Legacy effects from historical grazing enhanced carbon sequestration in a desert steppe

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ARTICLE INFO

ABSTRACT

Legacy effects are the ecological inheritances produced by preceding actions, which have been underlined more on agricultural land use, wildfire, invasive and removal species, forest management, and extreme climates in previous research; however, very few studies have shown concern toward the grazing legacy effects on key ecosystem functions such as the carbon cycle. A nested random block design was employed in 2012, with historical grazing as the block factor and precipitation as a nested factor, to explore the regulatory mechanisms on the carbon fluxes in a desert steppe. This long-term grazing practice had exerted unique legacy effects on community composition through increasing the proportion of *Stipa breviflora Griseb.* (P_{stipa}) by 61.53%, and decreasing species richness (R_{sp}) by 30.70%, cover by 21.87%, aboveground biomass (AGB) by 31.34%, and carbon allocation (the ratio of ANPP/BNPP) by 15.18%. Moreover, plants had differential adaptations to herbivores. Remarkably, these grazing legacies indirectly promoted plant photosynthesis (GEE) and carbon gain (NEE). Precipitation, as expected, accounted for the variability of GEE by 43% and NEE by 33%. The results revealed that precipitation controlled the magnitude of carbon fluxes while grazing legacies offset the adverse effects of current grazing and, therefore, mediated carbon sequestration.

1. Introduction

Legacy effects are the impacts from previous disturbances that continue to affect an ecosystem's structure and function (Bain et al., 2012; Kostenko et al., 2012; de Vries et al., 2012). In the semi-arid regions of Eurasia, such as on the Mongolian Plateau, grazing has been the primary land use or disturbance whose influence does not cease after the grazing enclosure (Adler et al., 2004). Understanding the long-lasting effects of grazing in this region is crucial for accurate forecasting of ecosystem functions as well as for developing future management plans. In Midwestern Inner Mongolia, the prohibition of grazing under the national policy of China has created an increasing number of "land closures" in recent decades (Qi et al., 2012). These policy-induced land enclosures create great

opportunities for us to assess the legacy effects of the historic grazing.

Historic grazing, which differs from current grazing, is the ecological inheritance of herbivores on forage grasses, where these changes persist extensively and evolve to form the unique structure and function of the pasture ecosystem after the ceasing of this activity (Coughenour, 1985). While grazing directly changes the community structure and composition of an ecosystem, it also produces indirect effects on ecosystem functions such as carbon cycling. Herbivory, through selective foraging, excreta, and trample, exerts substantial effects on aboveground communities and, thus, alters the quality of the plant litter (Rossignol et al., 2011) and causes asymmetric effects on differential species (Guitian and Bardgett, 2000; Medina-Roldan et al., 2012) and belowground characteristics via alterations in the soil community (Klumpp et al., 2009; Kotzé et al., 2013; Kulmatiski and Beard, 2011; Tessema et al., 2011; van de Voorde et al., 2011) and triggers root exudation (Hamilton and Frank, 2001). These changes in community

structure, composition, and processes could affect carbon productivity by reallocating carbon between belowground and aboveground activities (Hafner et al., 2012), thereby altering the carbon exchange of the plant canopy and reducing the root respiration (Olsen et al., 2011). Meanwhile, species may respond to herbivory in different ways. Some species are inclined to adapt to grazing pressure (e.g., through enhanced photosynthesis ability) (Cronin et al., 2003; Garrido et al., 2012; Prunier et al., 2012), while others will strengthen some of their traits to make them less attractive to foraging animals (e.g., forming less-tender leaves or growing tasteless forage; Taylor et al., 2002).

For the dryland ecosystems, precipitation is the most important climatic driver on ecosystem processes and functions (Qi et al., 2012; Wang et al., 2013). Del Grosso et al. (2008) report that precipitation is the vital driver to net primary production (NPP) in a non-tree-dominated ecosystem. Additionally, some studies report that there exist threshold values between precipitation pulses and ecosystem responses when the causal relationships will shift. Small precipitation events only activate the simple physiological actions of soil microbes, while large precipitation events could trigger ecosystem-wide vegetation growth, resulting in substantial improvement in carbon assimilation (Schwinning et al., 2004). Furthermore, it has been demonstrated that the importance of a rain event and its duration are dependent on the drought conditions prior to the event (Huxman et al., 2004; Yahdjian and Sala, 2006).

Our overall study objective is therefore to examine the coupled effects of historic grazing and precipitation concerning carbon fluxes in a desert steppe of northern Inner Mongolia. We hypothesize that: 1) the legacy effects of historic grazing remain significant in shaping ecosystem composition and function; 2) the magnitudes of the legacy effects on ecosystem carbon losses (respiration) and gains (photosynthesis) are different, leading the system to a carbon sink; and 3) precipitation is a determinant climatic cue in carbon sequestration magnitude for the desert steppe. To test our hypotheses, we developed a nested design with nine experimental blocks of no grazing (CK), low grazing stocking rate (LevA), and high stocking rate (LevC) to explore the impacts of historic grazing. Water addition treatments were implemented within each of the blocks to examine how changes in precipitation would alter the legacy effects in a desert steppe in Inner Mongolia.

2. Materials and methods

2.1. Study site

The study area is a temperate desert steppe located in the southwest of the grassland zone of the Mongolian Plateau (41°47′ N, 111°53′ E, 1450 m a.s.l.), which is often referred to as the transitional ecosystem between the typical steppe and a desert (John et al., 2009; Sternberg, 2008). The dominant species include *Stipa breviflora Griseb.*, *Cleistogenes squarrosa*, *Cleistogenes songorica*, and *Artemisia frigida*. The mean annual precipitation is 230 mm, mainly occurring in the growing season of May through October. The average annual temperature is 3.4 °C. The soil is classified as chestnut soil (FAO classification).

2.2. Experimental design

A randomized block design was applied to establish a grazing experiment on the desert prairies over a 50-ha land area since 2003. Grazing activities were performed yearly from May through November with four levels: a low stocking rate of 0.93 sheep ha^{-1} (LeA), a moderate stocking rate of 1.82 sheep ha^{-1} (LeB), a high stocking rate of 2.71 sheep ha^{-1} (LeC), and no grazing (CK, i.e., the

reference). Each level of the area is 4 ha and was replicated three times (i.e., twelve blocks).

A nested design was used within the grazing blocks to manipulate precipitation in 2012. At each of the nine blocks, other than LeB, we installed 9 × 9 m enclosures before field measurements, with two layers of wire fences to prohibit sheep disturbance. Within each enclosure, four 1 × 1 m plots set 1 m apart were laid out for measurements of net ecosystem exchange (NEE) and ecosystem respiration (ER). Another ten 1 × 1 m plots were used for measuring canopy height (H), cover, aboveground biomass (AGB), belowground biomass (BGB), and leaf area index (LAI). Among these fourteen plots, seven plots were randomly watered for carbon fluxes (two plots) and plant characteristics (five plots). About 5 mm of water were added by hand sprinklers biweekly from May through Octobers in 2012, resulting in a total of 70 mm of water addition, which is ∼30% of the annual precipitation in this desert steppe.

2.3. Field measurements

An open-path eddy-covariance (EC) system was installed in one of the reference blocks to record the continuous changes of the net ecosystem exchanges of water, CO_2, and energy as well as the local microclimatic conditions (Shao et al., 2013). Continuous records of temperature, volumetric water content (VWC), and precipitation at the EC tower were used in this study. Canopy height, cover, AGB, and LAI were measured by species on a monthly basis from May through October of 2012. On each sampling date, the AGB was determined by harvesting aboveground plants using six quadrats (2 quadrats in each block × 3 replicated blocks for each treatment) of 0.5 × 0.5 m each within each treatment. Samples were divided into green, dead, and standing parts by species. Green leaves were removed from the stems and scanned to calculate leaf area (LA). The LAI was then determined from total LA and ground area (0.5 × 0.5 m). All material was subsequently dried for 48 h at 65 °C before weighing to obtain green, dead, and standing litter biomass. We used the AGB in August as the aboveground net primary productivity (ANPP).

BGB was sampled twice by extracting soil cores (7 cm diameter) from the clipped plot in mid-May and mid-August. The differences in root biomass between the two samplings were treated as the belowground net primary productivity (BNPP). The extracted soil columns were divided into four layers (0–10, 10–20, 20–30, and 30–50 cm depths). Roots were carefully removed from each soil layer and then washed and oven-dried at 65 °C for 48 h to obtain BGB. The soil was subsequently screened using a 2 mm sieve and divided into two parts: one dried in the open air for soil organic carbon and total nitrogen measurement and the other stored in the refrigerator at 4 °C for microbial biomass carbon (MBC) and nitrogen (MBN) measurements by the fumigation−extraction method using the soil in August.

Ecosystem CO_2 exchanges of NEE and ER were measured in the morning during 8:00−10:00 h using an infrared gas exchange analyzer (IRGA; LI-840, LI-COR, Inc., Lincoln, NE, USA), which was attached with a static chamber (0.5 × 0.5 × 0.5 m) that was equipped with an air pump and flow meter. A stainless steel square frame (0.5 × 0.5 m in area and 10 cm in height) was embedded in the center of each plot one week prior to the measurements to avoid disturbance effects. A transparent chamber was placed on the frame to measure the carbon exchange for 80 s. The chamber was lifted and vented before putting on the square again. Then, an opaque cloth was used to cover the chamber for ER measurements. Gross ecosystem exchange (GEE) was calculated as [NEE−ER]. Our field measurements of NEE and ER were made three to four times per month. For each measurement, soil temperature (T_s) was

recorded by a portable thermometer at a depth of 10 cm. Soil volumetric water content (VWC) was simultaneously measured at a depth of 10 cm adjacent to the frame using a portable TDR-300 (Spectrum Technologies, Inc., Plainfield, IL, USA).

2.4. Statistical analyses

A nested block design was applied in our analysis of variance (ANOVA), with grazing as the main factor and precipitation as the nested factor so that the interactive effects between the two factors were prohibited from testing in this experiment. All data was transformed to normalized data by a log or sine function (i.e., removing the diurnal patterns). Nested two-way ANOVAs were used to examine the effects of grazing and precipitation on species richness (R_{sp}), ANPP, BNPP, MBC, and MBN in the peak of the growing season (i.e., August). Nested repeated measures analysis of variances (Nested RM-ANOVAs) were used to examine the effects of grazing and precipitation on T_s, VWC, proportion of dominant species (P_{stipa}), cover, H, AGB, LAI, NEE, ER, and GEE. The effects of grazing and precipitation on ecosystem carbon fluxes (NEE, ER, and GEE) and abiotic factors (T_s, VWC) were calculated as: absolute values (VALUE$_{treat}$−VALUE$_{control}$) and relative values (VALUE$_{treat}$−VALUE$_{control}$)/VALUE$_{control}$. We treated the relative values as classification variables, including the changes of carbon fluxes as dependent variables in the nested RM-ANOVAs to test the relative effects induced by grazing and watering. Regression analyses were also performed to evaluate the relationships between carbon fluxes and abiotic variables by treatment.

3. Results

3.1. Microclimate

The precipitation in 2012 was 359.80 mm, which is evidently higher than the average of the previous ten years (230 mm). 87.83% of the precipitation occurred in the growing season (May–October). Frequent rain events (94 times) occurred throughout the
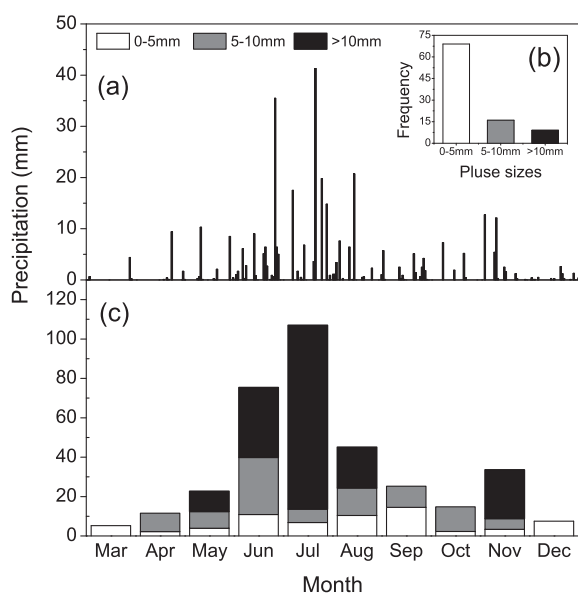

Fig. 1. (a) Daily precipitation in 2012; (b) the frequency of each rain events' sizes by dividing each event into groups of 0–5 mm, 5–10 mm, and >10 mm; (c) the cumulative amount of each rain event by group and month in 2012.

year, while a large proportion of precipitation (51.30%) was associated with the very limited rain pulses (>10 mm) (Fig. 1). The precipitation in the watered plots reached 429.80 mm. Daily mean VWCs at 10 cm depths in the control plots were 11.60%, 21.80%, and 9.98% in the early, peak, and late growing season and 8.68% in the non-growing season. The mean soil temperature (14.37 °C) at 10 cm had a one-peak pattern (Fig. 2). The historic grazing showed no effects on T_s or VWC. Watering stimulated VWC ($P < 0.001$), with 14.06% increases, whereas no significant difference existed on T_s ($P = 0.928$) (Tables 1–3).

3.2. Changes in community composition and structure

The long-term grazing over the immediate ten years prior to the experiment in 2012 greatly altered the community composition and structure. The canopy cover was reduced from 19.82% in the reference plot to 15.13% at LeA and 15.83% at LeC under no watering treatments ($P < 0.001$). Species richness (R_{sp}) was significantly reduced ($P = 0.001$) from 7.33 ± 0.42 in the reference plot to 4.83 ± 0.48 at LeA and 5.33 ± 0.42 in LeC. Grazing enhanced the proportion of dominant *Stipa breviflora Griseb.* (P_{stipa}) by 27% in LeA and 24% in LeC ($P < 0.001$). Interestingly, we found no grazing effect on LAI ($P = 0.658$). For productivity, as expected, the historic grazing significantly reduced AGB from 1152.30 kg ha^{-1} to 777.00 kg ha^{-1} (32.57% reduction) and 805.40 kg ha^{-1} (30.11% reduction) in LeA and LeC ($P < 0.001$), respectively. A similar reduction was also found for ANPP (34.32% and 26.15% for LeA and LeC, respectively, $P = 0.003$), but not for BNPP ($P = 0.279$) (Tables 2–4). Grazing stimulated MBC by 29.58% and 40.56% relative to the reference plot (244.25 mg kg^{-1}) of no water additions at LeA and LeC, respectively, and 0.54% and 9.07% in the precipitation plots (312.29 mg kg^{-1}) in the LeA and LeC under-watered plots ($P = 0.001$). There were no significant changes to MBN (Table 4, $P = 0.150$).

Precipitation significantly altered the canopy characteristics. Canopy cover was enhanced by 24.47% with water addition ($P = 0.001$) and 19.82% in the reference plot, but there were no obvious effects of watering on R_{sp}, H, LAI ($P = 0.070$; $P = 0.154$; $P = 0.915$, respectively), and P_{stipa} ($P = 0.873$) (Tables 2–4). Watering stimulated AGB ($P = 0.013$) and it was 30.60% higher in watered plots than non-watered plots. However, there were no significant changes in ANPP or BNPP ($P = 0.143$; $P = 0.249$, respectively) (Tables 2–4). MBC was significantly enhanced by 8.76% ($P = 0.022$) and MBN was significantly improved by 35.55% under the control plots, 4.35% under high grazing HG plots, and suppressed by 0.10% under light grazing plots ($P = 0.009$) (Table 4).

3.3. Seasonal changes in carbon fluxes

A greater GEE than ER in each measuring date lead to a carbon sink in 2012 (i.e., a wet year). The temporal changes in NEE, ER, and GEE followed a single peak pattern, with the maximum value occurring in early August, corresponding to the peak values of soil moisture and plant growth. In the control plots, the values of the carbon sink were lower in May (2.59 μmol m^{-2} s^{-1}) and October (3.75 μmol m^{-2} s^{-1}) and higher (16.98 μmol m^{-2} s^{-1}) in August (Fig. 3).

Historic grazing caused a significant ER reduction by 14.13% in the LeA plots ($P < 0.001$), but no effects were found in the LeC plots. Additionally, there appeared to be no obvious effects on NEE ($P = 0.108$) or GEE ($P = 0.068$). Watering increased ER by 12.57% (CK: 17.11%; LG: 8.29%; HG: 12.30%; $P < 0.001$). However, no changes were found for NEE ($P = 0.709$) or GEE ($P = 0.385$) (Tables 2 and 3).
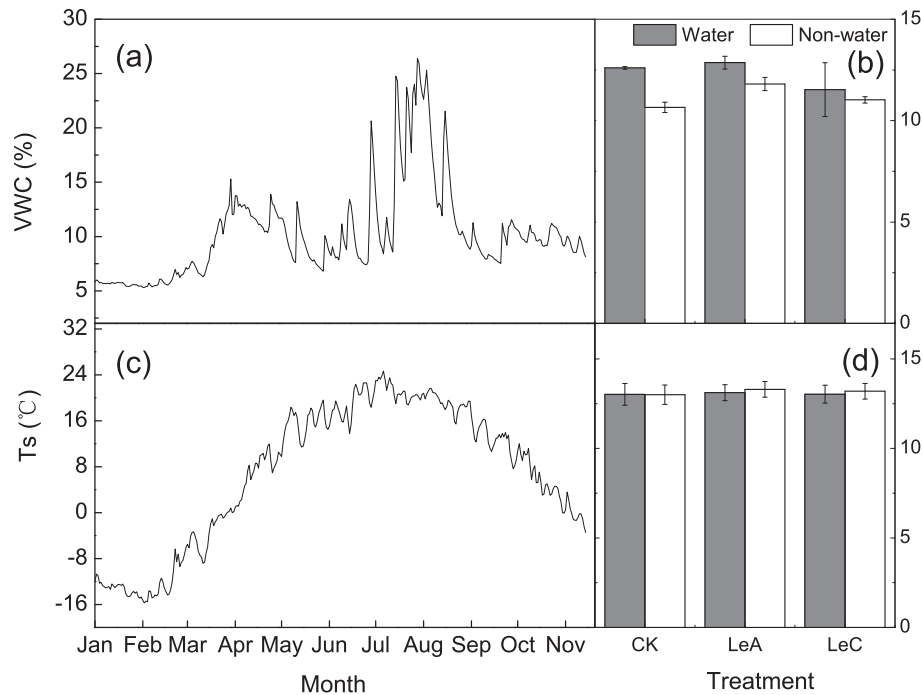
Fig. 2. (a) Daily mean volumetric soil moisture (VWC), (c) soil temperature (T_s) at the depth of 10 cm in the control plot, and (b, d) their annual means (Mean ± SE) under six treatments from a manipulative experiment in 2012.

3.4. Positive grazing effects on carbon fluxes

Grazing had marginal effects on changes of ER ($P = 0.064$) and produced no effects on changes of NEE or GEE (Table 5). However, there were significant differences on changes of NEE, ER, and GEE over time (Table 5). The logistic curves of NEE and GEE induced by relative grazing effects along the sampling dates showed that the negative effects of grazing on NEE and GEE were alleviated and tended to be near zero in August and then the positive effects were gradually amplified (NEE: adj.r^2 = 0.65, $P < 0.001$; GEE: adj.r^2 = 0.89, $P < 0.001$) (Fig. 4).

Table 1
Abbreviations of the variables and units applied in this paper.

Full name	Abbreviation
Aboveground live biomass (kg ha^{-1})	AGB
Aboveground net primary productivity (kg ha^{-1} yr^{-1})	ANPP
Belowground NPP (kg ha^{-1} yr^{-1})	BNPP
Canopy height (cm)	H
Control group	CK
Control plus no watering	CK_0
Control plus watering	CK_1
Ecosystem respiration (μmol m^{-1} s^{-2})	ER
Gross ecosystem exchange (μmol m^{-1} s^{-2})	GEE
Leaf area index	LAI
Level A: low stocking rate	LeA
Level A plus no watering	LeA_0
Level A plus watering	LeA_1
Level C: high stocking rate	LeC
Level C plus no watering	LeC_0
Level C plus watering	LeC_1
Microbial biomass carbon content (mg kg^{-1})	MBC
Microbial biomass nitrogen Content (mg kg^{-1})	MBN
Net ecosystem exchange (μmol m^{-1} s^{-2})	NEE
Proportion of Stipa breviflora Grisb.	P_{stipa}
Richness of species	R_{sp}
Soil temperature (°C)	T_s
Volumetric soil moisture (%)	VWC

3.5. Precipitation effects

Ambient precipitation had significant effects on the fluctuations of carbon exchanges (NEE, ER, GEE); however, for soil temperature, only ER was significantly dependent on it under good water conditions (Figs. 5 and 6). We found linear relationships between VWC and carbon exchanges (NEE, $P < 0.001$, ER, $P < 0.001$, and GEE, $P < 0.001$), where VWC explained the changes of NEE, ER, and GEE by 33%, 55%, and 43%, respectively, over the growing season. More interestingly, we found that a higher exponential correlation existed between soil temperature and ER only under high soil moisture (VWC > 15%). Watering also had a positive exponential relationship with the changes of NEE ($P < 0.001$) and GEE ($P < 0.001$). The changes of VWC explained the changes of NEE and GEE by 53% and 32%, respectively (Fig. 7a, b).

4. Discussion

4.1. The grazing legacies on vegetative communities

Selective foraging by herbivores directly modified the composition and structure of a plant community. Historic grazing at our site enhanced the proportion of dominant Stipa breviflora Griseb. (P_{stipa}) by 27% at LeA and 24% at LeC and reduced the species richness. These results were consistent with a study in a semi-natural mountain grassland (Medina-Roldan et al., 2012) where grazing also indirectly affected plant–soil relationships and modified the competition among species. More importantly, the arid, nutrient-scarce environment tended to select species associated with low forage quality and high resistance to grazing (i.e., the functional traits of the graminoids; Adler et al., 2004). In turn, these asymmetric competitions between species have been theorized as differential adaptation strategies of species to herbivory (Garrido et al., 2012; Parachnowitsch and Lajeunesse, 2012).

Ecosystem responses to historic grazing are embedded into the relationships of soils and plants to co-evolve and subsequently

Table 2
Annual averages of the biotic and abiotic variables in six treatments in 2012. The full name of each abbreviation can be found in Table 1. Values are Mean (SE) for $n = 6$ replicates for each treatment. The canopy height was calculated by the weighted means of individual species.

		CK_0	CK_1	LeA_0	LeA_1	LeC_0	LeC_1
Climate	T_s	14.37 (0.61)	14.35 (0.63)	14.73 (0.53)	14.49 (0.55)	14.55 (0.52)	14.34 (0.58)
	VWC	11.55 (0.34)	13.53 (0.13)	12.69 (0.27)	13.69 (0.32)	12.05 (0.29)	14.11 (0.59)
Structure & composition	P_{stipa}	0.43 (0.09)	0.41 (0.08)	0.70 (0.04)	0.65 (0.02)	0.67 (0.05)	0.63 (0.04)
	H	12.67 (0.62)	14.16 (0.80)	10.52 (0.88)	11.57 (0.76)	8.51 (0.41)	10.27 (0.74)
	R_{sp}	7.33 (0.42)	7.50 (0.56)	4.83 (0.48)	6.33 (0.21)	5.33 (0.42)	6.50 (0.67)
	Cover	19.82 (0.85)	27.14 (1.46)	15.13 (0.50)	17.10 (0.72)	15.83 (0.80)	19.54 (1.64)
	LAI	0.44 (0.01)	0.58 (0.15)	0.41 (0.04)	0.50 (0.10)	0.42 (0.09)	0.43 (0.07)
Productivity	NEE	−4.49 (0.33)	−5.58 (0.54)	−4.45 (0.27)	−4.67 (0.26)	−4.78 (0.49)	−5.40 (0.58)
	ER	3.53 (0.13)	4.13 (0.32)	3.03 (0.13)	3.28 (0.10)	3.32 (0.14)	3.73 (0.28)
	GEE	−8.01 (0.44)	−9.80 (0.86)	−7.49 (0.38)	−7.94 (0.36)	−8.10 (0.63)	9.12 (0.84)
	MBC	244.3 (19.14)	312.3 (19.55)	316.5 (11.07)	314.0 (7.45)	343.3 (8.98)	340.6 (15.40)
	MBN	47.59 (4.61)	64.51 (4.75)	56.71 (2.05)	56.70 (1.38)	60.68 (0.75)	63.33 (3.54)
	AGB	1152 (12.28)	1540 (12.78)	777 (3.65)	1035 (9.63)	805 (5.23)	995 (12.34)
	ANPP	2594 (40.4)	3578 (52.4)	1704 (18.4)	2282 (24.8)	1916 (20.9)	2084 (32.3)
	BNPP	5616 (105.1)	18732 (1048)	5448 (192.4)	7675 (230.5)	5031 (136.1)	5402 (86.1)
	ANPP/BNPP	0.56 (0.13)	0.60 (0.24)	0.44 (0.16)	0.50 (0.11)	0.51 (0.12)	0.44 (0.09)

form polymorphic populations and phenotypically plastic communities (Coughenour, 1985; Cronin et al., 2003; Parachnowitsch and Lajeunesse, 2012). Nevertheless, previous grazing-related studies emphasized the carbon stock and partition, the shift of species composition, and roots as well as their controls on soil microbial communities in a typical steppe of the Mongolian Plateau (Adler et al., 2004; Liu et al., 2012; Schönbach et al., 2011), a wet grassland (Rossignol et al., 2011), a mountain meadow (Virtanen, 2003), a Tibetan montane (Hafner et al., 2012; Unteregelsbacher et al., 2012), a tropical pasture (Wilsey et al., 2002), and a salt marsh (Olsen et al., 2011), but they were focused on the effects of concurrent grazing effects. Based on the ten-year grazing experiment, we found that reduced canopy AGB and cover and the ratio of ANPP/BNPP were the legacy effects that altered the biomass and reallocation of carbon from aboveground to belowground. Plants remained dwarfed in response to historic grazing, which may be the species legacies of evasive actions to avoid excessive foraging. However, lowered AGB, cover, and height did not reduce the canopy LAI as expected, revealing the adaptation ability of plants to acquire more energy from photosynthesis to alleviate tissue losses. The reduced ratio of ANPP/BNPP was beneficial to the belowground carbon storage to prevent species extinction under the changing climate, which may also be an adaptation of substantial morphological changes after long-term herbivory. However, clear challenges remain to distinguish the responses to and feedbacks of the relationship between ecosystems and historic grazing.

Historic grazing with high intensity produced greater legacies on soils. Higher MBC found in high grazing at the non-water-added plots indicated that a relatively high grazing intensity could strengthen MBC while precipitation had a weak effect on MBC. Similar results had been reported in maize fields (Nat Holland, 1995) and a temperate salt mash (Olsen et al., 2011). One possible explanation offered by Hamilton and Frank (2001) was that enhanced root carbon exudation induced by herbivores was sharply assimilated into the microbial population in the rhizosphere, which would, in turn, result in a higher MBC in grazing blocks.

4.2. Seasonal changes in carbon gains and losses

In the desert steppe, frequent precipitation pulses ($\sim$94 times in 2012) with medium or strong rain events (i.e., >5 mm) regulated the large annual net carbon sinks (4.48 μmol m^{-2} s^{-1}) in the control plots, which were higher than those in typical steppe (2005 rainfall: 322.8 mm, NEE: 3.17 μmol m^{-2} s^{-1}; 2006 rainfall: 407.7 mm, NEE: 2.77 μmol m^{-2} s^{-1}) (Niu et al., 2008). Seasonal variations of ER and GEE appeared as unimodal distributions, which were consistent with the changes in soil moisture (Figs. 2 and 3). ER ranging from 1.48 μmol m^{-2} s^{-1} to 10.13 μmol m^{-2} s^{-1} and GEE ranging from −2.59 μmol m^{-2} s^{-1} to −22.85 μmol m^{-2} s^{-1} in the CK plots indicated differential magnitudes and sensitivities of respiration and photosynthesis to water addition.

4.3. Grazing legacies promoting carbon uptake

Overall, no significant changes were found in NEE or GEE, but a reduction occurred in ER. This reduction in ER was consistent with the distinctive decreases in cover, height, AGB, and ANPP, demonstrating that the internal mechanism of the respiration process is consistent in all living cells of plants. Therefore, any changes in biomass-related variables will also be strongly correlated with ecosystem respiration. Additionally, higher ER in the LeC plots (3.52 μmol m^{-2} s^{-1}) than in LeA plots (3.12 μmol m^{-2} s^{-1}) may be ascribed to the higher microbial respiration from microbial activities. Grazing did not affect GEE, which matched well with no changes in LAI, leading to a potential equivalent photosynthesis among all treatments (Tables 2 and 3).

Table 3
Statistical results (P-values) of Nested Repeated-Measures ANOVAs in a nested random block design on the effects of measuring date (D), grazing (G), watering within grazing plots (W), and interactions between the classification factors (G, W) and date (D) on these variables during the growing season of 2012. The full name of each abbreviation can be found in Table 1. The canopy height was calculated by the weighted mean of individual species in plots. There are six replicates for each treatment.

	T_s	VWC	AGB	LAI	Cover	H	P_{stipa}	NEE	ER	GEE
D	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
D × G	<0.001	<0.001	0.005	0.639	0.093	<0.001	0.351	0.012	<0.001	0.001
D × W	0.021	0.052	0.201	0.454	0.403	0.408	0.122	0.155	0.011	<0.001
G	0.827	0.168	<0.001	0.658	<0.001	<0.001	<0.001	0.108	<0.001	0.068
W	0.928	<0.001	0.013	0.915	0.001	0.154	0.873	0.709	<0.001	0.385

Table 4
Statistical results (*P*-values) of the nested ANOVAs in a nested random block design on R_{sp}, ANPP, BNPP, MBC, and MBN in 2012. These variables were only measured in August, with six replicates for each treatment.

	R_{sp}	ANPP	BNPP	MBC	MBN
G	0.001	0.003	0.279	0.001	0.150
W	0.070	0.143	0.249	0.022	0.009

Table 5
Results (*P*-values) of nested RM-ANOVAs of the relative effects of grazing and watering on the changes of ecosystem CO_2 fluxes in 2012.

Treatments effects	$\triangle$ NEE	$\triangle$ ER	$\triangle$ GEE
D	0.002	<0.001	0.019
D × Relative grazing effects	0.169	0.772	0.333
Relative grazing effects	0.338	0.064	0.199
D	0.209	0.065	0.161
D × Relative watering effects	0.383	0.084	0.251
Relative watering effects	0.026	0.128	0.128

Relative grazing effects were referred to: $(VALUE_{LeA\_0}-VALUE_{CK\_0})/VALUE_{CK\_0}$; $(VALUE_{LeC\_0}-VALUE_{CK\_0})/VALUE_{CK\_0}$; $(VALUE_{LeA\_1}-VALUE_{CK\_1})/VALUE_{CK\_1}$; $(MEAN_{LeC\_1}-MEAN_{CK\_1})/VALUE_{CK\_1}$.
Relative water effects were referred to: $(VALUE_{CK\_1}-VALUE_{CK\_0})/VALUE_{CK\_0}$; $(VALUE_{LeA\_1}-VALUE_{LeA\_0})/VALUE_{LeA\_0}$; $(VALUE_{LeC\_1}-VALUE_{LeC\_0})/VALUE_{LeB\_0}$.

Grazing legacies in communities distinctly promoted photosynthesis and carbon sequestration over time. So far, studies on the legacy effects of disturbances have mainly underlined the neutral or even negative consequences in the fields of agricultural land use (Bellemare et al., 2002; Hermy and Verheyen, 2007; Schaffner et al., 2012), wildfire (Gough et al., 2007; Lorente et al., 2013; Zarin et al., 2005), invasive and removal species (Elgersma et al., 2011), forest management (Franklin et al., 2002; Gimmi et al., 2013; Gough et al., 2007; Royo et al., 2010; Saunders et al., 2002), and extreme climate (Edmondson et al., 2013; Goransson et al., 2013; Reichmann et al., 2013; de Vries et al., 2012). Wildfire and forest harvest disturbances remarkably changed the ecosystem plant quality and successional status and decreased the forest carbon storage (Lorente et al., 2013). The legacies of species removal resulted in decreased primary productivity by 40−60% after 90 months in a near-shore ecosystem (Tait and Schiel, 2011). Drought legacies of the preceding two years accounted for 20% of the carbon stock changes in a desert steppe (Reichmann et al., 2013). Different from these legacy effects, we argued that the distinctly positive results of the historic grazing effects on NEE and GEE may increase over time, which was ascribed to the comprehensive accumulated effects of the community rather than one single-factor effect. This founding was also contrary to the research of current grazing on carbon fluxes (Cao et al., 2004). The cause for this different consequence was that long-term herbivory activities shape community composition, which could reverse the negative grazing effects.

4.4. Precipitation regulating the strength of carbon uptake

As expected, water played a dominant role in the variability of carbon fluxes in our dryland ecosystem (Austin and Sala, 2009; Jongen et al., 2011). The fact that we found no significant correlations between the carbon fluxes (NEE, ER, GEE) and temperatures at any treatment in our study stimulated our effort in seeking the roles of water and temperature in this system. Changes in soil moisture could explain the variability of NEE, ER, and GEE by 33%, 54%, and 43%, respectively (Fig. 5). The experimental watering treatment-induced changes in NEE and GEE were also highly correlated with the alterations of the related soil moisture (Fig. 7a, b), indicating that water is the critical abiotic determinant for the dominancy of the seasonal changes of carbon fluxes in the desert steppe. For ER, our finding that water was a dominant variable that stimulates carbon fluxes was inconsistent with the commonly accepted conception of temperature-regulating respiration (Atkin and Tjoelker, 2003). There are two reasons to explain this phenomenon. First, frequent rain events and more available precipitation (i.e., >3 mm) in the growing season contribute to the rapid
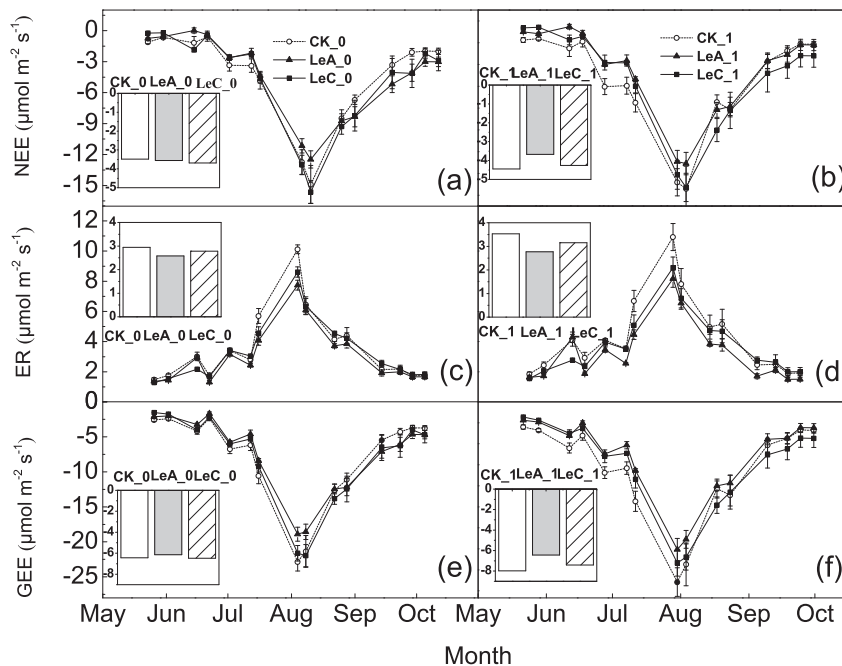

Fig. 3. Seasonal variability of net ecosystem exchange (NEE) (a, b), ecosystem respiration (ER) (c, d), and gross ecosystem exchange (GEE) (e, f) in 2012. The first column was under no watering and the second column was under watering treatment. CK_0, no grazing; LeA_0, 0.93 sheep ha^{-1} half a year^{-1}; LeC_0, 2.71 sheep ha^{-1} half a year^{-1}; CK_1, no grazing plus watering; LeA_1, 0.93 sheep ha^{-1} half a year^{-1} plus watering; LeC_1, 2.71 sheep ha^{-1} half a year^{-1} plus watering.
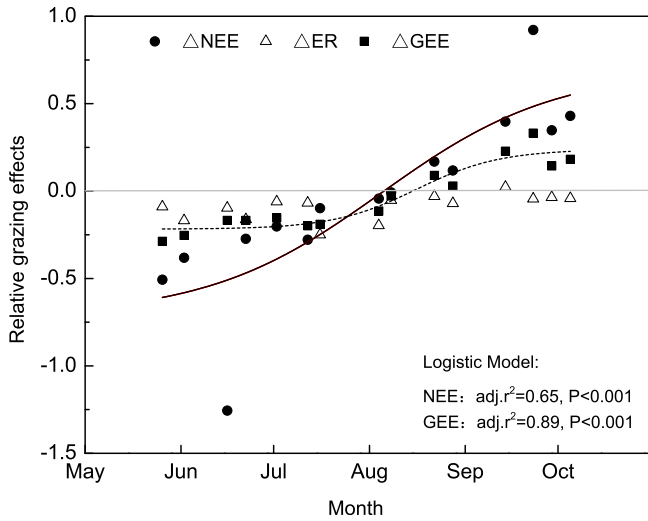
Fig. 4. The relative grazing effects on NEE (solid line) and GEE (dash line) over time. We calculated the relative light grazing and heavy grazing effects according to the equations in Table 5 for each sampling and then they were averaged in order to obtain the mean effects of the grazing.

Fig. 6. Volumetric soil water contents (VWCs) were divided into two groups with a VWC of 15% as the threshold point. We analyzed the dependence of ecosystem respiration (ER) on soil temperature (T_s) under the two VWC conditions.

growth of plants (i.e., higher ER) as water could promote the absorption of nutrients. Second, although some frequent rain pulses occurred in the growing season of 2012, they cannot change the fact that drought played an overwhelming role in the desert steppe (i.e., VWC in most periods of the growing season was below 15%). Thus, when we divided this data into two groups according to the VWC of 15%, a significant exponential function occurred between soil temperature and ER, which revealed that the dependence of ER on the soil temperature was under no other limiting or existing factors (Fig. 6). We concluded that water is the most important abiotic determinant for regulating the magnitude of carbon exchange in a desert steppe.
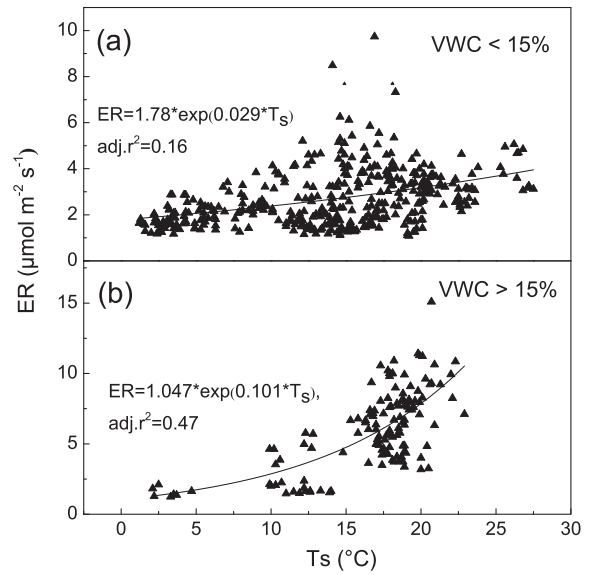
5. Conclusions

Through a manipulative experiment of grazing intensity and watering, we found that although precipitation regulated the magnitude of carbon exchange in the desert steppe, as expected, grazing legacies offset the adverse consequences of current grazing via promoting carbon sequestration, which is caused by modified community composition and function. However, this carbon sink is under the condition of the moderate grazing that could not cause catastrophes such as desertification. On the Mongolian Plateau, grazing (i.e., disturbance) is the main avenue for gaining social
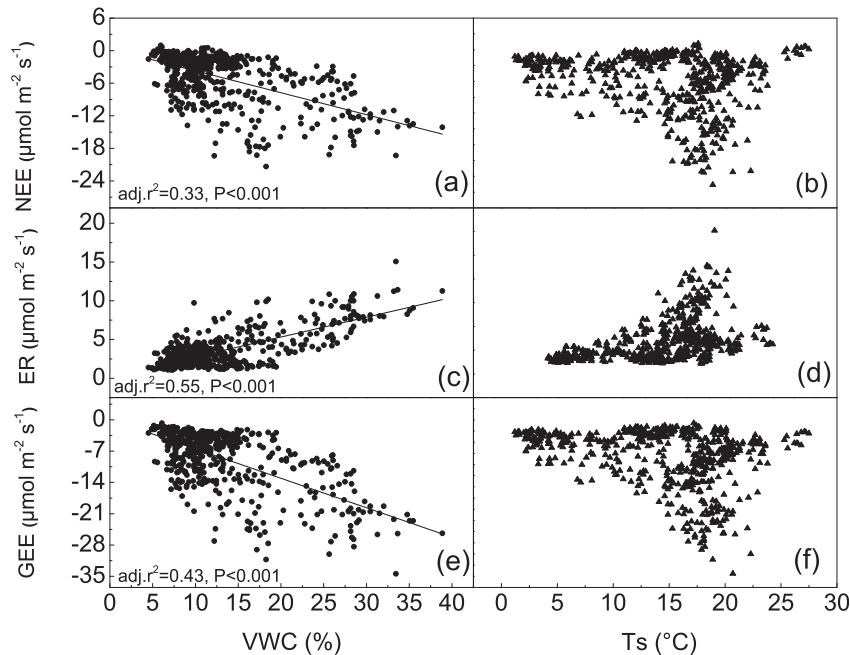

Fig. 5. The correlations of volumetric soil moisture (VWC), soil temperature (T_s) with net ecosystem exchange (NEE) (a, b), ecosystem respiration (ER) (c, d), and gross ecosystem exchange (GEE) (e, f).
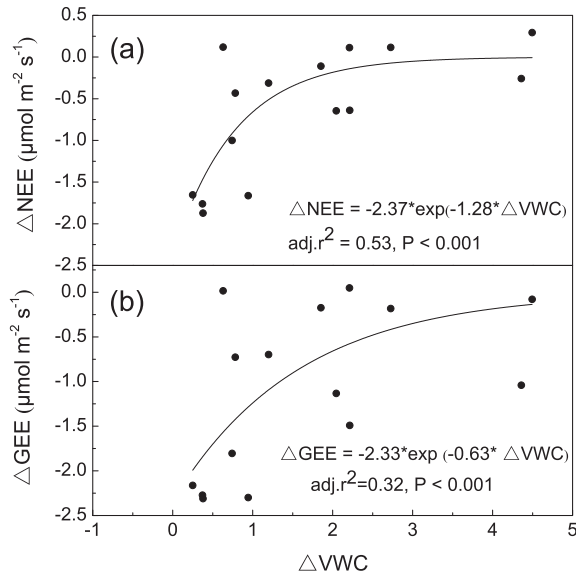
Fig. 7. Dependence of the water-induced changes in net ecosystem carbon exchange (NEE), a) and gross ecosystem carbon exchange (GEE), b) on the water-induced percent changes in volumetric soil moisture (VWC).

products and, to some extent, will tip the balances of pasture ecosystems for their functions. Therefore, the research related to the degree of grazing will continue to be an important issue for future investigations.

Acknowledgments

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