Relationship between Grassland Caterpillar (Gynaephora Alpherakiif) Populations and Alpine Vegetation Under Grazing Disturbance

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Abstract. The herbivorous grassland caterpillar (Gynaephora alpherakiif, Lepidoptera: Lymantriidae) is an important primary consumer in alpine meadow ecosystems. Its frequent population outbreaks threaten the sustainability of alpine grasslands. Human activities and climate change may increase populations of grassland caterpillars and affect alpine plant communities. However, due to the rapid population turnover and significant fluctuations in their numbers, the relationship between grassland caterpillar population and plant community characteristics under grazing disturbance remains unclear. Based on our long-term experiment of grazing and enclosure in an alpine grassland on the eastern edge of the Qinghai-Tibet Plateau. We examined the effect of grazing disturbance on both caterpillar populations and alpine vegetation communities through detailed investigations of caterpillar counts and vegetation characteristics, combined with generalized linear mixed models (GLMM). Throughout the observation periods, i) compared with the enclosure treatment, the grazed grasslands exhibited reduced caterpillar populations, fewer individuals of sedges and grasses, and reduced biomass of sedges, grasses, and forbs, but grazing increased the abundance of legumes in the community. The species richness among functional groups showed no significant differences between grassing and enclosure treatments. ii)In grassing, enclosure and overall sites, grassland caterpillar populations had a significant positive correlation with the individual count of sedges and grasses (with a tendency towards positive correlation with forb biomass), but a negative correlation with the biomass and individual count of legumes. Caterpillar numbers did not affect species richness across plant functional groups, the individual count of forbs, or the biomass count of sedges and grasses. iii) Although spatiotemporal variability and Random factors (observational or population fluctuations) significantly influenced variation in grassland caterpillar populations, the effect of grazing and enclosure treatments on caterpillar populations was significant and consistent. Grazing reduces the individual count and biomass of sedges, grasses, and forbs, subsequently decreasing the grassland caterpillar population and mitigating its effect on the grassland. Future studies should focus more on the role of plant functional diversity in interactions with small herbivorous animals under random influences, as well as the effects of human disturbances and environmental changes on both.

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1 Introduction

Grasslands are a crucial component of the Qinghai-Tibet Plateau ecosystem and cover approximately 55.5% of the total area [1]. Grasslands play a vital role in climate regulation, soil conservation, windbreak and sand fixation, and carbon sequestration [2]. The effects of economic and social development, combined with climate change, have resulted in grassland degradation [3]. This degradation has caused several changes in ecosystem functions, including an increase in grassland caterpillar populations [4]. Grassland caterpillars are common herbivorous insects in the grassland ecosystems of the Qinghai-Tibet Plateau. These caterpillars directly alter plant community characteristics by consuming forage resources [5,6] and indirectly influencing grassland ecosystem functions and services [7]. Moderate populations of grassland caterpillars do not significantly affect vegetation, but large population outbreaks can cause rapid grassland degradation and reduce the health of the grassland ecosystem [8,9]. Vegetation is strongly affected by the activities of grassland caterpillars, while caterpillar activities, reproduction, and predation are also influenced by factors such as plant species richness, individual abundance, and biomass [10]. When sedges or grasses are removed, grassland caterpillar populations decline significantly, whereas the removal of forbs or legumes tends to increase caterpillar numbers. [11]. Knowledge of the relationship between grassland caterpillar populations and alpine vegetation may aid in the control of caterpillar outbreaks and the effective management of grasslands.

Grasslands are primarily used for grazing, and management of grazing disturbance is important in maintaining grassland sustainability [12,13]. Research on the effect of grazing on grassland ecosystems has previously focused on factors such as grazing intensity, grazing methods, grazing timing, and their interactions with environmental changes. These studies have examined the effects on plant productivity, plant community characteristics (e.g., species richness and diversity), herbivorous insects, soil physicochemical properties, and grassland carbon-nitrogen and nutrient cycling [14,2]. However, studies on the effect of grazing on herbivorous insects are uncommon. Research in China and other countries has focused on locusts, butterflies, beetles, leafhoppers, and ants rather than on grassland caterpillars [13]. Most studies conclude that grazing affects herbivorous insects not only through direct mechanisms such as consumption, trampling, and excretion but also indirectly by altering plant community structure and soil properties [15,16]. However, research on the interaction between large herbivores (e.g., yaks) and small herbivorous insects (e.g., grassland caterpillars) is limited. Understanding the relationship between grassland caterpillars and alpine vegetation under grazing disturbance can provide insights into the causes of caterpillar outbreaks and useful strategies for sustainable grassland management. The population dynamics of grassland caterpillars exhibit high spatiotemporal variability and significant randomness [17,18]. To obtain insight into the relationship between grazing disturbance, grassland caterpillars, and alpine vegetation, repeated measurements across different months are necessary. However, such studies are rare.

The present study focused on grazing livestock and grassland caterpillars. We employed a combination of grazing enclosure treatments and controlled caterpillar release observations. The study was conducted on the eastern edge of the Qinghai-Tibet Plateau and investigated the effect of grazing disturbance on grassland caterpillar population dynamics and plant diversity while clarifying the interactions between caterpillar populations and alpine vegetation. Previous studies have shown that grassland caterpillars prefer to feed on sedges and grasses and have less preference for legumes and forbs [5–7,10]. Yaks, which primarily graze on high-quality forage (sedges and grasses), compete strongly with grassland caterpillars for these food resources [19–22]. Based on this information, we propose the following hypothesis: Compared with enclosure treatments, grazing should reduce the abundance of sedges and grasses and lead to a decline in grassland caterpillar populations. The goal of this study was to demonstrate how grazing influences grassland caterpillar population dynamics and plant community characteristics under the influence of random processes.

2 Materials and Methods

2.1 Study Area and Experimental Design

The experiment was conducted at the Alpine Meadow and Wetland Ecosystem Field Observation Station (Azi Station) of Lanzhou University, located on the eastern edge of the Qinghai-Tibet Plateau (33°40′N, 101°52′E) at an average altitude of 3540 m. The region has an annual average temperature of 1.2°C, with a mean growing season temperature of 9.84°C. The frost period exceeds 270 days per year, and the annual precipitation averages 620 mm, with 471.3 mm occurring during the growing season [23,24]. The vegetation type is classified as alpine meadow, with the primary growth season being June to September. The dominant plant species in the alpine meadow is Kobresia capillifolia [25,26]. The area supports a range of herbivores, including yaks, Tibetan sheep, plateau pikas, and grassland caterpillars. In July 2021, a south-facing mountain ridge with similar vegetation was selected near the observation station to establish a grazing and enclosure experimental platform. The enclosure area had been under year-round grazing exclusion since May 2011, with manual removal of dry grass each October. In the grazing area, vegetation begins to grow in April, experiences peak growth from June to August, and becomes senescent in mid-to-late September. Within both the grazing and enclosure sites, ten 1.5 m × 1.5 m plots were established per treatment. The plots were arranged in a "Z"-shaped pattern from the base of the mountain to the top, with relatively flat terrain and sufficient spacing between plots. Grassland caterpillars were introduced into each plot, and within each plot, 0.5 m × 0.5 m subplots were designated for vegetation community surveys.

2.2 Grassland Caterpillar Census and Plant Community Survey

Before conducting the grazing and enclosure experiment, a preliminary survey indicated that approximately 20 grassland caterpillars were present per square meter, primarily in areas with abundant sedges and grasses[11]. Their activity was observed

mainly during cool and humid weather conditions [27,28]. Based on this observation, from July to August 2021, we collected 400 grassland caterpillars from outside the experimental plots. In mid-July, we added up to 20 grassland caterpillars (in addition to the original population) into each of the 20 sample plots. The caterpillar population was recorded every 2 days for a total of five observations, continuing until most plots contained no remaining caterpillars. In early August, the caterpillar collection, introduction, and census procedures were repeated. In early September, we measured plant species richness, individual abundance, and aboveground biomass within each 0.5 m × 0.5 m subplot across the 20 experimental plots to characterize plant community features.

2.3 Data Analysis

We analyzed the explanatory power and overall effect of month, repeated observations within each month, and grazing/enclosure treatments on grassland caterpillar numbers, total plant species richness, individual abundance, aboveground biomass, and the abundance of different plant functional groups. We used a general linear model (GLM) without considering interaction effects among the explanatory variables. Grassland caterpillar counts, plant species richness, and individual abundance followed a Poisson distribution, while aboveground biomass followed a Gaussian distribution(Tables 1 and 2; Fig. 2). To determine how repeated observations over 2 months affected the effect of grazing and enclosure treatments on grassland caterpillar population dynamics, we used a nested general linear mixed model (GLMM) to analyze the effect of grazing on caterpillar populations from July to August 2021. The enclosure treatment was used as the control group, and repeated observations were set as a random variable (Fig. 1). To examine the relationship between plant community characteristics and grassland caterpillar population dynamics, we used a GLMM to assess the effects of total plant species richness, individual abundance, aboveground biomass, and functional group abundance on caterpillar numbers in each plot (Fig. 3). In this analysis, the relationship between plant community characteristics and grassland caterpillar populations included month as a random variable (because month only explained 5.9% of caterpillar population variation). Because repeated observations within each month significantly influenced caterpillar counts (decreasing from 20 caterpillars initially to nearly zero by the fifth observation), we conducted separate analyses on caterpillar counts from the first four observations, as well as on the median value across multiple observations in relation to plant community characteristics. Grazing disturbance had no significant effect on the species richness of the four plant functional groups (sedges, grasses, forbs, and legumes), so this dataset was excluded from the final analysis. All analyses were performed using R (v.3.6.3). The "lme4" package was used to implement the GLMM, while the "ggplot" and "sjPlot" packages were used to visualize the results [29,30].

3 Results and Analysis

3.1 Effect of Grazing on the Grassland Caterpillar

We used GLM to analyze the effects of month, repeated observations, and grazing/enclosure treatments on grassland caterpillar populations. We applied a nested GLMM to examine the effect of grazing and enclosure treatments on caterpillar populations under the influence of stochastic processes (repeated observations) from July to August. The results showed significant monthly variation in caterpillar populations. The number of grassland caterpillars observed was significantly lower in August than in July ($P < 0.001$). However, overall, month had a relatively small effect, explaining only 5.9% of the variation in caterpillar population dynamics (Table 1). Repeated observations and residual variance had a major effect on caterpillar numbers. Repeated observations accounted for 31.6% of the variation, while residual variance (differences among replicates within the same treatment) explained 36% of the variation. Compared with the first observation, caterpillar counts significantly decreased in all subsequent observations ($P < 0.001$; Table 1). Grazing had a smaller effect than repeated observations and residual variance but still significantly reduced caterpillar numbers. Grazing accounted for 26.6% of the variation in caterpillar populations. Compared with the enclosure treatment, grazing significantly reduced caterpillar numbers ($P< 0.001$; Table 1). In July, the number of caterpillars was significantly lower in the grazed plots than in the enclosure plots ($P< 0.001$; Fig. 1). Similarly, in August, caterpillar numbers were significantly lower in the grazed plots than in the enclosure plots ($P< 0.001$; Fig. 1).

Table 1. Effect of month, repeated measurements, and grazing/enclosure treatments on grassland caterpillar numbers assessed by GLM

Effect size	Estimated slopes ± Std.
Months (variability(%)|FP 5.9%|29.7***)	
August vs. July	−0.36 ± 0.04***
Repeated measurements (variability (%)|FP 31.6%|19.8***)	
2th observation vs. 1th observation	−0.24 ± 0.06***
3th observation vs. 1th observation	−0.63 ± 0.07***
4th observation vs. 1th observation	−0.81 ± 0.08***
5th observation vs. 1th observation	−1.18 ± 0.09***
Grazing/enclosure treatments (variability (%)|FP 26.6%|13.3***)	
Grazing vs. enclosure	−0.72 ± 0.05***
Residual variability (%)	36%

Note: The table values measure the variability (%, F-value and P-value) and slopes (mean ± Std. Error) of fixed factors (month, repeated measurements, and grazing/enclosure treatments) on caterpillar numbers. Positive and negative values, numeric size, and significant effect indicate the influence of month (vs. July), repeated measurements (vs. 1th observation), and treatment (vs. enclosure) on caterpillar numbers. A positive value means increase, while a negative value means decrease;*: $P < 0.05$.

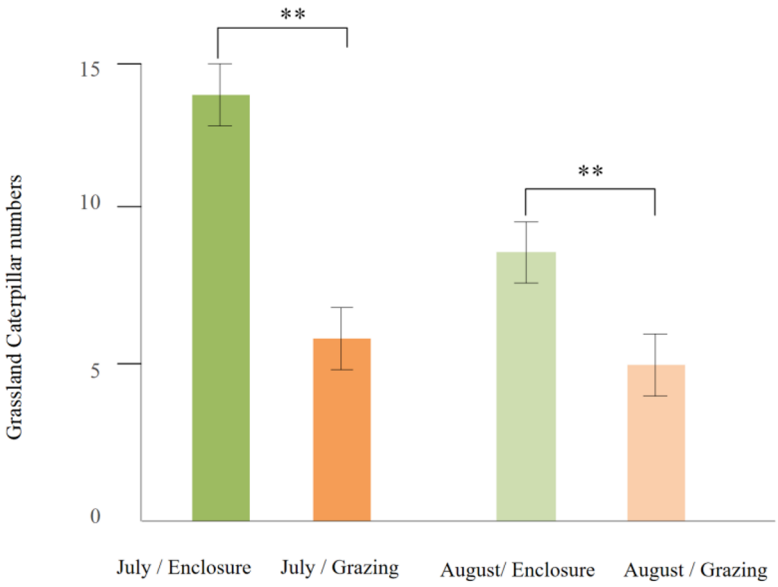


Fig. 1. Effect of grazing on numbers of grassland caterpillars over 2 months (mean ± SE). Note: GLMM was implemented, with treatment nested within months as fixed factors and repeated measurements as a random effect, to evaluate their impacts on grassland caterpillar abundance

3.2 Effect of Grazing on Plant Community Characteristics

We used a GLM to analyze the effects of grazing on plant community characteristics. Grazing had a minor effect on overall species richness and individual abundance. Grazing explained only 1.6% of the variation in total species richness and 2.1% of the variation in total individual abundance. Grazing had a greater effect on functional group abundance, explaining 19.1% of the variation in grass species richness and 16.2% of the variation in grass individual abundance. Grazing explained 14.6% of the variation in sedge species richness and 12.7% of the variation in sedge individual abundance (Table 2). Grazing significantly affected total biomass. It accounted for 36.3% of the variation in total biomass and had a strong effect on functional group abundance, explaining 46.2% of the variation in sedge biomass, 23.3% of the variation in grass biomass, and 19.6% of the variation in forb biomass (Table 2). Compared with the enclosure treatment, grazing significantly reduced the total number of individuals as well as sedge and grass individuals while increasing the number of legumes. However, it did not affect forb individual abundance (Table 2 and Fig. 2a). Grazing significantly decreased total biomass, as well as sedge, grass, and forb biomass, but had no significant effect on legume biomass (Table 2 and Fig. 2b). Grazing did not significantly alter total species richness or the species richness of individual functional groups (Table 2).

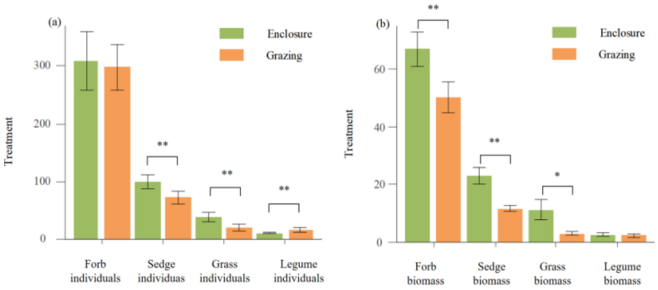


Fig. 2. Effect of grazing on plant community characteristics in each functional group (mean ± SE).

Note: The significance of the influence of grazing on individual numbers and biomass in each functional group was assessed using a GLM.A Subsection Sample

Table 2. Effect of grazing on plant community characteristics assessed using a GLM

Plant community characteristics	Variability (%)|FP	Enclosure/grazing Estimated slopes ± Std. Error	Residuals variability
Total species richness	1.6%|0.6	−0.04 ± 0.06	98.4%
Total individuals	2.1%|0.8	−0.12 ± 0.02***	97.9%
Total biomass	36.3%|21.7***	−36.53 ± 7.85***	63.7%
Sedge richness	14.6%|6.5*	0.21 ± 0.21	85.4%
Sedge individuals	12.7%|5.5*	−0.32 ± 0.03***	87.3%
Sedge biomass	46.2%|32.6***	−11.36 ± 2.00***	53.8%
Grass richness	19.1%|9.0**	−0.27 ± 0.17	80.9%
Grass richness	16.2%|7.3*	−0.68 ± 0.06***	83.8%
Grass biomass	23.3%|11.6**	−8.20 ± 2.41**	76.7%
Forb richness	0.2%|0.06	−0.01 ± 0.07	99.8%
Forb individuals	0.2%|0.1	−0.04 ± 0.02	99.8%
Forb biomass	19.6%|9.2**	−16.70 ± 5.5**	80.4%
Legume richness	3.0%|1.2	−0.16 ± 0.20	97.0%
Legume individuals	6.7%|2.7	0.40 ± 0.09***	93.2%
Legume biomass	0.7%|0.3	−0.27 ± 0.54	99.3%

Note: The effects of grazing on total plant species richness, individuals and biomass, and plant community of each functional group are measured in this table. Positive and negative values, numeric size, and significant effect indicate the influence of treatment (vs. enclosure) on caterpillar numbers. A positive value means increase, while a negative value means decrease;*: $P < 0.05$. Plants were measured only once in September 2021, so there was no effect of month and repeated measurement on the plant community.

3.3 Relationship between Plant Community Characteristics and the Grassland Caterpillar

Month was treated as a random variable to examine the relationship between plant community characteristics and grassland caterpillar counts from repeated observations each month. Total plant species richness had no significant effect on caterpillar numbers in any observation, but total plant biomass and individual abundance were strongly correlated with caterpillar population fluctuations. The only exception was the fourth observation, where biomass was not significantly correlated with caterpillar numbers (Fig. 3a–e). The individual abundance and biomass of different functional plant groups had a substantial effect on caterpillar numbers, and these two variables were highly correlated (Fig. 3f–y). Grassland caterpillar numbers increased with the biomass of sedges, grasses, and forbs. Caterpillar numbers decreased with increasing legume biomass and had a significant negative correlation. Caterpillar numbers significantly increased with sedge and grass individual abundance. Caterpillar numbers tended to increase with forb individual abundance, but this was not significant. Caterpillar numbers significantly decreased as legume individual abundance increased.

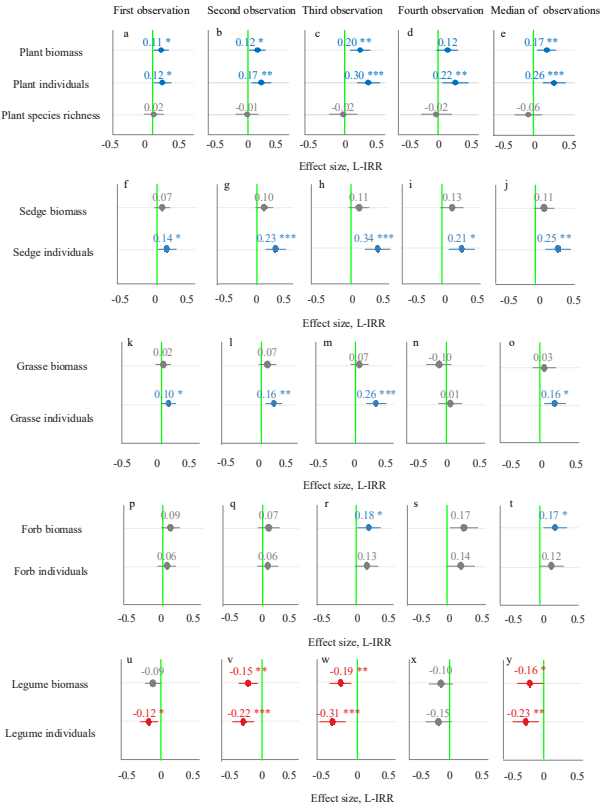


Fig. 3. Effect of plant community characteristics on numbers of grassland caterpillars assessed by GLMM

4 Discussion

4.1 Effects of Grazing on Grassland Caterpillar Populations

Cao Hui et al. conducted a simulated warming and grazing experiment at the Haibei Alpine Meadow Research Station to determine how these factors affect grassland caterpillars. Moderate grazing and its interaction with warming significantly increased caterpillar growth rates [31]. Light or moderate grazing can reduce plant community carbon content and vegetation height while increasing nitrogen and phosphorus content in plants, thereby promoting the regrowth of tender plant tissues and maintaining plant community stability. These ultimately benefit the growth of grassland caterpillars [25,32–34]. However, Chen Kelu et al. found that as grazing intensity increased, caterpillar populations first increased and then declined [35]. The present study showed that grazing significantly reduced grassland caterpillar populations. This may be because the experimental site experienced moderate to heavy grazing, where livestock extensively consumed and trampled grasses. This activity prevented plants from regenerating at a sufficient rate to compensate for damage [34,36]. As a result, the food resources preferred by grassland caterpillars (sedges and grasses) declined [5,10] and led to a reduction in caterpillar numbers. These research findings are consistent with the aforementioned hypothesis, which supports the use of grazing intensity as a predictor for changes in grassland caterpillar population dynamics.

4.2 Relationship between Grassland Caterpillar Populations and Functional Group Abundance Under Grazing Disturbances

As grazing intensity increases, the abundance of high-quality forage grasses (sedges and grasses) decreases [19,20]. Different livestock combinations and grazing schedules also reduce the biomass of sedges and grasses compared with ungrazed control areas [37]. However, moderate grazing and short-term grazing exclusion can promote the growth of Alpine meadow forage [38]. We found that grazing significantly reduced sedge and grass abundance, which led to a decrease in caterpillar populations. This result aligns with our hypothesis. One possible explanation is that in our moderately to heavily grazed experimental site, livestock consumed sedges and grasses, reducing their ecological niche and allowing less palatable plant species to expand their coverage [20]. Because grassland caterpillars prefer the same types of plants, their numbers consequently declined. Another explanation could be that excessive grazing reduces nitrogen and phosphorus availability in the soil [39], especially affecting grasses [40-42], which can lead to a decrease in plant diversity and a subsequent decline in caterpillar populations. Niu Yujie et al. conducted grazing experiments in northeastern Qinghai-Tibet Plateau grasslands and demonstrated that forb abundance (observed values) decreased with increased grazing intensity, whereas the relative importance of forbs within the community increased [20]. Similarly, Zhou Guoli et al. found that as grazing intensity increased, the proportion of high-quality forage plants declined, while forb abundance increased [19]. Moderate grazing can promote forb regrowth through intraspecific var-

iation [25]. However, seasonal grazing and changes in livestock structure had no significant effect on forb abundance when compared with control conditions [37]. We found that grazing significantly reduced forb biomass but did not significantly affect grassland caterpillar populations. This may be because moderate to heavy grazing led to extensive plant trampling and consumption resulting in an overall reduction in total biomass and, consequently, a decline in forb biomass. However, the reduction in forbs was smaller than the decline in sedges and grasses, which explains why sedge and grass abundance had a greater effect on caterpillar populations than forbs under grazing conditions. Han Bing et al. conducted grazing and enclosure experiments in Gannan Prefecture, Gansu Province, China, showing that grazing led to overconsumption of forage grasses, which allowed less palatable or toxic legumes (e.g., Thermopsis lanceolata) to persist [43]. Other studies have also shown that grassland caterpillars do not prefer nitrogen-rich legumes [10], although many herbivorous insects rely on legumes [44]. This finding explains why grazing increased legume individual abundance in our study and why some caterpillar observations had a significant negative correlation with legume abundance.

4.3 Effects of grazing on Grassland Caterpillar Population Dynamics Under the Dominance of Stochastic Processes

We found that both a simple model, excluding month and repeated observations, and a nested model incorporating these random effects showed that grazing had a significant and consistent effect on grassland caterpillar population dynamics. Although monthly repeated observations and residual variance were the dominant factors influencing caterpillar population changes, grazing/enclosure treatments remained a significant and stable predictor of caterpillar populations. These results suggest that, due to the high spatiotemporal variability and stochasticity of grassland caterpillar populations [17,18], long-term repeated observations are necessary to understand the relationship between grazing disturbance, caterpillar populations, and alpine vegetation.

Future studies should focus on the significant role of plant functional diversity and small herbivores under the influence of stochastic processes, as well as the effects of human disturbances and environmental changes.

5 Conclusion

In this paper, a grazing and enclosure experiment platform was set up in the alpine grassland on the eastern edge of the Qinghai Tibet plateau for a growing season. The population and vegetation characteristics of grassland caterpillars were investigated in detail. The effects of grazing disturbance on the population of grassland caterpillars and alpine vegetation and the relationship between the population of grassland caterpillars and alpine vegetation were analyzed and studied. The conclusion is as follows.

(1) The number of grassland caterpillars, the number of sedges and grasses, and the biomass of sedges and grasses in grazing grassland were lower, which increased the

abundance of legumes in the community, but the species richness of each functional group had no significant difference;

(2) Further analysis showed that although the random effect (observation or population fluctuation) had a great impact on the number of grassland caterpillars, the effect of grazing enclosure on grassland caterpillars was still significant and consistent;

(3) There was a significant positive correlation between the number of grassland caterpillars and the biomass and individual number of Cyperus, grasses and weeds, and a negative correlation between the number of grassland caterpillars and the biomass and individual number of legumes, but it had no effect on the species richness of each functional group;

(4) The population of grassland caterpillars can be reduced by reducing the individual number and biomass of sedge, grass and weeds, so as to reduce the harm of grassland caterpillars to grassland.

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Disclosure of Interests

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