Long-term light grazing does not change soil organic carbon stability and stock in the biocrust layer in hilly regions of drylands (Postprint)

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(Note: Chinese names in academic contexts are typically transliterated using the Pinyin system. "PAN Xinghui" is already in standard academic format, with the surname in all caps. If a journal prefers standard capitalization, it may appear as "Pan Xinghui" .), XU Mingxiang

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Abstract

Livestock grazing is the most extensive land use in global drylands and one of the most extensive stressors of biological soil crusts (biocrusts). Despite widespread concern about the importance of biocrusts for global carbon (C) cycling, little is known about whether and how long-term grazing alters soil organic carbon (SOC) stability and stock in the biocrust layer. To assess the responses of SOC stability and stock in the biocrust layer to grazing, from June to September 2020, we carried out a large scale field survey in the restored grasslands under long-term grazing with different grazing intensities (represented by the number of goat dung per square meter) and in the grasslands strictly excluded from grazing in four regions (Dingbian County, Shenmu City, Guyuan City and Ansai District) along precipitation gradient in the hilly Loess Plateau, China. In total, 51 representative grassland sites were identified as the study sampling sites in this study, including 11 sites in Guyuan City, 16 sites in Dingbian County, 15 sites in Shenmu City and 9 sites in Ansai District. Combined with extensive laboratory analysis and statistical analysis, at each sampling site, we obtained data on biocrust attributes (cover, community structure, biomass and thickness), soil physical-chemical properties (soil porosity and soil carbon-to-nitrogen ratio (C/N ratio)), and environmental factors (mean annual precipitation, mean annual temperature, altitude, plant cover, litter cover, soil particle-size distribution (the ratio of soil clay and silt content to sand content)), SOC stability index (SI) and SOC stock (SOCS) in the biocrust layer, to conduct this study. Our results revealed that grazing did not change total biocrust cover but markedly altered biocrust community structure by reducing plant cover, with a considerable increase in the relative cover of cyanobacteria (23.1%) while a decrease in the relative cover of mosses (42.2%). Soil porosity and soil C/N ratio in the biocrust layer under grazing decreased significantly by 4.1%-7.2% and 7.2%-13.3%, respectively, compared with those under grazing exclusion. The shifted biocrust community structure ultimately resulted in an average reduction of 15.5% in SOCS in the biocrust layer under grazing. However, compared with higher grazing (intensity of more than 10.00 goat dung/m2), light grazing (intensity of 0.00-10.00 goat dung/m2 or approximately 1.20-2.60 goat/(hm2 • a)) had no adverse effect on SOCS. SOC stability in the biocrust layer remained unchanged under long-term grazing due to the offset between the positive effect of the decreased soil porosity and the negative effect of the decreased soil C/N ratio on the SOC resistance to decomposition. Mean annual precipitation and soil particle-size distribution also regulated SOC stability indirectly by influencing soil porosity through plant cover and biocrust community structure. These findings suggest that proper grazing might not increase the CO2 release potential or adversely affect SOCS in the biocrust layer. This research provides some guidance for proper grazing management in the sustainable utilization of grassland resources and C sequestration in biocrusts in the hilly regions of drylands.

Full Text

Preamble

Long-term light grazing does not change soil organic carbon stability and stock in biocrust layer in the hilly regions of drylands

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Abstract: Livestock grazing is the most extensive land use in global drylands and one of the most significant stressors on biological soil crusts (biocrusts). Despite widespread concern about the importance of biocrusts for global carbon (C) cycling, little is known about whether and how long-term grazing alters soil organic carbon (SOC) stability and stock in the biocrust layer. To assess the responses of SOC stability and stock in the biocrust layer to grazing, we conducted a large-scale field survey from June to September 2020 in restored grasslands under long-term grazing with different intensities (represented by goat dung counts per square meter) and in grasslands strictly excluded from grazing across four regions (Dingbian County, Shenmu City, Guyuan City, and Ansai District) along a precipitation gradient in the hilly Loess Plateau, China. In total, 51 representative grassland sites were identified as sampling sites, including 11 sites in Guyuan City, 16 sites in Dingbian County, 15 sites in Shenmu City, and 9 sites in Ansai District. Combined with extensive laboratory and statistical analyses, we obtained data at each sampling site on biocrust attributes (cover, community structure, biomass, and thickness), soil physical-chemical properties (porosity and carbon-to-nitrogen ratio (C/N ratio)), environmental factors (mean annual precipitation, mean annual temperature, altitude, plant cover, litter cover, and soil particle-size distribution (ratio of clay and silt content to sand content)), SOC stability index (SI), and SOC stock (SOCS) in the biocrust layer.

Our results revealed that grazing did not change total biocrust cover but markedly altered biocrust community structure by reducing plant cover, with a considerable increase in the relative cover of cyanobacteria (23.1%) and a decrease in the relative cover of mosses (42.2%). Soil porosity and soil C/N ratio in the biocrust layer under grazing decreased significantly by 4.1%-7.2% and 7.2%-13.3%, respectively, compared with grazing exclusion. The shifted biocrust community structure ultimately resulted in an average reduction of 15.5% in SOCS in the biocrust layer under grazing. However, compared with higher grazing intensity (>10.00 goat dung/m^2), light grazing (intensity of 0.00-10.00 goat dung/m^2 or approximately 1.20-2.60 goat/(hm^2 · a)) had no adverse effect on SOCS. SOC stability in the biocrust layer remained unchanged under long-term grazing due to the offsetting effects of decreased soil porosity (positive effect on SOC resistance to decomposition) and decreased soil C/N ratio (negative effect). Mean annual precipitation and soil particle-size distribution also regulated SOC stability indirectly by influencing soil porosity through plant cover and biocrust community structure. These findings suggest that proper grazing might not increase CO$_2$ release potential or adversely affect SOCS in the biocrust layer. This research provides guidance for proper grazing management in the sustainable utilization of grassland resources and C sequestration in biocrusts in the hilly regions of drylands.

Keywords: biological soil crusts; livestock grazing; soil organic carbon; biocrust community structure; soil carbon-to-nitrogen ratio; dryland ecosystems; Loess Plateau

1 Introduction

Hyper-arid, arid, semi-arid, and dry sub-humid ecosystems (drylands) are critical components of the terrestrial carbon (C) cycle, occupying approximately 45.0% of the terrestrial surface and accounting for over 25.0% of Earth' s soil organic carbon (SOC) reserves [?, ?, ?]. Accordingly, dryland soils play a major role in stabilizing atmospheric carbon dioxide (CO_2) concentrations [?, ?]. In dryland ecosystems with sparse vascular plants, biological soil crusts (biocrusts) are the dominant living cover (up to 70.0% of ground surface) and important modulators of the C cycle [?, ?]. Biocrusts are composed of mosses, lichens, cyanobacteria, fungi, bacteria, and other microorganisms [?, ?]. As reported, biocrusts are an important SOC source, fixing approximately 2.4 Pg of C from the atmosphere annually [?, ?] and enriching organic C in the topsoil (biocrust layer) [?, ?]. Moreover, they substantially and complexly regulate soil CO_2 efflux dynamics [?, ?]. Briefly, biocrusts are considered crucial determinants of soils' potential as a sink for atmospheric CO_2 stabilization in drylands. Quantifying SOC stability in the biocrust layer is important for understanding soil CO_2 release potential and the role of biocrusts in dryland ecosystem C balance.

SOC stability, reflecting the tendency of organic C in soils to resist change and/or loss [?, ?], is an important indicator of soil C sequestration and mineralization potential. It is considered closely negatively related to the amounts of active C fractions [?, ?]. It has been confirmed that the lability and mineralization potential of SOC in the biocrust layer are remarkably higher than those in subsurface layers [?, ?]. Additionally, the degree of biocrust effects on active SOC fractions and SOC stability is closely correlated with crust types and succession stages. With biocrust succession, communities develop stronger C fixation ability [?, ?] and secrete greater amounts and diversity of metabolites, leading to higher labile-C content. It was found that SOC content, labile-C content, and its proportion relative to SOC in mid- to late-successional biocrusts dominated by mosses or lichens were 2.4–2.9, 2.9–6.8, and 1.2–2.3 times higher than those in early successional biocrusts dominated by cyanobacteria, respectively [?, ?, ?]. Moreover, biocrust succession affects other soil properties important for C cycling and turnover. It is well known that biocrust succession positively influences soil aggregation [?, ?], meso-macropore number (meso-macroporosity increased from 3.5%–4.2% to approximately 23.6% in lichens) [?, ?], microbial biomass and community diversity [?, ?], and enzymatic activities (e.g., β-glucosidase, cellulase, and urease) involved in C and nitrogen (N) cycling [?, ?, ?]. These soil properties, in turn, regulate SOC stability by affecting SOC accessibility to microbes [?, ?]. Thus, changes in biocrust attributes, such as successional stages, compositions, and cover, may drive variations in labile-C content and SOC stability in the biocrust layer and ultimately affect C balance in biocrust-dominated drylands.

Livestock grazing is the most extensive grassland use and a common disturbance source to biocrust communities in drylands worldwide [?, ?, ?]. Grazing effects on SOC and biocrust attributes have been a global concern [?, ?, ?, ?, ?]. Grazing significantly reduces total biocrust cover [?, ?] and promotes a shift in biocrust community structure to an early successional state [?, ?, ?]. Additionally, livestock trampling compacts soils and destroys soil aggregate structure, resulting in decreased soil porosity [?, ?], which can affect biocrust layer humidity and temperature [?, ?, ?] and influence microbial activity [?, ?]. Until now, many researchers have explored grazing effects on SOC without considering the biocrust layer [?, ?, ?], while only a few have focused on responses of CO_2 exchange and SOC sequestration to livestock trampling in biocrust-dominated drylands. It was found that soil CO_2 efflux and SOC showed different responses to brief simulated grazing disturbance versus long-term grazing in different soil types [?, ?, ?, ?, ?]. However, it is poorly understood whether and how grazing affects SOC stability in the biocrust layer. This research gap limits evaluation of soil C balance in biocrust-dominated drylands where livestock grazing is widespread.

On China' s Loess Plateau, implementation of a large-scale grazing withdrawal program for decades has allowed vast areas of grasslands and biocrusts to restore naturally, with total biocrust cover as high as 70.0% [?, ?]. Free livestock grazing in restored grasslands around rural settlements has been widespread for approximately 10 years. However, in this area, the effects of long-term grazing (approximately 10 years) on biocrust attributes and functions have been neglected. In particular, the effects of long-term grazing on SOC stability and stock in the biocrust layer and the underlying mechanisms have not been fully studied. Therefore, the Loess Plateau is an ideal location to explore grazing effects on SOC stability in biocrusts.

The objectives of this study were to: (1) analyze how long-term grazing impacts biocrust attributes (cover, community structure, biomass, and thickness) and soil physical-chemical properties (soil porosity and soil carbon-to-nitrogen ratio (C/N ratio)) in the biocrust layer; (2) evaluate whether and how long-term grazing with different intensities affects SOC stability and stock in the biocrust layer; and (3) determine the mechanisms by which long-term grazing affects SOC stability in the biocrust layer under the influences of environmental conditions (mean annual precipitation (MAP), soil particle-size distribution, and plant cover). We hypothesized that (1) grazing would decrease biocrust cover, biocrust biomass, soil porosity, and soil C/N ratio, and alter biocrust community structure; (2) grazing would reduce SOC stock (SOCS) in the biocrust layer; and (3) grazing and environmental factors would regulate SOC stability by affecting biocrust attributes (cover, community structure, and biomass) and soil physical-chemical properties (soil porosity and soil C/N ratio) in the biocrust layer. The results of this study are expected to provide baseline information for quantifying soil C balance in biocrust-dominated drylands and guidance for sustainable grassland resource utilization and SOC sequestration in biocrusts on the Loess Plateau and similar dryland regions worldwide.

2.1 Study Area

On China's Loess Plateau, a large-scale grazing withdrawal program launched in 2001 has reversed grassland degradation trends and promoted grassland productivity. As a result, vegetation cover and forage quantity and quality improved markedly in restored grasslands. However, in the last decade, as local residents' cost of living and production increased, livestock grazing in restored grasslands has re-emerged.

Four independent, typical regions with similar grassland restoration histories and grazing patterns were selected along a precipitation gradient on the Loess Plateau [Figure 1: see original paper]: Dingbian County (37°35 N, 107°35 E; 1303-1907 m a.s.l.), Shenmu City (38°50 N, 110°29 E; 739-1449 m a.s.l.), and Ansai District (36°51 N, 109°19 E; 1012-1731 m a.s.l.) in Shaanxi Province, and Guyuan City (36°00 N, 106°17 E; 1675-2148 m a.s.l.) in Ningxia Hui Autonomous Region. Mean annual precipitation (MAP) varied between 374 and 571 mm over the 2001-2020 period, with 60.0% or more falling between June and September. Mean annual temperature (MAT) ranged from 7.8°C to 9.9°C during 2001-2020. MAP and MAT data were acquired from the National Meteorological Information Centre of the China Meteorological Administration (https://data.cma.cn/). The ratio of soil clay and silt content to sand content, representing soil particle-size distribution, ranged from approximately 0.38 to 0.95 across the four regions . All four regions have consistent topography, representing hilly or undulating terrain in semi-arid areas. Goats are the most common livestock, typically walking and foraging freely under herder supervision in summer and autumn, while being fed primarily with crop grains, crop residue leftovers, or other supplements during winter and early spring. The proportion of heavily grazed grasslands is limited due to grazing withdrawal program restrictions.

Biocrusts are widely distributed across all four regions, dominated by cyanobacteria and mosses. Common cyanobacteria species include *Tolypothrix metamorpha*, *Microcoleus vaginatus*, *Phormidium tenue*, *Phormidium calciola*, and *Nostoc* spp., while moss species are dominated by *Didymodon tectorum*, *Didymodon vinealis*, and *Bryum argenteum*. Lichens are less common, with cover seldom reaching 10.00% [**?**, **?**]. The main soil types include Regosols and Umbrisols according to the World Reference Base for Soil Resources [**?**, **?**].

2.2 Field Survey and Sampling

From June to September 2020 (the rainy season), we investigated approximately 65 grassland sites based on livestock data from the China Statistical Yearbook (county-level) [**?**, **?**] and current livestock production situations. We used goat dung counts per square meter as a proxy for grazing intensity [**?**, **?**, **?**] and referenced the frequency of goats entering grasslands as reported by nearby rural residents. Laing et al. (2003) confirmed a strong positive correlation between grazing intensity and livestock dung quantity per unit area. Goat dung counts were measured in four to six 5 m × 5 m quadrats at each grassland site [**?**, **?**]. Finally, 42 representative grassland sites were identified as sampling sites, covering the widest possible range of goat dung counts per square meter while removing sites with similar grazing intensities. Due to grazing withdrawal program restrictions, only 2 of the 42 sampling sites had grazing intensities exceeding 30.00 goat dung/m^2 (39.28 and 73.20 goat dung/m^2, respectively). To represent the full range of grazing intensities on the Loess Plateau, these 2 sites were retained after careful consideration. We also sampled 3 strictly grazing-excluded sites per region as controls. Because grasslands excluded from grazing for over 30 years in Guyuan City were completely covered by plant basal area and litter without biocrusts, the final sample size was reduced to 51 sites: 11 in Guyuan City, 16 in Dingbian County, 15 in Shenmu City, and 9 sites in Ansai District . Each sampling site exceeded 1 hm^2 and was located at least 3 km from all other sites.

A 25 cm × 25 cm quadrat frame was used to survey total biocrust cover (%) and the cover of two major visible components (cyanobacteria and mosses) [**?**, **?**]. Each quadrat frame was divided into 25 grids (5 cm × 5 cm) to survey the presence and frequency of visible components (cyanobacteria, mosses, and lichens) and assess biocrust community cover. Survey quadrat frames were placed at 25–35 random locations within each sampling site. Biocrust community structure was assessed as the relative cover of the two major components [**?**, **?**]. The relative cover of cyanobacteria (or mosses) (%) was calculated as the ratio of cyanobacteria cover (or moss cover) to total biocrust cover. Biocrust thickness (mm) was measured with a vernier caliper. Additionally, six random quadrats (1 m × 1 m) were used to investigate main plant species, plant cover (%), and litter cover (%) at each site [**?**, **?**]. Altitude (m) and slope gradient (°) were recorded at each sampling site.

After these surveys, eight samples (8 cm × 8 cm) of the biocrust layer (approximately 4.00–13.00 mm thick) were randomly collected using a spatula at each site, with sampling points kept away from grass tussocks to avoid potential interference from plant roots. The eight samples were homogenized to provide one composite sample. Meanwhile, six random undisturbed samples of the biocrust layer were collected using Petri dishes. All samples were dried and sent to the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau. In the laboratory, after removing biocrustal organism tissues and other impurities, composite samples were sieved to 1.00 mm and 0.25 mm for subsequent analysis.

2.3 Laboratory Analysis

Undisturbed samples were used to determine soil bulk density (g/cm^3) of the biocrust layer and biocrust biomass (moss biomass (g/dm^2) and cyanobacterial biomass (mg/m^2)). Soil bulk density was determined using the wax-coated water immersion method [**?**, **?**]. Soil porosity (%) was calculated from soil particle density (taken as 2.65 g/cm^3) and soil bulk density using the following empirical equation [**?**, **?**]:

$$\text{Soil porosity} = \left(1 - \frac{\text{soil bulk density}}{\text{soil particle density}}\right) \times 100\%$$

Moss biomass was estimated using the dry weight of mosses per unit area (g/dm^2) [?, ?]. Cyanobacterial biomass was represented by chlorophyll *a* content per unit soil surface area (mg/m^2). Chlorophyll *a* was double-extracted with ethanol and measured spectrophotometrically at 665 nm [?, ?]. Mosses were completely removed when preparing cyanobacteria crust samples.

Composite samples were used to determine soil particle-size distribution, SOC content, soil total N content, and SOC fractions with different lability. Soil particle-size distribution was determined using laser diffraction (Mastersizer 2000 Laser Diffraction Particle Analyzer, Malvern Instruments Ltd., Worcestershire, UK) [?, ?]. SOC content (g/kg) was determined by the Walkley-Black method [?, ?]. Total N content (g/kg) was determined using the Kjeldahl method [?, ?]. The soil C/N ratio was calculated as SOC content divided by total N content.

SOC fractions with different lability were measured by potassium permanganate ($KMnO_4$) oxidation [?, ?, ?]. The change in $KMnO_4$ concentration was used to estimate oxidized C content, assuming that 1.00 mmol/L of MnO_4^- consumed ($Mn^{7+} \rightarrow Mn^{2+}$) oxidized 0.75 mmol/L (9.00 mg) of C. Four C fractions with different lability were measured using three $KMnO_4$ concentrations: C1 represents very labile C (g/kg), oxidized by 33.00 mmol/L $KMnO_4$; C2 represents labile C (g/kg), oxidized by 167.00 mmol/L $KMnO_4$ but not by 33.00 mmol/L; C3 represents less labile C (g/kg), oxidized by 333.00 mmol/L $KMnO_4$ but not by 167.00 mmol/L; and C4 represents nonlabile C (g/kg), not oxidized by 333.00 mmol/L $KMnO_4$.

For decades, the ratio of passive C fraction content to active C fraction content has been a reliable method for determining SOC stability [?, ?]. Specifically, Chan et al. (2001) defined C1 and C2 as active C fractions and C3 and C4 as passive C fractions. In this study, the SOC stability index (SI) was calculated as:

$$\text{SI} = \frac{C_{\text{passive}}}{C_{\text{active}}} = \frac{C3 + C4}{C1 + C2}$$

where C_{passive} is the passive C fraction (g/kg) and C_{active} is the active C fraction (g/kg).

SOCS of the biocrust layer (Mg/hm^2) was calculated using SOC content, soil bulk density, biocrust thickness, and total biocrust cover:

$$\text{SOCS} = \text{SOC content} \times \text{soil bulk density} \times \text{biocrust thickness} \times \text{total biocrust cover} \times 0.01$$

2.4 Statistical Analysis

Linear and nonlinear (exponential) regression analyses were used to explore changes in SOC content, SOC fractions, SI, SOCS, biocrust attributes, and soil physical-chemical properties with increasing grazing intensity. Grazing intensity was divided into four grades based on goat dung counts per square meter: 0.00, 0.00–10.00, 10.00–20.00, and \$ 20.00$goatdung/m$^{2}\$. SOCS data were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variance using Levene’ s test. Differences among grazing intensity grades were analyzed using one-way ANOVA and least significant difference tests. To reduce the influence of environmental conditions on SOCS across the four regions, multi-way analysis of covariance (ANCOVA) was performed with grazing intensity grade as a fixed factor and environmental factors (MAP, MAT, altitude, plant cover, litter cover, and soil particle-size distribution) as covariates. These analyses were performed using SPSS 25.0 (SPSS Inc., Chicago, USA). Figures were generated using Origin 2022 (Origin Lab Corp., Northampton, USA).

A structural equation model (SEM) was applied using Amos 21.0 (SPSS Inc., Chicago, USA) to explore how grazing affected SOC stability in the biocrust layer under different environmental conditions. We hypothesized that grazing intensity, MAP, soil particle-size distribution, and plant cover in each region have direct or indirect effects (via biocrust attributes, soil porosity, and soil C/N ratio) on SOC stability. To determine which biocrust attribute best represented grazing effects on SOC stability under different environmental conditions, Pearson correlation analysis identified which attribute (cover, community structure, biomass, or thickness) was most strongly correlated with SI, MAP, soil particle-size distribution, plant cover, soil porosity, and soil C/N ratio. After model construction, maximum likelihood estimation was used to parameterize the model, and goodness-of-fit was tested (chi-square test; Joreskog’ s goodness-of-fit index (GFI)). In the chi-square test, a high P value is desired ($P > 0.05$). Other fit indices were interpreted using rules-of-thumb: ^{2}/df < 2.000, root mean square error of approximation (RMSEA) < 0.080, and Joreskog’ s GFI > 0.950 indicate good fit [**?**, **?**].

3 Results

3.1 Variations in Biocrust Attributes and Soil Physical-Chemical Properties with Grazing Intensity

Figures 2 and S1 show grazing effects on biocrust attributes and soil physical-chemical properties. Grazing did not significantly change total biocrust cover ($P = 0.441$; Fig. S1a) but altered cyanobacteria and moss cover (Fig. 2a and d). With increasing grazing intensity, cyanobacteria cover increased with a nonsignificant trend ($P = 0.069$), while moss cover decreased significantly and linearly ($P = 0.014$). For biocrust community structure, the relative cover of cyanobacteria increased on average from 64.9% under grazing exclusion to 79.9%

under grazing (Fig. 2c). Mosses comprised 20.0% of cover in grazed biocrust communities compared with 34.6% under grazing exclusion (Fig. 2f). Thus, compared with grazing exclusion, mean relative cyanobacteria cover increased by 23.1% under grazing, while mean relative moss cover decreased by 42.2%. Similar to community structure changes, mean cyanobacterial biomass increased by 8.8% and mean moss biomass decreased by 33.4% under grazing compared with grazing exclusion (Fig. 2b and e). Mean biocrust thickness under grazing was 14.2% lower than under grazing exclusion (Fig. 2g).

Soil particle-size distribution was not significantly related to grazing ($P = 0.926$; Fig. S1c). However, soil porosity ($P = 0.007$) and soil C/N ratio ($P = 0.031$) in the biocrust layer decreased significantly by 4.1%-7.2% and 7.2%-13.3% under grazing, respectively, compared with grazing exclusion (Fig. 2h and i).

3.2 Variations in SOC Fractions and Stability Index (SI) with Grazing Intensity

Figure 3 shows variations in SOC content, SOC fractions, and SI with increasing grazing intensity. Overall, SOC content in the biocrust layer ranged from 4.43 to 26.16 g/kg and decreased exponentially with grazing intensity ($P = 0.007$; Fig. 3a). Compared with grazing exclusion, SOC content under grazing was reduced by 1.2%-26.2%. For SOC fractions, C1 content decreased exponentially by 0.0%-25.6% ($P = 0.014$; Fig. 3b) and C4 content decreased significantly by 4.3%-27.8% ($P = 0.045$; Fig. 3e) under grazing compared with grazing exclusion. However, no significant decreases were observed in C2 content ($P = 0.150$; Fig. 3c) or C3 content ($P = 0.570$; Fig. 3d). Additionally, no significant variations were found in the relative proportions of C1 ($P = 0.470$), C2 ($P = 0.630$), C3 ($P = 0.526$), and C4 ($P = 0.469$) to SOC (Fig. S2). On average, the relative proportions of C1, C2, C3, and C4 to SOC were 9.6%, 9.2%, 10.1%, and 71.1%, respectively. Long-term grazing had no significant effect on SI in the biocrust layer. The average SI was 4.24 under grazing and 4.52 under grazing exclusion (Fig. 3f).

3.3 Effect of Grazing on SOCS in the Biocrust Layer

Soil bulk density in the biocrust layer increased significantly with grazing intensity ($P = 0.007$; Fig. S1b). Based on changes in SOC content, biocrust cover, and thickness, SOCS decreased significantly and linearly with grazing intensity ($P = 0.020$), ranging from 0.13 to 1.30 Mg/hm^2 (Fig. 4a). Mean SOCS under grazing (0.49 Mg/hm^2) was 15.5% lower than under grazing exclusion (0.58 Mg/hm^2).

After grading grazing intensity by goat dung counts per unit area, no statistically significant difference was found between SOCS under 0.00-10.00 goat dung/m^2 (mean 0.61 Mg/hm^2) and grazing exclusion (mean 0.58 Mg/hm^2) (Fig. 4b). SOCS under >10.00 goat dung/m^2 (mean 0.41 Mg/hm^2) was not significantly different from grazing exclusion but was significantly lower than under

0.00-10.00 goat dung/m^2. Multi-way ANCOVA results indicated that grazing intensity and other environmental factors (MAP, MAT, litter cover, and soil particle-size distribution) had no significant effect on SOCS, while altitude and plant cover had significant effects ($P = 0.008$ and $P = 0.036$, respectively; Table 3).

3.4 Influence Mechanism of Grazing on SOC Stability

SI and soil porosity were more strongly correlated with the relative cover of cyanobacteria and mosses than with total biocrust cover, cyanobacteria cover and biomass, moss cover and biomass, or biocrust thickness (Table 4). Moreover, the relative cover of cyanobacteria and mosses was significantly related to plant cover and soil particle-size distribution. No biocrust attributes had significant relationships with MAP or soil C/N ratio. Consequently, the relative cover of cyanobacteria was used to represent biocrust attributes under grazing and environmental conditions.

To reveal the mechanism by which grazing influenced SOC stability under different environmental conditions, we constructed an SEM to determine how grazing regulated SOC stability by affecting biocrust attributes and soil physical-chemical properties (Fig. 5). The final model explained 25% of variance in SOC stability and fit the data well (^{2}/df = 1.106, $P = 0.356$, $R^2 = 0.250$, GFI = 0.963, RMSEA = 0.046). SEM results showed that grazing intensity, MAP, and soil particle-size distribution indirectly affected SOC stability by influencing soil porosity and soil C/N ratio. Specifically, grazing directly decreased soil porosity (standardized path coefficient (β) = -0.26, $P = 0.027$) and soil C/N ratio (β = -0.35, $P = 0.010$), and indirectly decreased soil porosity by increasing relative cyanobacteria cover due to reduced plant cover. Additionally, MAP and soil particle-size distribution in each region affected soil porosity directly and indirectly by influencing plant cover and thereby regulating relative cyanobacteria cover. Finally, soil porosity (β = -0.38, $P = 0.025$) and soil C/N ratio (β = 0.28, $P = 0.049$) directly influenced SOC stability negatively and positively, respectively. These results imply that decreased soil porosity caused by grazing, either directly or indirectly, could promote SOC stability, whereas decreased soil C/N ratio caused by grazing could reduce SOC stability.

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4 Discussion

4.1 Long-Term Grazing Effects on SOCS in the Biocrust Layer

Biocrusts occupy large portions of soil surface in dryland ecosystems and play multiple critical ecological roles, particularly in organic C accumulation and stabilization [?, ?]. Livestock grazing is a common disturbance to biocrust communities in drylands worldwide and an important factor affecting SOC stability and C balance [?, ?, ?, ?, ?]. Contrary to our hypothesis, total biocrust cover under grazing did not decrease as significantly as in previous studies [?, ?, ?]. This contrasting pattern may relate to common networks of livestock tracks formed by long-term goat trampling on hilly or undulating topography [?, ?] [Figure 1b: see original paper]. Biocrusts persist in non-track areas and may be protected from goat trampling. Nevertheless, grazing promoted a shift to early successional states, with increased relative cyanobacteria cover and decreased relative moss cover (Fig. 2c and f). This shift is closely related to cyanobacteria' s high resistance and resilience to grazing and to changed microenvironmental conditions. First, cyanobacteria readily colonize soil surfaces vacated by moss removal due to their protective polysaccharide sheaths, greater ability to move through soil and disperse via wind and water, and high tolerance to wide environmental ranges (low to high light, UV, soil temperature, and moisture) [?, ?]. Additionally, grazing-induced plant cover reduction limited moss growth and development (Fig. 5), promoting a shift to cyanobacteria-dominated early successional states [?, ?]. The shifted community structure resulted in lower C fixation ability, reflected by reduced SOC content and SOCS under higher grazing intensity ($ 10.00*goatdung/m*^{2}$) [?, ?, ?].

SOCS represents the net result of long-term SOC gain and loss changes [?, ?]. Thomas (2012) found that SOCS responses to grazing in biocrusts varied across soil types. Largely consistent with studies in China' s Mu Us Sandy Land [?, ?], our study found no adverse effect of light grazing on SOCS (Fig. 4b), possibly due to slower water evaporation from broken biocrust patches and longer photosynthetic activity duration. Additionally, livestock track formation may alter hydrological processes, leading to different spatial water distribution patterns [?, ?]. However, mechanisms underlying negative SOC balance responses to intermediate and heavy grazing may differ, as no sand burial was observed in our study. Further research is needed to verify whether grazing worsens soil erosion and affects SOCS through soil C loss from erosion in hilly regions.

Grazing impacts on ecosystem services strongly depend on environmental conditions (climate, soil, and other biotic features) [?, ?]. In this study, besides plant cover, altitude regulated grazing effects on SOCS (Table 3; Fig. S3a). Altitude alters solar radiation, soil temperature, and moisture, influencing biocrust photosynthesis. Moreover, lower soil temperatures at higher altitudes can suppress soil microorganisms and their activities, resulting in less SOC decomposition and indirectly promoting SOC accumulation [?, ?, ?]. MAP indirectly affected biocrust attributes and SOCS by influencing plant cover (Table 3; Fig. 5), likely because increased precipitation promotes plant growth, especially in drylands [?, ?]. Additionally, the soil matrix serves as the SOC vessel, modifying SOC stability and turnover through physical structure and chemical processes (Figs. 5 and S3b) [?, ?]. It can also influence soil moisture and fertility retention capacity, ultimately altering biocrust community structure by affecting plant growth (Fig. 5) [?, ?]. However, soil particle-size distribution had no significant effect on SOCS [?, ?].

4.2 SOC Stability in the Biocrust Layer Remained Unchanged Under Long-Term Grazing

SOC stability in the biocrust layer, which is enriched with organic C, is an important factor affecting CO_2 emissions and soil C balance in dryland ecosystems. Livestock excrement provides easily decomposed C resources [?, ?], compensating for C1 and C2 content reductions caused by shifted biocrust community structure (Fig. S4), thus maintaining a stable ratio of active to passive C fractions under long-term grazing. The ratio of passive C fraction (resistant to microbial decomposition) to active C fraction (easily decomposed) in the biocrust layer did not change, meaning the potential for CO_2 release from biocrust soils remained unchanged. This result contrasts with Yang et al. (2020), who found that short-term trampling increased the relative content of active organic C to SOC. This difference may stem from inconsistent disturbance patterns (uniform human vs. livestock disturbance) and different grazing durations (short-term vs. long-term). Short-term trampling lacks livestock track networks that protect biocrusts.

Unchanged SOC stability under grazing was regulated by variations in biocrust attributes and soil physical-chemical properties. As shown in the SEM, grazing balanced SOC stability by regulating soil porosity and soil C/N ratio. First, livestock trampling’ s downward compressional forces increased soil bulk density and broke down macroporosity [?, ?, ?]. Additionally, biocrust reverse succession not only reduced soil porosity but also transformed pores from larger, interconnected elongated and irregular shapes to smaller, unconnected rounded forms [?, ?]. Increased fine particles could also promote total pore space and relative small pore numbers [?, ?]. Decreased soil porosity and reduced large interconnected pores impede soil gas diffusion, reducing bacterial abundance and making SOC inaccessible to microorganisms and enzymes [?, ?, ?], thereby limiting organic matter decomposition and enhancing SOC stability [?, ?].

Additionally, due to N resources from livestock excrement deposition, soil C/N ratio decreased significantly with grazing intensity [?, ?]. Soil C/N ratio and biocrust community structure shifts could directly affect soil microbial community structure and function [?, ?, ?]. It was confirmed that grazing disturbance could decrease fungal functional groups [?, ?] and increase bacterial/fungal biomass ratios [?, ?]. Xu et al. (2016) found that active and slow SOC pool decomposition rates decreased with increasing soil C/N ratio. Thus, contrasting with reduced soil porosity effects, grazing-induced lower soil C/N ratio changed microbial C use efficiency, ultimately favoring soil respiration and SOC lability [?, ?]. In summary, various environmental conditions (climate, topography, and soil texture) and grazing durations (long-term and short-term) in different regions may produce different SOC stability patterns in the biocrust layer.

4.3 Implications for Grassland Management

In drylands, water scarcity causes biocrusts to occupy large soil surface areas and play key roles in the soil C cycle, particularly in the biocrust layer; likewise, large human populations depend heavily on livestock grazing for subsistence [?, ?]. However, grazing effects on SOC stability and sequestration in the biocrust layer have often been neglected [?, ?, ?]. This study focused on biocrusts, which play important roles in ecosystem stability and development, and found that light grazing (0.00–10.00 goat dung/m^2) could maintain SOCS in the biocrust layer. We also found that light grazing promoted vegetation community development, increasing average cover, biomass, and diversity [?, ?]. Additionally, for another important biocrust ecological function in hilly or mountainous regions, it is encouraging that average biocrust cover under light grazing was 43.2%, exceeding the threshold for effective soil erosion control [?, ?]. We estimated grazing intensity (goat/($hm^2 \cdot a$)) based on the quantitative relationship between grazing intensity and goat dung counts per unit area from controlled grazing experiments in fenced grasslands in the same area (Fig. S5), revealing that 0.00–10.00 goat dung/m^2 corresponds to approximately 1.20–2.60 goat/($hm^2 \cdot a$). Therefore, compared with grazing exclusion, light grazing (approximately 1.20–2.60 goat/($hm^2 \cdot a$)) could improve local farmers' income without degrading ecosystem services in restored grasslands. Our findings provide a key basis for future government policy decisions on effective management of restored grasslands under the grazing withdrawal program on China' s Loess Plateau.

Moreover, the mechanisms by which long-term grazing balanced SOC stability in the biocrust layer may extend to other hilly, undulating, or mountainous dryland regions. Livestock track formation is largely biogenic on such topography, as using near-horizontal tracks for foraging is energy-efficient for goats [?, ?]. Protecting these typical livestock track networks may be important for maintaining biocrust ecological functions under grazing in hilly regions. However, grazing may not have equal effects on C sequestration and ecosystem services across areas due to regional environmental differences. For instance, livestock trampling tends to compress plain surfaces more severely, potentially causing distinct changes in SOC stability and stock. Furthermore, in most arid and semi-arid desert areas, livestock trampling often turns soils over and buries biocrust organisms, making biocrusts on sandy soils more susceptible to rapid degeneration, with slower or prevented recovery [?, ?, ?, ?]. Additionally, biocrust-vascular plant interactions are complex under different climate conditions. In humid areas, vascular plants dominate vegetation communities, restricting biocrusts to small open patches; grazing-induced plant cover decreases may increase biocrust cover [?, ?]. In contrast, in arid areas, biocrusts occupy interspaces between sparse vascular plants due to high desiccation tolerance; biocrust attributes and functions may respond negatively to livestock trampling [?, ?]. Grazing effects on biocrusts under different climate conditions will inevitably lead to different SOCS responses in the biocrust layer. More research worldwide could improve understanding of grazing effects on SOC stability and sequestration in biocrusts and their regulatory pathways. Much work remains to determine optimal grazing intensity, frequency, and timing according to local conditions without harming biocrust attributes and ecological functions.

Although estimated grazing intensity may not exactly match true grazing intensity, this should not be a major limitation [**?**, **?**, **?**]. Due to grazing withdrawal program restrictions, results from only 2 sites with >30.00 goat dung/m^2 may not accurately represent SOC stability and stock under high grazing intensity; however, the direction of variation with grazing intensity was established. Because sampling sites were large enough (approximately 1 hm^2) and conditions (slope and aspect) were similar among sites, they may still provide true representation. Another important point is that retaining the maximum range of grazing intensity presented on the Loess Plateau is significant for regional practical guidance.

5 Conclusions

Biocrusts are important components of dryland ecosystems, enriching the upper millimeters of soil with organic C. In the context of global climate change, determining responses of SOC stability and stock in the biocrust layer to grazing is crucial for quantifying C balance in biocrust-dominated drylands where livestock grazing is widespread. Our results showed that long-term grazing did not change SOC stability but indirectly decreased mean SOCS by 15.5% in the biocrust layer in dryland hilly regions. However, light grazing did not adversely affect SOCS. Specifically, long-term grazing altered biocrust community structure and decreased soil porosity and soil C/N ratio, rather than biocrust cover. Grazing regulated SOC stability via variations in biocrust community structure (relative cyanobacteria cover), soil porosity, and soil C/N ratio under different environmental conditions (MAP, soil particle-size distribution, and plant cover). Therefore, proper grazing might not increase CO_2 release potential or adversely affect SOCS in the biocrust layer in dryland hilly regions. These findings provide effective guidance for scientific grazing management in sustainable grassland resource utilization and C sequestration in biocrusts in dryland hilly regions.

Conflict of interest: The authors declare no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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Appendix

Fig. S1 Variations in total biocrust cover (a), soil bulk density (b), and soil particle-size distribution (c) in the biocrust layer with increasing grazing intensity. Soil particle-size distribution is the ratio of soil clay and silt content to sand content.

Fig. S2 Variations in the relative contents of C1, C2, C3, and C4 to SOC in the biocrust layer with grazing intensity. (a) C1/SOC; (b) C2/SOC; (c) C3/SOC; (d) C4/SOC. C1, very labile C; C2, labile C; C3, less labile C; C4, nonlabile C.

Fig. S3 Relationships of SOC content in the biocrust layer with altitude (a) and soil particle-size distribution (b).

Fig. S4 Relationships of relative cyanobacteria cover with the relative contents of C1, C2, C3, and C4 to SOC in the biocrust layer. (a) C1/SOC; (b) C2/SOC; (c) C3/SOC; (d) C4/SOC.

Fig. S5 Quantitative relationship between grazing intensity and the number of goat dung per square meter.

Note: Figure translations are in progress. See original paper for figures.

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