.13455>
- Meisner A, Jacquioud S, Snoek BL, Ten Hooven FC, Van der Putten WH (2018) Drought legacy effects on the composition of soil fungal and prokaryote communities. *Front Microbiol* 9:294. <https://doi.org/10.3389/fmicb.2018.00294>

- Meuriot F, Morvan-Bertrand A, Noiraud-Romy N, Decau ML, Escobar-Gutiérrez AJ, Gastal F et al (2018) Short-term effects of defoliation intensity on sugar remobilization and N fluxes in ryegrass. *J Exp Bot* 69:3975–3986. <https://doi.org/10.1093/jxb/ery211>
- Nguyen LT, Osanai Y, Anderson IC, Bange MP, Tissue DT, Singh BK (2018) Flooding and prolonged drought have differential legacy impacts on soil nitrogen cycling, microbial communities and plant productivity. *Plant Soil* 431:371–387. <https://doi.org/10.1007/s11104-018-3774-7>
- Ott JP, Klimešová J, Hartnett DC (2019) The ecology and significance of below-ground bud banks in plants. *Ann Bot* 123:1099–1118. <https://doi.org/10.1093/aob/mcz051>
- Petrie MD, Peters DP, Yao J, Blair JM, Burruss ND, Collins SL et al (2018) Regional grassland productivity responses to precipitation during multiyear above- and below- average rainfall periods. *Glob Chang Biol* 24:1935–1951. <https://doi.org/10.1111/gcb.14024>
- Qian J, Guo Z, Muraina TO, Te N, Griffin-Nolan RJ, Song L et al (2022) Legacy effects of a multi-year extreme drought on below-ground bud banks in rhizomatous vs bunchgrass-dominated grasslands. *Oecologia* 198:763–771. <https://doi.org/10.1007/s00442-022-05133-8>
- Shao C, Chen J, Li L, Zhang L (2012) Ecosystem responses to mowing manipulations in an arid Inner Mongolia steppe: an energy perspective. *J Arid Environ* 82:1–10. <https://doi.org/10.1016/j.jaridenv.2012.02.019>
- Shen W, Jenerette GD, Hui D, Scott RL (2016) Precipitation legacy effects on dryland ecosystem carbon fluxes: Direction, magnitude and biogeochemical carryovers. *Biogeosciences* 2:9613–9650. <https://doi.org/10.5194/bg-13-425-2016>
- Sloat LL, Gerber JS, Samberg LH, Smith WK, Herrero M, Ferreira LG et al (2018) Increasing importance of precipitation variability on global livestock grazing lands. *Nat Clim Chang* 8:214–218. <https://doi.org/10.1038/s41558-018-0081-5>
- Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N et al (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J Ecol* 100:1391–1399. <https://doi.org/10.1111/j.1365-2745.2012.02020.x>
- Socher SA, Prati D, Boch S, Müller J, Baumbach H, Gockel S et al (2013) Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic Appl Ecol* 14(2):126–136. <https://doi.org/10.1016/j.baae.2012.12.003>
- Song S, Zhu J, Zheng T, Tang Z, Zhu J (2020) Long-term grazing exclusion reduces species diversity but increases community heterogeneity in an alpine grassland. *Front Ecol Evol* 8:1–12. <https://doi.org/10.3389/fevo.2020.00066>
- Veron SR, Paruelo JM (2010) Desertification alters the response of vegetation to changes in precipitation. *J Appl Ecol* 47:1233–1241. <https://doi.org/10.1111/j.1365-2664.2010.01883.x>
- Wan C, Sosebee RE (2002) Tiller recruitment and mortality in the dryland bunchgrass *Eragrostis curvula* as affected by defoliation intensity. *J Arid Environ* 51:577–585. <https://doi.org/10.1006/jare.2001.0939>
- Wang K, Zhong S, Sun W (2020) Clipping defoliation and nitrogen addition shift competition between a C₃ grass (*Leymus chinensis*) and a C₄ grass (*Hemarthria altissima*). *Plant Biol* 22:221–232. <https://doi.org/10.1111/plb.13064>
- Williams AP, Cook ER, Smerdon JE, Cook BI, Abatzoglou JT, Bolles K et al (2020) Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 368:314–318. <https://doi.org/10.1126/science.aaz9600>
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Glob Chang Biol* 17:927–942. <https://doi.org/10.1111/j.1365-2486.2010.02302.x>
- Wu X, Liu H, Li X, Ciais P, Babst F, Guo W et al (2018) Differentiating drought legacy effects on vegetation growth over the temperate Northern Hemisphere. *Glob Chang Biol* 24:504–516. <https://doi.org/10.1111/gcb.13920>
- Xu Z, Zhou G, Shimizu H (2010) Plant responses to drought and rewatering. *Plant Signal Behav* 5:649–654. <https://doi.org/10.4161/psb.5.6.11398>
- Yang Z, Minggagud H, Baoyin T, Li FY (2020) Plant production decreases whereas nutrients concentration increases in response to the decrease of mowing stubble height. *J Environ Manag* 253:109745. <https://doi.org/10.1016/j.jenvman.2019.109745>
- Yuan ZQ, Yu KL, Wang BX, Zhang WY, Zhang XL, Siddique KH et al (2015) Cutting improves the productivity of lucerne-rich stands used in the revegetation of degraded arable land in a semi-arid environment. *Sci Rep* 5:1–11. <https://doi.org/10.1038/srep12130>
- Zhang J, Romo JT (1994) Defoliation of a northern wheatgrass community: above-and belowground phytomass productivity. *J Range Manage* 4:279–284
- Zhang J, Huang Y, Chen H, Gong J, Qi Y, Yang F et al (2016) Effects of grassland management on the community structure, above-ground biomass and stability of a temperate steppe in Inner Mongolia. *China J Arid Land* 8:422–433. <https://doi.org/10.1007/s40333-016-0002-2>
- Zhang Y, Loreau M, He N, Zhang G, Han X (2017) Mowing exacerbates the loss of ecosystem stability under nitrogen enrichment in a temperate grassland. *Funct Ecol* 31:1637–1646. <https://doi.org/10.1111/1365-2435.12850>
- Zhang Y, Keenan TF, Zhou S (2021) Exacerbated drought impacts on global ecosystems due to structural overshoot. *Nat Ecol Evol* 5:1490–1498. <https://doi.org/10.1038/s41559-021-01551-8>
- Zhang F, Bennett JA, Zhang B, Zhao M, Han G (2022) Intensification of disturbance destabilizes productivity through effects on dominant species. *Ecol Indic* 143:109383. <https://doi.org/10.1016/j.ecolind.2022.109383>

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