Degradation leads to dramatic decrease in topsoil but not subsoil root biomass in an alpine meadow on the Tibetan Plateau, China (postprint)

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Abstract

Understanding the effects of degradation on belowground biomass (BGB) is essential for assessment of carbon budget of the alpine meadow ecosystem on the Tibetan Plateau, China. This ecosystem has been undergoing serious degradation owing to climate change and anthropogenic activities. This study examined the response of the vertical distribution of plant BGB to degradation and explored the underlying mechanisms in an alpine meadow on the Tibetan Plateau. A field survey was conducted in an alpine meadow with seven sequential degrees of degradation in the Zoige Plateau on the Tibetan Plateau during the peak growing season of 2018. We measured aboveground biomass (AGB), BGB, soil water content (SWC), soil bulk density (SBD), soil compaction (SCOM), soil organic carbon (SOC), soil total nitrogen (STN), soil total phosphorus (STP), soil available nitrogen (SAN), and soil available phosphorus (STP) in the 0–30 cm soil layers. Our results show that degradation dramatically decreased the BGB in the 0–10 cm soil layer (BGB0–10) but slightly increased the subsoil BGB. The main reason may be that the physical-chemical properties of surface soil were more sensitive to degradation than those of subsoil, as indicated by the remarked positive associations of the trade-off value of BGB0–10 with SWC, SCOM, SOC, STN, SAN, and STP, as well as the negative correlation between the trade-off value of BGB0–10 and SBD in the soil layer of 0–10 cm. In addition, an increase in the proportion of forbs with increasing degradation degree directly affected the BGB vertical distribution. The findings suggest that the decrease in the trade-off value of BGB0–10 in response to degradation might be an adaptive strategy for the degradation-induced drought and infertile soil conditions. This study can provide theoretical support for assessing the effects of degradation on the carbon budget and sustainable development in the alpine meadow ecosystem on the Tibetan Plateau as well as other similar ecosystems in the world.

Full Text

Preamble

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Abstract: Understanding the effects of degradation on belowground biomass (BGB) is essential for assessing the carbon budget of alpine meadow ecosystems on the Tibetan Plateau, China. These ecosystems have undergone serious degradation due to climate change and anthropogenic activities. This study examined how the vertical distribution of plant BGB responds to degradation and explored the underlying mechanisms in an alpine meadow on the Tibetan Plateau. We conducted a field survey during the peak growing season of 2018 in an alpine meadow with seven sequential degradation gradients on the Zoige Plateau. We measured aboveground biomass (AGB), BGB, soil water content (SWC), soil bulk density (SBD), soil compaction (SCOM), soil organic carbon (SOC), soil total nitrogen (STN), soil total phosphorus (STP), soil available nitrogen (SAN), and soil available phosphorus (SAP) in the 0–30 cm soil layers. Our results show that degradation dramatically decreased BGB in the 0–10 cm soil layer ($\mathrm{BGB}_{0\ 10}$) but slightly increased subsoil BGB. The primary reason appears to be that surface soil physical-chemical properties were more sensitive to degradation than subsoil properties, as indicated by the marked positive associations of the trade-off value of $\mathrm{BGB}_{0\ 10}$ with SWC, SCOM, SOC, STN, SAN, and STP, as well as the negative correlation between the trade-off value of $\mathrm{BGB}_{0\ 10}$ and SBD in the 0–10 cm layer. Additionally, an increase in the proportion of forbs with increasing degradation degree directly affected BGB vertical distribution. These findings suggest that the decrease in the trade-off value of $\mathrm{BGB}_{0\ 10}$ in response to degradation might represent an adaptive strategy to degradation-induced drought and infertile soil conditions. This study provides theoretical support for assessing degradation effects on the carbon budget and sustainable development in alpine meadow ecosystems on the Tibetan Plateau and other similar ecosystems worldwide.

Keywords: belowground biomass; soil properties; plant community structure; degradation; alpine meadow; Tibetan Plateau

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1 Introduction

Grasslands occupy over 25% of Earth' s terrestrial surface and store approximately 30% of the global terrestrial carbon (C) pool (Hewins et al., 2015). Soil C sequestration in grasslands occurs at an estimated rate of 0.5 Pg C/a globally, accounting for roughly a quarter of the world's potentially sequestered soils (Qiu et al., 2013). The Tibetan Plateau, where alpine meadows cover approximately 35% of the area (Zheng et al., 2000), represents about 44% of China's total grasslands and approximately 6% of grasslands worldwide (Piao et al., 2012). Alpine grasslands are vital for local livestock husbandry development and ecological functions, including soil and water conservation, biodiversity maintenance, and C sequestration (Li et al., 2013; Qin et al., 2018). However, these grasslands are extremely fragile due to unique climate and harsh environmental conditions (Sun and Wang, 2016; Sun et al., 2019a), and have undergone serious degradation under the influence of climate change and anthropogenic activities (Harris, 2010; Sun et al., 2014; Dong et al., 2020), greatly threatening local economic development and ecological security (Huo et al., 2013).

Belowground biomass (BGB) serves as a main source of the soil C pool and plant C stock, playing a crucial role in terrestrial ecosystem C cycles (Mokany et al., 2010; Sun et al., 2013), especially in grasslands where over 25% of plant C is stored in roots (Li et al., 2008; Yang et al., 2009). On the Tibetan Plateau, BGB constitutes the core portion of grassland total primary productivity (Li et al., 2011), with root-to-shoot ratios reaching as high as 5.8 (Yang et al., 2009). The alpine grassland ecosystem of the Tibetan Plateau currently functions as a C sink (Yang et al., 2008), largely because roots account for a notably large proportion of alpine plants (Wu et al., 2011). Therefore, precise estimation of root biomass and turnover rate is essential for reliable scientific assessment of the C budget in this ecosystem. However, due to methodological difficulties and high costs, the distribution and transfer of plant BGB in response to grassland degradation remain poorly understood (Sun et al., 2018a).

Roots serve as primary pathways for plant nutrient and water uptake (Wu et al., 2011) and provide anchorage to the soil. As resource consumers, roots engage in underground competition with other plants (Hortal et al., 2017), form complex mutualistic relationships with beneficial bacteria and fungi (Duran et al., 2018), and compete with detrimental microbes (Rey and Schornack, 2013). The root system' s overall structure and ability to adapt to habitat conditions—termed plasticity—represent a crucial determinant of plant adaptability (Gruber et al., 2013; Rogers and Benfey, 2015). For example, roots of perennial plants, particularly legumes, can alter the physical properties of compacted soils (Głąb and Szewczyk, 2014), and by enhancing water retention properties, such roots can regenerate physically degraded soils. However, some species exert different effects on the soil environment due to their unique root morphologies (Silva et al., 2014). Additionally, root systems influence plant growth through nutrient foraging, gaseous exchange, and absorption of beneficial microorganisms (Pieterse et al., 2014; Verbon and Liberman, 2016).

Key root system properties include length, biomass, volume, anatomy, and surface area (Lynch and Brown, 2012). These characteristics facilitate plant survival under various biotic and abiotic stresses, including salinity, extreme temperatures, waterlogging, drought, and nutrient deficiency (Dukes et al., 2005; Rodrigues et al., 2015). Thus, roots constitute an important factor determining the competitive ability of individual plants under environmental stress, which affects how plant community structure responds to environmental changes (Haichar et al., 2008). Grass root characteristics and morphology are closely linked to environmental conditions, and these roots exhibit highly dynamic lifespans ranging from days to weeks (Tingey et al., 2010). Previous research has revealed that plant root biomass distribution can be affected by various environmental factors, including soil physical-chemical and biological properties, climatic conditions, and plant characteristics (Rodriguez et al., 2007; Macinnis-Ng et al., 2010; Li et al., 2011). For instance, Zhang et al. (2019) found that plants allocate more root biomass to deeper soils to maintain water acquisition and growth under drought stress. As grassland degradation induces dynamics in soil water, nutrients, microenvironment, and plant properties, BGB distribution patterns may also fluctuate during degradation. However, little information exists regarding the variation in direction and magnitude of BGB distribution patterns in response to alpine meadow degradation. We hypothesized that topsoil BGB, but not subsoil BGB, may be more vulnerable to degradation because surface soil loses water and nutrients relatively quickly compared with subsoil.

This study examined variations in BGB distribution patterns along degradation gradients in an alpine meadow on the Tibetan Plateau of China. Our aims were: (i) to verify our hypothesis regarding BGB dynamics at different soil depths in response to grassland degradation; and (ii) to explore the underlying mechanisms driving changes in BGB vertical distribution in degraded alpine meadows. Our results may offer insights into grassland degradation and, more specifically, the effects of degradation on the carbon budget of alpine meadow ecosystems.

2.1 Study area

The study was conducted in an alpine meadow on the Zoige Plateau (32°20 -34°00 N, 101°30 -103°30 E), located in the northeastern Tibetan Plateau of China (Fig. 1 [Figure 1: see original paper]). The Zoige Plateau has an average altitude of 3500 m and covers an area of 6180 km^2 (Liu et al., 2020a). The climate is cold and humid, with mean annual temperature of 1.5°C, mean July temperature of 11.1°C, and mean January temperature of -9.7°C (Liu et al., 2020b). Mean annual precipitation is approximately 700-800 mm, with most occurring from May to August (Liu et al., 2020a). The plant community at our study site is dominated by *Kobresia tibetica*, *Stipa capillata*, and *Carex lasiocarpa* (Liu et al., 2020b). Soils are classified mainly as Cambisols according to the World Reference Base for Soil Resources (WRB) and as Inceptisols using the United States Department of Agriculture (USDA) soil taxonomy (Liu et al., 2020a).

Fig. 1 Location of sampling site at the Zoige Plateau on the Tibetan Plateau of China (a), photograph showing the landscape of sampling site (b), and schematic illustration of experimental design (c)

2.2 Experimental design and soil sampling

We sampled nine degraded grasslands and selected seven sequential degradation gradients based on vegetation coverage and plant community structure, a common classification method for such studies (Ma et al., 2002; Zhang et al., 2019; Liu et al., 2020a). All grasslands were freely grazed, primarily by yaks and horses, which contributed significantly to degradation. Table 1 provides detailed information on the seven degradation gradients, which were adjacent and thus shared similar topography and environmental conditions; heterogeneity within each degradation gradient was relatively low. The sampling survey was conducted in August 2018 (peak growing season). We selected three representative sampling plots (approximately 50 m × 20 m) as replicates for each degradation gradient. Within each plot, three quadrats (1 m × 1 m) were randomly selected for plant and soil sampling. Plant species were recorded, and soil compaction (SCOM) was determined using portable time-domain reflectometry equipment (TDR 100, Spectrum Technologies Inc., Chicago, IL, USA).

Table 1 Information on the seven degradation gradients

<table>
<tr><th>Degradation gradient</th><th>Coordinates</th><th>Altitude (m)</th><th>Main species</th><th>Coverage (%)</th></tr>
<tr><td>1</td><td>33°13 37.53 N,-102°36 51.26 E</td><td></td><td>*Stipa capillata*, *Carex tristachya*</td><td>89.00$±5.13||2|33°13′37.44″N, 102°36′51.69
| ∗
Stipacapillata∗, ∗Anaphalissinica∗
|78.00±3.26||3|33°13′37.11″N, 102°36′50.87′
| ∗
Stipacapillata∗, ∗Carextristachya∗
|67.00±4.15||4|33°13′36.93″N, 102°36′51.46′
| ∗
Carextristachya∗, ∗Stipacapillata∗
|50.00±4.71||5|33°13′37.84″N, 102°36′51.11′
| ∗
Carextristachya∗, ∗Artemisiadesertorum∗
|38.00±3.52||6|33°13′37.62″N, 102°36′50.97′
| ∗
Artemisiadesertorum∗, ∗Agrostismatsumu
|29.00±2.20||7|33°13′37.39″N, 102°36′51.25′
| ∗
Artemisiadesertorum∗, ∗Oxytropiskansue
|17.00±$2.44</td></tr>
</table>

Note: Mean±SE.

We clipped aboveground plant parts at ground level using scissors and separated them by species. Belowground plant parts were collected from 0–30 cm soil depth (0–10, 10–20, and 20–30 cm layers) using soil cores (5 cm diameter), with three replicates per layer within each quadrat. Samples were transported to the laboratory and soaked in water to remove residual soil using a 0.5-mm sieve. Plant samples were oven-dried at 65°C to constant weight to determine aboveground biomass (AGB) and BGB. Soil samples were also collected from three replicate soil profiles at 0–30 cm depth (0–10, 10–20, and 20–30 cm layers) using 5 cm diameter soil cores and 200 cm^3 cutting rings. For chemical analysis, soil samples were handpicked to extract fine roots and organic materials, then air-dried and sieved through a 2.0-mm mesh. For physical analysis, soil samples were oven-dried at 105°C to constant weight to measure soil water content (SWC) and soil bulk density (SBD). Soil organic carbon (SOC), soil total nitrogen (STN), soil total phosphorus (STP), soil available nitrogen (SAN), and soil available phosphorus (SAP) were determined using the external heating method ($K_2Cr_2O_7$ volumetric method), a vario MACRO cube elemental analyzer (Elementar Analysensysteme GmbH, Germany), the $NaHCO_3$ alkali digestion method with molybdenum antimony colorimetry, the continuous alkali-hydrolyzed reduction-diffusion method, and the Olsen method, respectively (Olsen et al., 1954; Bao, 2000).

2.3 Data analysis

The benefit of BGB in a given soil layer is expressed as the relative deviation from the mean of an objective observation calculated via the following equation (Bradford and Damato, 2012; Sun et al., 2018b):

$$B_i = \frac{x_i - x_{\min}}{x_{\max} - x_{\min}}$$

where B_i is the magnitude of the benefit for objective i; x_i is the measured value of i; and $x_{\min}$ and $x_{\max}$ are the minimum and maximum values for all x_i, respectively. A three-dimensional trade-off method was used to describe BGB trade-offs among the three soil layers (0–10, 10–20, and 20–30 cm) (Li et al., 2019). The vertical distance (l) from the objective point x to the zero trade-off line indicates the magnitude of BGB benefit in each soil layer (Fig. 2 [Figure 2: see original paper]). The trade-off was decomposed into components in the a, b, and c directions by tracing BGB in the 0–10, 10–20, and 20–30 cm soil layers, respectively (Fig. 2). Trade-off components in each direction were calculated by finding the point on the zero trade-off line using Euclidean distance.

Fig. 2 Illustration of trade-offs among objective belowground biomass (BGB) values in the three soil layers (0–10, 10–20, and 20–30 cm). The zero trade-off line represents equal BGB benefits in each layer. $\text{BGB}_{0\ 10}$, $\text{BGB}_{10\ 20}$, and $\text{BGB}_{20\ 30}$ represent BGB in the 0–10, 10–20, and 20–30 cm soil layers, respectively.

Differences in soil properties across soil layers along degradation gradients were analyzed using one-way analysis of variance in SPSS 19.0 software (SPSS Inc., Chicago, IL, USA). We used linear piecewise quantile regression analysis and linear regression in SigmaPlot for Windows, version 10.0 (Systat Software, Inc., Chicago, IL, USA; Windows version 14.0) to visualize changes in AGB of graminoids and forbs along degradation gradients. The ggplot2 and corrgram packages in R version 3.3.2 (R Core Team, 2016) were employed to explore variation in BGB trade-off values among the three soil layers along degradation gradients and to determine correlations among BGB trade-off values, soil variables, and plant community structure.

3.1 Changes in soil characteristics along the degradation gradients

SOC, STN, STP, SAN, SCOM, and SWC decreased gradually with increasing degradation degree, whereas SAP and SBD showed no significant changes (Table 2). Most soil components, including SOC, STN, SAN, and SAP, were significantly higher in the uppermost soil layer than in subsoil layers. Similar patterns were found for SWC in the first and second degradation gradients (Table 2).

3.2 Variations in plant aboveground biomass (AGB) and belowground biomass (BGB) along the degradation gradients

With increasing degradation degree, AGB of graminoids decreased dramatically until the fourth degradation gradient then declined slowly, whereas AGB of forbs changed little (Fig. 3 [Figure 3: see original paper]). Graminoids had higher AGB than forbs in the first degradation gradient, while forbs accounted for most AGB after the fourth degradation gradient.

Fig. 3 Changes in aboveground biomass (AGB) of graminoids and forbs along the seven degradation gradients. Information on the seven degradation gradients is shown in Table 1.

BGB clearly decreased along degradation gradients. BGB in the 0-10 cm soil layer ($BGB_{0\ 10}$) decreased dramatically with increasing degradation degree (Fig. 4 [Figure 4: see original paper]). In contrast, BGB in the 10-20 cm soil layer ($BGB_{10\ 20}$) remained virtually unchanged along degradation gradients. BGB in the 20-30 cm soil layer ($BGB_{20\ 30}$) tended to first decrease then increase along degradation gradients. $BGB_{20\ 30}$ was similar to $BGB_{10\ 20}$ but clearly lower than $BGB_{0\ 10}$ in most degradation gradients, except the seventh gradient (Fig. 4).

Fig. 4 Changes of belowground biomass (BGB) in the three soil layers (0-10, 10-20, and 20-30 cm) along the seven degradation gradients

3.3 Relationships among BGB and soil and plant characteristics

Figure 5 [Figure 5: see original paper] shows variations in trade-off values of BGB in the three soil layers (0-10, 10-20, and 20-30 cm) along degradation gradients. The trade-off value of $BGB_{0\ 10}$ decreased remarkably with increasing degradation degree ($R^2 = 0.71$, $P < 0.05$). In the 0-10 cm soil layer, the trade-off value of $BGB_{0\ 10}$ exhibited significant positive correlations with SWC ($R^2 = 0.82$), SCOM ($R^2 = 0.93$), SOC ($R^2 = 0.77$), STN ($R^2 = 0.76$), STP ($R^2 = 0.69$), and SAN ($R^2 = 0.69$), and with the ratio of AGB of graminoids to that of forbs (AGB(G/F); $R^2 = 0.66$). However, it was negatively correlated with SBD ($R^2 = 0.72$) at the 95% confidence level (Fig. 6 [Figure 6: see original paper]).

Fig. 5 Changes in trade-off values of BGB in the three soil layers (0-10, 10-20, and 20-30 cm) along the seven degradation gradients. The gray area represents 95% confidence intervals.

Fig. 6 Correlations among the trade-off value of BGB in the 0-10 cm soil layer ($BGB_{0\ 10}$), topsoil physical-chemical properties, and plant community structure. SBD, soil bulk density; SAP, soil available phosphorus; SCOM, soil compaction; SWC, soil water content; STP, soil total phosphorus; SOC, soil organic carbon; STN, soil total nitrogen; AGB(G/F), the ratio of AGB of graminoids to that of forbs; SAN, soil available nitrogen. Color depth represents correlation strength, with deeper colors indicating stronger correlations. Blue and red represent positive and negative correlations, respectively.

4.1 Variations of soil properties along the degradation gradients

Consistent with previous studies demonstrating that degradation causes considerable nutrient loss, which then accelerates further degradation (Wen et al., 2013; Pan et al., 2017; Zhang et al., 2019), our results indicated that soil nutrients such as SOC, STN, STP, and SAN decreased dramatically with increasing degradation degree (Table 2). These findings may be attributed to several factors. First, degradation-induced reductions in vegetation biomass and coverage decrease soil organic matter (SOM) input (Wang et al., 2009) while enhancing water and soil erosion, resulting in nutrient losses (Zhu et al., 2011; Dlamini et al., 2014). Second, changes in the microenvironment (e.g., SWC and SBD) along degradation gradients increase SOM dissolution (Wang et al., 2008). Third, degradation-induced turnover in species composition—for example, the replacement of grasses by ruderal species during grassland degradation—affects fixed soil C content (Wu et al., 2014; Han et al., 2018). Finally, changes in litter quantity and quality can significantly affect SOC (Mehta et al., 2013) and STN variation (Che et al., 2018). Specifically, degradation reduces C and nitrogen (N) storage by altering litter input to the soil (Sun et al., 2018a).

In this study, SWC decreased gradually with increasing degradation degree (Table 2), consistent with numerous previous studies (Wei et al., 2010; Yi et al., 2012). This may result from negative effects of retrogression on soil water-holding capacity (Fu et al., 2015) and increased evaporation due to strong radiation following degradation-induced plant cover reduction (Wang et al., 2009). Additionally, the decrease in SCOM with increasing degradation degree indicates that degradation reduces soil cohesion by decreasing clay content and increasing silt content (Yi et al., 2012). Notably, most soil physical-chemical properties were more vulnerable to degradation in the upper soil layer (0–10 cm) than in subsoil layers (10–20 and 20–30 cm) (Table 2). Other studies have reported similar patterns (Bardgett et al., 2005; Pan et al., 2017), indicating that degradation impacts on soil characteristics appear primarily in the upper soil layer, likely because degradation-induced decreases in vegetation cover and root grasp directly expose surface soil to wind, rainfall, and surface flow (Pan et al., 2017).

4.2 Effects of habitat and plant community structure on the dynamics of BGB distribution patterns

We found that BGB distribution was depth-dependent, with more than 50% concentrated in the 0–10 cm soil layer, except in extremely degraded grasslands (Fig. 4). This pattern agrees overall with Li et al. (2011) in alpine grasslands on the Tibetan Plateau and exceeds values reported for Inner Mongolia, China

(47%; Ma et al., 2008) and temperate zone grasslands worldwide (44%; Jackson et al., 1996). Unique environmental conditions on the Tibetan Plateau, such as high soil rigidity and permafrost, may contribute to this depth dependence (Li et al., 2011). Most relevant to our study, the trade-off value of BGB in the 0-10 cm soil layer ($\text{BGB}_{0\ 10}$) decreased dramatically along degradation gradients, a finding that can be explained by several direct and indirect mechanisms.

Soil physical-chemical properties strongly affected changes in BGB vertical distribution. The apparent positive association between the trade-off value of $\text{BGB}_{0\ 10}$ and SCOM in topsoil (Fig. 6) suggests that deeply rooted plants provide resilience against strong winds in cohesionless soil (Vo and Johnson, 2001). Moreover, soil with higher SBD is generally less porous, limiting root respiration, microbial activities, and thus root growth (Yan et al., 2018), reflected in the negative correlation between the trade-off value of $\text{BGB}_{0\ 10}$ and $\text{SBD}_{0\ 10}$ (SBD in the 0-10 cm soil layer) (Fig. 6). Additionally, SWC, which is tightly linked to nutrient availability, plays an important role in plant physiological activities (e.g., transpiration) and strongly affects plant growth (Swift et al., 2004). The significant positive correlation between the trade-off value of $\text{BGB}_{0\ 10}$ and $\text{SWC}_{0\ 10}$ (SWC in the 0-10 cm soil layer) in our study (Fig. 6) indicated that deeper-rooted plants could utilize water from subsoil when soil water in the upper layer decreased dramatically with increasing degradation degree (Hu et al., 2013).

Plants growing in infertile soil produce deep root systems to access nutrients from deeper layers (Wang et al., 2006; Han et al., 2011). In this study, we found significant positive correlations between the trade-off value of $\text{BGB}_{0\ 10}$ and SOC, STN, STP, and SAN in the 0-10 cm soil layer (Fig. 6). Soil nutrients play crucial roles in multiple plant physiological activities: SOM provides energy for heterotrophic N-fixing microbes and facilitates plant N fixation (Reed et al., 2011; Zheng et al., 2019); soil N significantly affects leaf N content and plant photosynthesis (Yue et al., 2019); low soil P can greatly limit plant growth and functioning (Quesada et al., 2009; Sun et al., 2019b). Consequently, soil nutrient changes can drive species turnover by affecting plant facilitation and competitive exclusion (Marriott et al., 2002; Guo, 2003).

Dynamics in plant community structure directly affect BGB vertical distribution patterns. Our results showed a dramatic decrease in AGB of graminoids and a slight increase in AGB of forbs with increasing degradation degree (Fig. 3), suggesting that plant communities shift from graminoids to forbs following degradation, demonstrating successive vegetation reversal with degradation of plant community structure (Wang et al., 2009; Wu et al., 2009). This pattern occurs primarily because free grazing—the main cause of grassland degradation at our study site—involves selective foraging that decreases the proportion of palatable graminoids. Moreover, forbs exhibit stronger competitive capacity than graminoids in the increasingly hostile environment resulting from increasing degradation degree (Sun et al., 2009; Han et al., 2011). Graminoids have shallow roots that extend horizontally in surface soil, whereas forbs produce deep axial roots (Wang et al., 2004), contributing directly to reduced root biomass in topsoil, as indicated by the significant positive correlation between the trade-off value of $\text{BGB}_{0\ 10}$ and AGB(G/F) (Fig. 6).

5 Conclusions

In this study, we selected an alpine meadow with sequential degradation degrees at the Zoige Plateau as a typical degraded grassland to analyze variations in plant BGB distribution under degradation. The trade-off value of BGB in the 0-10 cm soil layer clearly decreased with increasing degradation degree and exhibited significant positive correlations with SWC, SCOM, SOC, STN, and STP. Our findings suggest that alpine grassland degradation dramatically reduces belowground net primary production in topsoil owing to degradation-induced deterioration of soil conditions and changes in plant community structure. These results provide valuable information for scientific assessment of degradation effects on soil C pool distribution in alpine meadows on the Tibetan Plateau and similar areas worldwide. Future studies should employ larger-scale transect surveys to further explore the general response of root biomass distribution to grassland degradation.

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