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# Plant biomass partitioning in alpine meadows under different herbivores as influenced by soil bulk density and available nutrients

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ABSTRACT

Biomass allocation is a key mechanism for understanding the response of alpine meadow plants to environmental changes. However, the two major theories of plant biomass partitioning, that is, optimal and equidistant allocation, are highly controversial. This study aimed to test these hypotheses by using the biomass allocation pattern of Qinghai–Tibetan Plateau alpine meadows under different herbivore assemblages and enclosures and to identify the key physicochemical factors driving changes in biomass allocation. The results showed that fencing and grazing lead to the allocation of more biomass to roots and shoots, respectively. Additionally, our results support the optimal allocation hypothesis, which is mainly regulated by changes in soil physicochemical properties. Specifically, the trade-off between aboveground- and belowground biomass negatively correlated with the soil bulk density, soil moisture, available nitrogen, and available phosphorus but positively correlated with available potassium. In terms of biomass trade-offs, co-grazing yaks and Tibetan sheep at a 1:6 ratio with moderate grazing intensity may be a reasonable method to use and protect alpine meadows on the Qinghai-Tibetan Plateau.

## 1. Introduction

Studying trade-off mechanisms between the aboveground biomass (AGB) and belowground biomass (BGB) of plants is crucial to understanding plant resource allocation strategies, physiological integration patterns, and the environmental adaptations of plant growth and development (Gao et al., 2021). Under the influence of external environmental stress, plants actively allocate biomass to different organs, increasing their efficiency in resource acquisition and use. Two main theories, that is, optimal and isometric allocation, are currently used to explain biomass allocation patterns (Sun et al., 2018). The theory of optimal allocation suggests that plants actively regulate the distribution of biomass among different organs to ensure that they can acquire resources in the most efficient way in an environment in which resources are scarce (Bloom et al., 1985). This means that biomass allocation is dominated by changes in trade-offs. For example, when soils are nutrient-poor, plants prioritize biomass allocation to the root system to ensure nutrient uptake and utilization, whereas plants prioritize biomass allocation to the stems and leaves when soils are nutrient-rich to ensure photosynthesis (Maire et al., 2009). In contrast, the isometric allocation theory suggests that the distribution of plant biomass is not constrained by the external environment and that biomass is equally distributed to different organs regardless of the environment (Enquist and Niklas, 2002). Therefore, clarifying the patterns of plant biomass allocation in different environments not only contributes to enhancing the understanding of how plants utilize diverse resources to adapt to different environmental conditions but also provides valuable insights for ecosystem management, thereby facilitating improvements in ecosystem management practices.

The Qinghai–Tibetan Plateau (QTP) is renowned as the highest, largest, and most biodiverse region worldwide because of its distinctive geographical positioning (Mao et al., 2021). Spanning more than 60 % of the plateau's total surface area, the alpine grasslands on the QTP play a crucial role in conserving soil and water, sequestering carbon and nitrogen, sustaining herders' livelihoods, and maintaining stable ecosystem functions (Schirpke et al., 2017; Li et al., 2018).

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Unfortunately, these valuable alpine meadows have experienced considerable degradation in recent decades due to overgrazing and climate change (Dong and Sherman, 2015). To prevent the further degradation of alpine meadows, the local government introduced a series of measures to protect alpine grasslands including enclosures (Dong et al., 2020; Sun et al., 2021). Notably, one of these protective measures, the Grassland Contract Responsibility System, has effectively prevented the degradation of alpine grasslands but created new problems. The fundamental approach of the Grassland Contract Responsibility System involves the demarcation of pasturelands through the implementation of fencing, thereby allocating these areas to individual pastoralists and establishing privately-owned small-scale grazing enclosures. However, this system leads to the fragmented utilization of alpine meadows, which is not conducive to the sustainable use of alpine meadows (Niu et al., 2019). Additionally, different herder management choices and preferences have resulted in three grassland use patterns (i.e., herders grazing only Tibetan sheep or only yaks or co-grazing yaks and Tibetan sheep) gradually becoming the main form of grassland use in QTP alpine meadows (Liu et al., 2023). Different types of grazing livestock will further exacerbate the fragmented utilization of alpine meadows. For example, various types of grazing livestock were shown to affect both directly and indirectly the biomass allocation of alpine meadow plants through selective intake and their difference in trampling and dung return frequencies, respectively (Yang et al., 2019). Therefore, determining the biomass allocation pattern of alpine meadow plants under different herbivore assemblages and clarifying which herbivore assemblage can best maintain the ecosystem function of alpine meadows is important.

Researchers have primarily examined the effects of various grazing intensities, restoration years, and fencing measures on biomass allocation patterns in alpine meadows (Gong et al., 2015; Wu et al., 2019; Zhou et al., 2021). However, research on alterations in the trade-off between AGB and BGB in alpine meadow plants under diverse herbivore assemblages is relatively limited. Therefore, elucidating changes in plant biomass trade-offs and their drivers in alpine meadows with different herbivore assemblages is essential for the conservation and rational use of fragile alpine meadow ecosystems (Sun and Wang, 2016). In this study, we hypothesized that the patterns of plant biomass allocation in alpine meadows under different herbivore assemblages follow the optimal allocation theory and that their variations are significantly modulated by changes in the soil physicochemical properties. Thus, we investigated the trade-offs between biomass allocation and soil physicochemical properties in different herbivore assemblages to (a) clarify how they affect changes in AGB and BGB trade-offs and (b) identify the main physicochemical factors driving changes in biomass trade-offs in alpine meadows. To test our hypothesis, using experimental treatments and to determine the effects of the plant community and physicochemical properties of the soil in alpine meadows on the QTP, we investigated the three distinct herbivore grazing configurations, namely, yak grazing, Tibetan sheep grazing, and the co-grazing of yaks and Tibetan sheep, at varying proportions.

## 2. Materials and methods

### 2.1. Study site

The research was conducted at the Qinghai Provincial Alpine Grassland-livestock Adapative Management Technology Platform, organized by Qinghai University (latitude 36°56′ N, longitude 100°53′ E, altitude 3038 m) within Haiyan County, Haibei Autonomous Prefecture, Qinghai Province (Fig. 1). In this area, no absolute frost-free days occur. The average annual temperature is 1.4 °C; the temperature varies from −24.8 °C during the non-growing season to 12.5 °C during the growing season (Shi et al., 2022). The average annual precipitation is 425 mm. The soil type is Gelic Cambisol with an average thickness of 0.65 m, and is classified as World Reference Base for Soil Resources (Wang et al., 2018a). The grassland type is an alpine meadow dominated by *Stipa purpurea*, *Kobresia humilis*, *Leymus secalinus* (Georgi) Tzvel., and *Potentilla acaulis*.

### 2.2. Experimental design and sampling measurements

In 2013, we selected an $\sim 1 \times 10^5$ $m^2$ area of alpine meadow with flat terrain and a relatively uniform environment and plant cover for fencing to prevent livestock grazing. Before the grazing experiment, we surveyed the aboveground biomass of edible forage grass in the meadow and determined the grazing intake of yaks and Tibetan sheep. Studies have shown that alpine meadows with moderate grazing intensity exhibit the highest plant diversity and AGB (Gao and Carmel, 2020). One year after fencing, we initiated a grazing experiment with different herbivore assemblages in the alpine meadows by using moderate grazing intensity (3.86 sheep units/ha). All grazing treatments in this study were conducted at a moderate grazing intensity. To ensure this moderate grazing intensity, we adjusted the area of grazing plots based on the aboveground biomass of edible forage grass of the meadow and the grazing intake of livestock. Additionally, we dynamically adjusted the grazing days during the grazing period to maintain a grass utilization rate between 50 % and 55 %. When the grass utilization rate exceeded

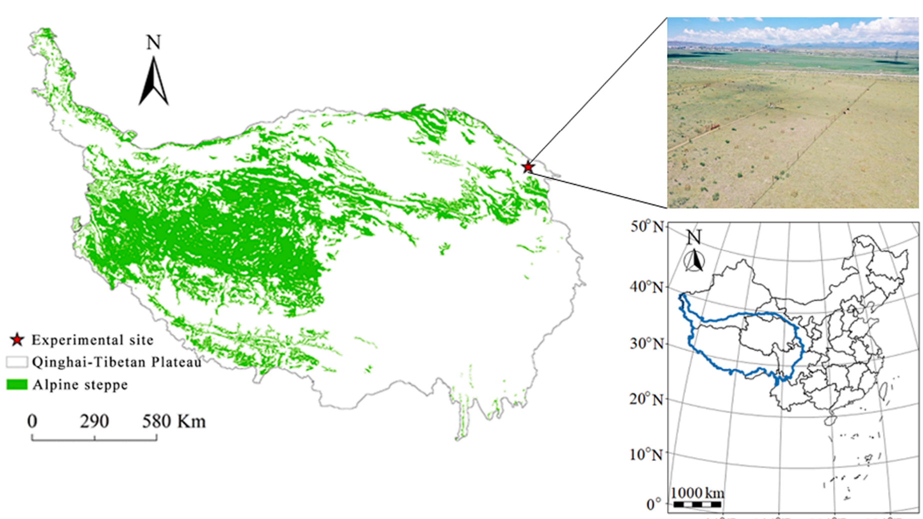


**Fig. 1.** The location of the sampling site.

55 %, livestock were moved to nearby pastures for grazing. At this time, the calculated grazing intensity was 3.86 sheep units/ha (moderate grazing intensity). All grazing treatments in this study were conducted at a moderate grazing intensity. We selected eighteen plots and established six treatments: yak grazing (YG), Tibetan sheep grazing (SG), mixed grazing of yaks and Tibetan sheep at a ratio of 1:2 (MG 1:2), mixed grazing of yaks and Tibetan sheep at a ratio of 1:4 (MG 1:4), mixed grazing of yaks and Tibetan sheep at a ratio of 1:6 (MG 1:6), and grazing exclusion (NG). Details are presented in Table 1 and Fig. S1. The male yaks (100 ± 5 kg, 1.5 years old) and male Tibetan sheep (30 ± 2 kg, 1 year old) were from local herders. Grazing occurred consistently every year between June and October for seven years until 2021. Throughout the grazing period, no additional food but ample drinking water was provided.

Annually, starting in 2014, we conducted plant sample collection on August 15 that lasted no more than 5 d. We randomly selected 3 quadrats (0.5 m × 0.5 m) at least 15 m apart within each plot annually to determine the plant community composition; nine quadrats were selected per treatment, totaling 54 quadrats. Plant richness, height, and coverage were recorded for each quadrat (Liu et al., 2022) (Table S1). In each quadrat, the AGB of various functional groups, including Gramineae, Cyperaceae, Leguminosae, and forbs, and the BGB were assessed. For the accurate determination of biomass, the AGB and BGB samples were subjected to oven-drying at 65 °C until a constant weight was reached. Subsequently, they were weighed in a laboratory to a precision of 0.001 g (Sun et al., 2018). For AGB, the plants were harvested at the soil surface within each quadrat; BGB was measured by extracting soil cores, using a 7 cm diameter root drill and reaching a depth range of 0–10, 10–20, and 20–30 cm (Chen et al., 2022).

In August 2021, after the plant community survey was completed, we collected soil samples within the quadrats. Soil bulk density (BD) was determined using a cutting ring with a volume of 100 $cm^3$ at depths ranging from 0 to 10, 10–20, and 20–30 cm in each quadrat. Soil moisture (SM) was determined using a drying method that used 105 °C for each quadrat. For chemical analysis, soil samples were collected using an auger with a diameter of 3.5 cm, extending to depths ranging from 0 to 10 cm, 10–20 cm, and 20–30 cm. Three replicates were collected from each quadrat and combined into a single composite sample, with a total of 3 replicates × 3 soil layers × 3 plots × 6 treatments = 162 soil samples. These soil samples were divided into two parts. One part was stored at 4 ℃ for the determination of available nitrogen (AN), and the other part was air-dried, sieved through a 2 mm mesh, and ground to facilitate chemical analysis. Multiple soil chemical properties were measured, such as the soil total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), available phosphorus (AP), available potassium (AK), and soil pH. The measurement of all physicochemical properties of the soil used the methodology in Wang et al., (2022a).

**Table 1**
Grazing experiment design details.

| Treatment | Number of yaks | Number of Tibetan sheep | Area of plot/ $m^2$ | Grazing intensity sheep units/ ha | Number of plots |
|---|---|---|---|---|---|
| YG | 1 | 0 | $2.6 \times 10^3$ | 3.86 | 3 |
| SG | 0 | 2 | $1.7 \times 10^3$ | 3.86 | 3 |
| MG 1:2 | 1 | 2 | $4.3 \times 10^3$ | 3.86 | 3 |
| MG 1:4 | 1 | 4 | $6.0 \times 10^3$ | 3.86 | 3 |
| MG 1:6 | 1 | 6 | $7.7 \times 10^3$ | 3.86 | 3 |
| NG | 0 | 0 | $0.5 \times 10^3$ | 3.86 | 3 |

YG: yak grazing; SG: Tibetan sheep grazing; MG 1:2: mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4: mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6: mixed grazing of yaks and Tibetan sheep at a ratio of 1:6, NG: grazing exclusion.

## 2.3. Data analysis

### 2.3.1. Analysis of plant and soil characteristics

First, the Kolmogorov–Smirnov test was used to verify the data normality. Next, descriptive statistics and one-way ANOVA followed by a multiple comparison post-hoc Tukey test were performed to examine variations in richness, height, coverage, AGB and BGB, and soil physical and chemical properties among treatments. To explore the contribution of grazing years, grazing activities, and their interaction due to the changes in AGB and BGB, we conducted a linear mixed-effects model analysis based on the "glmm.hp" package (Lai et al., 2022). Grazing years and grazing treatment were fixed factors, and the surveyed blocks were random factors. Additionally, the effects of different herbivore assemblages on AGB and BGB, and on physicochemical properties were quantified and compared by using the following formula in the form of response ratios:

$$R = Ln\left(\frac{T}{C}\right) \tag{1}$$

T represents the specific observed values of biomass or physicochemical properties for different herbivore assemblages, and C denotes the specific observed values of biomass or physicochemical properties within the enclosure. We also used cumulative response ratios to represent the overall effects of all grazing treatments. When calculating the cumulative response ratio for each treatment group, we divide its effect value by the effect value of the control group and then multiply these ratios together. Positive response ratio values indicate an increase in the indicator under this treatment, and negative values indicate the opposite trend (Sun et al., 2021).

### 2.3.2. Calculation of the trade-off between AGB and BGB

The trade-off between the AGB and BGB was evaluated within each quadrat by calculating the root-mean-square error (RMSE):

$$RMSE = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}\left(RB - \overline{B}\right)^2} \tag{2}$$

where $RB$ is the relative benefit of biomass, and $\overline{B}$ is the expected benefit of $i$ number AGB or BGB. When the biomass trade-off was towards the aboveground biomass, we defined the value as positive. When the biomass trade-off is towards the belowground biomass, we defined the value as negative.

The $RB$ of the biomass was calculated as:

$$RB = \frac{B_i - B_{min}}{B_{max} - B_{min}} \tag{3}$$

where $B_i$ is the observed biomass value, $B_{min}$ is the observed lowest biomass value, and $B_{max}$ is the highest biomass value (Gao et al., 2021; Feng et al., 2023).

### 2.3.3. Random forest analysis, correlation analysis, and structural equation mode

First, we conducted random forest analysis by using the "randomForest" package to identify key physicochemical factors influencing the trade-offs in AGB and BGB in alpine meadows. We considered that the model passed the test when the model's $P$-value was less than 0.05, indicating a high level of reliability. Next, to examine the relationship between changes in physicochemical factors and variations in AGB and BGB, we used the "Hmisc" package to perform Pearson correlation analysis. Finally, on the basis of the selection results from the random forest model, we used the "piecewiseSEM" package to construct a piecewise structural equation model (SEM) to investigate the primary mechanisms through which soil physicochemical factors regulate changes in AGB and BGB trade-offs in alpine meadows(Lefcheck, 2016). We considered that the SEM passed the test when the SEM's *P*-value was less than 0.05 and the lower the Akaike information criterion (AIC) value and Fisher's C value of the SEM, the higher the model accuracy. All statistical analyses and figure plotting were conducted in R 4.0.3 (R Development Core Team, 2020).

## 3. Results

### 3.1. Effects of herbivore assemblages on AGB and BGB changes in alpine meadows

Starting from the third year of grazing, grazing activities significantly reduced the AGB of alpine meadow plants (Fig. 2a and S2). However, only the BGB of alpine meadow plants in 2021 was significantly reduced in the MG 1:2 treatment (Fig. 2b and S3). The results of the mixed-effects model showed that grazing activities had a greater impact on the AGB and BGB changes (Fig. 2c, d). The changes in functional group proportion showed that starting from the sixth year of grazing, the proportion of Gramineae plants in AGB was always higher in the MG:16 treatment than in the other treatments (Fig. 3a). Similarly, starting from the sixth year of grazing, the proportion of BGB in the 0–10 cm soil layer in all treatments exceeded 70 % of the total BGB. Grazing results in the concentration of plant roots in the surface soil (Fig. 3b). Additionally, grazing was identified to be a factor causing a noteworthy disparity in the nutrient composition between the surface and deeper soil in alpine meadows, with the former exhibiting significantly elevated levels of available nutrients (Table S2).

### 3.2. Trade-off between AGB and BGB

When the grazing intensity in the alpine meadow is intermediate, plant biomass is preferentially allocated to the shoots, indicating a beneficial state for the AGB. When the alpine meadow is under fencing, plant biomass is preferentially allocated to the roots, implying a beneficial state for the BGB. Starting from 2018, the trade-off values of all grazing treatments remained relatively stable; thus, we only used the trade-off values from 2021 as an example for further analysis (Fig. 4a). When fenced, the trade-off value between AGB and BGB was 0.07. Among the grazing treatments, the highest trade-off values were observed for the MG 1:2 and MG 1:4 treatments (both 0.05), and the lowest trade-off values were observed for the YG and MG 1:6 treatments (both 0.01; Fig. 4b).

### 3.3. Grazing increases soil available nutrients in alpine meadows

For total nutrients, YG and MG 1:2 significantly decreased the TOC content. SG and MG 1:6 significantly increased the TN and TP content. MG 1:4 significantly increased the TOC. Among available nutrients, AN significantly increased among the herbivore assemblages, and AK significantly decreased. Except for that of MG 1:4, the AP content significantly increased in the other herbivore assemblages. Regarding soil physical properties, SM significantly increased in YG, SG, and MG at the 1:6 ratio. The BD in different herbivore assemblages significantly increases. The soil pH significantly increased for MG at the 1:6 ratio (Fig. 5).

### 3.4. Effects of soil factors on the allocation of plant biomass

Random forest analysis was used to determine the key factors affecting the balance between AGB and BGB. The primary influencers in

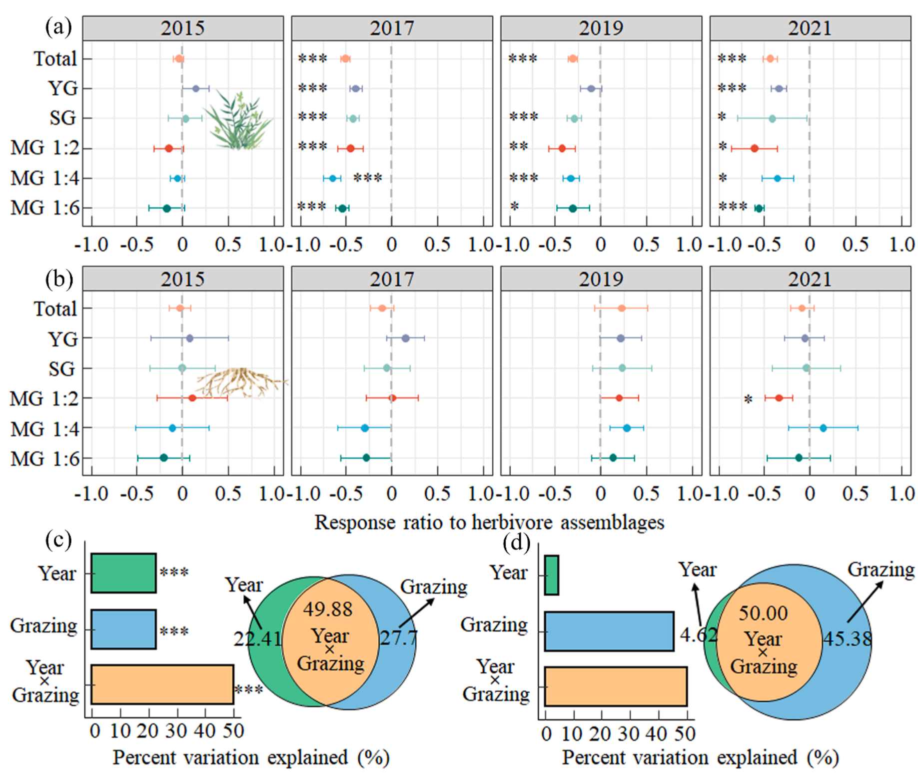


**Fig. 2.** Response ratios of aboveground biomass (AGB, a) and belowground biomass (BGB, b) to herbivore assemblages under different grazing years; The contribution of grazing years, grazing, and their interaction to the changes in aboveground biomass (c) and belowground biomass (d). Total: cumulative response ratios of all grazing treatments; YG: yak grazing; SG: Tibetan sheep grazing; MG 1:2: mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4: mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6: mixed grazing of yaks and Tibetan sheep at a ratio of 1:6. Asterisks indicate significant differences from zero. *0.01 < $P$ < 0.05; **0.001 < $P$ < 0.01; ***$P$ < 0.001.

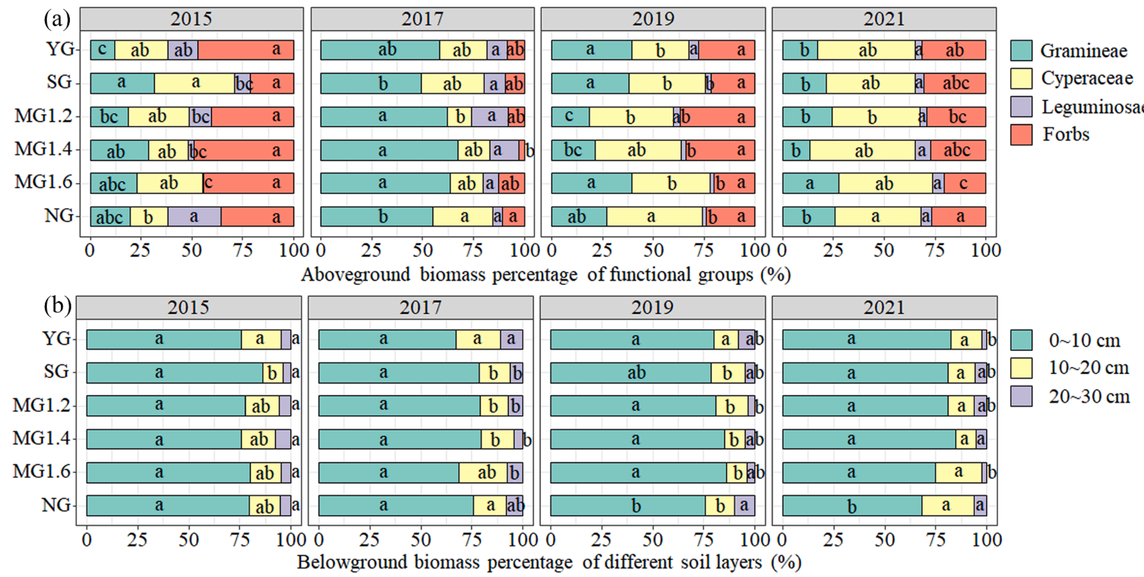


**Fig. 3.** Percentage of aboveground biomass of functional groups among herbivore assemblages under different grazing years (a), percentage of belowground biomass of different soil layers among herbivore assemblages under different grazing years (b). YG: yak grazing; SG: Tibetan sheep grazing; MG 1:2: mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4: mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6: mixed grazing of yaks and Tibetan sheep at a ratio of 1:6, NG: grazing exclusion. Different lowercase letters indicate significant differences in the same indicator among different treatments ($P < 0.05$).

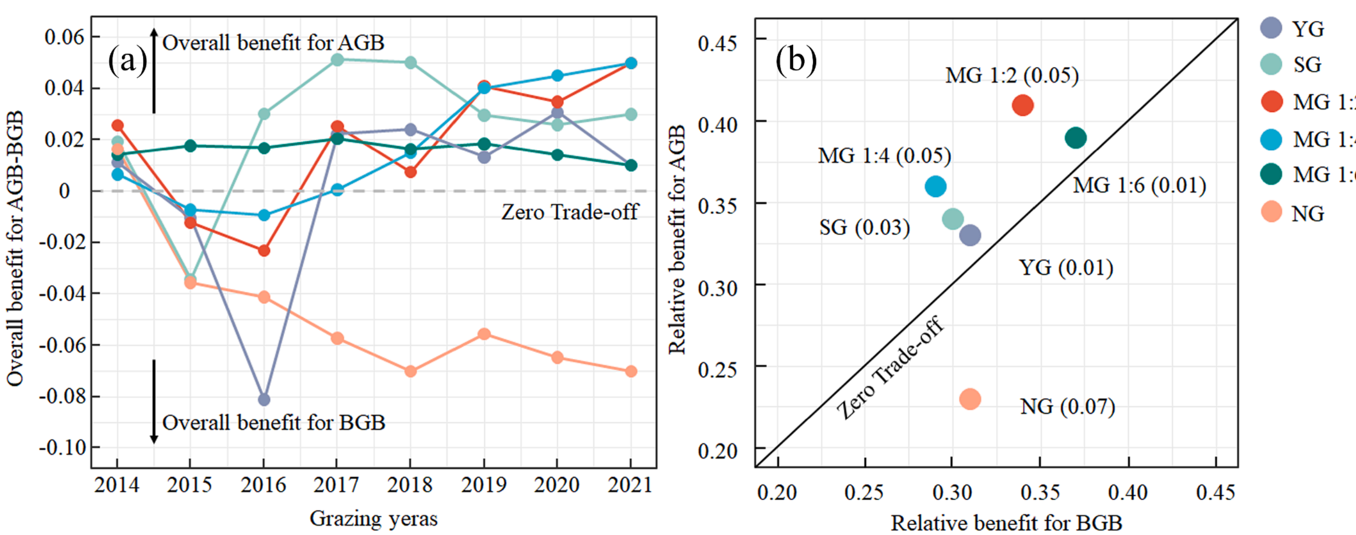


**Fig. 4.** The trade-off changes in aboveground biomass (AGB) and belowground biomass (BGB) of herbivore assemblages under different grazing years (a); The trade-off changes in aboveground biomass and belowground biomass of herbivore assemblages in 2021 (b). YG: yak grazing; SG: Tibetan sheep grazing; MG 1:2: mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4: mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6: mixed grazing of yaks and Tibetan sheep at a ratio of 1:6, NG: grazing exclusion.

this trade-off were BD, AK, AN, SM, AP, and TP (Fig. 6a). Correlation analysis showed that AGB positively correlated with TOC and AP but negatively correlated with BD. By contrast, BGB was positively associated with TN but negatively associated with SM (Fig. 6b).

Path analysis accounted for 83 % of the variability in the trade-off between AGB and BGB. The SEM indicated that the trade-off was positively affected by factors such as BD and AK, and had negative correlations with SM, AN, and AP. Additionally, BD indirectly affected the trade-off by exerting a positive effect on AN and AP. BD and SM also indirectly affected the trade-off by negatively influencing AK. Similarly, SM indirectly affected the trade-off through its positive effect on AN (Fig. 7a). The standardized effect sizes of the drivers further indicated that the trade-off had a negative relationship with BD, SM, AN, and AP and a positive relationship with AK (Fig. 7b).

## 4. Discussion

### 4.1. Grazing promotes allocation of plant biomass to shoots in alpine meadows

The trade-off between AGB and BGB responds differently to herbivore assemblages and enclosures. Plants preferentially allocate more biomass to roots than to shoots when the alpine meadow is fenced, and they allocate more biomass to shoots than to roots when the alpine meadow is moderately grazed, independent of changes in herbivore assemblages. The highest trade-off value for the alpine meadow biomass was 0.07 when fenced. The main reasons for this phenomenon may be that the alpine meadow is less disturbed by herbivore activity during fencing, especially excluding the effects of intake and trampling by

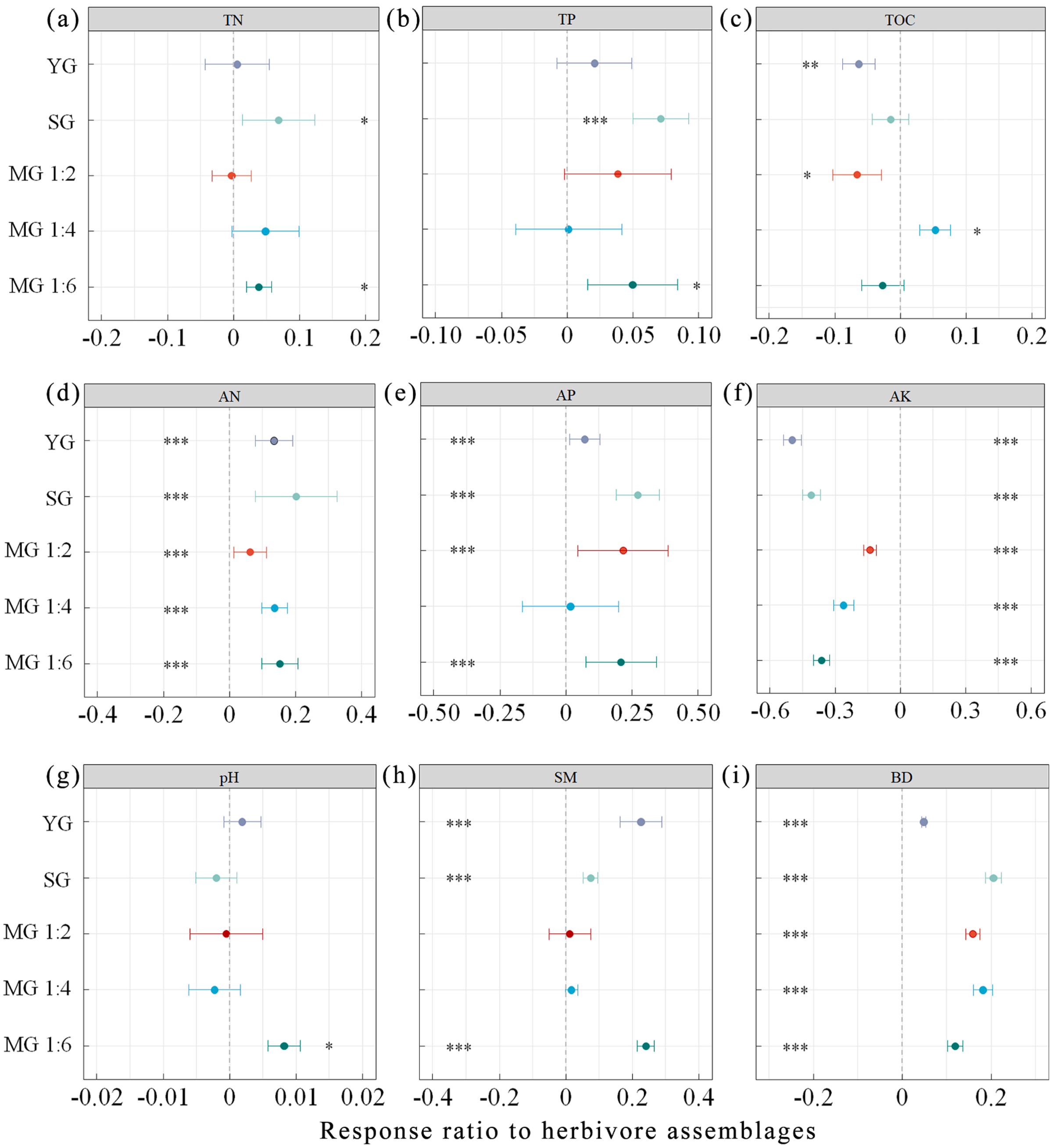


**Fig. 5.** The response ratios of different soil physicochemical properties to herbivore assemblages. TN: total nitrogen; TP: total phosphorus; TOC: total organic carbon; AN: available nitrogen; AP: available phosphorus; AK: available potassium; pH: soil pH; SM: soil moisture; BD: bulk density. YG: yak grazing; SG: Tibetan sheep grazing; MG 1:2: 1:2 ratio co-grazing of yaks and Tibetan sheep; MG 1:4: 1:4 ratio co-grazing of yaks and Tibetan sheep; MG 1:6: 1:6 ratio co-grazing of yaks and Tibetan sheep. YG: yak grazing; SG: Tibetan sheep grazing; MG 1:2: mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4: mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6: mixed grazing of yaks and Tibetan sheep at a ratio of 1:6. Asterisks indicate significant differences from zero. *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$.

herbivores, which effectively improves the moisture and aeration of the soil and significantly reduces the BD of the soil, thus favoring the growth of plant roots and accumulation of root biomass (Sun et al., 2018). By contrast, grazing grasslands experience a significant increase in the soil BD due to livestock trampling, leading to increased resistance to root penetration (Wang et al., 2019). Our study revealed a notable concentration of plant roots in the surface soil layer (0–10 cm) of alpine meadows subjected to moderate grazing intensity. There are two main reasons for this phenomenon: 1) higher soil capacity and poorer moisture and oxygen conditions are not conducive to root growth in deeper soils, and 2) the return of excreta from grazing livestock can increase the ease with which plant roots to obtain the nutrients they need from the surface soil layer. The findings of this study showed that the nutrient content in the topsoil was substantially higher than that in the subsoil layers. Consequently, the roots in the alpine meadow vegetation exhibited aggregation towards the topsoil layer, particularly under grazing conditions. This result supports the initial hypothesis of this study, which suggests that plant biomass trade-offs in alpine meadows undergo significant changes in response to various grazing practices. Additionally, the observed biomass allocation pattern aligns with the principles outlined in optimal allocation theory. In the literature, researchers have mainly focused on the effects of various grazing

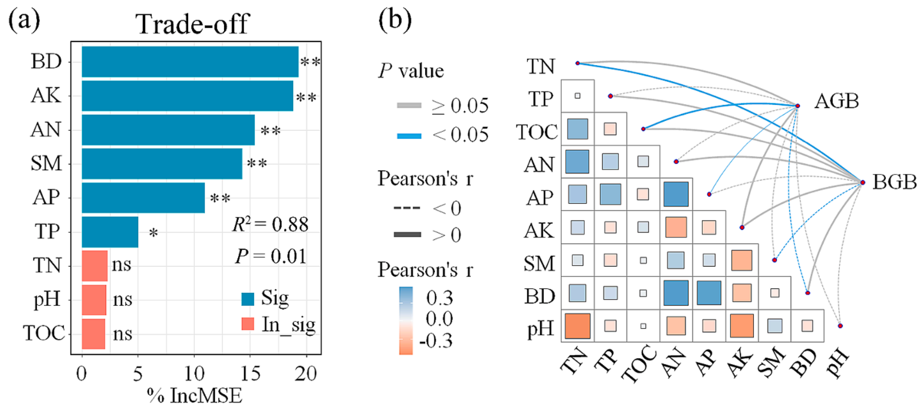


**Fig. 6.** Random forest analysis identified key physicochemical factors that dominate changes in trade-off (a); Pearson correlation between biomass and soil physicochemical properties (b). BD: bulk density; AK: available potassium; AN: available nitrogen; SM: soil moisture; AP: available phosphorus; TP: total phosphorus; TN: total nitrogen; pH: soil pH; TOC: total organic carbon; AGB: above ground biomass; BGB: below ground biomass. *0.01 < $P$ < 0.05; **0.001 < $P$ < 0.01.

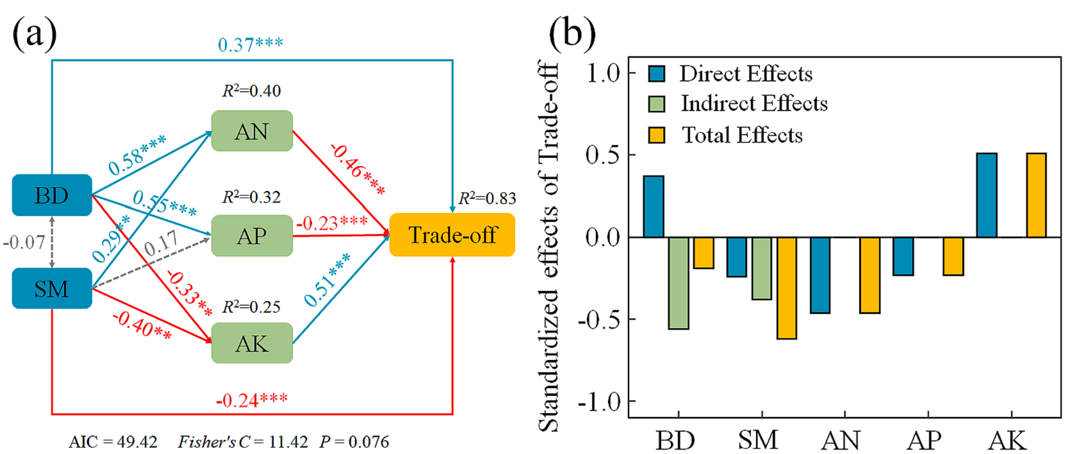


**Fig. 7.** Effect of soil bulk density (BD), soil moisture (SM), available nitrogen (AN), available phosphorus (AP), available potassium (AK) on trade-off (a); Standardized effects of driving factors on trade-off (b). Blue solid lines and solid red lines represent significantly positive and negative relationships, respectively, while the gray dotted lines indicate insignificant relationships. *0.01 < $P$ < 0.05; **0.001 < $P$ < 0.01; ***$P$ < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

intensities or enclosures on the net primary productivity, species richness, and plant community composition in alpine grassland ecosystems (Wang et al., 2018b; Wang et al., 2022b). However, they predominantly examined the responses of aboveground components to grazing disturbances, neglecting the potential changes in belowground components. Because of the significance of alpine meadows on the QTP, understanding the synergistic effects of aboveground- and belowground elements in response to grazing disturbances is important. Additionally, investigating alterations in AGB and BGB trade-offs and their underlying drivers in different alpine meadow ecosystem states is essential for sustainable management.

### 4.2. *Soil available nutrients dominate plant biomass trade-offs in alpine meadows*

Changes in the AGB and BGB trade-offs of alpine meadow plant communities during grazing are directly affected by the selective intake of grazing livestock and indirectly influenced by livestock trampling and the return of excreta. Many researchers have investigated the mechanisms based on which soil physical and chemical factors contribute to changing biomass trade-offs in alpine meadow plant communities. A study on free-grazing alpine meadows showed that the total and available soil nitrogen content significantly influences changes in biomass trade-offs (Sun et al., 2021). A study on alpine grasslands with different years of restoration also showed that available soil N is a key factor regulating changes in biomass trade-offs in alpine grassland vegetation communities (Gao et al., 2021). A similar pattern was observed in this study: soil available nutrients (AN, AP, and AK) modulate changes in alpine meadow plant biomass trade-offs in different manners. This finding confirms the second hypothesis of this study: changes in alpine meadow plant biomass trade-offs at moderate grazing intensities are significantly modulated by changes in soil physicochemical properties. The results of this study also showed that the biomass trade-off in alpine meadows is directly affected by soil available nitrogen and phosphorus, exhibiting a negative relationship, and soil available potassium has a positive influence. Several possible explanations exist for these results. In grassland ecosystems, soil nitrogen and phosphorus are critical factors limiting plant growth (Jiang et al., 2012; Zhang et al., 2018; He et al., 2020); the return of excreta through grazing livestock contributes to an increase in the available nitrogen content within the topsoil of alpine grasslands (Zhang et al., 2020), and the trampling activity of grazing livestock effectively increases mineralization; and the trampling activities of grazing livestock enhance soil phosphorus mineralization, leading to a substantial increase in the available phosphorus content within the surface soil of alpine grasslands (Dixon et al., 2020). This suggests that alpine grassland plants often compensate for the effects of grazing livestock (Li et al., 2022), although sufficient nutrients help maintain the biomass trade-off of alpine grassland plants in equilibrium (zero trade-off), resulting in the allocation of the biomass of alpine grassland plants to the shoots under grazing conditions. Additionally, available potassium in the soil is highly soluble and can be easily lost through trampling by grazing livestock (Cao et al., 2023). Thus, grazing activities have significantly reduced the soil available potassium content of alpine meadows. When the soil potassium availability is higher in alpine meadows, the soil is less disturbed and therefore has a positive effect on the alpine meadow plant biomass trade-off.

### *4.3. How to use and protect alpine meadows of the QTP in a rational way*

Overgrazing has long been identified as a leading cause of the degradation of alpine meadows on the QTP (Harris, 2010). Consequently, fencing has emerged as a widely adopted and cost-effective measure to restore degraded alpine meadows in this region (Sun et al., 2021). However, the results of previous studies showed that the recovery of alpine meadows on the QTP does not follow a linear trajectory with respect to the duration of enclosure (Wu et al., 2017; Li et al., 2018). Additionally, temporary grazing closures or rotational grazing during critical periods, such as spring or autumn, have proven more effective than long-term fencing in promoting the restoration of vegetation productivity (Zhang et al., 2019). Thus, adopting a reasonable land-use approach is crucial for safeguarding the health and longevity of alpine grassland ecosystems. The literature has indicated that the trade-off between AGB and BGB in alpine meadows gradually reaches a state of relative equilibrium (zero trade-off) after long-term fencing, resulting in the stabilization of plant communities and the structure within alpine meadows (Sun et al., 2018). Contrary to these findings, our results demonstrate that the trade-off between AGB and BGB continues to favor BGB. even after eight years of fencing. This difference could be explained the optimal allocation theory: (1) soil nutrients in alpine grasslands under long-term enclosure are relatively poor, and thus plants allocate more biomass to roots than to shoots to compete for nutrients (Song et al., 2006); and (2) soil nutrients in alpine meadows under moderate grazing intensity are relatively high, and thus plants allocate more biomass to shoots than to roots to compete for sunlight for photosynthesis (Peng et al., 2020). Additionally, the trade-off is 0.01 for YG or MG 1:6. The trade-off under these conditions is the most similar to that under fenced conditions, but MG 1:6 involves a higher proportion of grass biomass and a lower proportion of herb biomass. Therefore, MG 1:6 represents one of the more rational uses of the QTP. However, determining the rational use of alpine meadows from one perspective is a one-sided approach. Research on the microbial community of alpine meadows has shown that MG 1:2 represents the ideal use of alpine grasslands (Liu et al., 2023). Therefore, future studies should explore the appropriate use of alpine meadows on the QTP from different perspectives. Establishing comprehensive evaluation indicators to characterize the utilization status of alpine meadows is essential. Additionally, long-term monitoring is needed for future research to gain a clearer understanding of the sustainable utilization of alpine meadows.

### *4.4. Limitations of this study*

It is worth noting that this study was conducted in a small-scale paddock setting. Under normal circumstances, paddocks typically limit the range and duration of grazing livestock activities (Eldridge et al., 2018; Zhang et al., 2020), resulting in relatively uniform effects of grazing livestock on changes in the trade-off of plant biomass in controlled grazing experiments at small scales. However, when employing traditional grazing patterns in natural grasslands, grazing livestock not only can stay in the grassland for extended periods but also have a larger range of movement. For example, grazing livestock tend to follow fixed routes for grazing activities or to reach water sources and habitats (Pringle and Landsberg, 2004; Mizutanil et al., 2012; Stavi et al., 2021). This results in significant spatial heterogeneity in the trade-off of plant biomass in natural grazing grasslands at landscape scales. Therefore, in traditional grazing patterns in natural grasslands, grazing livestock will have a more significant impact on the trade-off of plant biomass in areas where they frequently move. This will be an important direction for future research.

## 5. Conclusions

Our results demonstrate that variations in herbivore assemblages and the implementation of fencing have distinct effects on the trade-offs associated with plant biomass allocation within alpine meadows. Specifically, grazing activities favor the allocation of AGB, whereas enclosures promote BGB allocation. Additionally, our results support the notion that the biomass allocation pattern in alpine meadows aligns with the principles of the optimal allocation theory. Notably, the effect of moderate grazing intensity on biomass allocation trade-offs relies primarily on alterations in the soil bulk density and nutrient availability. Therefore, in managing and conserving alpine meadows on the Qinghai-Tibetan Plateau, the optimization of the trade-off between AGB and BGB can be achieved by regulating soil bulk density and the content of available nitrogen and phosphorus. From the perspective of biomass trade-offs, the mixed grazing of yaks and Tibetan sheep at a ratio of 1:6 under moderate grazing intensity is one of the effective approaches for the sustainable utilization of alpine grasslands.

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## CRediT authorship contribution statement

**Yuzhen Liu:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Xinquan Zhao:** Writing – review & editing. **Wenting Liu:** Funding acquisition, Data curation. **Bin Feng:** Data curation. **Weidong Lv:** Data curation. **Zhenxiang Zhang:** Data curation. **Xiaoxia Yang:** Writing – review & editing, Funding acquisition, Data curation. **Quanmin Dong:** Supervision, Methodology, Funding acquisition.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2024.108017.

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