Agriculture, Ecosystems and Environment 393 (2025) 109834

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Precipitation and grazing intensity jointly shape plant compensatory growth and productivity in a semi-arid steppe ecosystem

Yanlong Li [a,b], Frank Yonghong Li [a,b,*], Chunjun Shi [a], Hao Wang [a], Lin Wu [a], Yadong Wang [a], Hugjiltu Minggagud [a,b]

[a] Ministry of Education Key Laboratory of Ecology and Resource Use of the Mongolian Plateau & Inner Mongolia Key Laboratory of Grassland Ecology, School of Ecology and Environment, Inner Mongolia University, Hohhot 010021, China

[b] Collaborative Innovation Center for Grassland Ecological Security, Ministry of Education of China, Inner Mongolia University, Hohhot 010021, China

ARTICLE INFO

Keywords:
Grazing intensity
Precipitation fluctuation
ANPP
Compensatory growth

ABSTRACT

Plant compensatory growth and productivity under animal grazing and their relations with climate have been one of the central topics in the ecology of natural grasslands. However, no consistent and general framework exists for the relationships of plant compensatory growth with grazing intensity and precipitation, especially in the semi-arid steppes of central Asia. We studied plant aboveground net primary productivity (ANPP) and compensatory growth (CG) of a semi-arid typical steppe grassland under different experimental grazing intensities, and over six years that were hugely variable with respect to precipitation in central Inner Mongolia (China). The grazing experiment used a random block-design consisting of four grazing intensities of nil (NG), light (LG), moderate (MG) and heavy grazing (HG), and replicated in four blocks. We found that (i) grazing with a defoliation rate ranging from 20 % (LG) to 60 % (HG) induced a plant over-compensatory growth, which significantly increased grassland ANPP, though the HG grassland showed a significantly lower potential production of plant aboveground biomass (AGB_p, i.e., peak AGB of the grazed grassland but not subject to grazing in the measurement year) than the NG grassland. (ii) Precipitation and grazing intensity interactively determined plant growth and production. Plant over-compensatory growth and ANPP showed a humpback curve on the grazing gradient, and grazing intensity with the highest over-compensatory growth and ANPP increased with annual precipitation. (iii) Plant community over-compensatory growth under grazing was mostly attributed to over-compensatory growth of dominant species *Leymus chinensis* and some subordinate annual species, while the C_4 grass *Cleistogenes squarrosa* had an under-compensatory growth at HG intensity. (iv) Precipitation enhanced grassland ANPP by promoting both AGB_p and the over-compensatory growth after grazing. Our study demonstrates a framework showing the interrelations of plant compensatory growth or ANPP with grazing intensity and annual precipitation, which has important implications for the development of sustainable grassland management systems to adapt to climate and land use changes.

1. Introduction

Plant compensatory growth and productivity under animal grazing and their relations with climate have been one of the central topics in the ecology of natural grasslands (Hilbert et al., 1981; McNaughton, 1979; Vail, 1992). Plants may have higher, equal or lower productivity and reproduction potential growth (i.e., have over-, equal- or under-compensatory growth) under grazing disturbance, contingent upon the disturbance intensity and external resource availability and their interactions (Alward and Joern, 1993; Belsky et al., 1993). The compensatory growth serves as an indication of the resilience and tolerance to disturbance. Empirical evidence shows that moderate grazing may enhance aboveground net primary productivity (ANPP) by inducing an over-compensatory plant growth in ecosystems characterized by high precipitation and abundant nutrient availability (McNaughton, 1979); however, heavy grazing has been reported to reduce soil fertility and regeneration of dominant perennial species (Dai et al., 2022; Török et al., 2018) and weakens the ANPP and

* Corresponding author at: Ministry of Education Key Laboratory of Ecology and Resource Use of the Mongolian Plateau & Inner Mongolia Key Laboratory of Grassland Ecology, School of Ecology and Environment, Inner Mongolia University, Hohhot 010021, China.

E-mail address: lifyhong@126.com (F.Y. Li).

https://doi.org/10.1016/j.agee.2025.109834
Received 22 February 2024; Received in revised form 17 June 2025; Accepted 25 June 2025
Available online 27 June 2025

below-ground productivity (Bai et al., 2015; Ganjurjav et al., 2015). The ANPP change along the grazing gradient is not only related with the changes in the regeneration capability of plants under varying grazing intensities, but also with the shift of plant species or plant functional groups (Herrero-Jáuregui and Oesterheld, 2018; Li et al., 2017). Grazing generally decreases the dominance of perennial species, especially perennial grasses, but fosters growth of annual and biennial species (Bork et al., 2019; Zainelabdeen et al., 2020). The change in species composition influences ANPP and its sensitivity to precipitation (Batbaatar et al., 2021; Felton et al., 2019).

ANPP in semi-arid natural grassland is sensitive to, and to a large extent, determined by fluctuating or changing climate factors, particularly precipitation (Maurer et al., 2020; Sloat et al., 2018; Su et al., 2023). Precipitation may affect ANPP directly by changing soil moisture and nutrient availability or indirectly via altering plant species composition of grassland community (Felton et al., 2019; Petrie et al., 2018; Willms et al., 1993). A decline in precipitation may induce a linear (Liu et al., 2018; Zeng et al., 2022) or non-linear reduction (Zhu et al., 2016), or little alteration of ANPP (Arredondo et al., 2016; Deng et al., 2017), depending on the precipitation patterns and grassland systems (Irisarri et al., 2016; Schönbach et al., 2011). Despite the increasing focus on the effects of precipitation and grazing on ANPP, most studies still consider only one of these factors (Irisarri et al., 2016; Knapp et al., 2017; Zhang et al., 2023). Both precipitation and grazing intensity affect plant compensatory growth and ANPP of grasslands (Irisarri et al., 2016; Schönbach et al., 2011), but the overall pattern of how compensatory growth and ANPP respond to the interactive effects of grazing intensity and precipitation fluctuation remains inconsistent across studies and ecosystems.

The temperate, semi-arid grassland in northern China is the easternmost region of the Eurasian steppe grassland and has historically served as traditional grazing land (Li et al., 2019; Zhu et al., 2023). Many studies have been done on the response of plant production to animal grazing intensity (Altesor et al., 2005; Dangal et al., 2016; Guo et al., 2023) and to fluctuating precipitation (Shaw et al., 2022; Su et al., 2020; Swemmer et al., 2007; Wilcox et al., 2017) in the grassland. Many studies have reported a ANPP decrease with grazing intensity (Dai et al., 2019; Zhang et al., 2018c), while a few other studies have demonstrated a plant over-compensatory growth under certain grazing intensities (Li et al., 2022; Schönbach et al., 2011). However, these studies on plant compensatory growth were either of short-term or under one or two grazing intensities, without a general framework being discussed on plant productivity variation in response to varying precipitation and animal grazing intensity. This general framework is, however, critically important for stocking rate adjustment in the semiarid environment (Díaz-Solis et al., 2003).

Here we conducted a 6-year field experiment in a typical steppe grassland in Inner Mongolia of Northern China, to explore the effect of animal grazing intensity and precipitation fluctuation on plant community productivity, with an emphasis on plant compensatory growth. We hypothesized that (i) plant productivity (ANPP) increases with annual precipitation, and that the increasing range of ANPP to precipitation differs under varying grazing intensities, with the highest ANPP appearing at a moderate grazing intensity; (ii) the grazing intensity with the highest plant compensatory growth or ANPP on grazing gradient increases with increasing precipitation; (iii) plant species differ in their capability of regrowth, contributing differently to plant compensatory growth under grazing. The confirmation of these hypotheses would provide insights into the mechanisms of ANPP responses to animal grazing and precipitation, and would be helpful in the development of grassland management regimes adapting to climate and land use changes.

2. Materials and methods

2.1. Study site

The study was conducted at the Grassland Ecosystem Research Station of Inner Mongolia University, located 60 km northeast of Xilinhot city, Inner Mongolia, China (116°31′18″ - 116°32′28″E, 44°15′24″ - 44°15′41″N, 1146 m a.s.1.). The region experiences a temperate semi-arid climate, with a long-term (1950–2022) mean annual temperature (MAT) of 2.7°C, and mean annual precipitation (MAP) of 284 mm. The vegetation is a typical steppe dominated by *Leymus chinensis, Cleistogenes squarrosa, Stipa grandis* and *Carex korshinskyi,* with 7 subordinate species (see Table 1). The soil is a sandy loam light chestnut soil (Calcic-rothic Aridisol in the US Soil Taxonomy classification system) (Wang et al., 2020). A 6-year grazing experiment (2017–2022 inclusive) was conducted to explore the interactive effects of grazing intensity and annual precipitation on grassland productivity. The MAT over the 6-year experimental period (4.3℃) was relatively higher compared to the long-term average; and the annual precipitation was markedly lower in 2017 and 2018, (dry years: 167.9 mm and 177.8 mm respectively), and higher in 2020–2022 (wet years: 293.5, 366.6, 386.2 and 406.2 mm respectively), than the long-term average (Fig. 1).

2.2. Experimental design

In 2016, a grazing experiment was initiated in a flat grassland area that had previously served as pastureland until 2012 when livestock grazing was prohibited to facilitate vegetation recovery. Sixteen experimental grazing paddocks of 0.25 hm^2 (50 m × 50 m) were employed to implement the four treatments of grazing intensity, that is, nil (NG), light (LG), moderate (MG), and heavy grazing (HG), replicated by four blocks. The four grazing intensities were realized by setting on 0, 3, 6, 9 sheep to graze the NG, LG, MG, or HG paddocks, respectively, in a rotational grazing system. The sheep were moved in the grassland

Table 1
Analysis of variance (*df* and *P* value) on the effects of grazing intensity, year and their interaction on ANPP, plant aboveground biomass in grazing exclusion (AGB_p), and plant belowground biomass (BGB) and its percentage in grassland productivity (relative BGB), at plant species (or subordinate species group) and community levels.

Effects		Grazing I.		Year		Grazing I. × Year	
		df	*F*	*df*	*F*	***df***	*F*
ANPP	*Leymus chinensis*	3	15.76***	5	62.28***	15	5.78***
	Stipa grandis	3	13.06***	5	15.73***	15	2.18*
	Cleistogenes squarrosa	3	0.75ns	5	17.04***	15	4.20* *
	Carex korshinskyi	3	10.62***	5	0.64ns	15	1.30ns
	Subordinate species	3	26.75***	5	21.49***	15	8.17***
	Plant community	3	14.84***	5	80.13***	15	3.34**
AGB_p	*Leymus chinensis*	3	9.75***	5	34.39***	15	3.55**
	Stipa grandis	3	2.73*	5	11.41***	15	10.42***
	Cleistogenes squarrosa	3	25.13***	5	30.39***	15	5.09***
	Carex korshinskyi	3	0.60ns	5	8.16***	15	1.83*
	Subordinate species	3	4.03**	5	9.46***	15	6.97***
	Plant community	3	16.64***	5	62.16***	15	20.03***
BGB (0–30 cm)		3	10.16***	5	2.14*	15	4.01***
Relative BGB		3	51.09***	5	6.393***	15	1.40ns

Note: *df* represents degrees of freedom. Significant levels are denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The mixture subordinate species refer to all the species except the four dominants listed in the Table, including *Thalictrum petaloidem, Astragalus galactites, Chenopodium album, Potentilla acaulis, Allium bidentatum, Lappula intermedia* and *Salsola collina.*

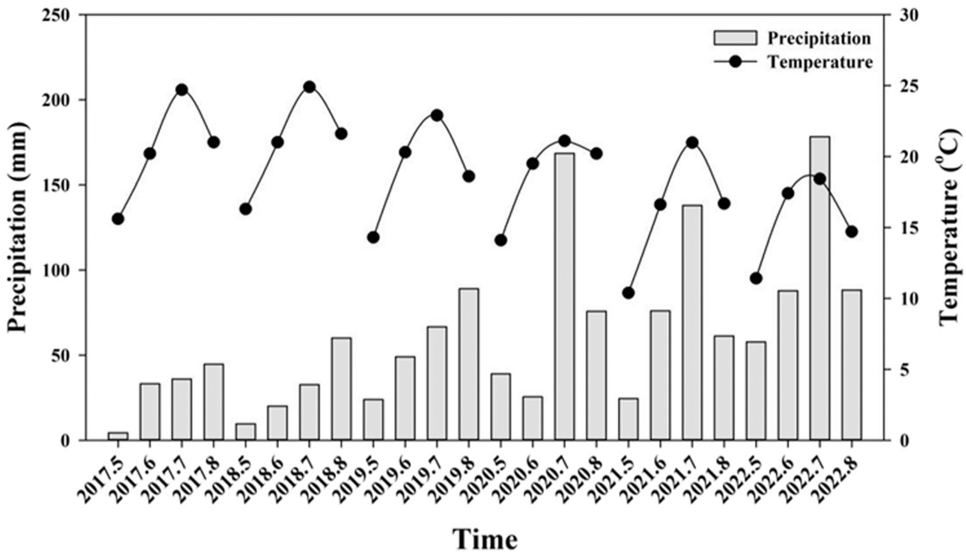

Fig. 1. Monthly mean temperature (℃) and total precipitation (mm) during the plant growing season (May-August) at the research site over the experimental period.

paddocks simultaneously on three occasions each year (in June, July and August). After grazing, they were removed, leaving a residual grassland height of approximately 6 cm in the MG paddocks, corresponding to plant aboveground biomass (AGB) of approximately 60 g dry matter m^{-2}. The experiment runs over six years from 2017 to 2022. The grazing sheep were Mongolia sheep, all aged 2 years, with an average body weight of 33 kg. During the 6-year experimental period, each paddock was grazed by a sheep flock of 0, 3, 6, 9 sheep for 190 days, i.e., for 0, 570, 1140, 1710 sheep-grazing days in NG, LG, MG or HG paddocks, respectively. These grazing intensities were equivalent to average stocking rates of 0, 1.04, 2.08 and 3.12 sheep·$ha^{-1}y^{-1}$ in NG, LG, MG or HG paddocks. Water was provided in each paddock for sheep drinking during the grazing period.

2.3. Sampling and measurements

Before sheep grazing commenced, three permanent cages measuring 1.2 m in length, 1.2 m in width, and 1.0 m in height were placed in each paddock. These cages served to safeguard the grassland from grazing throughout the plant growing season, being maintained until conclusion of the last grazing event each year. Also, another three moving cages were placed in each paddock to prevent grazing on the grassland before every sheep grazing rotation in June, July or August. Plant AGB was determined by harvesting (clipping) plant materials species by species from the ground surface at the end of each grazing rotation, both inside and outside each moving cages, using the quadrat of 1 m × 1 m, and then these cages were moved to other places for excluding sheep grazing in next rotation. The collected plant species biomass were separately oven-dried at 65°C for 48 h and weighed, and plant species biomass was summed up as plant community biomass. This process was carried out for four predominant species: *L. chinensis, C. squarrosa, S. grandis* and *C. korshinskyi,* as well as for the remaining species in mixture. Plant height of each species was measured and recorded in each quadrat. The plant AGB in the three permanent cages that excluded sheep grazing for the whole plant growing season were also determined in the same way at the time of determining plant AGB at the conclusion of the last grazing rotation of the year, and used to represent the ANPP under no grazing in the grazing grassland paddocks. Belowground biomass (BGB) was determined by sampling plant belowground parts to 30 cm in depth, by collecting three soil cores (of 7 cm-diameter) in each of the three vegetation quadrats after plant AGB being harvested in each paddock. The belowground parts were extracted from soil by rinsing them in water, and then oven-dried at 65°C for 48 h to get dry weight.

2.4. Description and calculation of livestock and plant parameters

(1) Peak plant AGB of the grazing grasslands (AGB_p): it was determined in the permanent grazing-exclusion cages in plant biomass peak time (mid-August) in all the grazing grassland paddocks. AGB_p represents the plant productivity of the grassland grazed in previous years but not in the measurement year.
(2) Plant residual AGB, i.e., plant standing AGB under grazing (AGB_g): it was dynamic and determined upon the completion of each grazing rotation.
(3) Grassland residual rate: the ratio of AGB_g to the plant AGB determined inside the moving grazing-exclusion cages (AGB_i) upon the completion of each grazing rotation (i.e., AGB_g/AGB_i). The rate is complementary to the defoliation rate, and its average over the three grazing rotations was used to gauge the grazing intensity.
(4) ANPP: the total herbage intake by animals throughout the plant growing season, combined with the AGB_g at the conclusion of the last grazing rotation in that season.
(5) Relative plant belowground biomass (relative BGB): that is, BGB/(BGB+ANPP), used to quantify plant biomass allocation between the below and the aboveground parts.
(6) Plant compensatory growth (CG): the difference between ANPP and AGB_p, i.e., CG = ANPP - AGB_p. CG can be positive (over-compensation) or negative (under-compensation).
(7) Daily herbage intake of grazing sheep (DI): the difference between plant AGB inside (AGB_i) and outside (AGB_g) of the moving cages upon the completion of each grazing rotation, i.e., DI = (ABG_i - ABG_g) × 2500 m / N_L / D_g, where DI was in g·$head^{-1}$·d^{-1}; AGB_i and AGB_g were in g·m^{-2}, N_L represents the number of grazing sheep, and D_g represents the number of grazing days.

2.5. Statistical analyses

All experimental data underwent normal distribution testing, and logarithmic transformation was applied to those that did not meet the normality criteria. A repeated measures mixed model ANOVA was employed, with grazing years as a within-subjects factor and grazing intensity as a between-subjects factors, to evaluate the effects of grazing intensity and grazing years on grassland community attributes, including height, AGB_g, AGB_g/AGB_i, BGB, ANPP, AGB_p, and relative biomass of dominant plant species. One-way ANOVA was used to compare the means of these plant production parameters at plant species and community levels among grazing intensity treatments.

Partial correlation coefficients were computed to differentiate the influences of grazing and precipitation on grassland CG and ANPP. A quadratic polynomial surface model was fit using the least-squares method to examine the response of ANPP and CG to animal grazing and precipitation. Data analysis and charting were done using SPSS 24.0 (IBM Crop., Armonk NY), Origin 2020 and R.4.1.1.

3. Results

3.1. Plant aboveground biomass dynamics and defoliation rates on the grazing gradient

Plant community height, standing aboveground biomass (AGB_g) and the residual rate (AGB_g/AGB_i) at the end of each grazing rotation decreased significantly with increasing grazing intensity and varied across years (Fig. 2). Plant AGB_g after each grazing rotation averaged 110, 65 and 40 g·m^{-2} under LG, MG and HG, respectively, over the 6-year period. Plant community height and AGB_g increased under NG and LG over the years, while the residual proportion of plant biomass (AGB_g/AGB_i) showed no significant difference across the years, averaging 80.5 %, 59.1 % and 39.4 %, which were equivalent to average defoliation rates of 19.5 %, 40.9 % and 60.6, respectively under LG, MG and HG (Fig. 2c).

3.2. Plant productivity and compensatory growth on the grazing gradient

Grazing intensity and year interactively affected the plant community ANPP and AGB_p ($P < 0.05$) (Table 1). The grassland under the grazing at all the three intensity levels had a significant higher plant community ANPP than no-grazing grassland over the 6-year period ($P < 0.05$) (Fig. 3a). However, the potential plant production with grazing excluded in the measurement year (AGB_p) were similar under NG, LG and MG, and were all significantly higher than that under HG over the 6-year period ($P < 0.05$) (Fig. 3b).

Plant compensatory growth (CG) at community level varied among grazing intensities and across years (Fig. 3c). Plant community showed a significant over-compensatory growth under LG consistently over the six years ($P < 0.05$), and a significant over-compensatory growth under MG and HG except in dry years (2017 and 2018) ($P < 0.05$), and the amount of compensatory growth was higher under MG and HG than LG ($P < 0.05$) in the wet years (2020–2022).

3.3. Plant species composition and their contribution to plant community compensatory growth

ANPP of the four dominant species *L. chinensis*, *C. squarrosa*, *S. grandis* and *C. korshinskyi* and that of mixed subordinate species were determined, which accounts for 36.8 %, 25.3 %, 28.2 %, 4.2 % and 5.5 % of plant community biomass, respectively, on average over the six-year period. Grazing intensity and year significantly and interactively affected the ANPP of the three dominant species and the subordinate species mixture in plant community ($P < 0.05$) (Table 1). The increase in plant community ANPP under grazing (Fig. 3a) was primarily attributed to the increased ANPP of the two dominants species (*L. chinensis* and *C. korshinskyi*) and mixture subordinate species ($P < 0.05$) (Fig. S1). The variation pattern of ANPP and AGB_p differs on the grazing gradient. Compared to the ANPP in the NG grassland, grazing at all three intensities significantly increased the ANPP of *L. chinensis*, whereas its AGB_p significantly decreased with increasing grazing intensity ($P < 0.05$) (Fig. S1 & 2). In contrast, grazing decreased both ANPP and AGB_p of *S. grandis* at HG, but not at LG and MG. Grazing did not significantly alter the ANPP of *C. squarrosa*, but increased its AGB_p at HG; grazing at MG and HG significantly increased the ANPP and AGB_p of the mixture subordinate species ($P < 0.05$) (Fig. S1 & 2).

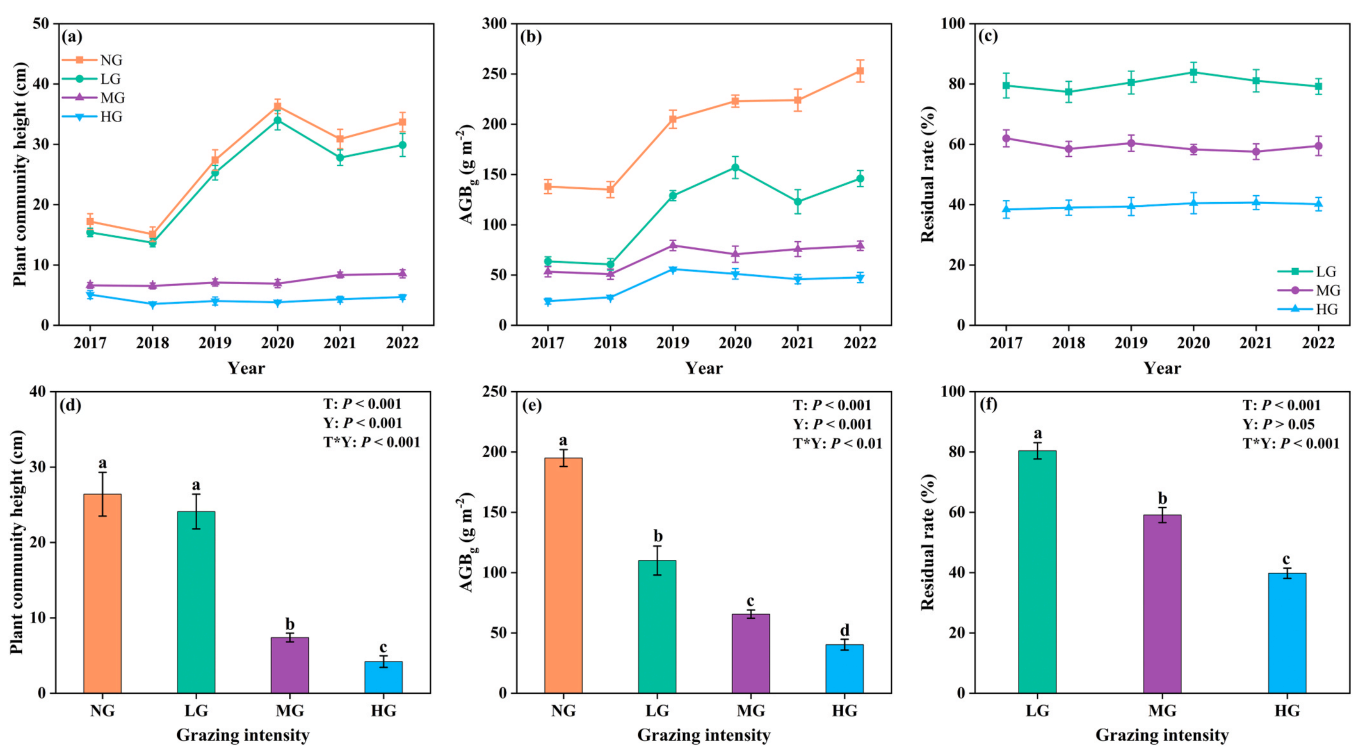

Fig. 2. Plant community height (a, d), residual plant aboveground biomass (AGB_g) (b, e), and residual rate (percentage of AGB_g in ANPP) (c, f) under different grazing intensities and across the 6-year experimental period. NG, no-grazing; LG, light-grazing; MG, moderate-grazing; HG, heavy-grazing. Each dot represents the mean and standard error of these vegetation parameters over the three grazing rotations each year (n = 12); and each column represents the mean and standard error of these vegetation parameters over the six-year period (n = 72). Distinct lowercase letters are used to denote statistically significant differences (P < 0.05) among grazing treatments.

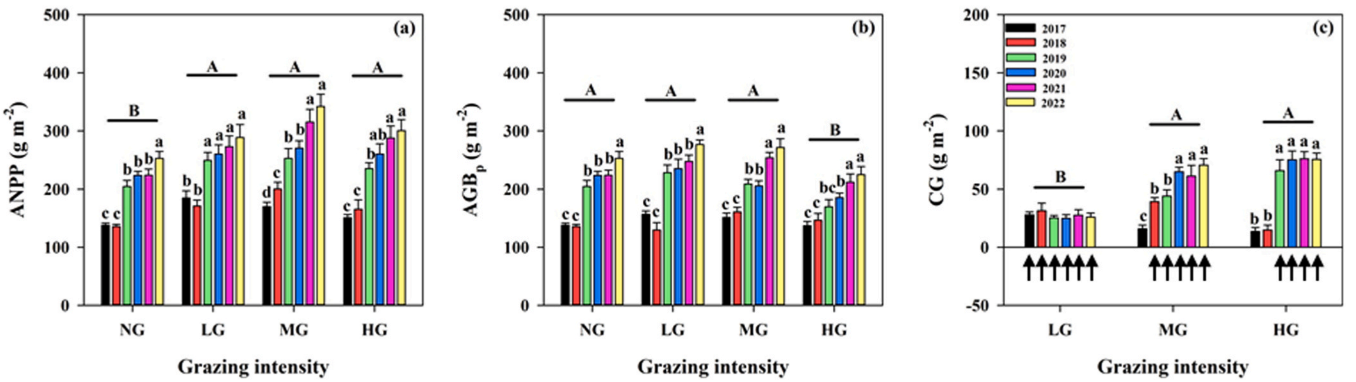

Fig. 3. Plant community productivity under grazing (a: ANPP = animal herbage intake + residual biomass), plant aboveground biomass at the peak biomass time determined under no-grazing in the current season (b: AGB_p), and plant compensatory growth (c: CG = ANPP - AGB_p) of the grasslands subject to summer grazing at different intensities in a typical steppe. Distinct lowercase letters signify a significant difference within the same grazing treatment across the years, while distinct uppercase letters indicate a significant difference between grazing intensities ($P < 0.05$). Each bar represents the mean and standard error (n = 12). An arrow beneath the bar of the CG for each year in (c) indicates a significant compensatory growth (i.e., CG > 0 at $P < 0.05$).

The increase of plant community ANPP and AGB_p over the years (Fig. 3) was mainly attributed to the ANPP and AGB_p increase of dominants *L. chinensis* and *S. grandis* over the years at all grazing intensities ($P < 0.05$) except that of *S. grandis* under HG ($P < 0.05$) (Fig. S1 & S2). The AGB_p but not ANPP, of *C. squarrosa*, significantly decreased under MG, but increased under HG; the ANPP and AGB_p of *C. korshinskyi* and the mixture subordinate species showed no significant change across years (Fig. S1 & 2).

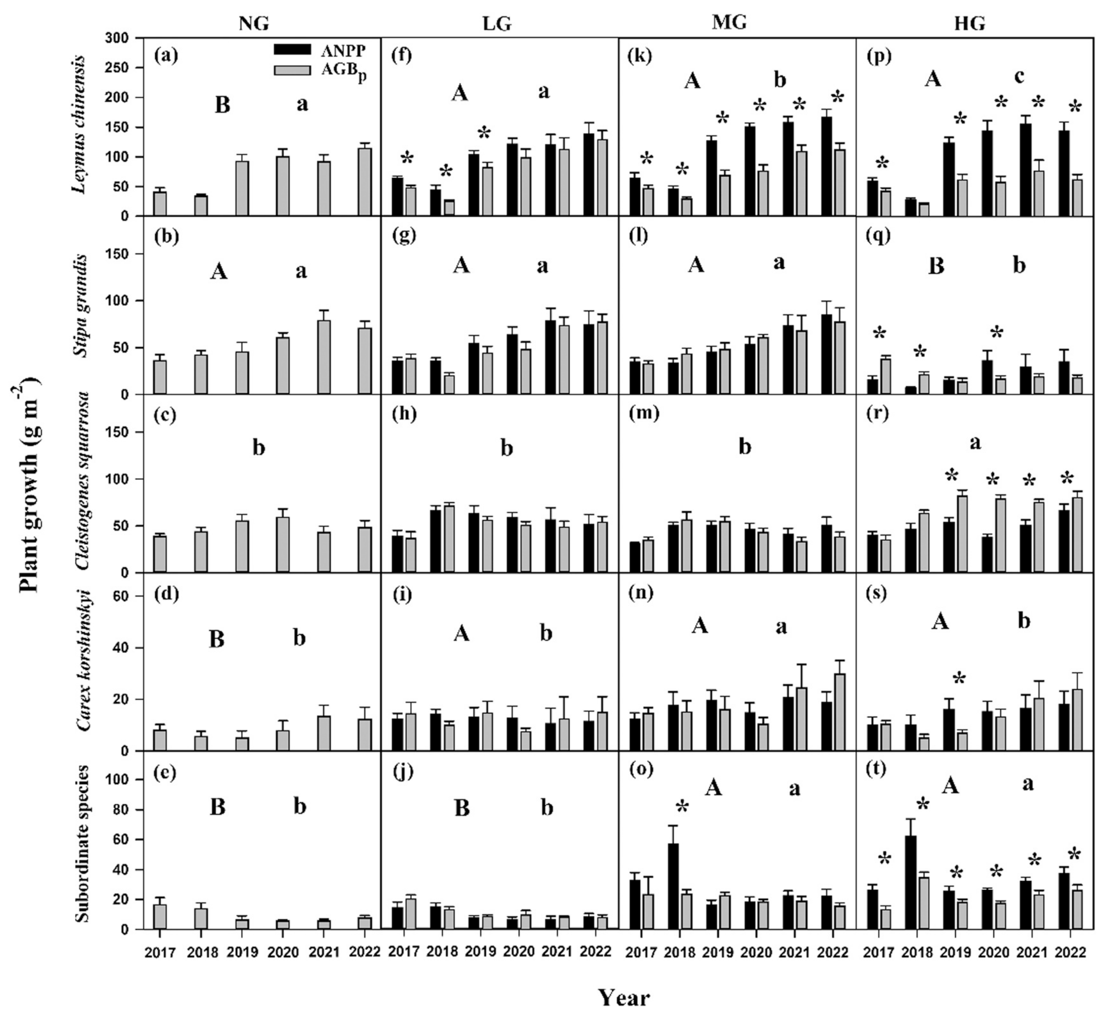

Fig. 4. A comparison of grassland ANPP under grazing (black bars) and plant aboveground biomass at the peak biomass time under no grazing in the current season (AGB_p; grey bars) of plant species in the grassland paddocks under NG, LG, MG and HG in a typical steppe. A significant difference between ANPP and AGB_p (marked with a '*') indicates a grazing induced plant compensatory growth ($P < 0.05$). Distinct uppercase letters indicate significant differences in ANPP ($P < 0.05$), while distinct lowercase letters indicate significant differences in AGB_p ($P < 0.05$), at the four grazing intensities over the six years.

Plant community compensatory growth (CG) under grazing was mainly attributed to the CG of dominant *L. chinensis*, which had a significant positive CG under all the three grazing intensity levels ($P < 0.05$) and over the six years, except that under LG from 2020 to 2022 and under HG in 2018 (Fig. 4a-p). *Stipa grandis* showed a significant under-compensatory growth in dry years (2017 & 2018), but an over-compensatory growth in wet 2020 under HG (Fig. 4q). *Cleistogenes squarrosa* showed an over-compensatory growth under HG in wet years (2019–2022) (Fig. 4r). The over-compensatory growth was also observed for *C. korshinskyi* under HG in a wet year (2019) (Fig. 4s), and for the subordinate species mixture under MG in 2018, and under HG in 2017–2022 (Fig. 4o, t).

3.4. Relationships of plant CG and ANPP with grazing intensity and precipitation

The polynomial model for the relationships of ANPP or CG with grazing intensity and precipitation showed that both grassland ANPP and CG demonstrated a humpback-like curve on grazing gradient at a certain precipitation (Fig. 5). The grazing intensity for the highest ANPP or CG on the grazing gradient increased with precipitation, from approximately LG to approximately MG, as shown by the ridge lines of the fitted ANPP or CG surface on the plane of grazing intensity and precipitation.

4. Discussion

4.1. Plant aboveground biomass and productivity on grazing gradient

Previous studies across diverse semi-arid grassland systems have documented variable effects of grazing on ANPP (Ferraro and Oesterheld, 2002; Milchunas and Vandever, 2013), and the effects vary with grazing intensity, season and regimes. Our study focuses on the influence of differences in grazing intensity on plant growth and ANPP under an adaptive rotational grazing management by setting off the grazing animals in each rotational grazing when the residual plant height or biomass reached a certain threshold. As a result, the defoliation rates of ANPP are controlled at approximately 80 %, 60 % and 40 % respectively at LG, MG and HG, and are consistent over the six experimental years (Fig. 2c). Our results show that, although plant community height and AGB_g decline with increasing grazing intensity, plant AGB_p declines under HG, but not under LG and MG; while ANPP increases under all the three grazing intensities (Fig. 3a, b). Many studies have shown that animal grazing may increase plant productivity under low to moderate grazing intensity, while heavy grazing damages grassland and leads to a reduction in plant productivity (Hilbert et al., 1981; Zhang et al., 2015), which supports our findings of the humpback-like curve of AGB_p variation along the grazing gradient. The divergent changes in ANPP versus AGB_p on grazing gradient implies the dependence of plant CG on grazing intensity. Our results are consistent with existing studies that grazing can increase grassland productivity by promoting plant over-compensatory growth (Li et al., 2022). The results may also reflect the heavy grazing, which consumes 60 % of ANPP, in our study may not be heavy enough to damage the grassland in such an adaptive grazing management system, and the compensatory growth under the HG may compensate for the decline in AGB_p.

Our results also show that both plant community ANPP and AGB_p increase significantly over the 6-years at all the three grazing intensities. This increase is a consequence of increasing precipitation over the experimental period (Su et al., 2019), not the successive or accumulative change of plant-soil system under different grazing intensities. This is indicated by the high correlation of ANPP or AGB_p with precipitation but not with the sequential year when the effects of sequential year are controlled in a partial correlation analysis, but not vice versa (Fig. S5a, b).

Plant CG is significantly and positively correlated with grazing intensity and precipitation, but its correlation with precipitation is significant only when the effect of grazing occurs (Fig. S5c). This result indicates that, though plant CG occurs only under grazing and varies with grazing intensity, precipitation modulates the amount of grazing-induced plant CG.

4.2. Mechanisms of plant compensatory growth under grazing

Plant compensatory growth serves as the primary strategy by which plants withstand defoliation disturbance. Several major processes can be identified for the grazing enhancement of plant growth and ANPP (Leriche et al., 2001). The first is the better re-growth of plant species after grazing due to the high photosynthetic rate of newly regrown young leaves and the reduction of plant self-shading (Borer et al., 2014;

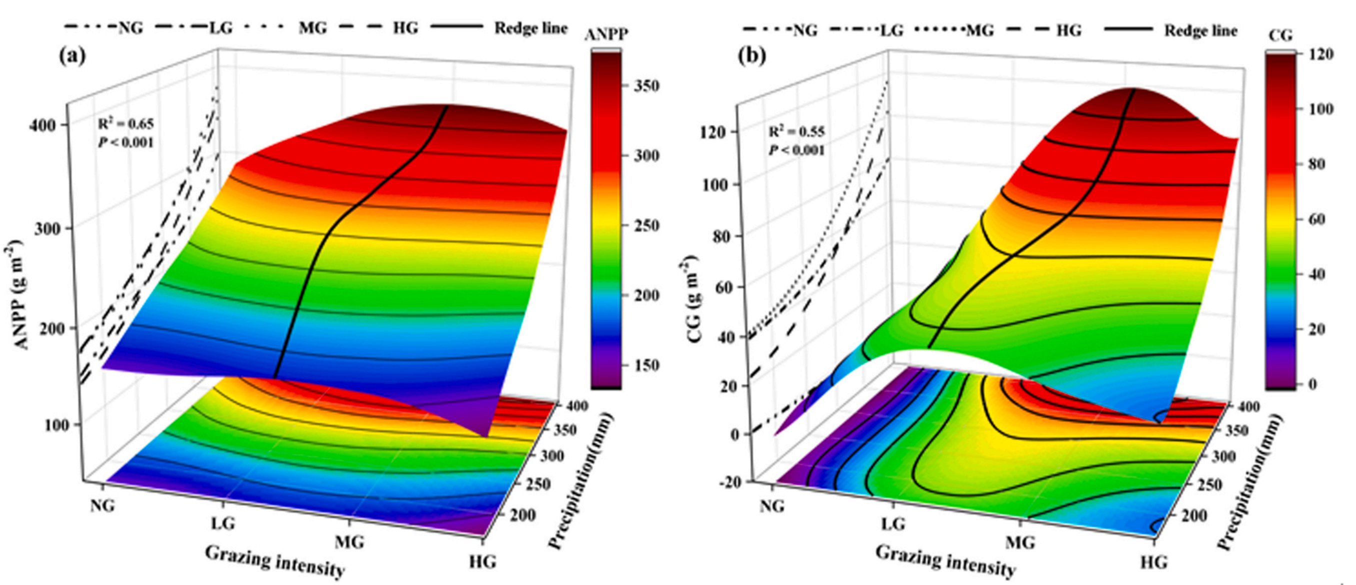

Fig. 5. The relationships of plant productivity (ANPP) (a) and compensatory growth (CG) (b) with grazing intensity and precipitation in a semi-arid steppe. The polynomial models are: ANPP = $-2.0g^2 + 0.002p^2 + 35.2$ g – 0.17p – 0.02gp + 37.3; CG = -2.83 $g^2 + 0.0016p^2 + 44.3$ g – 0.89p + 0.26gp – 57.8; where g and p represent grazing intensity (unit: sheep-grazing days/year) and annual precipitation (unit: mm), respectively.

Leriche et al., 2001). Our results show that plants differ in their regrowth capability. The significant increase in grassland ANPP is primarily attributable to the increased ANPP of two dominants *L. chinensis* and *C. korshinskyi* (Fig. S1). The rhizomatous *L. chinensis* exhibits a much stronger compensatory growth after grazing than other species (Fig. 4), which was also reported by Fanselow et al. (2011) in a short grazing experiment. The strong compensatory growth in *L. chinensis* is likely supported not only by its higher photosynthetic capacity (Ye et al., 2020), and it more effective light-harvesting complex and reduced self-shading (Jang and Mennucci, 2018; Rahman et al., 2018), but also by its well-developed rhizomatous clonal structure, which enable resource translocation among ramets and supports recovery after grazing (Wang et al., 2017). In contrast the other dominant species *S. grandis* does not show a significant over-compensatory growth under grazing, it even shows a downward trend under HG in dry years (Fig. 4 & S1). This is in agreement with the result of Ye et al. (2020) who showed that *S. grandis* does not show a compensatory growth even with abundant precipitation, mostly due to the downward change of its functional traits under the environmental stress, especially under HG. Plant CG is thought to be related with the high capability of plant species to adjust photosynthesis to acclimate to different grazing intensity levels, especially in wet years (Liu et al., 2019). This is realized by an improvement of photochemical efficiency evidenced by more developed light-harvesting complexes and reduced self-shading under grazing (Song et al., 2020), which is considered to be an adaptation to grazing (Ren et al., 2017). An under-compensatory growth (ANPP < AGB_p) is observed for *C. squarrosa* under HG in our study. This is related with the increased density of this short C_4-grass in HG grassland (Zhang et al., 2018a), and grazing exclusion in the measurement year allows it to grow better (a higher AGB_p) with improved solar radiation but no animal defoliation and tramping. Despite of the under-compensatory growth of this species, plant community ANPP increases in HG grassland.

Second, the grazing promotion of grassland ANPP is related to the changes in species composition. An increase in the mixed subordinate species, including mostly annuals and biennials, is observed with the increasing grazing intensity in the present study, which is in agreement with the reports of Li et al. (2008) and Baoyin et al. (2015). In addition, the increase in the relative contribution of subordinate species to overall ANPP can impact community ANPP sensitivity to inter-annual precipitation (Gaitán et al., 2014; Verón and Paruelo, 2010), as grasses and forbs exhibit differential sensitivity to water availability (Felton et al., 2019). It is worth to note that, while a grazing induced increase in annual and biennial species may contribute to plant biomass increase (Zhang et al., 2018b), it does not necessarily imply an improvement in grassland quality, as many of these annual and biennial species have lower palatability and quality compared to the dominant perennials like *L. chinensis*. However, in our studied grassland, the biomass increase form the over-compensatory growth of *L. chinensis* is much greater than that of annual and biennial species, thus the grazed grassland has overall higher quality than the un-grazed.

Third, plants may adjust the allocation of carbohydrates in response to an imbalance between sources and sinks (Briske et al., 1996). Thus, the increase in ANPP may have partly resulted from the different allocation of carbohydrates between above and belowground parts. Grazing significantly increases ANPP at all three grazing intensities, whereas it decreases BGB significantly at MG and HG in the present study (Fig. S3). These findings suggest that the ANPP increase may be, at least partly, realized at the expense of BGB. This mechanism was also reported by Belsky et al. (1993) who indicates that plant regrowth after defoliation is generally limited by carbon gain due to the loss of leaf area, thus, more carbon may be allocated to shoot growth. The strategy of allocating carbohydrates, including both previously stored and newly produced, to the growth of leaves at the expense of roots is a mechanism employed by plants to tolerate grazing (Belsky et al., 1993; Gao et al., 2008), leading to compensatory plant aboveground growth, affecting ANPP (Schönbach et al., 2011). Rhizomatous species, such as *L. chinensis*, generally have large belowground storage organs, which can reallocate carbohydrates to the aboveground, contributing to the stronger plant compensatory growth (Xie et al., 2016; Zhao et al., 2009).

Fourth, grazing acceleration of nutrient cycling of grassland ecosystem may also be a key process for grazing enhanced plant growth (Leriche et al., 2001). In addition to carbohydrates reallocation, the mobilization of nitrogen reserves from roots and stems to support the regrowth of leaves, may also positively impact plant regrowth (Gong et al., 2015). This is also true for the studied steppe grassland, as evidenced by 69 % and 86 % higher nitrogen and phosphorous cycling rates under moderate grazing than no-grazing, and the grazing-enhanced nutrient concentration in new growing leaves and more resorption at the end of the growing season (Zhang et al., 2020).

Our results also show that HG reduced plant community AGB_p, compared to that under NG; and the reduction in plant community AGB_p is primarily a result of the decrease in the AGB_p of the dominant plants *L. chinensis* and *S. grandis* (Fig. S2). The decrease in the AGB_p of dominant species, and the increase of AGB_p of subordinate species along the grazing intensity gradient are well supported by previous studies (Liu et al., 2015). The defoliation of the dominant species by herbivores, especially at HG, is the main driver for these changes (Gao et al., 2018).

4.3. Precipitation effects on plant compensatory growth and productivity in grazing grassland

Both precipitation and grazing disturbance determine plant biomass production in semi-arid grasslands (Lauenroth and Sala, 1992). The ANPP response to precipitation in grazing grassland is not solely contingent upon the environmental conditions such as soil moisture and nutrients, but also on plant species composition and traits, especially plant traits related with plant regrowth capability or tolerance to grazing stress (Fanselow et al., 2011; Liu et al., 2019; Ye et al., 2020). The peak AGB of the grazing grassland (but subject no grazing exclusion in the measurements year) reflects the plant production potential (AGB_p) of these grazing-altered plant communities. The grassland AGB_p shows no significant difference among NG, LG and MG, but is higher under these three grazing intensities than under HG (Fig. S2), suggesting a decline in grassland production potential after the HG over years.

Our results demonstrate a strong modulation of precipitation on plant community CG and ANPP under grazing, as evidenced by the increase of the grazing intensity with increasing precipitation for the highest ANPP or CG on the grazing gradient (Fig. 5). In other words, precipitation is the most preponderant factor for plant production in semi-arid regions (Batbaatar et al., 2021; Le Houérou et al., 1988), and its positive effects on ANPP can be enhanced by grazing in wet years (Schönbach et al., 2011).

5. Conclusion

We conclude that adaptive grazing with a defoliation rate less than 60 % in each grazing rotation enhances grassland aboveground net primary productivity (ANPP) through plant over-compensatory growth, although it may reduce grassland aboveground biomass production potential (AGB_p). The interaction between grazing intensity and precipitation shapes plant compensatory growth and ANPP: they both exhibit a hump-shaped response along the grazing gradient, with the optimal grazing intensity increase under wetter conditions. Dominant rhizomatous species *Leymus chinensis* and subordinate species group demonstrate strong compensatory capacity across grazing intensities, whereas the C_4 short grass *Cleistogenes squarrosa* shows an under-compensatory growth to heavy grazing. These findings suggest that adaptive grazing strategies, maintaining moderate grazing pressure and adjusting stocking rates according to annual precipitation and plant production, can improve productivity while preserving grassland aboveground biomass production potential in semi-arid grasslands. Our study offers a valuable framework for sustainable grassland management under increasing climate variability and grazing demands.

CRediT authorship contribution statement

Yanlong Li: Writing – original draft, Investigation, Data curation. **Hugjiltu Minggagud:** Investigation. **Yadong Wang:** Investigation, Data curation. **Chunjun Shi:** Investigation. **Frank Yonghong Li:** Writing – original draft, Funding acquisition, Data curation. **Lin Wu:** Investigation. **Hao Wang:** Investigation, Data curation.

Funding

This work was supported by the National Natural Science Foundation of China [Grant No. 32261143732] and by Department of Science and Technology of Inner Mongolia Autonomous Region [Grant for the Development of Research Capability in Grassland Ecology, and for Ecosystem Functions and Services Research & Grant No. 2019ZD007].

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109834.

Data availability

Data will be made available on request.

References

Altesor, A., Oesterheld, M., Leoni, E., Lezama, F., Rodríguez, C., 2005. Effect of grazing on community structure and productivity of a Uruguayan grassland. Plant Ecol. 179, 83–91. https://doi.org/10.1007/s11258-004-5800-5.

Alward, R.D., Joern, A., 1993. Plasticity and overcompensation in grass responses to herbivory. Oecologia 95, 358–364. https://doi.org/10.1007/BF00320989.

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agric. For. Meteor. 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011.

Bai, W., Fang, Y., Zhou, M., Xie, T., Li, L., Zhang, W.H., 2015. Heavily intensified grazing reduces root production in an Inner Mongolia temperate steppe. Agric. Ecosyst. Environ. 200, 143–150. https://doi.org/10.1016/j.agee.2014.11.015.

Baoyin, T., Li, F.Y., Minggagud, H., Bao, Q., Zhong, Y., 2015. Mowing succession of species composition is determined by plant growth forms, not photosynthetic pathways in Leymus chinensis grassland of Inner Mongolia. Landsc. Ecol. 30, 1795–1803. https://doi.org/10.1007/s10980-015-0249-6.

Batbaatar, A., Bork, E.W., Broadbent, T., Alexander, M.J., Cahill Jr, J.F., Carlyle, C.N., 2021. Grazing alters the sensitivity of plant productivity to precipitation in northern temperate grasslands. J. Veg. Sci. 32, e13008. https://doi.org/10.1111/jvs.13008.

Belsky, A.J., Carson, W.P., Jensen, C.L., Fox, G.A., 1993. Overcompensation by plants: Herbivore optimization or red herring? Evol. Ecol. 7, 109–121. https://doi.org/10.1007/BF01237737.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Yang, L.H., 2014. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508, 517–520. https://doi.org/10.1038/nature013144.

Bork, E.W., Lyseng, M.P., Hewins, D.B., Carlyle, C.N., Chang, S.X., Willms, W.D., Alexander, M.J., 2019. Herbage biomass and its relationship to soil carbon under long-term grazing in northern temperate grasslands. Can. J. Plant. Sci. 99, 905–916. https://doi.org/10.1139/cjps-2018-0251.

Briske, D.D., Boutton, T.W., Wang, Z., 1996. Contribution of flexible allocation priorities to herbivory tolerance in C_4 perennial grasses: an evaluation with ^{13}C labeling. Oecologia 105, 151–159. https://doi.org/10.1007/BF00328540.

Dai, L., Guo, X., Ke, X., Zhang, F., Li, Y., Peng, C., Du, Y., 2019. Moderate grazing promotes the root biomass in Kobresia meadow on the northern Qinghai–Tibet Plateau. Ecol. Evol. 9, 9395–9406. https://doi.org/10.1002/ece3.5494.

Dai, Y., Guo, J., Li, Y., Dong, Z., Li, H., 2022. Soil physical and chemical properties affected by long-term grazing on the desert steppe of Inner Mongolia, China. Catena 211, 105996. https://doi.org/10.1016/j.catena.2021.105996.

Dangal, S.R.S., Tian, H., Lu, C., Pan, S., Pederson, N., Hessl, A., 2016. Synergistic effects of climate change and grazing on net primary production of Mongolian grasslands. Ecosphere 7, e01274. https://doi.org/10.1002/ecs2.1274.

Deng, Q., Aras, S., Yu, C.L., Dzantor, E.K., Fay, P.A., Luo, Y., Hui, D., 2017. Effects of precipitation changes on aboveground net primary production and soil respiration in a switchgrass field. Agric. Ecosyst. Environ. 248, 29–37. https://doi.org/10.1016/j.agee.2017.07.023.

Díaz-Solis, H., Kothmann, M.M., Hamilton, W.T., Grant, W.E., 2003. A simple ecological sustainability simulator (SESS) for stocking rate management on semi-arid grazinglands. Agric. Syst. 76, 655–680. https://doi.org/10.1016/S0308-521X(01)00115-9.

Fanselow, N., Schönbach, P., Gong, X.Y., Lin, S., Taube, F., Loges, R., Dittert, K., 2011. Short-term regrowth responses of four steppe grassland species to grazing intensity, water and nitrogen in Inner Mongolia. Plant Soil 340, 279–289. https://doi.org/10.1007/s11104-010-0694-6.

Felton, A.J., Zavislan-Pullaro, S., Smith, M.D., 2019. Semiarid ecosystem sensitivity to precipitation extremes: weak evidence for vegetation constraints. Ecology 100, e02572. https://doi.org/10.1002/ecy.2572.

Ferraro, D.O., Oesterheld, M., 2002. Effect of defoliation on grass growth. A quantitative review. Oikos 98, 125–133. https://doi.org/10.1034/j.1600-0706.2002.980113.x.

Gaitán, J.J., Oliva, G.E., Bran, D.E., Maestre, F.T., Aguiar, M.R., Jobbágy, E.G., Massara, V., 2014. Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. J. Ecol. 102, 1419–1428. https://doi.org/10.1111/1365-2745.12273.

Ganjurjav, H., Duan, Mj, Wan, Yf, Zhang, W.N., Gao, Q.Z., Li, Y., Guo, H.B., 2015. Effects of grazing by large herbivores on plant diversity and productivity of semi-arid alpine steppe on the Qinghai-Tibetan Plateau. Rangel. J. 37, 389–397. https://doi.org/10.1071/RJ14127.

Gao, S., Zheng, Z., Wang, Y., Liu, L., Zhao, N., Gao, Y., 2018. Drought and grazing drive the retrogressive succession by changing the plant–plant interaction of the main species in Inner Mongolia Steppe. Ecol. Evol. 8, 11954–11963. https://doi.org/10.1002/ece3.4652.

Gao, Y.Z., Giese, M., Lin, S., Sattelmacher, B., Zhao, Y., Brueck, H., 2008. Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant Soil 307, 41–50. https://doi.org/10.1007/s11104-008-9579-3.

Gong, X.Y., Fanselow, N., Dittert, K., Taube, F., Lin, S., 2015. Response of primary production and biomass allocation to nitrogen and water supplementation along a grazing intensity gradient in semiarid grassland. Eur. J. Agron. 63, 27–35. https://doi.org/10.1016/j.eja.2014.11.004.

Guo, X., Arshad, M.U., Zhao, Y., Gong, Y., Li, H., 2023. Effects of climate change and grazing intensity on grassland productivity—a case study of Inner Mongolia, China. Heliyon 9, e17814. https://doi.org/10.1016/j.heliyon.2023.e17814.

Herrero-Jáuregui, C., Oesterheld, M., 2018. Effects of grazing intensity on plant richness and diversity: a meta-analysis. Oikos 127, 757–766. https://doi.org/10.1111/oik.04893.

Hilbert, D.W., Swift, D.M., Detling, J.K., Dyer, M.I., 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia 51, 14–18. https://doi.org/10.1007/BF00344645.

Irisarri, J.G.N., Derner, J.D., Porensky, L.M., Augustine, D.J., Reeves, Justin L., Mueller, K.E., 2016. Grazing intensity differentially regulates ANPP response to precipitation in North American semiarid grasslands. Ecol. Appl. 26, 1370–1380. https://doi.org/10.1890/15-1332.

Jang, S., Mennucci, B., 2018. Delocalized excitons in natural light-harvesting complexes. Rev. Mod. Phys. 90, 035003. https://doi.org/10.1103/RevModPhys.90.035003.

Knapp, A.K., Ciais, P., Smith, M.D., 2017. Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change. N. Phytol. 214, 41–47. https://doi.org/10.1111/nph.14381.

Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. Ecol. Appl. 2, 397–403. https://doi.org/10.2307/1941874.

Le Houérou, H.N., Bingham, R.L., Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. J. Arid Environ. 15, 1–18. https://doi.org/10.1016/S0140-1963(18)31001-2.

Leriche, H., LeRoux, X., Gignoux, J., Tuzet, A., Fritz, H., Abbadie, L., Loreau, M., 2001. Which functional processes control the short-term effect of grazing on net primary production in grasslands? Oecologia 129, 114–124. https://doi.org/10.1007/s0044201006907.

Li, F., Wang, Y., Guo, K., Wesche, K., 2019. Grasslands of China. In (pp. 1-12). https://doi.org/10.1016/B978-0-12-409548-9.12120-7.

Li, W., Xu, F., Zheng, S., Taube, F., Bai, Y., 2017. Patterns and thresholds of grazing-induced changes in community structure and ecosystem functioning: species-level responses and the critical role of species traits. J. Appl. Ecol. 54, 963–975. https://doi.org/10.1111/1365-2664.12806.

Li, Y., Wang, W., Liu, Z., Jiang, S., 2008. Grazing gradient versus restoration succession of *Leymus chinensis* (Trin.) Tzvel. Grassland in Inner Mongolia. Restor. Ecol. 16, 572–583. https://doi.org/10.1111/j.1526-100X.2007.00332.x.

Li, Y., Shi, C., Zhang, T., Wang, H., Yang, Z., Tang, S., Li, F.Y., 2022. Summer grazing by three livestock species at moderate intensity enhances primary productivity and drives community divergence in a semi-arid steppe. Appl. Veg. Sci. 25, e12683. https://doi.org/10.1111/avsc.12683.

Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., He, J., 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. PANS 115, 4051–4056. https://doi.org/10.1073/pnas.1700299114.

Liu, J., Feng, C., Wang, D., Wang, L., Wilsey, B.J., Zhong, Z., 2015. Impacts of grazing by different large herbivores in grassland depend on plant species diversity. J. Appl. Ecol. 52, 1053–1062. https://doi.org/10.1111/1365-2664.12456.

Liu, M., Gong, J., Yang, B., Ding, Y., Zhang, Z., Wang, B., Hou, X., 2019. Differences in the photosynthetic and physiological responses of Leymus chinensis to different levels of grazing intensity. BMC Plant Biol. 19, 558. https://doi.org/10.1186/s12870-019-2184-1.

Maurer, G.E., Hallmark, A.J., Brown, R.F., Sala, O.E., Collins, S.L., 2020. Sensitivity of primary production to precipitation across the United States. Ecol. Lett. 23, 527–536. https://doi.org/10.1111/ele.13455.

McNaughton, 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. Am. Nat. 113, 691–703. https://doi.org/10.1086/283426.

Milchunas, D.G., Vandever, M.W., 2013. Grazing effects on aboveground primary production and root biomass of early-seral, mid-seral, and undisturbed semiarid grassland. J. Arid Environ. 92, 81–88. https://doi.org/10.1016/j.jaridenv.2013.01.012.

Petrie, M.D., Peters, D.P.C., Yao, J., Blair, M., Burruss, N.D., Collins, S.L., Steiner, J.L., 2018. Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods. Glob. Change Biol. 24, 1935–1951. https://doi.org/10.1111/gcb.14024.

Rahman, S., Duursma, R.A., Muktadir, M.A., Roberts, T.H., Atwell, B.J., 2018. Leaf canopy architecture determines light interception and carbon gain in wild and domesticated Oryza species. Environ. Exp. Bot. 155, 672–680. https://doi.org/10.1016/j.envexpbot.2018.08.008.

Ren, W., Hu, N., Hou, X., Zhang, J., Guo, H., Liu, Z., Li, X., 2017. Long-term overgrazing-Induced memory decreases photosynthesis of clonal offspring in a perennial grassland plant. Front Plant Sci. 8. https://doi.org/10.3389/fpls.2017.00419.

Schönbach, P., Wan, H., Gierus, M., Bai, Y., Müller, K., Lin, L., Taube, F., 2011. Grassland responses to grazing: effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. Plant Soil 340, 103–115. https://doi.org/10.1007/s11104-010-0366-6.

Shaw, E.A., White, C.T., Silver, W.L., Suding, K.N., Hallett, L.M., 2022. Intra-annual precipitation effects on annual grassland productivity and phenology are moderated by community responses. J. Ecol. 110, 162–172. https://doi.org/10.1111/1365-2745.13792.

Sloat, L.L., Gerber, J.S., Samberg, L.H., Smith, W.K., Herrero, M., Ferreira, L.G., West, P. C., 2018. Increasing importance of precipitation variability on global livestock grazing lands. Nat. Clim. Change 8, 214–218. https://doi.org/10.1038/s41558-018-0081-5.

Song, L., Pan, Y., Gong, J., Li, X., Liu, M., Yang, B., Baoyin, T., 2020. Physiology of *Leymus chinensis* under seasonal grazing: implications for the development of sustainable grazing in a temperate grassland of Inner Mongolia. J. Environ. Manag. 271, 110984. https://doi.org/10.1016/j.jenvman.2020.110984.

Su, F., Wei, Y., Wang, F., Guo, J., Zhang, J., Wang, Y., Hu, S., 2019. Sensitivity of plant species to warming and altered precipitation dominates the community productivity in a semiarid grassland on the Loess Plateau. Ecol. Evol. 9, 7628–7638. https://doi.org/10.1002/ece3.5312.

Su, J., Zhang, Y., Xu, F., 2023. Divergent responses of grassland productivity and plant diversity to intra-annual precipitation variability across climate regions: a global synthesis. J. Ecol. 111, 1921–1934. https://doi.org/10.1111/1365-2745.14149.

Su, R., Yu, T., Dayananda, B., Bu, R., Su, J., Fan, Q., 2020. Impact of climate change on primary production of Inner Mongolian grasslands. Glob. Ecol. Conserv 22, e00928. https://doi.org/10.1016/j.gecco.2020.e00928.

Swemmer, A.M., Knapp, A.K., Snyman, H.A., 2007. Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. J. Ecol. 95, 780–788. https://doi.org/10.1111/j.1365-2745.2007.01237.x.

Török, P., Penksza, K., Tóth, E., Kelemen, A., Sonkoly, J., Tóthmérész, B., 2018. Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. Ecol. Evol. 8, 10326–10335. https://doi.org/10.1002/ece3.4508.

Vail, S.G., 1992. Selection for overcompensatory plant responses to herbivory a mechanism for the evolution of plant-herbivore mutualism. Am. Nat. 139, 1–8. https://doi.org/10.1086/285309.

Verón, S.R., Paruelo, J.M., 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.

Wang, D., Du, J., Zhang, B., Ba, L., Hodgkinson, K.C., 2017. Grazing intensity and phenotypic plasticity in the clonal grass Leymus chinensis. Rangel. Ecol. Manag. 70, 740–747. https://doi.org/10.1016/j.rama.2017.06.011.

Wang, X., Li, F.Y., Tang, K., Wang, Y., Suri, G., Bai, Z., Baoyin, T., 2020. Land use alters relationships of grassland productivity with plant and arthropod diversity in Inner Mongolian grassland. Ecol. Appl. 30, e02052. https://doi.org/10.1002/eap.2052.

Wilcox, K.R., Shi, Z., Gherardi, L.A., Lemoine, N.P., Koerner, S.E., Hoover, D.L., Luo, Y., 2017. Asymmetric responses of primary productivity to precipitation extremes: a synthesis of grassland precipitation manipulation experiments. Glob. Change Biol. 23, 4376–4385. https://doi.org/10.1111/gcb.13706.

Willms, W., McGinn, S., Dormaar, J., 1993. Influence of Litter on herbage production in the mixed prairie. J. Range. Manag. 46, 320–324. https://doi.org/10.2307/4002466.

Xie, X., Hu, Y., Pan, X., Liu, F., Song, Y., Dong, M., 2016. Biomass allocation of stoloniferous and rhizomatous plant in response to resource availability: a phylogenetic meta-analysis. Front Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00603.

Ye, R., Liu, G., Chang, H., Shan, Y., Mu, L., Wen, C., Li, F., 2020. Response of plant traits of *Stipa breviflora* to grazing intensity and fluctuation in annual precipitation in a desert steppe, northern China. Glob. Ecol. Conserv 24, e01237. https://doi.org/10.1016/j.gecco.2020.e01237.

Zainelabdeen, Y.M., Yan, R., Xin, X., Yan, Y., Ahmed, A.I., Hou, L., Zhang, Y., 2020. The impact of grazing on the grass composition in Temperate Grassland. Agronomy 10, 1230. https://doi.org/10.3390/agronomy10091230.

Zeng, X., Hu, Z., Chen, A., Yuan, W., Hou, G., Han, D., Luo, D., 2022. The global decline in the sensitivity of vegetation productivity to precipitation from 2001 to 2018. Glob. Change Biol. 28, 6823–6833. https://doi.org/10.1111/gcb.16403.

Zhang, F., Zheng, J., Bennett, J.A., Zhang, B., Wang, Z., Li, Z., Zhao, M., 2023. The legacy effects of grazing and precipitation variability on grassland productivity in a temperate steppe. Agric. For. Meteor. 343, 109788. https://doi.org/10.1016/j.agrformet.2023.109788.

Zhang, M., Li, X., Wang, H., Huang, Q., 2018a. Comprehensive analysis of grazing intensity impacts soil organic carbon: a case study in typical steppe of Inner Mongolia, China. Appl. Soil Ecol. 129, 1–12. https://doi.org/10.1016/j.apsoil.2018.03.008.

Zhang, R., Wang, Z., Han, G., Schellenberg, M.P., Wu, Q., Gu, C., 2018c. Grazing induced changes in plant diversity is a critical factor controlling grassland productivity in the Desert Steppe, Northern China. Agric. Ecosyst. Environ. 265, 73–83. https://doi.org/10.1016/j.agee.2018.05.014.

Zhang, R., Wang, Z., Han, G., Schellenberg, M.P., Wu, Q., Gu, C., 2018b. Grazing induced changes in plant diversity is a critical factor controlling grassland productivity in the Desert Steppe, Northern China. Agric. Ecosyst. Environ. 265, 73–83. https://doi.org/10.1016/j.agee.2018.05.014.

Zhang, T., Li, F.Y., Shi, C., Li, Y., Tang, S., Baoyin, T., 2020. Enhancement of nutrient resorption efficiency increases plant production and helps maintain soil nutrients under summer grazing in a semi-arid steppe. Agric. Ecosyst. Environ. 292, 106840. https://doi.org/10.1016/j.agee.2020.106840.

Zhang, Y., Huang, D., Badgery, W., Kemp, D., Chen, W., Wang, X., Liu, N., 2015. Reduced grazing pressure delivers production and environmental benefits for the typical steppe of north China. Sci. Rep. 5, 16434. https://doi.org/10.1038/srep16434.

Zhao, W., Chen, S.P., Han, X.G., Lin, G.H., 2009. Effects of long-term grazing on the morphological and functional traits of Leymus chinensis in the semiarid grassland of Inner Mongolia, China. Ecol. Res. 24, 99–108. https://doi.org/10.1007/s11284-008-0486-0.

Zhu, K., Chiariello, N.R., Tobeck, T., Fukami, T., Field, C.B., 2016. Nonlinear, interacting responses to climate limit grassland production under global change. PNAS 113, 10589–10594. https://doi.org/10.1073/pnas.1606734113.

Zhu, N., Yan, Y., Bai, K., Zhang, J., Wang, C., Wang, X., Chen, J., 2023. Conversion of croplands to shrublands does not improve soil organic carbon and nitrogen but reduces soil phosphorus in a temperate grassland of northern China. Geoderma 432, e116407. https://doi.org/10.1016/j.geoderma.2023.116407.