Deng *et al. Carbon Research* (2023) 2:19
https://doi.org/10.1007/s44246-023-00051-7

Carbon Research

ORIGINAL ARTICLE

Open Access

Carbon in Chinese grasslands: meta-analysis and theory of grazing effects

Lei Deng[1,2], Zhouping Shangguan[1,2*], Stephen Mackenzie Bell[3], Andrey V. Soromotin[4], Changhui Peng[5], Shaoshan An[1,2], Xing Wu[6], Xingliang Xu[7], Kaibo Wang[8], Jianping Li[9], Zhuangsheng Tang[10], Weiming Yan[1,2], Fengbao Zhang[1,2], Jiwei Li[2], Jianzhao Wu[1] and Yakov Kuzyakov[11,12]

Abstract

Globally, livestock grazing is an important management factor influencing soil degradation, soil health and carbon (C) stocks of grassland ecosystems. However, the effects of grassland types, grazing intensity and grazing duration on C stocks are unclear across large geographic scales. To provide a more comprehensive assessment of how grazing drives ecosystem C stocks in grasslands, we compiled and analyzed data from 306 studies featuring four grassland types across China: desert steppes, typical steppes, meadow steppes and alpine steppes. Light grazing was the best management practice for desert steppes (< 2 sheep ha^{-1}) and typical steppes (3 to 4 sheep ha^{-1}), whereas medium grazing pressure was optimal for meadow steppes (5 to 6 sheep ha^{-1}) and alpine steppes (7 to 8 sheep ha^{-1}) leading to the highest ecosystem C stocks under grazing. Plant biomass (desert steppes) and soil C stocks (meadow steppes) increased under light or medium grazing, confirming the '*intermediate disturbance hypothesis*'. Heavy grazing decreased all C stocks regardless of grassland ecosystem types, approximately 1.4 Mg ha^{-1} per year for the whole ecosystem. The regrowth and regeneration of grasslands in response to grazing intensity (i.e., *grazing optimization*) depended on grassland types and grazing duration. In conclusion, grassland grazing is a double-edged sword. On the one hand, proper management (light or medium grazing) can maintain and even increase C stocks above- and belowground, and increase the harvested livestock products from grasslands. On the other hand, human-induced overgrazing can lead to rapid degradation of vegetation and soils, resulting in significant carbon loss and requiring long-term recovery. Grazing regimes (i.e., intensity and duration applied) must consider specific grassland characteristics to ensure stable productivity rates and optimal impacts on ecosystem C stocks.

Highlights

(1) Light grazing can maintain and even increase C stocks in grassland biomasses.

(2) Human-induced overgrazing leads to significant carbon loss that requires long-term recovery.

(3) Heavy grazing decreases C stocks regardless of grassland ecosystem types.

(4) Grassland state before grazing is critical to the response of grassland to grazing duration.

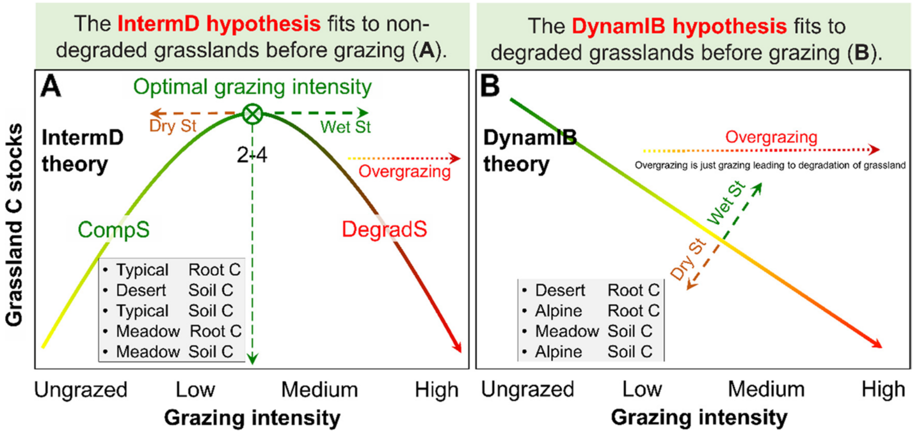
(5) The '*intermediate disturbance hypothesis*' fits to non-degraded grasslands before grazing.

Keywords Grazing duration, Grazing intensity, Grassland, Overgrazing, Plant and soil, Carbon dynamics, Land use change

Handling editor: Hailong Wang.

*Correspondence:
Zhouping Shangguan
shangguan@ms.iswc.ac.cn
Full list of author information is available at the end of the article

Graphical Abstract



1 Introduction

Global grasslands cover approximately 40% of terrestrial area, store 10%–30% of soil organic carbon (C) with a sequestration rate of 0.5 Pg yr^{-1}, and harbor more than 10% of terrestrial biomass C (Booker et al. 2013; Dlamini et al. 2016). Due to their large area and potential for sequestering atmospheric CO$_2$, grasslands are critical to the global C cycle (Deng et al. 2017; Abdalla et al. 2018; Bai and Cotrufo 2022). However, about 49% of global grassland area has been degraded to some extent by overgrazing (Bardgett et al. 2021). In China, nearly 61% of grasslands suffer from degradation due to intensive grazing (Zhou et al. 2014). Degraded grasslands not only fail to provide subsistence for the local people (Zhao et al. 2017; Bardgett et al. 2021), but also fail to mitigate climate change owing to the negative effect on ecosystem C stocks (Wang et al. 2016; Deng and Shangguan, 2021). Therefore, there is a new challenge to increase or at least maintain C sequestration in grassland ecosystems and protect existing terrestrial C stocks in the context of climate change.

Grazing intensity is the main factor affecting the C source/sink function of grasslands directly (Zhao et al. 2017). Most studies have shown that overgrazing strongly declined C stocks in grassland (Dlamini et al. 2016; Jiang et al. 2020; Liu et al. 2018). Grassland primary productivity dramatically drops because of overgrazing, thereby reducing the C input from vegetation to soil (Derner et al. 2006; Zuo et al. 2018). Overgrazing accelerates CO$_2$ emission from the soil due to organic matter decomposition, thus speeding up C transfers into the atmosphere and promoting soil erosion (Chen et al. 2016; Zhao et al. 2017; Moinet et al. 2016). Although light and medium grazing can actually be beneficial for soil C accumulation (Hafner et al. 2012; Jiang et al. 2020), the absence of grazing can lead to soil C loss because litter accumulation decreases with little stimulation of grass growth (Gao 2007; Hassan et al. 2021). Thus, there are complex interactions between grazing and grassland C stocks (Milchunas and Laurenroth 1993). The ecosystem C stocks in various grassland types may have specific response patterns to increasing grazing intensities because of the differences in: 1) climate, 2) net primary production, 3) composition of plant communities, and, 4) soil properties. Accurate estimations of the thresholds of grazing intensity (i.e., stocking rates) is particularly important for promoting C sequestration in different grassland types. While it is known that grassland ecosystem C stocks are affected by grazing intensities and grazing animals (Eldridge et al. 2017), grazing duration must also be considered in any robust synthesis (Zhang et al. 2017; Deng et al. 2017). Even under light grazing conditions, grassland ecosystems can degrade through long-term grazing (Jiang et al. 2020), sometimes leading to woody encroachment (Gao et al. 2021) which decreases productivity and biodiversity (Bai et al. 2012; Zhang et al. 2021a). Additionally, heavy grazing during the few first years may have no noticeable effects on grassland C stocks (Milchunas et al. 1998; Elmore and Asner 2006). Soil C content has also been shown to linearly increase under light grazing for more than 40 years (Conant et al. 2001). This indicates that the effects of grazing duration on ecosystem C stocks remain largely unclear, and the optimal grazing duration and intensities for C sequestration need to be quantified based on a broad meta-analysis taking into account the specifics of grassland types.

Grazing effects on C stocks depend on plant biomass, vegetation diversity, and soil properties (Deng et al., 2014a; McSherry & Ritchie 2013; Abdalla et al. 2018), all of which are affected by local climate and environmental conditions, e.g., precipitation, temperature, light intensity and duration of the vegetation restoration (Altesor et al. 2005; Yan et al. 2013; Deng et al. 2017). While the aboveground biomass decreases with grazing pressure (Zhu et al. 2016, 2018), soil nutrient turnover is accelerated (Pineiro et al. 2009; Dong et al. 2021). This is attributed to the addition of animal dung and urine, which in turn affects soil C dynamics and microbial activities (Vandandorj et al. 2017). Grazing also affects soil properties such as nitrogen (N) content, pH, bulk density, infiltration rate, microporosity, and moisture, all of which are closely related to ecosystem C stocks (Han et al. 2008). Although many individual studies have clarified the effects of grazing on soil C stocks and the underlying mechanisms (Conant et al. 2001; Hafner et al. 2012; Jiang et al. 2020; Bai and Cotrufo 2022), generalized relationships are still unclear due to regional differences in climate, soil properties, and grassland types, as well as disturbance factors such as grazing intensities/stocking rates and grazing duration. Therefore, a more systematic analysis as well as a theoretical review is required.

Four hypotheses have been proposed for the structure and functions of grassland ecosystems in responses to grazing: the '*intermediate disturbance hypothesis*' (Tilman and Downing 1994), the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986), the '*dynamic balance hypothesis*' and the '*dynamic imbalance hypothesis*' (Palmer et al. 2016). The '*intermediate disturbance hypothesis*' suggests that light or medium grazing changes the existing vegetation stock and stimulates regrowth leading to increased photosynthesis, more biomass production per vegetation season, and more C input belowground (Tilman and Downing 1994). This regrowth was termed as a "compensatory effect", which is linked to the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986). However, the increasing grazing reduces the recovery potential of the vegetation, and consequently, this means that further grazing intensity leads to the collapse of the grassland ecosystem (McNaughton 1979). The '*dynamic balance hypothesis*' refers to the coordinated and stable-state achieved in an ecosystem within a certain period, including the stability of ecosystem structure, functions, and energy input and output (Palmer et al. 2016). Finally, the '*dynamic imbalance hypothesis*' proposes that the structure and functions of an ecosystem are increased or decreased under grazing, implying difficulties maintaining the ecosystem steady-state (Palmer et al. 2016). Unfortunately, these theories have been individually developed for specific grassland types, grazing intensities, grazing durations, and ecosystem components. To our knowledge, no study has been conducted to test each of these theories based on a large dataset including all these factors.

The grassland area in China covers 265 million ha, accounting for 27.6% of the country's total land area (http://www.gov.cn/xinwen/2021-08/26/content_5633497.htm). Based on the temperature, precipitation and altitude ranges, the grassland ecosystems in China are usually classified into four major types: desert steppes, typical steppes, meadow steppes, and alpine steppes (Kang et al. 2007; Yan et al. 2013). Nearly all uncultivated Chinese grasslands are grazed by large mammals such as cattle, sheep, goats and yak (Yan et al. 2013), and thus, grazing is a critical factor affecting ecosystem function (Deng et al. 2014a, 2017; Eldridge et al. 2017; Bai and Cotrufo 2022). Despite this, only two meta-analyses reported the effects of grazing on C stocks in China's grasslands (Yan et al. 2013; Jiang et al. 2020), and they mainly evaluated grazing intensity based on limited databases without considering the effects of grassland types, grazing duration and stocking rate. Here, we conducted a more in-depth investigation into the wider effects of grazing on C stock in grassland ecosystems. We hypothesized that grassland carbon stocks' response to grazing are diversified among different grassland ecosystems and their responses to grazing intensity are affected by grazing duration. This synthesis compiled and analyzed data from 306 studies carried out on 216 sites in China, in an effort to answer two research questions: (a) How do ecosystem C stocks (above- and belowground) respond to increasing grazing intensities in four dominant grassland types: desert, typical, meadow, and alpine steppes? (b) What are the temporal patterns of ecosystem C stocks during grazing duration under each grazing intensity? By using these data to verify theories of grassland response to grazing and to explore pathways towards sustainable grassland management, this study provides new insights and a foundation for management decisions regarding global grasslands.

2 Materials and methods

2.1 Data compilation

To develop a comprehensive database in China, peer-reviewed journal articles published before 2021 were searched using Web of Science (http://apps.webofknowledge.com/), Google Scholar (http://scholar.google.com/), and China Knowledge Resource Integrated Database (http://www.cnki.net/) with the following search term combinations: 'grazing' or 'grazing intensity' and 'biomass' or 'soil carbon' and 'grassland' or 'pasture' or 'meadow' or 'rangeland' and 'China'. We also searched for articles that were cited in the publications we found in the previous step. To avoid bias in the selection and increase relevance, we extracted papers based on the following criteria:

(a) Only studies using paired-site and/or chronosequence approaches, with similar soil and climatic conditions for both the grazed and ungrazed sites were selected for the database; studies were excluded if the experiments were not adequately replicated or if the paired sites were confounded by different soil types.
(b) Grazing intensity was clearly defined in quantitative or qualitative terms for stocking rate, grazing duration, and livestock type (i.e., cattle, sheep, or others),
(c) Experiments with durations of less than one growing season were excluded to avoid short term noise,
(d) Soil C stocks were provided or could be calculated based on SOC or SOM content, bulk density, and soil depth,
(e) Sampling depths for belowground biomass varied in studies. Considering that most root biomass is distributed in the top 50 cm and most studies sampled roots to this depth, data of root biomass in 0–50 cm were used to investigate the C stocks in belowground biomass,
(f) Only the first rotation of grazing was considered and data for 0–100 cm soil layers were extracted. The synthesis only estimated soil C stocks for the top 20 cm because more than 90% of the studies were conducted at this soil depth.

In total, the final dataset comprised of 306 studies (Appendix Dataset S1), including 216 sites in 16 provinces of China (Fig. 1), which represented most of the grassland area of China. This dataset is the largest compiled thus far with a focus on the effects of grazing on grassland C stocks in China. The latitude of the study sites ranged from 25.21° to 49.34° N and the longitude ranged from 81.00° to 148.16° E. Altitude ranged from 140 to 4730 m. Grazing intensity provided in the collected studies ranged from low to medium and high grazing. Grasslands in China range from the high-altitudes of the Qinghai-Tibetan plateau to the low-altitude steppes of Inner Mongolia. The grassland ecosystems in China are classified into four major types (Kang et al. 2007): desert steppes, typical steppes, meadow steppes, and alpine steppes. The classifications were mostly provided in the individual studies, but when they were absent, we defined the grassland types based on the temperature, precipitation and altitude ranges (Yan et al. 2013). The climatic conditions for each grassland type are presented in Fig. 1.

The raw data were either obtained from tables or extracted by digitizing graphs using the GetData Graph Digitizer (version 2.24, ver. 2.24, http://getdata-graph-digitizer.com, Russian Federation). For each study, the following information was compiled: sources, location (i.e., longitude and latitude), climatic data (i.e., mean annual precipitation, and mean annual temperature), elevation, land use types (including grazing exclusion sites and grazing sites), grassland types (i.e., desert, typical, meadow and alpine steppes), dominant species, grazing intensity, stocking rates (i.e., yak, cattle, sheep or horse per hectare), grazing duration (i.e., years since grazing), grassland utilization rate (i.e., aboveground biomass utilization rate), grazing period (i.e., growth period, ungrowth period or whole year), above- and belowground biomasses or C stocks, litters biomasses or stocks, total biomasses or C stocks, plant coverage, plant height, plant diversity (i.e., species richness, Shannon–wiener Index, Margalef richness Index, Pielou Evenness Index), soil depth from soil surface, bulk density, soil pH, soil organic C (SOC) content and total N content (TN) in each layer of 0–100 cm soil depths. Stocking rates and grassland utilization rates (Eq. 1) corresponding to different grazing intensities in the four grassland types of the dataset are shown in Fig. S1. The grazing intensities were categorized based on the text of each study, that is ungrazed, light, medium, and heavy. To make different units of stocking rate comparable among different sites, we normalized the raw values of stocking rates to standardized animal units by using the criteria: one yak equivalent for three sheep/goat, and one cow-calf or horse equivalent for four sheep/goat (Vallentine 1990). If climatic factors were not reported, we extracted these data from the WorldClim database (http://www.worldclim.org/) based on site location information (latitude and longitude). Moreover, to depict more apparent trends of the C pools, the ages of grazing duration were divided into six groups: 1, 2–3, 4–5, 6–10, 11–20, and > 20 years. We divided the stocking rate into six stocking rate categories to explore the effects on the grassland C stock changes: < 2, 2–4, 5–6, 7–8, 9–10, and > 10 sheep units per hectare.

2.2 Data calculation

2.2.1 Grassland utilization rate

As animal stocks only feed on the aboveground biomass in grasslands, we used the following equation to calculate the grassland utilization rate:

$$R_u = \frac{AGB_{CK} - AGB_G}{AGB_{CK}} \times 100\% \tag{1}$$

In which, R_u is the grassland utilization rate (%), AGB_{CK} is the aboveground biomass in the ungrazed sites (g m^{-2}),

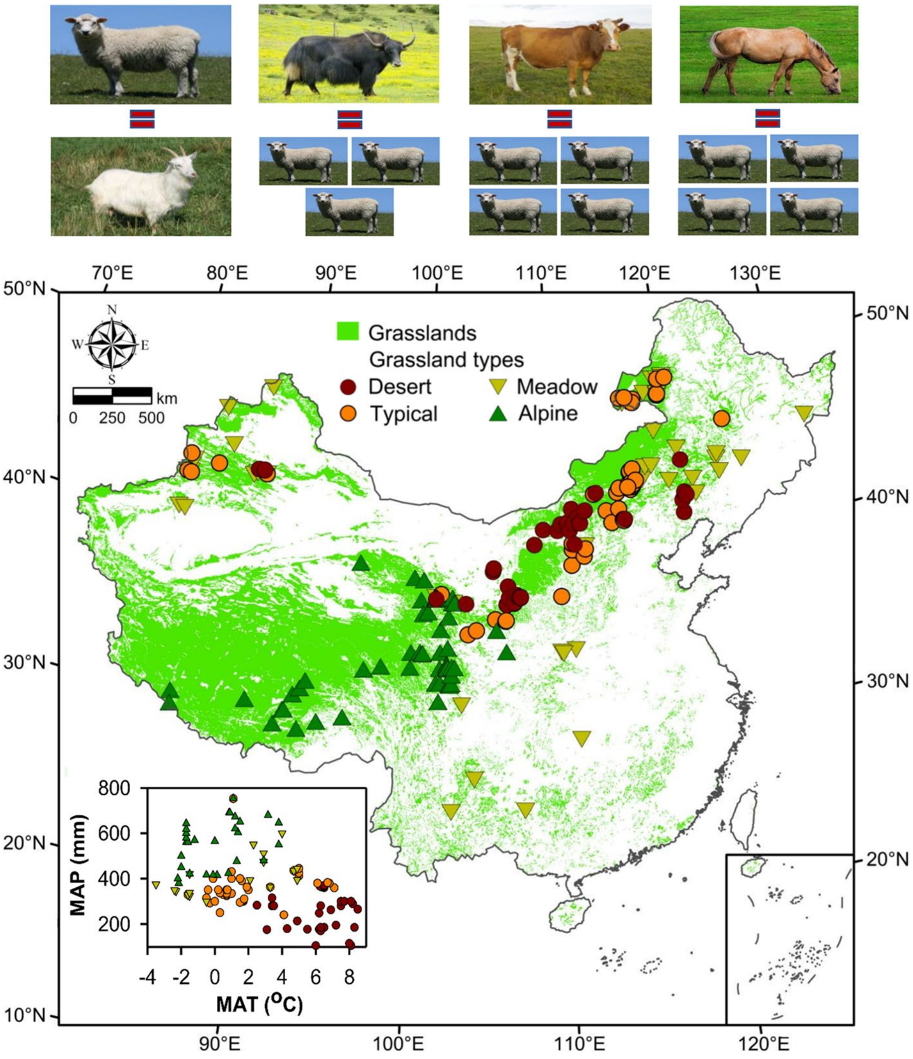


Fig. 1 Locations of the sampling sites reported in the individual studies collected in this synthesis. The grassland ecosystems are classified into four major types (Kang et al. 2007): typical steppes, meadow steppes, desert steppes and alpine steppes. The above figures indicate the livestock equivalents as follows: one goat equivalent for one sheep, one yak equivalent for three sheep/goats, and one cow-calf or horse equivalent for four sheep/goat, which is estimated by the herbivorous value of the livestock (Vallentine 1990). The left bottom inset figure indicates the range of mean annual temperature (MAT) and mean annual precipitation (MAP) for the sites of the four grassland steppes in this meta-analysis

and AGB_G is the aboveground biomass in the grazing sites (g m^{-2}).

2.2.2 Vegetation C stock

For vegetation C stock, we used the following equation (Deng et al. 2017):

$$C_B = B \times C_f \tag{2}$$

In which, C_B is the vegetation C stock (g m^{-2}), B is the vegetation biomass (g m^{-2}) or litter biomass (g m^{-2}), and C_f is the plant or litter biomass C content. The plant biomass C coefficient for estimating the herbaceous C stock was set at 0.45 (Deng et al. 2017). If the samples reported only had aboveground biomass (AGB) or belowground biomass (BGB), the study used the root/shoot ratio (R/S) of each grassland type and grazing intensities to calculate their belowground biomass (BGB) or aboveground biomass (AGB) (Fig. S2).

2.2.3 Soil C stocks

If the samples reported only had SOM, their SOC was calculated by the relation between SOM and SOC as follows (Deng et al. 2017):

$$SOC = SOM \times 0.58 \tag{3}$$

where SOC is the soil organic C concentration (g kg^{-1}) and SOM is the soil organic matter (g kg^{-1}).

The SOC stocks were calculated using the following equation (Deng et al. 2017):

$$C_s = \frac{SOC \times BD \times D}{10} \quad (4)$$

in which, C_s is soil organic C stocks (Mg ha^{-1}); SOC is soil organic C content (g kg^{-1}); BD is soil bulk density (g cm^{-3}), and D is soil thickness (cm).

Soil BD estimates are critical for calculations of C_s, but many studies did not measure this. We established an empirical relationship between SOC content and soil BD with the reported values for ungrazed sites and grazed sites from the Appendix Dataset S1. Then, the missing values of soil BD were interpolated using the predicted values from the empirical functions (*Exponential Decay, Double, 4 Parameter*, Fig. S3, Eqs. 5 and 6):

$$BD_{UnG} = 1.53e^{0.01SOC} - 0.13, r^2 = 0.47, p < 0.0001,\ \mathrm{n} = 113 \quad (5)$$

$$BD_{GG} = 1.27e^{0.01SOC} + 0.20, r^2 = 0.42, p < 0.0001,\ \mathrm{n} = 333 \quad (6)$$

To increase the comparability of data derived from different studies, the original soil C data were converted to soil C stocks in the top 20 cm using the depth functions developed by Jobbágy and Jackson (2000) according to the following equations:

$$Y = 1 - \beta^d \quad (7)$$

$$X_{20} = \frac{1 - \beta^{20}}{1 - \beta^{d0}} \times X_{d0} \quad (8)$$

where Y represents the cumulative proportion of the soil C stock from the soil surface to depth (d, cm); β is the relative rate of decrease in the soil C stock with soil depth; X_{20} denotes the soil C stock in the upper 20 cm; *d*0 denotes the original soil depth (cm); X_{d0} is the original soil C stock. Although Jobbágy and Jackson (2000) provided the depth distribution of soil C for 11 biome types globally, there was no significant difference in the depth distribution among biome types or between individual biomes and the global average. Therefore, in the present study, the global average depth distributions for C were adopted to calculate β (i.e., 0.9786) in the equations (Li et al. 2012).

It should be noted that potential uncertainties may be introduced by this dataset standardization, mainly due to the difference in C distribution through the soil profile between ungrazed and grazing sites, and among the different stages following grazing exclusion. However, as it has been stated, there was no significant difference among the 11 biome types included in Jobbágy and Jackson's study (2000) or between individual biomes and the global average in terms of soil C distribution with depth. Previous meta-analyses have also used the same method, and concluded that depth corrections did not alter the overall pattern of soil C stock dynamics during vegetation development (Li et al. 2012; Deng et al. 2014b, 2017; Yu et al. 2023).

2.3 Data analysis

Analysis of variance (ANOVA) was conducted to evaluate whether the changes in plant C stocks, soil C stocks, plant height, plant coverage, R/S, soil pH, and soil C/N were significantly different depending on grazing intensity, grazing duration, grassland types, or grazing periods. Differences were evaluated at the 0.05 significance level ($p < 0.05$). When the homogeneity of variance was confirmed and significance was observed at the $p < 0.05$ level, a least significant difference (LSD) test was used for multiple comparisons. Pearson correlations were used to analyze ecosystem C stocks with climate (MAP, MAT), elevation, grassland utilization rate, grazing duration, R/S, and plant community characteristics in the different grazing grasslands (Table S1). Regression analysis was conducted to analyze the relationships among plant biomass C stocks as well as the relationships between soil C stocks and above- or belowground biomass C stocks, the relationships of R/S, soil C/N ratios with stocking rates or grazing duration, and the relationships of soil N stocks and soil C stocks, TN content and SOC content (Table S2). In addition, a multivariable linear regression analysis was conducted to quantify the relationships between ecosystem C stocks and five driving factors of MAP, MAT, elevation, stocking rate, and grazing duration in the four grassland types. All statistical analyses were performed using the SPSS software program, ver. 17.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 Grassland C stocks change with grazing intensity

Grassland type and grazing intensity affected ecosystem C stocks (Fig. 2). Heavy grazing decreased plant biomass and soil C stocks in all grassland types, but light grazing slightly increased the above- and belowground biomass stocks only in the desert steppes (Fig. 2). Light grazing increased belowground plant biomass (roots) in typical steppes, but had no effects on roots in alpine and meadow steppes (Fig. 2). Both light grazing and medium grazing increased the soil C stocks in all grassland types, except in alpine steppes (Fig. 2). In terms of ecosystem C accumulation, light grazing is good for desert steppes and typical steppes, whereas medium grazing is the best option for meadow steppes and alpine steppes (Fig. 2).

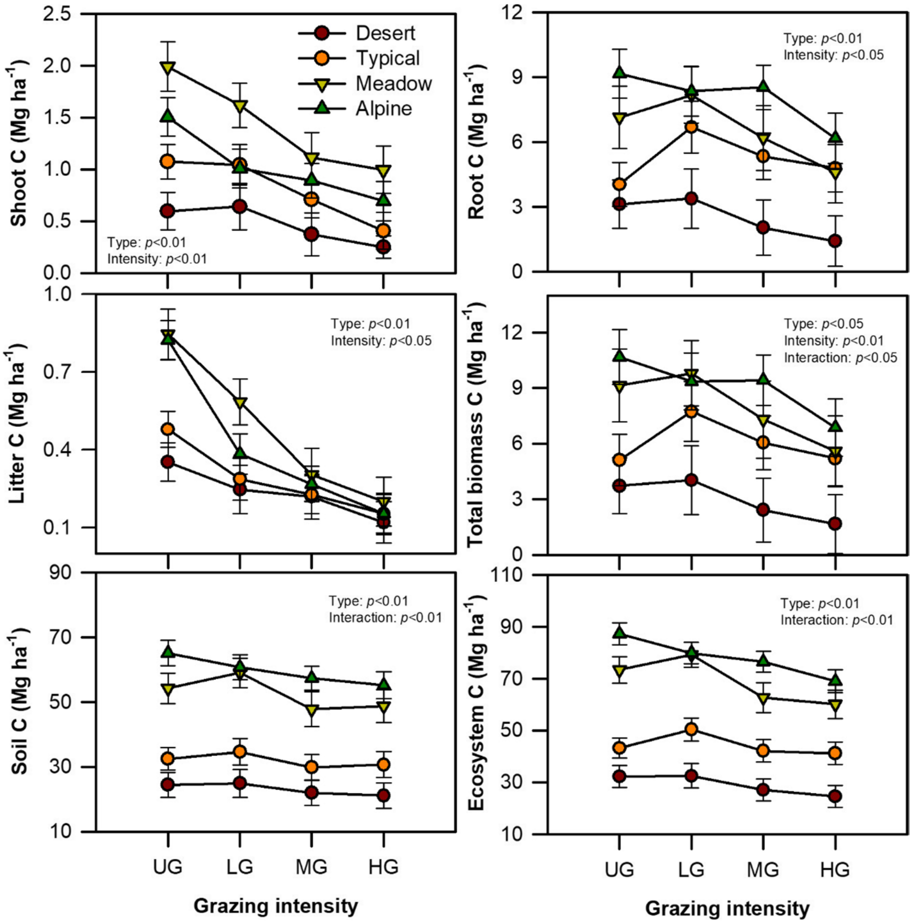


Fig. 2 Carbon stocks depending on grazing intensity in the four grassland types of desert, typical, meadow and alpine steppes. UG, Ungrazed; LG, Low grazing; MG, Medium grazed; HG, High grazed. Shoot C, aboveground biomass carbon stocks; Root C, belowground biomass carbon stocks; Litter C, litter biomass carbon stocks; Total biomass C, total biomass carbon stocks including both shoot C and root C; Soil C, soil carbon stocks; Ecosystem C, ecosystem carbon stocks including all plant biomass C, litter C and soil C. $p < 0.05$ indicates significant differences among the grassland types or grazing intensities or their interactions at 0.05 level. All the data are presented as Mean ± SE

Grazing intensities depend on stocking rates. Overall, higher stocking rates reduced plant and soil C stocks. Along with the increasing grazing intensities, aboveground biomass carbon stocks decreased from 0.6 Mg ha^{-1} to 0.1 Mg ha^{-1}, from 1.1 Mg ha^{-1} to 0.5 Mg ha^{-1}, from 2.0 Mg ha^{-1} to 0.4 Mg ha^{-1} and from 1.3 Mg ha^{-1} to 0.8 Mg ha^{-1} in the desert steppes, typical steppes, meadow steppes and alpine steppes, respectively (Fig. 3). Compared with ungrazed grasslands, grazed grassland C stocks did not change at the stocking rates of about 1 ~ 2, 3 ~ 4, 5 ~ 6, and 7 ~ 8 sheep units per hectare for desert steppes, typical steppes, meadow steppes, and alpine steppes, respectively (Fig. 3, Fig.S4).

3.2 Grassland C stocks change with grazing duration

Grazing duration is an important factor of ecosystems C stocks. Of the 72 potential carbon, intensity and grassland type effects, two-thirds showed significant linear declines, but 16 showed a unimodal response, generally increasing up to 2 or 4 years, then declined (Fig. 4). Grassland ecosystem C stocks increased in the early grazing duration (< 3 yr) under light grazing (Figs. 4 and S5), especially in the desert, typical, and meadow steppes. For the short-term grazing duration (< 6 years), light grazing increased plant biomass C stocks in the desert steppes, but they declined during long-term grazing (Fig. 4). Light grazing (2 to 4 sheep ha^{-1}) increased belowground biomass in the typical steppes (Fig. 4). The belowground biomass in the meadow steppes under light grazing (1 to 2 sheep ha^{-1})

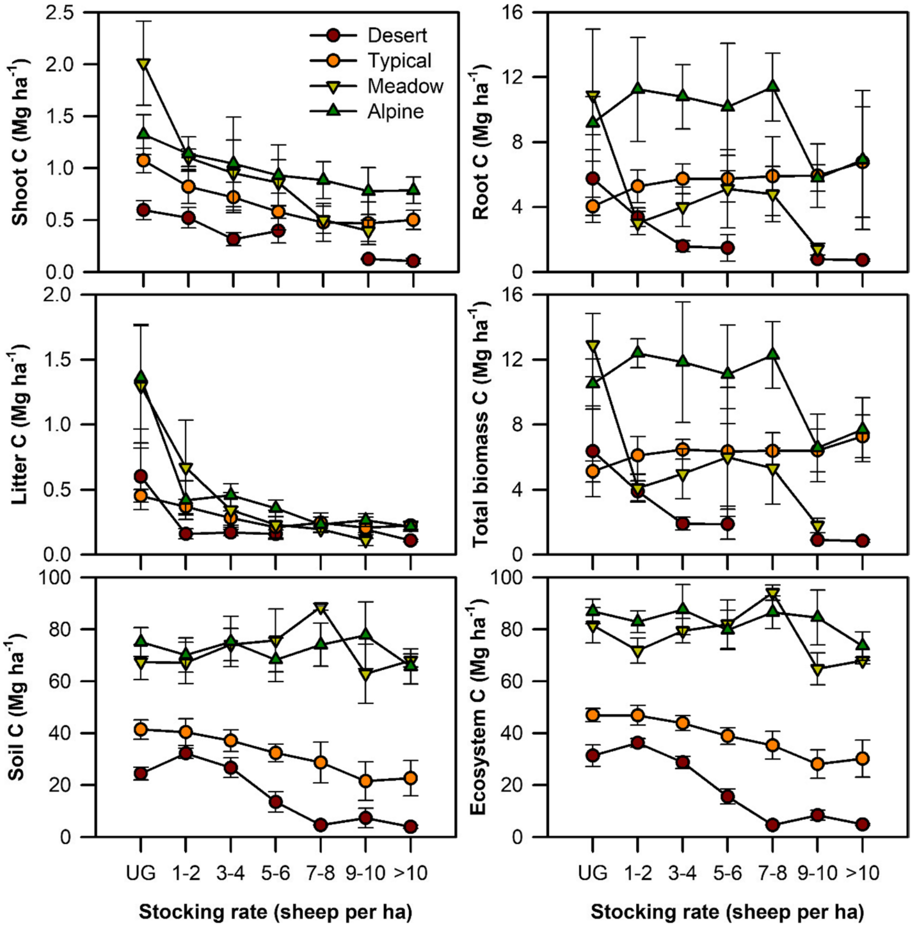


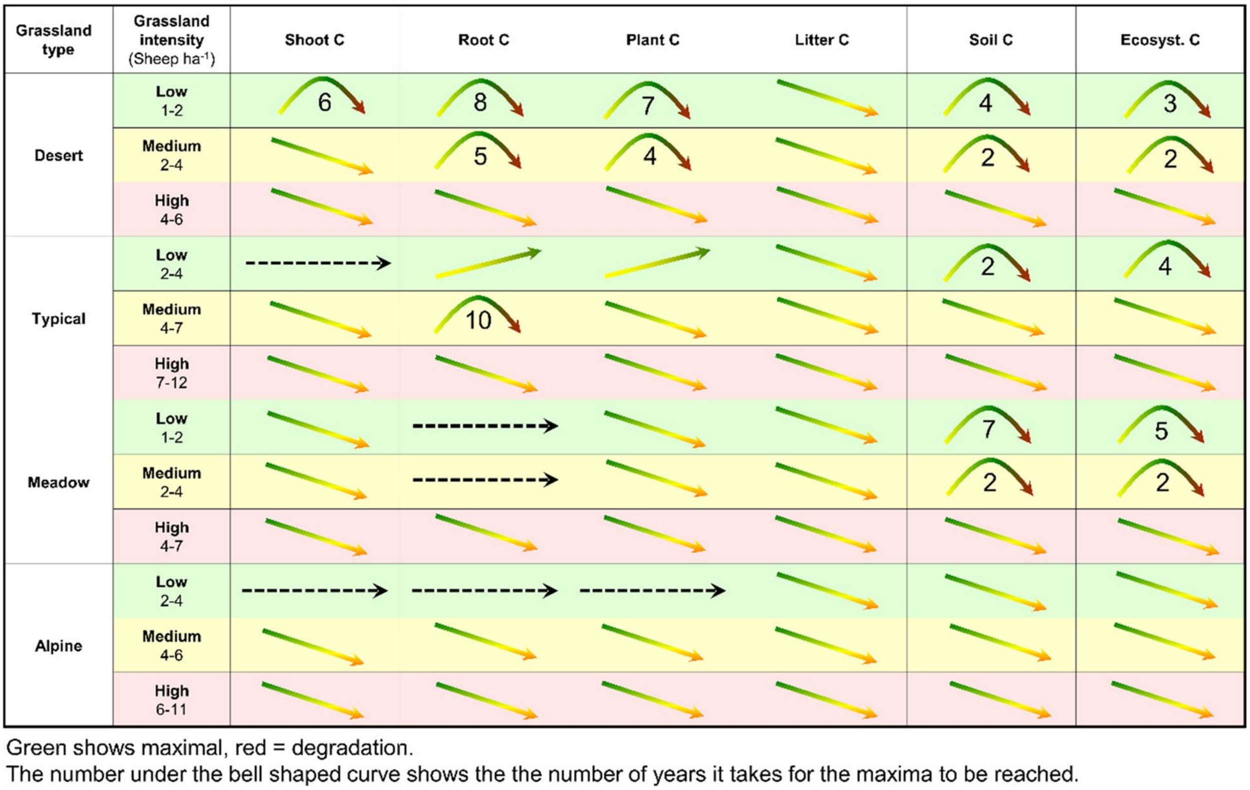
Fig. 3 Grassland carbon stocks depending on stocking rates in the four grassland types of desert, typical, meadow and alpine steppes. Note: UG, Ungrazed. Shoot C, aboveground biomass carbon stocks; Root C, belowground biomass carbon stocks; Litter C, litter biomass carbon stocks; Total biomass C, total biomass carbon stocks including both shoot C and root C; Soil C, soil carbon stocks; Ecosystem C, ecosystem carbon stocks including all plant biomass C, litter C and soil C. All the data are presented as Mean ± SE

and medium grazing (2 to 4 sheep ha^{-1}) were stable even under long-term grazing (Fig. 4). Plant biomass C stocks in the alpine steppes were also stable under light grazing (2 to 4 sheep ha^{-1}), though C stocks decreased for litter, soil and the whole ecosystem (Fig. 4). When the grazing duration is longer than 2 years, soil C stocks decrease faster than aboveground or belowground biomass (Fig. S5). Overall, soil C stocks decreased from 59.6 Mg ha^{-1} to 26.4 Mg ha^{-1}, from 64.3 Mg ha^{-1} to 14.8 Mg ha^{-1}, from 53.2 Mg ha^{-1} to 18.5 Mg ha^{-1} in the light, medium, and heavy grazing, respectively (Fig. S5). All litter C stocks decreased linearly with grazing duration, regardless of grassland types (Fig. 4). It is worth noting that heavy grazing decreased C stocks linearly with grazing duration, at about 1.4 Mg ha^{-1} per year in the whole grassland ecosystems (Fig. S6), mainly linked to the decline in soil C stocks.

3.3 Factors affecting grassland C stocks depending on grazing

Climate is an important factor affecting grassland ecosystems (Fig. 5, Tables S1 and S2). Plant C stocks in grasslands usually increased with precipitation but they were not influenced by temperature (Fig. 5). This phenomenon was only found in the ungrazed grasslands (Fig. 5). However, grazing offset the correlations between plants C stocks and climate conditions (Table S1). Plant C stocks remained stable independent of MAP or MAT under all the grazing intensities (Table S1). Soil C stock increased with precipitation, but it was reduced with temperature (Fig. 5). In the light and medium grazed grasslands, soil C stocks decreased with stocking rates, but there were no correlations in the heavy grazing grasslands (Table S1).

Ecosystem C stocks in the light grazing grasslands decreased with increasing Pielou index, indicating that light grazing increased the evenness of the grasslands. Higher plant coverage increased soil C stocks (Table



Grassland type	Grassland intensity (Sheep ha-1)	Shoot C	Root C	Plant C	Litter C	Soil C	Ecosyst. C
Desert	Low 1-2	⌒ 6	⌒ 8	⌒ 7	↘	⌒ 4	⌒ 3
	Medium 2-4	↘	⌒ 5	⌒ 4	↘	⌒ 2	⌒ 2
	High 4-6	↘	↘	↘	↘	↘	↘
Typical	Low 2-4	⇢	↗	↗	↘	⌒ 2	⌒ 4
	Medium 4-7	↘	⌒ 10	↘	↘	↘	↘
	High 7-12	↘	↘	↘	↘	↘	↘
Meadow	Low 1-2	↘	⇢	↘	↘	⌒ 7	⌒ 5
	Medium 2-4	↘	⇢	↘	↘	⌒ 2	⌒ 2
	High 4-7	↘	↘	↘	↘	↘	↘
Alpine	Low 2-4	⇢	⇢	⇢	↘	↘	↘
	Medium 4-6	↘	↘	↘	↘	↘	↘
	High 6-11	↘	↘	↘	↘	↘	↘

Green shows maximal, red = degradation.
The number under the bell shaped curve shows the the number of years it takes for the maxima to be reached.

Fig. 4 Response of grassland C stocks to grazing duration (maximum ~ 30 years) under each grazing intensity in the four grassland types. The values below each grazing intensity indicate the corresponding stocking rate (sheep ha^{-1}) in the dataset of this synthesis. The numbers under the bell shaped curves show the period when the maxima will be reached in years. Shoot C, aboveground biomass carbon stocks; Root C, belowground biomass carbon stocks; Litter C, litter biomass carbon stocks; Total biomass C, total biomass carbon stocks include both shoot C and root C; Soil C, soil carbon stocks; Ecosyst. C, ecosystem carbon stocks include all plant biomass C, litter C and soil C

S1). The multivariable linear regression model analysis showed that soil C stocks were mainly affected by the climate factors, stocking rate, and grazing duration in all grassland types, but factors affecting plant C stocks were determined by the grassland types (Table S2). In the typical meadow steppes, plant C stocks were mainly affected by grazing intensity and duration. In the desert and alpine steppes, the MAP and MAT were the main factors influencing plant C stocks (Table S2).

4 Discussions

4.1 Effects of grazing on plant biomass C stocks

Grazing disturbance is crucial for the growth and development of plant species, and thus can change the community composition, structure, diversity, and productivity (Fig. S7; Zhao et al. 2017; Mou et al. 2018). Our meta-analysis showed that grazing decreased the shoot biomass in the desert, typical and meadow steppes, especially under heavy grazing (Fig. 2), because shoots were removed and the remaining stubbles were damaged by livestock trampling (Ferraro and Oesterheld 2002). Light grazing, however, slightly increased the shoot and root biomass of the desert steppes (Fig. 2) because: 1) the vegetation productivity index was the highest under light grazing by stimulating the compensatory plant growth (Evju and Mysterud 2010; Zhu et al. 2018); and, 2) livestock increases the evenness of the grasslands (Table S1) and reduces the competition of dominant species for resources (water, nutrients, light), which provides space for the survival of alien species and the fast recovery of native species (Yan et al. 2013; Zhu et al. 2018; Gao et al. 2021). This conforms to the '*intermediate disturbance hypothesis*' (Tilman and Downing 1994). Therefore, rotational grazing intensity maintains or increases grassland productivity and is an important grassland management strategy to increase C stocks.

Light grazing, however, had no effects on shoot biomass in the alpine steppes (Fig. 2), because alpine meadows have higher compensatory growth or over-compensatory growth under grazing (Kuzyakov et al. 2002; Lu et al. 2017) and thus increase the primary productivity (Sun et al. 2019). Heavy grazing strongly decreased the shoot and root C stocks (Figs. 2, 3 and 4), as overgrazing (i.e., grazing leading to degradation of grassland) with higher

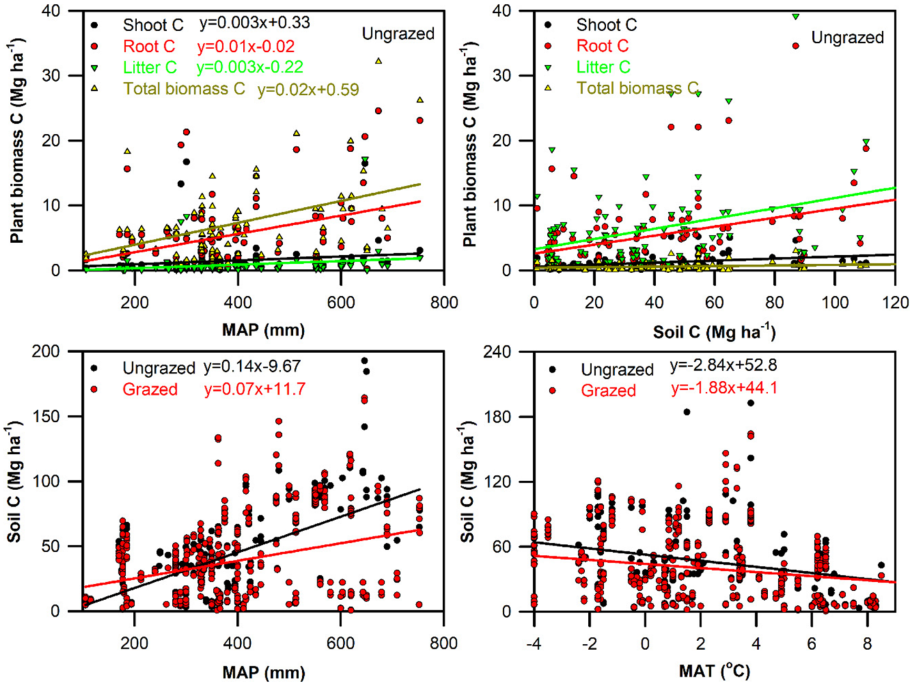


Fig. 5 Effects of the MAP (mean annual precipitation) on plant biomass C stocks in the ungrazed sites, and of the MAP and MAT (mean annual temperature) on soil C stocks in ungrazed and grazing sites, as well as the relationships between soil C stocks and plant biomass C stocks in ungrazed sites. Shoot C, aboveground biomass carbon stocks; Root C, belowground biomass carbon stocks; Litter C, litter biomass carbon stocks; Total biomass C, total biomass carbon stocks including both shoot C and root C; Soil C, soil carbon stocks. All regression lines are significant at $p < 0.01$ (except Litter C, which is at $p < 0.05$)

stocking rates reduced the growth and regeneration of grassland plants, and reduced C allocation belowground (Kuzyakov et al. 2002; Unteregelsbacher et al. 2012; Liu et al. 2015). Overgrazing altered the distribution of matter and energy among the plant organs, leading to a small leaf area index (LAI), short grass height, sparse plant coverage (Fig. S7), and low light interception. Consequently, photosynthesis decreased, especially in the high grazing intensity. If the grassland is overgrazed during the seed-bearing period, the livestock decreases the tiller number, leaf, plant height, growth rate, and total biomass (Zheng et al. 2010; Eldridge et al. 2016), and thus, it affects the productivity of the entire grassland (Milcu et al. 2016). Therefore, the compensatory regeneration of herbage is weak, and present C stocks of plant biomass are low under overgrazing (Patty et al. 2010).

4.2 Effects of grazing on soil C stocks

Soil C stocks depend on the balance between the C inputs by plants and soil organic matter decomposition (Deng et al. 2014b, 2017). According to our meta-analysis, grazing decreased the soil C stocks in typical steppes (Fig. 3) because: 1) grazing decreases shoot biomass and photosynthesis, which reduces the belowground C input (Zheng et al. 2010; Unteregelsbacher et al. 2012; Zhu et al. 2018); 2) selective feeding by livestock reduces the litter amounts and litter inputs (Fig. 3), thus reducing the soil C content (Sun et al. 2011; Qu et al. 2022); 3) trampling, particularly in the heavy grazing, destroys soil structure and increases soil erosion which reduces C in topsoils (Zhao et al. 2017); and, 4) soil CO_2 emissions increase due to soil acidification (decreased soil pH) under intensive grazing (Fig. 7; Zamanian et al. 2018; Raza et al. 2020). Light grazing can increase the soil C stocks in the desert steppes, typical steppes, and meadow steppes (Fig. 2) because grazing has a stimulatory effect on root growth (Fig. 4). More assimilation products are allocated to the roots as storage for regrowth following grazing (Kuzyakov et al. 2002; Pucheta et al. 2004; Hafner et al. 2012), thereby increasing root/shoot ratios (Fig. S2 and S8). Additionally, soil organic matter increases with animal manure brought outside (Liu et al. 2020) and declines in organic matter decomposition due to low microbial activities under grazing (Zhao et al. 2017; Zheng et al. 2021), leading to an increase in soil C stocks. However, light grazing and medium did not affect soil C stocks in the alpine steppes (Fig. 3) because: 1) appropriate (light – medium) grazing does not reduce C inputs from the plants into soils due to higher compensatory growth or over-compensatory growth of the alpine steppes (Fig. 3); 2) animal manure inputs can offset the C losses due to trampling (Milchunas and Laurenroth 1993); and, 3) grazing changes the composition of plant species in the alpine steppes, and increased plant diversity promotes soil organic matter formation (Zhao et al. 2009; Gao et al. 2021). The stability of soil C stock in alpine grasslands indicates good adaptability and resistance to grazing (Wang et al. 2016).

C-N interactions are very important factors in determining whether C sinks in ecosystems can be sustained over the long term (Luo et al. 2006; Deng et al. 2017). In the grazed grasslands, soil C/N decreased during the first 4–5 years (Fig. 6) due to a fast decline in the soil C pools (Fig. S5). Under long-term grazing (> 10 yr), the declining soil C pool reached a stable level (Fig. S5). However, long-term grazing also leads to higher N mineralization and N_2O emissions (McNaughton et al. 1997) due to the activities of heterotrophs, nitrifiers, and denitrifiers (Patra et al. 2005), leading to more soil N losses than in the earlier stages. Long-term intensive grazing reduces the biological nitrogen fixation capacity (Zhang et al. 2021b). So, soil C/N ultimately increased following long-term grazing (Fig. 6). More soil N loss also means a lack of nutrients for plant growth, which in turn reduces grassland productivity (Hao and He 2019; Deng et al. 2021) and a decrease in ecosystem C stocks. In summary, this decrease in ecosystem C stocks under long term grazing is due to: 1) low plant productivity and carbon inputs (Gamoun 2014; Deng et al. 2021); 2) soil N deficiencies due to higher N losses, which limit plant growth (McNaughton et al. 1997); and, 3) high proportions of heterotrophic microorganisms that accelerate soil organic matter decomposition (Patra et al. 2005; Raza et al. 2020).

4.3 Effects of grazing on ecosystem C stocks

Grazing affects grassland ecosystems through trampling, feeding and the excrements of livestock (McSherry and Ritchie 2013; Deng et al. 2017; Wilson et al. 2018). Grazing duration is an important factor influencing C stocks. The short-term (1 yr) grazing, light grazing and medium grazing slightly increased the above- or belowground biomass (Fig. 4 and S5), but heavy grazing did not (Fig. S6). Compared with ungrazed conditions, light or medium grazed grasslands, heavy grazing reduced plant coverage and density, and species diversity (Fig. S7), and thus decreased plant biomass (Gamoun 2014).

The short-term grazing effects also confirm the '*intermediate disturbance hypothesis*' (Tilman and Downing 1994): medium grazing maintained and even increased

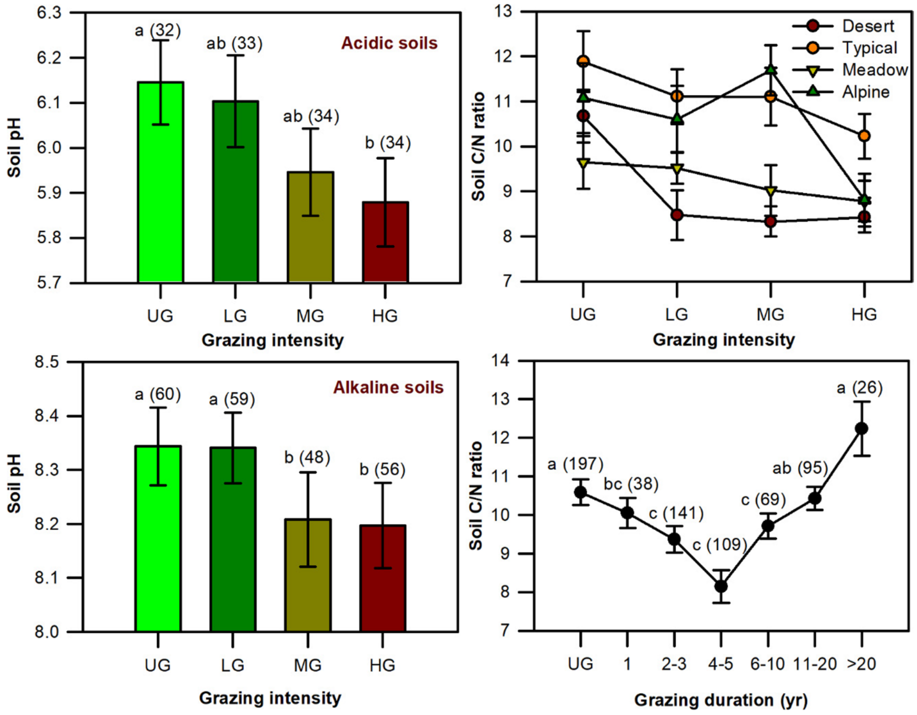


Fig. 6 Soil pH and soil C/N ratios depending on grazing intensities in the acidic and alkaline soils, and the C/N ratios depending on grazing duration. UG, Ungrazed; LG, Low grazing; MG, Medium grazed; HG, High grazed. Small letters above the error bars indicate significant differences among the grazing intensities or grazing duration at $p < 0.05$. Values in parenthesis are the numbers of observations. All the data are presented as Mean ± SE

vegetation productivity and diversified the community structure. However, regardless of the grazing intensity, all ecosystem C pools increased with short-term grazing (2 ~ 3 yr) to various degrees (Fig. 4 and S5). This could be attributed to the rapid turnover of nutrients, acceleration of plant growth, and the transformation of organic matter, indicating that grasslands have a compensatory response to grazing. These findings, as impacted by the grazing duration, also confirm the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986) because grass growth is stimulated during short-term grazing (< 3 yr), after which the compensatory effect disappears (Fig. S5).

The best grazing intensity maintaining the highest ecosystem C stocks for desert and typical steppes is light grazing (Fig. 2). Medium grazing is the best grazing intensity for ecosystem C stocks in meadow steppes and alpine steppes (Fig. 2). When the grazing intensity exceeds the tipping-point, the ecosystem C stocks will drop. These results also confirm the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986). Before the stocking rate increases to the optimal level, the ecosystem C stocks increase, and then decrease with the increase of grazing intensity. Light or medium grazing increases the ecosystem C stocks because plants undergo over-compensatory growth (Zhu et al. 2018). Under heavy grazing, the rate of plant regeneration cannot compensate for the biomass removal rate, and thus the total net primary productivity drops (Fig. S6, Zhu et al. 2018). Plant productivity is the main driving force for ecosystem C sequestration because soil and ecosystem C stocks increase with the above- and belowground plant biomass (Fig. 7, Deng et al. 2021). Therefore, optimal grazing intensities must always be considered to maintain original production rates and ensure that the grassland ecosystems remain stable and sequester C (Fig. 4).

4.4 Theory of grazing effects on ecosystem C stocks

The structure and functions of grassland ecosystem responses to grazing fit four theories, i.e., the '*intermediate disturbance hypothesis*' (Tilman and Downing 1994), the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986), the '*dynamic balance hypothesis*' and the '*dynamic imbalance hypothesis*' (Palmer et al. 2016). Based on the results of this synthesis, we summarize these conceptual models to reflect the response of grassland C stocks to grazing intensity and duration (Fig. 8).

The '*intermediate disturbance hypothesis*' assumes that moderate disturbance is beneficial to maintain higher community productivity and diversity, and medium grazing accelerates vegetation growth, reduces canopy shielding to solar radiation, increases forage photosynthetic capacity, and thus enables compensatory effects on forage growth (Tilman and Downing 1994). The compensatory effect on forage growth is further developed in the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986), which

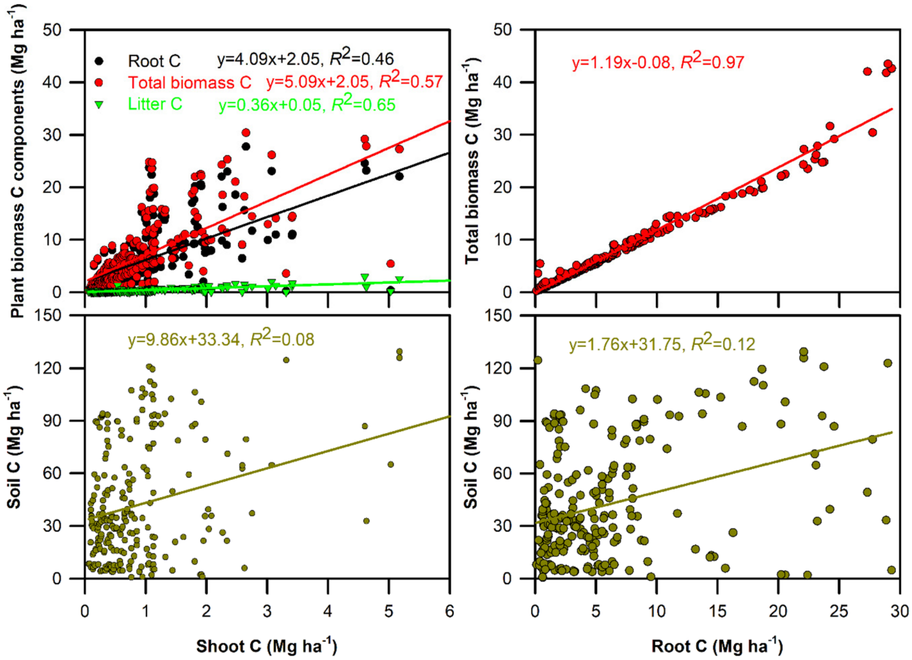


Fig. 7 The relationships among plant biomass carbon (C) stocks ($n = 286$) as well as the relationships between soil C stocks ($n = 253$) and shoot or root C stocks. Shoot C, aboveground biomass carbon stocks; Root C, belowground biomass carbon stocks; Litter C, litter biomass carbon stocks; Total biomass C, total biomass carbon stocks including both shoot C and root C; Soil C, soil carbon stocks. $R.^2$ is the coefficient of determination. All regression lines are significant at $p < 0.001$

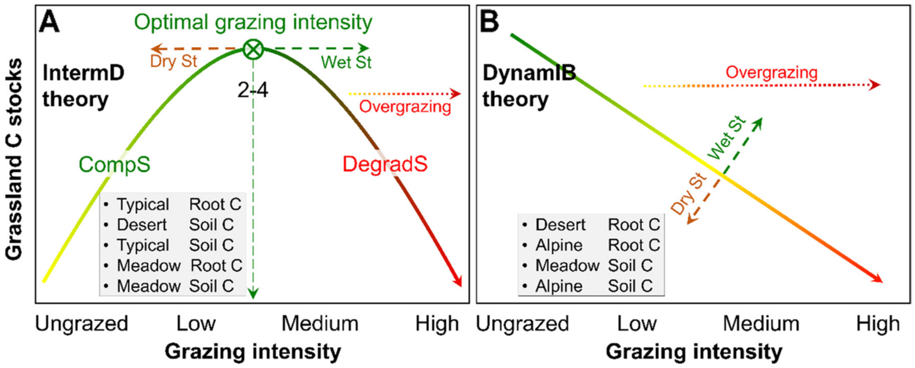


Fig. 8 Conceptual models of the response of grassland C stocks to grazing intensity from ungrazed through low grazing and medium grazing to high grazing. The conceptual models reflect the response of grassland C stocks to grazing duration elucidated in this synthesis. The 'Unimodal curve' in panel A indicates the first increase of grassland C stocks to a maximum, and then the subsequent decrease. Panel A fits the '*Intermediate disturbance hypothesis*' (IntermD hypothesis) (Tilman and Downing 1994). Panel B fits the '*dynamic imbalance hypothesis*' (DynamIB hypothesis) (Palmer et al. 2016). The grassland response cycle to grazing intensity can be divided into two stages of C stock changes, that is CompS, compensatory growth stage, and DegradS, degradation stage (**A**). The green "cross circle" in panel A indicates the optimal grazing intensity, where grazing has a positive effect on grassland C stocks. The model only reflects the general C stock response to grazing intensity and it does not cover all cases (e.g., some grasslands can be grazed with low intensity for a very long time without reaching degradation). Grassland state before grazing is critical to the response of grassland to grazing duration. The ModerD hypothesis fits to non-degraded grasslands before grazing (**A**). And the DynamIB hypothesis fits to degraded grasslands before grazing (**B**). It is worth noting that dry steppes (Dry St) have a lower optimal grazing intensity than wet steppes (Wet St) (**A**), and the grassland C stocks decreased faster in dry steppes than in wet steppes (**B**). Dry St are steppes located in arid and semi-arid areas, and Wet St are steppes located in humid areas. The grey boxes in panels **A** and **B** reflect the grassland ecosystem C components of each of the grassland types that fit the corresponding models. Overgrazing indicates grazing that leads to the degradation of a grassland

assumes that the primary production increases first and then decreases with rising grazing intensity (Deng et al. 2014a). The primary productivity reached the peak when the grazing intensity was medium, corresponding to the optimal stocking rates (McNaughton 1979). The '*intermediate disturbance hypothesis*' and the '*grazing optimization hypothesis*' can have the same outcome when grasslands do not suffer from extreme grazing. In our meta-analysis, the plant biomass and soil C stocks in the desert steppes confirm the '*intermediate disturbance hypothesis*' responding to grazing intensity (Fig. 8), indicating that appropriate grazing intensity of less than 2 sheep ha^{-1} is better for increasing ecosystem C stocks (Fig. 8) in the desert steppes.

The belowground biomass C stocks in the typical steppes increased after light grazing (Fig. S6), which confirms the '*grazing optimization hypothesis*' (Edelstein-Keshet 1986). The specific performance of grazing optimization is the compensatory growth of plants (Lu et al. 2017). Compensatory growth is the result of coadaptation and coevolution among grasslands, livestock and environment responding to disturbance, occurring at various organizational levels of plant organs, individual plants, populations and communities (McNaughton 1979). Along with increasing grazing duration, the belowground biomass C stocks of the typical steppes linearly increase under light grazing, but a "unimodal" trend is common under medium grazing (Figs. 4 and 8). Soil C stocks increased in desert, typical and meadow steppes during the first 3 years of grazing (Fig. 4 and 8). The compensation effect will gradually disappear with the increase in grazing duration, until they reach a new equilibrium (Fig. 8). The turning point after the compensatory growth stage could represent the optimal grazing duration (Fig. 8). Therefore, the compensatory effect is related to grazing duration and intensity.

The '*dynamic balance hypothesis*' refers to the stable state achieved by interactions between organisms and environment within a certain period, including the stability of ecosystem structure, functions and energy (Palmer et al. 2016). The shoot C stocks in the typical steppes and root C stocks in alpine steppes under light grazing remained independent of grazing duration (Figs. 4 and 8). They confirmed the '*dynamic balance hypothesis*' responding to grazing. The dynamic balance of the C stocks is determined by grazing intensities. For example, the root C stocks in the meadow steppes was unchanged at or below medium grazing but reduced significantly under heavy grazing (Fig. 2). So, heavy grazing disturbs the balanced C budget. Soil C stocks in the alpine steppes (Figs. 2 and 3) decreased with grazing (Fig. 8), indicating that grazing imbalanced C inputs and outputs. It confirmed the '*dynamic imbalance hypothesis*' (Palmer et al. 2016). Therefore, plant and soil C stocks' responses to grazing intensity are related to the grassland type and grazing duration.

4.5 Implications for grazing management in grasslands

Grazing is the primary use for natural grassland ecosystems (Yan et al. 2013; Zhou et al. 2014; Dlamini et al. 2016). The C stocks in grassland ecosystems of China could increase by up to 0.21 Pg yr^{-1} (i.e., 1.7 Mg ha^{-1} yr^{-1}) if the comprehensive 'Returning Grazing Land to Grassland' Project is implemented (Deng et al. 2017). However, a total cessation of grazing is in conflict with the policy goal of increasing food production, so grazing exclusion is therefore not feasible. Based on this meta-analysis, there are four options for grazing land management strategies:

(1) Reasonable grazing intensity is conducive to maintaining grassland ecosystem C pools. The appropriate intensity of grazing utilization, whether light grazing or medium grazing, has positive effects on ecosystem C stocks (Fig. 2). The best stocking rates in the desert steppes, typical steppes, meadow steppes and alpine steppes are about 1 ~ 2, 3 ~ 4, 5 ~ 6 and 7 ~ 8 sheep units per hectare, respectively (Fig. S5). At these grazing intensities, livestock will not decrease C stocks, and they may even increase C stocks of grassland ecosystems.

(2) Rotational grazing cycles are conducive to the healthy development of grasslands. All the components of ecosystem C in the short-term grazing (<3 yr) do not indicate degradation, regardless of the grazing intensity (Fig. S4). Although grazing exclusion has no effects on shoot biomass after 3 years, it can increase shoot biomass to some extent in the first 3 years (i.e., synthesis of grazing exclusion effects; Deng et al. 2017). Accordingly, every 3 years (i.e., 3 years of grazing followed by 3 years of rest) may be the optimal grazing rotation cycle to maintain stable pastures.

(3) Grazing in the non-growing season helps to maintain C sequestration. Non-growing season grazing strongly increased ecosystem C stocks due to the higher productivity in alpine steppes, compared with grazing during the growing season or the whole year. However, whether non-growing season grazing is beneficial for improving grassland C stocks in other grassland types requires further study.

(4) Reasonable grazing improves the ability of ecosystems to cope with climate change. Grazing can change the correlations between plants C stocks and climate conditions (Table S1). Plant C stocks remained unchanged with climate change under all grazing intensities (Fig. 5), and soil C stocks responded slower to climate change under grazing than when they were under ungrazed condition (Fig. 5). So, reasonable grazing may reduce the sensitivity of grasslands to climate change.

5 Conclusions

The '*intermediate disturbance hypothesis*' and the '*grazing optimization hypothesis*' are most relevant for the early stages of light grazing, such as in desert steppes. The '*dynamic balance hypothesis*' is most relevant for light grazing conditions such as in typical steppes and alpine steppes and the over-degradation stage due to overgrazing. The '*dynamic imbalance hypothesis*' is most relevant for the intermediate stage of light grazing and medium grazing, or the stages prior to degradation under heavy grazing. However, it should also be noted that the grassland state before grazing is critical for the response of the grassland to the grazing duration. If the grassland is not degraded before grazing, it fits the '*intermediate disturbance hypothesis*'; if the grassland is in different degradation states, it is more in line with the '*dynamic imbalance hypothesis*'. The model of grassland response to grazing is regulated by the grassland's type, grazing intensity, and grazing duration. In conclusion, grassland grazing is a double-edged sword. On the one hand, proper management can maintain and even increase the grassland C stock and the harvest livestock products. On the other hand, grassland degradation can be accelerated by human induced overgrazing, resulting in serious carbon losses. So, more appropriate and customized management strategies should be considered whenever possible, such as light or medium grazing, rotational grazing or non-growing season grazing, to promote C sequestration on grasslands and climate change mitigation.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s44246-023-00051-7.

Additional file 1: TableS1. Pearson correlations of ecosystem carbon (C) stocks with climate (MAP, mean annual precipitation; MAT, mean annual temperature), elevation and grassland utilization rate, grazing duration, root/shoot ratio (R/S) and plant community characteristics in the grasslands with four grazing intensities. **TableS2.** Multivariable linear regression model analysis between ecosystem carbon (C) stocks and five driving factors: MAP (x1), MAT (x2), elevation (x3), stocking rate (x4) andgrazing duration (x5) in four grassland types under grazing. **FigureS1.** Stockingrates and grassland utilization rates (see below) corresponding to three grazing intensities in the four grassland types of the dataset, as well as the relationships between stocking rate and grassland utilization rates. **FigureS2.** Root/shoot ratios (R/S) depending on grazing intensities in the four grassland types of typical, desert, meadow and alpine steppes. **FigureS3.** Empirical functions to estimate the missing soil bulk density based ondata from studies reporting organic carbon content and bulk density in the ungrazed (n=133) and grazed (n=333) sites. **Figure. S4** Plant biomass, litter and soil carbon (C) stocks depending on stocking rates in the four grassland types. **FigureS5.** Plant biomass, litter and soil carbon (C) stocks depending on grazing duration underthe three grazing intensities of light, moderate and heavy grazing. **Figure S6.** Grassland carbon stocks change with grazing duration under the heavy grazing. **FigureS7.** Plant community height and coverage change with grazing intensities in the four grassland types in China. **FigureS8.** There lationships of root/shoot ratios (R/S) with stocking rates (A) and grazing duration (B). **FigureS9.** Grassland carbon (C) stocks depending on grazing periods of alpine steppes.

Additional file 2: Appendix Dataset S1.

Acknowledgements
This study was supported by the National Natural Science Foundation of China (42277471), the Second Tibetan Plateau Scientific Expedition and Research Program of the Chinese Academy of Sciences (2019QZKK0603), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA23070201), the Scientific and Technological Innovation Project of Shaanxi Forestry Academy of Sciences (SXLK2021-0206), the RUDN University Strategic Academic Leadership Program, and the Tyumen Oblast Government project No. 89-DON

Authors' contributions
L.D., Z.S. and Y.K. designed the research, L.D., J.L., and J.W. collected the data, L.D. performed the research, K.W., J.L., Z.T., W.Y. and F.Z. contributed new analytical tools, L.D. and X.W. analysed the data, and L.D., Z.S., S.B., A.S., C.H., S.A., X.X. and Y.K. wrote the paper. The author(s) read and approved the final manuscript.

Availability of data and materials
All research data of the current study are accessible from the corresponding author on reasonable request.

Declarations

Competing interests
All the authors declare no competing interests.

Author details
[1]State Key Laboratory of Soil Erosion and Dryland Farming On the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, No. 26 Xinong Road, Yangling 712100, Shaanxi, China. [2]Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, Shaanxi, China. [3]Institute of Environmental Science and Technology (ICTA), Universitat Autònoma de Barcelona (UAB), Bellaterra, Spain. [4]Research Institute of Ecology and Natural Resources Management, Tyumen State University, 6 Volodarskogo Street, 625003 Tyumen, Russia. [5]Center of CEF/ESCER, Department of Biological Science, University of Quebec at Montreal, Montreal H3C 3P8, Canada. [6]State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China. [7]Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China. [8]State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an 710075, Shaanxi, China. [9]School of Agriculture, Ningxia University, Yinchuan 750021, Ningxia, China. [10]Key Laboratory of Grassland Ecosystem of the Ministry of Education, College of Grassland Science, Gansu Agricultural University, Lanzhou 730070, Gansu, China. [11]Department of Soil Science of Temperate Ecosystems, Department of Agricultural Soil Science, University of Göettingen, Göttingen, Germany. [12]Peoples Friendship University of Russia (RUDN University), 117198 Moscow, Russia.

Received: 6 December 2022 Revised: 2 April 2023 Accepted: 10 April 2023

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