






Original Article



Effects of long-term grazing exclusion on vegetation structure, soil water holding capacity, carbon and nitrogen sequestration capacity in an alpine meadow on the Tibetan Plateau


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Abstract: Grazing exclusion is one of the primary management practices used to restore degraded grasslands on the Tibetan Plateau. However, to date, the effects of long-term grazing exclusion measures on the process of restoring degraded alpine meadows have not been evaluated. In this study, moderately degraded plots, in which the vegetation coverage was approximately 65% and the dominant plant species was *Potentilla anserina* L, with grazing exclusion for

2 to 23 years, were selected in alpine meadows of Haibei in Qinghai-Tibet Plateau. Plant coverage, plant height, biomass, soil bulk density, saturated water content, soil organic carbon (SOC) and total nitrogen (TN) were evaluated. The results were as follows: (1) With increased grazing exclusion duration, aboveground biomass and total saturated water content at 0-40 cm depth, the average SOC and TN contents in moderately degraded alpine meadows increased as a power function, and the plant height increased as a log function. (2) The average soil bulk density at 0-40 cm depth first decreased and then increased with increasing grazing exclusion duration,

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and the minimum value of $0.90 \text{ g}\cdot\text{cm}^{-3}$ was reached at 15.23 years. The plant coverage, total belowground biomass at 0-40 cm depth, total aboveground and belowground biomass first increased and then decreased, their maximum values (80.49%, $2452.92 \text{ g}\cdot\text{m}^{-2}$, $2891.06 \text{ g}\cdot\text{m}^{-2}$) were reached at 9.41, 9.46 and 10.25 years, respectively. Long-term grazing exclusion is apparently harmful for the sustainable restoration of degraded alpine meadows. The optimal duration of grazing exclusion for the restoration of moderately degraded alpine meadows was 10 years. This research suggests that moderate disturbance should be allowed in moderately degraded alpine meadows after 10 years of grazing exclusion.

Keywords: Long-term grazing exclusion; Soil water holding capacity; Soil carbon and nitrogen sequestration; Biomass; Alpine meadow

1 Introduction

The total area of grassland on the Tibetan Plateau (TP) is $1.52 \times 10^6 \text{ km}^2$, which accounts for approximately one-third of the grassland in China. The sustainability of these grasslands plays a very important role in traditional means of livelihood associated with animal husbandry, protecting biodiversity and maintaining ecological balance (Wen et al. 2012; Li et al. 2006a). As one of the main components of water source conservation, alpine meadows are a widespread land cover type and contain the representative vegetation type for the TP (Cao et al. 2004). Due to the harsh environment and vulnerable biomes in alpine meadow regions (Sun et al. 2020), alpine meadow ecosystems are extremely sensitive to climate change and human activities. By the end of the 20th century, due to the combined effects of global warming and disturbance from human activities (e.g., overgrazing, overexploitation, development, etc.), the alpine meadows on the TP had become seriously degraded (Shang and Long 2007). Extremely degraded alpine meadows are common in the headwaters of the Yangtze and Yellow Rivers of the TP (Wang and Fu 2004), where they account for approximately 30 percent of the alpine grassland (Zhou et al. 2005; Shang and Long 2007). To restore and improve the environmental quality in degraded alpine meadows, the Chinese government has invested substantial labour and material resources in recent decades and has implemented many measures to control alpine meadow degradation, including

grazing exclusion (Wu et al. 2010); grazing reduction; rodent, pest and poisonous weed control; and comprehensive management (Shang et al. 2008). Among these measures, grazing exclusion, which has low investment costs and immediate benefits, has been widely adopted by the local and central government to restore degraded alpine grasslands since 2003 (Wu et al. 2010; Sun et al. 2020).

Although there have been some studies on the effects of grazing exclusion on vegetation structure, species diversity (Shang et al. 2013; Zhang et al. 2015; Yao et al. 2019) and soil physicochemical properties (Yang et al. 2016; Li et al. 2017b) reported in recent years, most of them have focused only on short-term grazing exclusion (Wu et al. 2009, 2010). Little research has been conducted on the effects of long-term grazing exclusion on water conservation, soil nutrients and vegetation structure in alpine meadows, especially the effects of grazing exclusion durations greater than 15 years. This shortcoming has seriously limited the accurate assessment of the effects of grazing exclusion duration on the restoration of degraded alpine meadows.

Some research has shown that long-term grazing exclusion (9 years) not only inhibited the regeneration of plants and the formation of seedlings, decreased the conversion of vegetation productivity (Risser 1993; Altesor et al. 2005) and the biodiversity of plants (Yao et al. 2019), but also directly caused mortality and injuries in a wide range of birds and mammals (Rey et al. 2012; Jones et al. 2014), and affected the reproduction of some wild animals (Said et al. 2016; Jakes et al. 2018). More importantly, long-term grazing exclusion inevitably reduced the income of herders and hindered economic development in pasture regions. Therefore, the sustainable economic development of animal husbandry in grasslands and the utilization and renewal of grassland resources in pastoral areas should be comprehensively considered. Many researchers believe that long-term grazing exclusion in grasslands is unreasonable (Micchunas et al. 1988; Agarwal et al. 1993; Adler et al. 2004), and they propose that after a certain grazing exclusion period, moderate grazing should be carried out in the grazing exclusion region (Risser 1993; Sun et al. 2020). However, because there were great differences in the climate, soil and plant conditions, and degradation degree in different grasslands on the TP, the optimal duration of grazing exclusion for the restoration of degraded grassland is expected to be

different in different grasslands (Sun et al. 2020; Xu et al. 2020). It is necessary to conduct specific research on the optimal duration of grazing exclusion for specific types of grazing lands, such as degraded alpine meadows. Therefore, we hypothesized that long-term grazing exclusion is likely not the most beneficial approach for the sustainable restoration of degraded alpine meadows on the TP. Furthermore, grazing exclusion measures in degraded alpine meadows probably have a certain time component that can be determined through data analysis, and moderate disturbances (e.g., seasonal grazing) should be allowed in alpine meadows after the optimal duration of grazing exclusion.

The objective of the present study was to quantify the effects of long-term grazing exclusion on vegetation structure, soil water holding capacity, and carbon and nitrogen sequestration capacity in an alpine meadow. Based on these analyses, we identify the beneficial and harmful effects of grazing exclusion in alpine meadows and the optimal duration of grazing exclusion for the restoration of degraded alpine meadows. We expect that these results will provide an essential data for ecological conservation and the sustainable development of animal husbandry in alpine meadows.

2 Materials and Methods

2.1 Study sites

The experiment was conducted in August 2018 at the Haibei alpine meadow research station (Haibei station). The Haibei station is located in the northeastern TP in a large valley oriented from NW–SE and surrounded on all sides by the Qilian Mountains, at latitude 37°29'–37°45'N and longitude 101°12'–101°23'E. The average elevation of the mountain area is 4000 m, and the average elevation of the valley area is 2900–3500 m. This area experiences a typical plateau continental climate with long severe winters and short cool summers. The average air temperature is -1.7°C, with a maximum of 27.6°C and a minimum of -37.1°C. The average annual precipitation ranges from 426 to 860 mm, 80% of which is in the form of rain during the short summer growing season from May to September. The annual average amount of sunlight is 2462.7 hrs. The soil type is mainly alpine meadow soil. The vegetation is

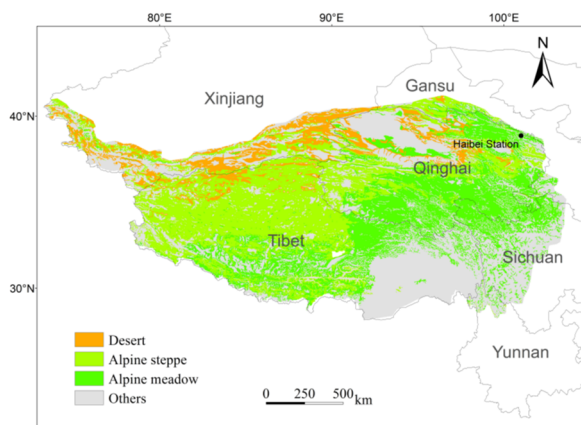
typical of an alpine meadow and is dominated by *Kobresia humilis*, *Gentiana straminea* Maxim, *Stipa aliena*, *Poa orinosa*, *Festuca ovina*, and *Elymus nutans*. Overgrazing had led to the degradation of 30% of pasturelands in the Haibei region before the end of the 20th century (Zhao and Zhou 1999).

2.2 Experimental design

To study the effects of grazing intensity, grazing exclusion, simulated warming and nutrient addition on the ecosystem functions of the alpine meadows, some grazing exclusion plots were established at Haibei station from the end of the twentieth century to the beginning of this century. Some of them were selected as the research subject to explore the effect of long-term grazing exclusion on vegetation structure, soil water holding capacity, carbon and nitrogen sequestration capacity by using the substitution method of space for time. In August 2018, 10 of these grazing exclusion sites, whose duration of grazing exclusion was 2, 6, 7, 11, 13, 15, 18, 19, 20, and 23 years, were selected for this study with the following characteristics: 1) the area of the grazing exclusion plot was at least 50 m²; 2) before grazing exclusion, the alpine meadow had degraded to the middle degradation level, where the vegetation coverage was approximately 65% (Zeng et al. 2013); the dominant plant species was *Potentilla anserina* L, and the associated plant species were *Pedicularis kansuensis* and *Ligularia virgaurea*. A grazing plot that had reached the middle degradation level was selected as a control treatment (CK). The grazing intensity for the control site was 5 sheep units per hm², the grazing time was from September to May of the following year, and the grazing animal was Tibetan sheep. Therefore, including 10 grazing exclusion sites and a CK treatment, there were 11 treatments in the current study. All 11 research sites were distributed within 8 km² of Haibei station; therefore, the topography, rainfall, temperature and other ecological factors were generally consistent, and their basic information is shown in Fig. 1.

2.3 Sample collection

Three 5 m×5 m (length × width) experimental plots were established at the 11 research sites, and the plant coverage and average plant height in each experimental plot were measured in August 2018.



(a) Location of the Haibei station in the Qinghai-Tibetan Plateau

Sampling sites	Grazing exclusion duration (yr)	Longitude (N)	Latitude (E)	Elevation. (m)
Site1(CK)	1	37°36'41.54"	101°18'16.27"	3190
Site2	2	37°36'40.99"	101°18'13.86"	3191
Site3	6	37°36'30.92"	101°18'12.27"	3187
Site4	7	37°36'37.84"	101°18'45.54"	3194
Site5	11	37°36'37.72"	101°18'43.30"	3195
Site6	13	37°36'38.74"	101°18'46.93"	3194
Site7	15	37°36'47.91"	101°18'16.60"	3197
Site8	18	37°36'38.43"	101°18'43.82"	3195
Site9	19	37°36'34.07"	101°18'20.36"	3190
Site10	20	37°36'37.03"	101°18'41.71"	3194
Site11	23	37°36'39.15"	101°18'46.03"	3190

(b) Location information of the sampling sites

Fig. 1 Locations and basic information of sampling points. Site 1 (CK) was grazing plots that reached moderate degradation levels. The grazing exclusion duration for CK was set to 1 year, because the relevant data could not be fit if their grazing exclusion duration was set to 0 in the figure which is shown in the results and analysis section.

Three sample locations (1 m × 1 m) were selected randomly in each experimental plot, and undisturbed soil cores were collected at depths of 0 to 10, 10 to 20, and 20 to 40 cm using the standard cutting ring method (Yang et al. 2016). The undisturbed soil cores in the cutting ring were prepared for measurements of soil bulk density and saturated water capacity. Additional soils from the three layers were collected in plastic Ziplock bags, and after careful removal of the roots, the soils were air dried and sifted through a 1 mm sieve and prepared for measurements of soil organic carbon (SOC) and total nitrogen (TN).

2.4 Measurements

2.4.1 Determination of plant coverage and height

Five 0.5 m × 0.5 m (length × width) quadrats in

the center and four diagonal corners of each experimental plot were selected in August 2018, and a point sampling frame (10 cm × 10 cm grid, 100 points per 100 cm × 100 cm) was used to measure the plant coverage in each experimental plot (Li et al. 2010). Thirty plants were randomly selected in each experimental plot to calculate the average height of the plants. When the number of plants in a quadrat was fewer than thirty, the height of all plants was measured. The determination of plant coverage and height at each experimental plot was replicated five times.

2.4.2 Determination of aboveground and belowground biomass

First, after removing litter from the soil surface in the quadrats, the litter was carefully collected in paper bags. Second, the aboveground parts of plants, which were cut by shears, were collected in paper bags. Third, the soil columns of the above quadrats were collected from depths of 0 to 10, 10 to 20, and 20 to 40 cm by a root auger with a diameter of 8 cm, and the soil columns were placed into nylon bags and brought indoors. After carefully removing any small stones, the soil columns were washed through a 1 mm sieve, and the clean plant roots were collected in paper bags. Finally, all collected aboveground parts and underground roots were placed in a drying oven at a temperature of 85°C to a constant weight, and they were weighed with a precision of 0.01 g.

2.4.3 Determination of soil bulk density and saturated water capacity

The undisturbed soil cores at depths of 0 to 10, 10 to 20 and 20 to 40 cm were placed in a square plastic basin, and water was poured into the plastic basin until the water level was flush with the surface of the undisturbed soil cores. When undisturbed soil cores were saturated completely, the undisturbed soil cores were carefully removed from the water and instantly weighed. Then, the undisturbed soil cores were placed in an oven at 105°C until they reached a constant weight. The soil bulk density and saturated water capacity were calculated using the equations included in Yang et al. (2018).

2.4.4 Determination of SOC and TN

After the soil samples were air-dried, the roots and gravel in the soil samples were carefully removed and sifted through a 0.25 mm sieve. The SOC content was measured using the heated dichromate/titration

method, and the TN concentration was determined by the semimicro Kjeldahl method (Wang et al. 2011).

2.5 Data analyses

Data are expressed as the mean ± standard error. Data were analysed for significance with one-way analysis of variance and the least significant difference test in SPSS 12.0 software (SPSS Inc., Chicago, IL, USA), with significance set at $P < 0.05$. The analysis of correlations among the different index values was performed in SAS 9.0 (SAS Institute, Inc., Cary, North Carolina).

3 Results and Analyses

3.1 Dynamic changes in plant coverage and height

With increasing duration of grazing exclusion, plant coverage of degraded alpine meadows first increased to a point and then decreased (Fig. 2). According to the regression equations for plant coverage, the maximum value of plant coverage (80.49%) was reached after grazing exclusion for 9.41 years. The plant height in the moderately degraded alpine meadow increased as a log function with increasing duration of grazing exclusion (Fig. 2). From the CK plot to the plot that had grazing exclusion for 2 years, the plant height was significantly increased by 110.61% ($P < 0.05$), and the increase rate was 3.65 cm·yr⁻¹. From the 6 year grazing exclusion plot to the 23 year grazing exclusion plot, the plant height gradually increased, but the degree of increase did not reach a significant level ($P > 0.05$).

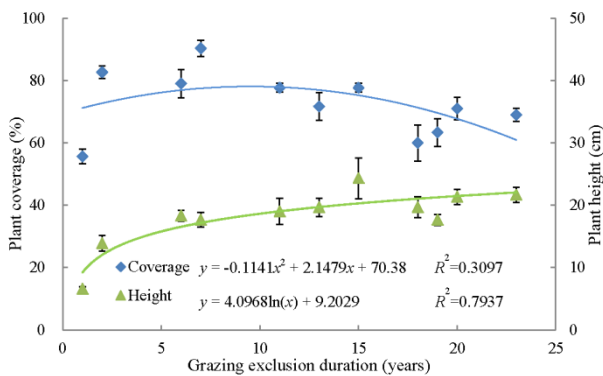


Fig. 2 Variation of plant coverage and plant height with grazing exclusion duration. Bars mean standard errors.

3.2 Dynamic changes in aboveground and belowground biomass

The total belowground biomass at 0-40 cm depth and the total aboveground and belowground biomass in the moderately degraded alpine meadow first increased and then decreased with increasing duration of grazing exclusion (Fig. 3a), and their maximum values (2452.92, 2891.06 g·m⁻²) were reached at 9.46, 10.25 years, respectively. The aboveground biomass in the moderately degraded alpine meadow increased as a power function with increasing duration of grazing exclusion. From CK to grazing exclusion for 7 years, the aboveground biomass of the moderately degraded alpine meadow significantly increased by 49.95%, and from grazing exclusion for 11 years to 23 years, the aboveground biomass showed no significant changes, which were generally stable at approximately 464.56 g·m⁻². The belowground biomass was significantly greater than the aboveground biomass in the alpine meadow, and the belowground biomass accounted for 82.86% of

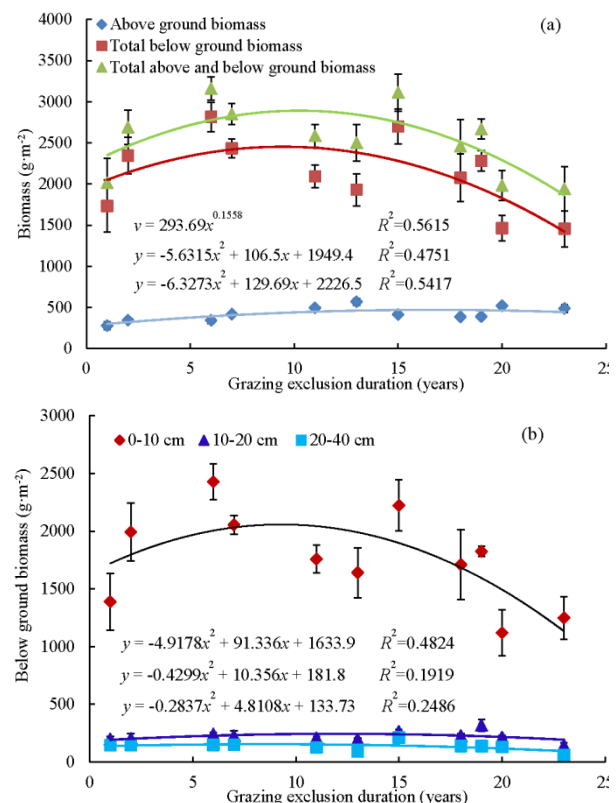
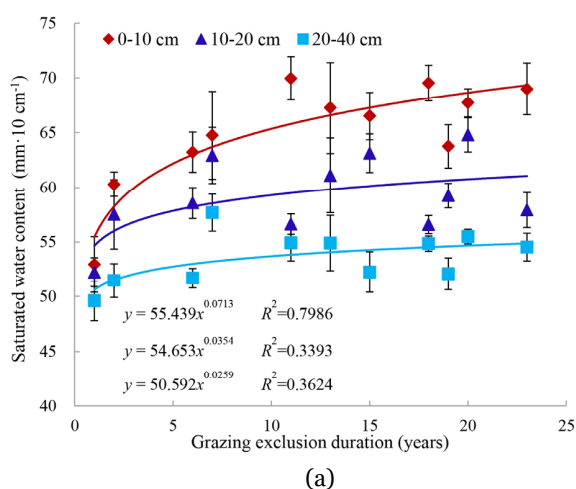


Fig. 3 Variation of above ground biomass, total below ground biomass, total above and below ground biomass (a) and below ground biomass at 0-10, 10-20, and 20-40 cm depths (b) with grazing exclusion duration. Bars mean standard errors.

the total aboveground and belowground biomass.

With increasing soil depth, the belowground biomass significantly decreased (Fig. 3b), and the belowground biomass was mainly concentrated at 0-10 cm depths. The belowground biomass at 0-10 cm accounted for 82.90% of the total belowground biomass at 0-40 cm depth. The belowground biomass at 0-10, 10-20 and 20-40 cm depths first increased and then decreased with increasing duration of grazing exclusion, reaching maximum values of 2057.99, 244.17 and 154.12 g·m⁻² at 9.29, 12.04 and 8.48 years, respectively.

3.3 Dynamic changes in saturated water content



content

The saturated water content at 0-10, 10-20, and 20-40 cm depth and the total saturated water content at 0-40 cm depth increased as a power function with increasing duration of grazing exclusion (Fig. 4). From CK to grazing exclusion for 7 years, the saturated water content at 0-10, 10-20, and 20-40 cm and the total saturated water content at 0-40 cm significantly increased by 22.31%, 20.48%, 16.31% and 18.93%, respectively ($P < 0.05$), and from grazing exclusion for 11 years to grazing exclusion for 23 years, the saturated water content at different depths gradually increased in fluctuation, but the degree of increase did not reach a significant level ($P > 0.05$).

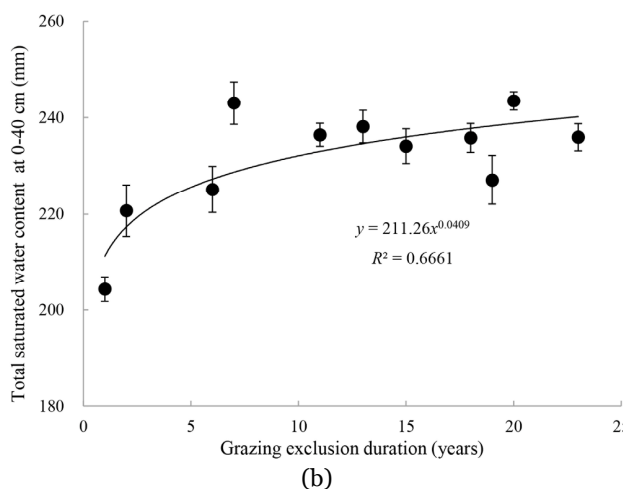


Fig. 4 Variation of saturated water content at 0-10, 10-20, and 20-40 cm depths (a) and total saturated water content of the 0-40 cm depth (b) with grazing exclusion duration. Bars mean standard errors.

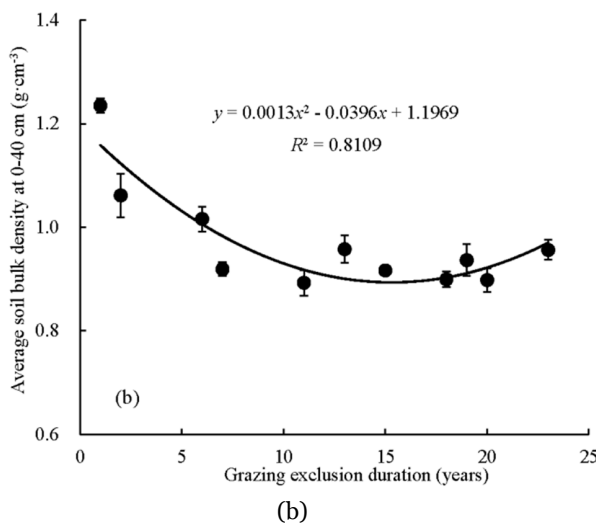
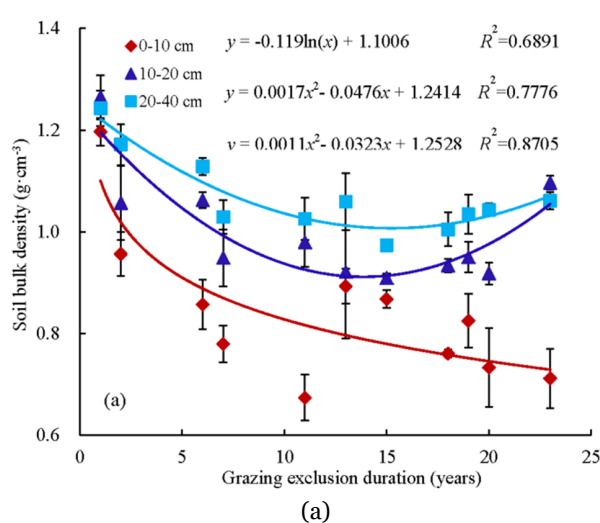


Fig. 5 Variation of soil bulk density at 0-10, 10-20, and 20-40 cm depths (a) and average soil bulk density of the 0-40 cm depth (b) with grazing exclusion duration. Bars mean standard errors.

3.4 Dynamic changes in soil bulk density

The effects of grazing exclusion duration on the soil bulk density of the alpine meadow were different due to the difference in soil depths (Fig. 5a). The soil bulk density at 0-10 cm depth decreased with increasing duration of grazing exclusion, with a decreasing rate of $0.02 \text{ g}\cdot\text{cm}^{-3}\cdot\text{yr}^{-1}$. The soil bulk density at 10-20 and 20-40 cm first decreased and then increased with increasing duration of grazing exclusion, and the minimum values of the soil bulk density at 10-20 and 20-40 cm (0.91 and $1.02 \text{ g}\cdot\text{cm}^{-3}$) were reached at 13.82 and 14.68 years, respectively. The average soil bulk density at 0-40 cm depth first decreased and then increased with increasing duration of grazing exclusion (Fig. 5b), reaching a minimum value of $0.90 \text{ g}\cdot\text{cm}^{-3}$ at 15.23 years.

3.5 Dynamic changes in SOC and TN

The extent of the influence of grazing exclusion on SOC content and TN content gradually decreased with increasing soil depth (Fig. 6a; Fig.7a). The SOC content and TN content at 0-10 and 10-20 cm increased as a power function with increasing grazing exclusion duration, and the increase rates of SOC content and TN content at 0-10 cm ($2.36 \text{ g}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$, $0.26 \text{ g}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$) were significantly greater than those at 10-20 cm ($0.70 \text{ g}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$, $0.14 \text{ g}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$) ($P < 0.05$). From CK to grazing exclusion for 2 years, the SOC content and TN content at 20-40 cm depth significantly increased. Later, they showed no significant change with increasing duration of grazing exclusion and were generally stable at approximately 30.76 and $3.32 \text{ g}\cdot\text{kg}^{-1}$, respectively. The average SOC

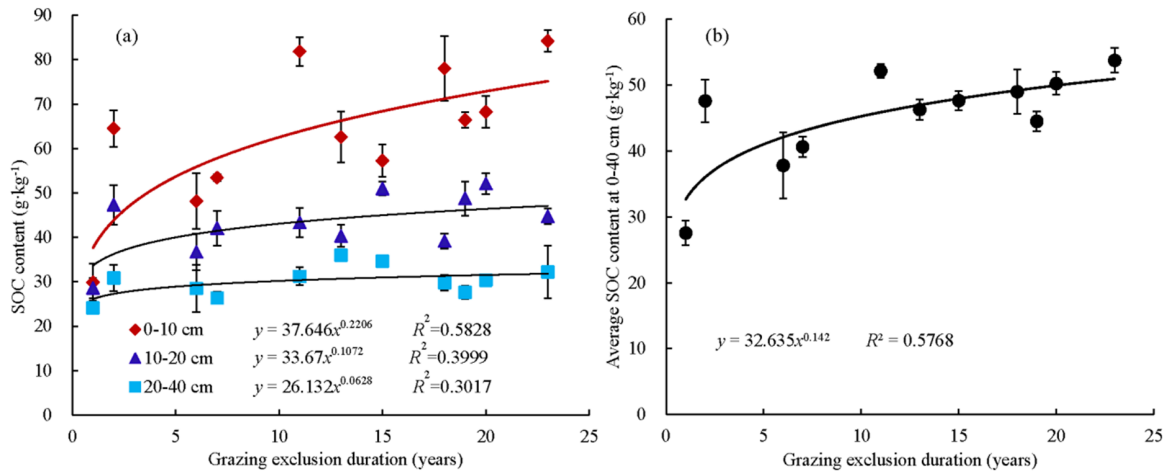


Fig. 6 Variation of SOC content at 0-10, 10-20, and 20-40 cm depths (a) and average SOC content of the 0-40 cm depth (b) with grazing exclusion duration. Bars mean standard errors.

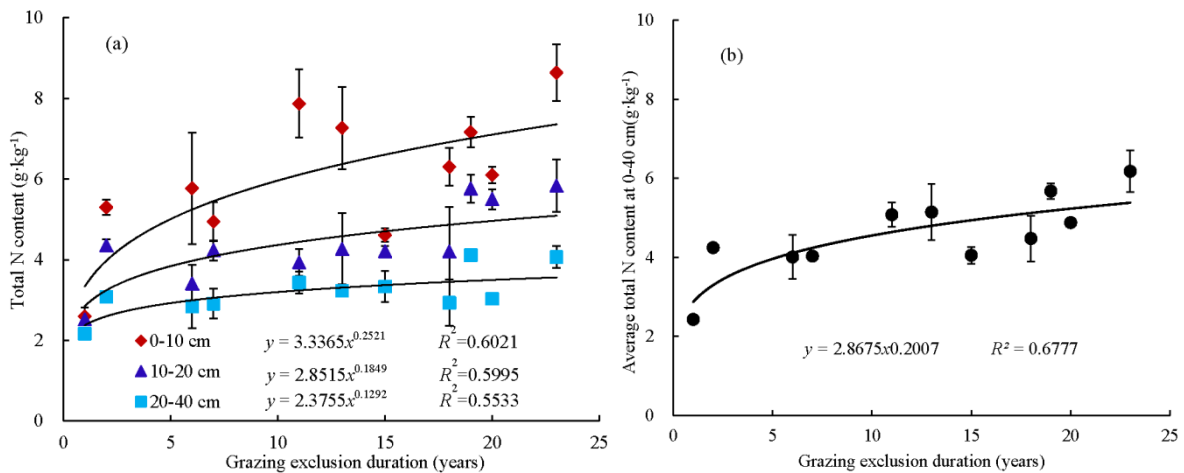


Fig. 7 Variation of total N at 0-10, 10-20, and 20-40 cm depths (A) and average total N of the 0-40 cm depth (B) with grazing exclusion duration. Bars mean standard errors.

content and TN content at 0-40 cm increased as a power function with increasing duration of grazing exclusion (Fig. 6b; Fig.7b), and their annual increase rates were 1.14 and 0.16 g·kg⁻¹·yr⁻¹, respectively.

3.6 Correlation analyses

Based on correlation analyses (Table 1), the plant coverage, total belowground biomass, total aboveground and belowground biomass were not correlated with grazing exclusion duration, but the other indicators were significantly correlated with grazing exclusion duration. The average SOC was significantly positively associated with the average TN. The total saturated water content was significantly positively associated with plant height, aboveground biomass, average SOC and average TN. The average soil bulk density was significantly negatively associated with plant height, aboveground biomass, total saturated water content, average SOC and average TN.

4 Discussion

4.1 Effects of long-term grazing exclusion on vegetation structure in alpine meadows

The results of this research indicate that the root biomass at different grazing exclusion durations decrease with increasing soil depth, and the root biomass at 0-10 cm depth accounts for 82.90% of the total belowground biomass at 0-40 cm, which was consistent with previous studies (Jing et al. 2014). This is because with the increase in soil depth, the soil moisture, soil temperature, soil nutrients and porosity

were reduced, and the soil compaction increased, which inhibited the growth of roots and directly reduced the root biomass (O’Grady et al. 2005; Mello et al. 2007). Wu et al. (2009) found that grazing exclusion measures could significantly enhance the aboveground and belowground biomass, while other researchers found that grazing exclusion had no significant effect on the belowground biomass in meadow steppes (Sun et al. 2015). The results of our research showed that grazing exclusion did not simply increase or have no effect on biomass in alpine meadows, but its effects mainly depended on the duration of grazing exclusion. At the early stages of grazing exclusion, because grazing exclusion prevented livestock from trampling and grazing on plants, and plants with relatively high light and nutrient competition capacity (for example, grasses and sedges) rapidly recovered (Wei et al. 2017), plant coverage increased, plant height was higher, aboveground and belowground biomass increased. With further increase in the duration of grazing exclusion, evidence suggests that the amount and thickness of litter in the grazing exclusion region will gradually increase, too (Zou et al. 2016). A thick and undecomposed litter layer forms due to the accumulation of litter, which inhibits the contact between seeds and soil, reduces the plant germination rate and affects the growth of seedlings (Wainwright et al. 2017). And litter coverage greatly decreases the light intensity at the bottom of a plant community, which inhibits the light competition capacity of some dwarf weeds, and these plants gradually disappear as their living space gradually decreases (Wu et al. 2009). In this study, it is believed that these effects caused the plant coverage and the belowground

Table 1 Correlation coefficients between soil physicochemical properties, vegetation structure and grazing exclusion duration

	GED	PC	PH	AGB	TBGB	TABGB	TSWC	ASBD	ASOC	ATN
GED	1									
PC	-0.31	1								
PH	0.66**	0.19	1							
AGB	0.53**	0.06	0.53**	1						
TBGB	-0.34	0.39*	0.07	-0.24	1					
TABGB	-0.25	0.41*	0.17	-0.06	0.98**	1				
TSWC	0.56**	0.27	0.72**	0.67**	-0.08	0.04	1			
ASBD	-0.66**	-0.25	-0.82**	-0.56**	-0.05	-0.16	-0.87**	1		
ASOC	0.63**	0.10	0.64**	0.56**	-0.18	-0.08	0.57**	-0.70**	1	
ATN	0.68**	-0.12	0.50**	0.55**	-0.17	-0.08	0.47**	-0.53**	0.65**	1

Notes: ** denotes probabilities ($P < 0.01$); * denotes probabilities ($0.01 < P < 0.05$); GED=grazing exclusion duration, PC=Plant coverage, PH=Plant height, AGB=Aboveground biomass, TBGB=Total belowground biomass, TABGB=Total above- and belowground biomass, TSWC=Total saturated water content, ASBD = Average soil bulk density; ASOC= Average SOC, ATN=Average total nitrogen.

biomass at 0-40 cm to first increase and then decrease, and the aboveground biomass gradually stabilized with the increase in the duration of grazing exclusion. Because the total aboveground and belowground biomass was mainly composed of the belowground biomass, the variation trend of the total aboveground and belowground biomass was consistent with that of the belowground biomass (Fig. 2), and their correlation reached a significant level (Table 1).

4.2 Effects of long-term grazing exclusion on SOC and TN in an alpine meadow

C and N are important elements in grassland systems, mainly stored in soils. The results of our research showed that the SOC content and TN content at 0-40 cm in the moderately degraded alpine meadow increased as a power function with increasing duration of grazing exclusion, which was consistent with Wu et al. (2010). The reasons for low SOC and TN contents in the moderately degraded alpine meadow are: (1) when the alpine meadow becomes moderately degraded, the relatively weak vegetation conditions (Fig. 2) result in little plant residue entering the shallow (0-10 cm) soil; (2) Only 10-25% of the vegetation roots, which are the main source of SOC and soil nitrogen (Cao et al. 2004; Liu et al. 2012) in an alpine meadow, are distributed at 10-40 cm depths (Wang et al. 2008). This condition leads to low SOC and TN contents in the 10-20 and 20-40 cm soil layers; (3) Alpine meadow degradation increases soil respiration (Wang et al. 2002), which accelerates the loss of SOC and nitrogen (Wang et al. 2009). With the implementation of grazing exclusion measures, the SOC content at 0-40 cm significantly increases, especially at the early stage of grazing exclusion. This result occurs because: (1) the roots and litter of vegetation increases after grazing exclusion (Zou et al. 2016), and the soil water content in the topsoil of the grazing exclusion region is greater than that of the grazing region (Jia et al. 2017), which increases the decomposition rate of the surface litter under grazing exclusion (Estavillo et al. 2002). These effects increase the return of organic matter to the soil (Shahzad et al. 2015; Xiao et al. 2016), especially to the shallow soil (0-10 cm); (2) The coverage and height of the alpine meadow vegetation rapidly increases after grazing exclusion, and the soil temperature is reduced in an alpine meadow (Zhu et

al. 2016), which inhibits the activity of soil microbes. The decomposition rate of the mineralized SOC is naturally reduced, which results in the accumulation of SOC (Leifeld et al. 2005); (3) The improvement of vegetation conditions increases the proportions of silt and clay in the soil (Li et al. 2006b), which indirectly improves the SOC content (Hu et al. 2012); (4) With increasing duration of grazing exclusion, the proportion of grasses and sedges with dense, fibrous root systems gradually increase (Yao et al. 2019; Dai et al. 2021), which induce the formation and accumulation of soil organic matter (Reeder and Schuman 2002) in the grazing exclusion region; (5) Although there are few plant roots distributed in the deep soils, the input of dissolved organic carbon leaching from shallow (0-10 cm) soil to deep (20-40 cm) soil increase in alpine meadows after grazing exclusion (Yang et al. 2016), which directly enhance the SOC content in the deep (20-40 cm) soil. With the further increase in the duration of grazing exclusion, the SOC content in deep soil gradually stabilizes. This phenomenon could be explained by the fact that after long-term grazing exclusion, the soil bulk density in the deep soil gradually increases, and its porosity naturally decreases, which directly reduces the input of dissolved organic carbon leaching from shallow soil to deep soil (Yang et al. 2016). The soil TN content is significantly correlated with the SOC content (Moges and Holden 2008; Fu et al. 2010), and the variation trends for soil TN content at different depths in the present research are basically consistent with those of SOC content. These results indicate that grazing exclusion is an important way to improve the carbon and nitrogen holding capacity in degraded alpine meadows, and they also indicate that with the extension of the alpine meadow ecosystem restoration process, the soil carbon and nitrogen holding capacity of these ecosystems will gradually decrease and finally reach a relatively stable condition.

4.3 Effects of long-term grazing exclusion on water conservation in an alpine meadow

Soil bulk density is considered to be an important factor affecting soil water holding capacity, and it is mainly affected by soil texture, soil structure and land use patterns (Zhao et al. 2016). The results of our research confirmed that the effects of grazing exclusion on the soil bulk density of the moderately degraded alpine meadow mainly depends on the

duration of grazing exclusion. When the duration of grazing exclusion is less than 15 years, the average soil bulk density at 0-40 cm in the moderately degraded alpine meadow decreases with increasing duration of grazing exclusion, which is consistent with Yang et al. (2016). This may occur because: (1) grazing exclusion prevents livestock from trampling and grazing on plants, this effect significantly improves the plant coverage, aboveground and belowground biomass of grass and sedge, which has good palatability for livestock (Yao et al. 2021). These effects improve soil porosity within the root zone of the vegetation and enhance the functions of root structure and mechanisms (Li et al. 2017a); (2) Grazing exclusion increases the SOC content at different depths, and the increasing SOC content characteristically results in a decrease in bulk density (Haynes and Naidu 1998); (3) Grazing exclusion decreases soil compaction by preventing livestock trampling (Castellano and Valone 2007). When the duration of grazing exclusion was greater than 15 years, the soil bulk density at 0-10 cm still decreased with increasing duration of grazing exclusion, while the soil bulk density at 10-40 cm increased with increasing duration of grazing exclusion. This phenomenon could be caused by the following: (1) after long-term grazing exclusion, the proportion of grasses and sedges (e.g., *Elymus nutans*, *Poa crymophila*, *Stipa purpurea*) with a fibrous root system, whose roots are mainly distributed at 0-10 cm, gradually increases (Yao et al. 2019; Dai et al. 2021); (2) After long-term grazing exclusion, the SOC content at 10-40 cm is relatively low and basically stable with the increase in duration of grazing exclusion, especially the SOC content at 20-40 cm, while the SOC content at 0-10 cm is relatively high and gradually increases with increasing duration of grazing exclusion; (3) Grazing exclusion increases the plant height in alpine meadows, which increases the interception of dust and fine particles by plants (Ma et al. 2016), thereby increasing the ratio of silt to clay content in the shallow soil (Yang et al. 2018). These effects directly decrease the soil bulk density (Heuscher et al. 2005) at depths of 0-10 cm. Overall, the average soil bulk density at 0-40 cm in the moderately degraded alpine meadow first decreases and then increases with increasing duration of grazing exclusion. In contrast to our results, other researchers found that grazing exclusion had no significant effect (Li et al. 2013) or reduced (Wu et al. 2010) the soil bulk density in alpine meadows. These contradictory

results could be related to differences in the duration of grazing exclusion. The duration of grazing exclusion in the present study was 23 years, but it was only 9 years and 3 years in the studies by Wu et al. (2010) and Li et al. (2013), respectively. This indicated that the difference in the duration of grazing exclusion could lead to contradictory results when determining the effects of grazing exclusion on soil bulk density, as demonstrated by our previous study (Yang et al. 2016).

Soil saturated water content can directly reflect soil water-holding capacity, which is the key to determining the water conservation function of alpine meadow ecosystems. In our research, the soil saturated water content at 0-40 cm in the moderately degraded alpine meadow increased as a power function with increasing duration of grazing exclusion, especially at 0-10 cm, which agrees with findings by Li et al. (2016). This phenomenon could be explained by the following reason: (1) there is a decrease in soil bulk density and an increase in SOC in the 0-40 cm depth, especially in the shallow soil (0-10 cm), with the increase in the duration of grazing exclusion (Fig. 5, Fig. 6); (2) The improvement of vegetation conditions increases the proportions of silt and clay in the soil (Li et al. 2006b), which directly improves the soil water retention capacity (Rawls et al. 2003). This result is also an indication that the soil infiltration and water retention capacity of the degraded alpine meadow would improve with increasing duration of grazing exclusion, which indirectly reveals the reason that alpine meadows are an important functional zone for water conservation on the TP.

4.4 Beneficial or harmful effects of grazing exclusion in alpine meadows

The present research found that the plant coverage, plant height, plant biomass, soil water holding capacity, carbon and nitrogen sequestration ability of the moderately degraded alpine meadow were quickly restored at the early stage of grazing exclusion, while with increasing duration of grazing exclusion, the restoration rates of plant height, aboveground biomass, saturated water content, carbon and nitrogen sequestration ability gradually decreased. Even the plant coverage, belowground biomass, soil bulk density, total aboveground and belowground biomass deteriorated after grazing

exclusion for 9.41, 9.46, 15.23 and 10.25 years, respectively. These results indicate that grazing exclusion for too long is harmful to the restoration of degraded alpine meadows; grazing exclusion measures have a time component. Further analysis found that after 9.41, 9.46 and 10.25 years of grazing exclusion, the plant coverage, belowground biomass, and total aboveground and belowground biomass all decreased with increasing duration of grazing exclusion. In other words, these indices decreased after 10 years of grazing exclusion. Although the plant height, aboveground biomass, soil saturated water content, soil bulk density, SOC and TN content still improved after 10 years of grazing exclusion, the degree of improvement was very limited (Fig. 2 to Fig. 7). Therefore, we contend that the optimal duration of grazing exclusion for the restoration of the moderately degraded alpine meadow is 10 years. To maintain the positive condition of energy flows and material circulation in the alpine meadow ecosystem, moderate disturbances (e.g., seasonal grazing) should be applied in long-term grazing exclusion alpine meadows. Research from Inner Mongolia (Li et al. 2008) found that moderate grazing in spring and winter could effectively remove litter, reduce growth redundancy, promote tiller formation, regenerate the pasture (Li et al. 2019) and be beneficial to nutrient circulation, humus formation and carbon sequestration in grassland soils (Reeder and Schuman 2002), which was in accordance with the grazing optimization hypothesis (Belsky 1986).

There are three important points worth noting from the present research. First, the restoration of degraded alpine meadows not only included the recovery of plant coverage, biomass, soil water holding capacity and soil nutrients, but also the recovery of herbage growth rate, species nutrient competition and soil microorganism change, especially the change in plant species composition and plant functional group. To accurately understand the role of long-term grazing exclusion in the process of restoring degraded alpine meadows, a more comprehensive study that consider the effects of long-term grazing exclusion on biodiversity, species nutrient competition and soil microorganisms is needed to fill these research gaps. Second, we only studied the effects of long-term grazing exclusion on vegetation structure, soil water holding capacity and soil carbon and nitrogen sequestration in a moderately degraded alpine meadow. These effects would likely be different from

those in lightly, severely and extremely degraded alpine meadows. Therefore, to comprehensively understand the interactive effects of long-term grazing exclusion on plant and soil ecosystems in alpine meadows at different degrees of degradation, more field studies are needed. Third, precipitation, especially growing season precipitation, plays a key role in plant growth, community composition, primary production, carbon and water cycles of alpine grassland ecosystems on the TP (Wu et al. 2013; Yan and Lu 2015), and it is well known that there are great differences in precipitation in different regions on the TP. Therefore, the optimal duration of grazing exclusion for different alpine grassland types would naturally be different, and a series of special studies on the optimal duration of grazing exclusion in specific areas on the TP are still needed.

5 Conclusion

With increasing duration of grazing exclusion, the aboveground biomass, total saturated water content at 0-40 cm depth, and average SOC and TN contents at 0-40 cm depth in the moderately degraded alpine meadow increased as a power function, the plant height increased as a log function, the plant coverage, total belowground biomass at 0-40 cm depth, total aboveground and belowground biomass in the moderately degraded alpine meadow first increased and then decreased, and the average soil bulk density at 0-40 cm depth in the moderately degraded alpine meadow first decreased and then increased. Long-term grazing exclusion is harmful for the sustainable restoration of degraded alpine meadows on the northeastern TP. The optimal duration of grazing exclusion for the restoration of these moderately degraded alpine meadows is approximately 10 years, and moderate disturbances should be allowed in following 10 years of grazing exclusion.

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