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The Response of Vegetation Biomass to Soil Properties along Degradation Gradients of Alpine Meadow at Zoige Plateau

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Abstract: Alpine grassland of the Tibetan Plateau has undergone severe degradation, even desertification. However, several questions remain to be answered, especially the response mechanisms of vegetation biomass to soil properties. In this study, an experiment on degradation gradients was conducted in an alpine meadow at the Zoige Plateau in 2017. Both vegetation characteristics and soil properties were observed during the peak season of plant growth. The classification and regression tree model (CART) and structural equation modelling (SEM) were applied to screen the main factors that govern the vegetation dynamics and explore the interaction of these screened factors. Both aboveground biomass (AGB) and belowground biomass (BGB) experienced a remarkable decrease along the degradation gradients. All soil properties experienced significant variations along the degradation gradients at the 0.05 significance level. Soil physical and chemical properties explained 54.78% of the variation in vegetation biomass along the degradation gradients. AGB was mainly influenced by soil water content (SWC), soil bulk density (SBD), soil organic carbon (SOC), soil total nitrogen (STN), and pH. Soil available nitrogen (SAN), SOC and pH, had significant influence on BGB. Most soil properties had positive effects on AGB and BGB, while SBD and pH had a slightly negative effect on AGB and BGB. The correlations of SWC with AGB and BGB were relatively less significant than those of other soil properties. Our results highlighted that the soil properties played important roles in regulating vegetation dynamics along the degradation gradients and that SWC is not the main factor limiting plant growth in the humid Zoige region. Our results can provide guidance for the restoration and improvement of degraded alpine grasslands on the Tibetan Plateau.

Keywords: vegetation biomass; soil properties; degradation gradients; structural equation modelling; Zoige Plateau

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1 Introduction

Desertification has become a global environmental problem (Schlesinger et al., 1990). It is defined in the United Nations Convention to Combat Desertification (Coscarelli et al., 2005; Albalawi and Kumar, 2013) as land

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degradation caused by human activities and climatic change in arid, semiarid and dry sub-humid regions. More than two-fifths of the world's land area suffers desertification (Verón and Paruelo, 2010), and it is widely believed that global warming or improper human management are critical drivers (Lu et al., 2014). In the typical arid and semiarid region in China, degradation has been extensively studied (Traylor, 1988; Sun et al., 2006; Wang et al., 2006; Zhu et al., 2007; Cao et al., 2007; Sun et al., 2008; Ge et al., 2016). The Tibetan Plateau, which claims to be the 'the third pole' (Sun et al., 2013), with the highest worldwide altitude (Pan et al., 2017), is the focus of this study due to its vulnerable ecological environment. This vulnerability has fostered serious degradation of the alpine grassland (Wang et al., 2007a) and even severe desertification (Yang et al., 2004) as a result of anthropogenic activities and climate change. For example, the area of degraded alpine grasslands across the Tibetan Plateau is approximately 5.0 × 10^5 km^2, 16% of which is severely degraded (Cui and Graf, 2009). In addition, the alpine meadow on the humid Zoige Plateau, (mean annual precipitation ranging from 615 to 753 mm), eastern of the Tibetan Plateau, is suffering from grievous degradation (Dong et al., 2010).

Recently, degradation has been studied with respect to its effect on ecosystems (De Pina Tavares et al., 2015; Sun et al. 2019), which could lead to various undesirable changes in ecosystem function and structure (Wang et al., 2007b) and the deterioration of soil properties and vegetation features (Allington and Valone, 2010; Gao et al., 2011; Zhang et al., 2013). Vegetation biomass, which is an important indicator of ecosystem function, acts as the major source of soil carbon (C) input and regulates terrestrial ecosystem C cycling and storage (Ma et al., 2008; Sun et al., 2013). Plant aboveground and belowground biomasses are closely related, and their interactions largely affect the processes and functions of terrestrial ecosystems (Fan et al., 2015; Wang et al., 2019). Biomass allocation stands for photosynthate allocation between aboveground and belowground components, which is an important parameter of plant physiological ecology (Mokany et al., 2006), and reflects an individual plant's adaptation to habitat after a long-term life history (Shipley and Meziane, 2002). Information about plant biomass changes in response to degradation is valuable for the protection and restoration of grasslands (Zhang et al., 2019) and for the assessment of terrestrial ecosystem C budgets.

Previous studies have revealed that soil water content (SWC) is a key requirement for vegetation growth that directly influences vegetation coverage and distribution (Belaroui et al., 2014) and temperature is an important factor that affects the distribution of vegetation at a global scale. In the Tibetan Plateau, local temperature variability is exhibited due to geographical location and altitude (Chen et al., 2011). The availability of N and P in soil could explain the adaptive changes in photosynthesis-related properties of common plant species for different stages of degradation reversal (Qiu et al., 2018), which further implicates their roles in the adaptation of plants to environmental changes. However, the response mechanism of vegetation biomass and soil properties to degradation gradients and the main indicative index of degradation in humid regions (average annual precipitation of approximately 700 mm in Zoige) remain unknown. Thus, the aim of this study was to analyse the dynamics of soil properties and vegetation biomass, to determine the main the soil properties that affect vegetation biomass, and to explore the internal mechanism of the mutual effect between soil properties and vegetation biomass along the degradation gradients. Consequently, the current study will provide a theoretical basis and practical guidance for effective alpine meadow management and regional sustainable development.

2 Materials and Methods

2.1 Study area

The Zoige region (32°20′–34°00′N, 101°30′–103°30′E) is in the northeast margin of the Tibetan Plateau, with an average altitude of 3500 m and an area of 6180 km^2 (Chen et al., 2016). It experiences a cold and wet climate in the Zoige Plateau corresponding to a mean annual temperature of approximately 1℃ and a mean annual precipitation of 700 mm, which occurs between May and August (Fig. 1). The vegetation is dominated by *Kobresia tibetica*, *Muli sedge*, and *Carex lasiocarpa* and belongs to subalpine meadow and wetland vegetation (Bai et al., 2013). Peat moor soils, alpine meadow soils and subalpine meadow soils are the major soil categories (Dong et al., 2010), with a mean pH value of 7.25 (Zhang et al., 2008). Since the 1970s, the Zoige plateau has undergone degradation, and wetlands, moist

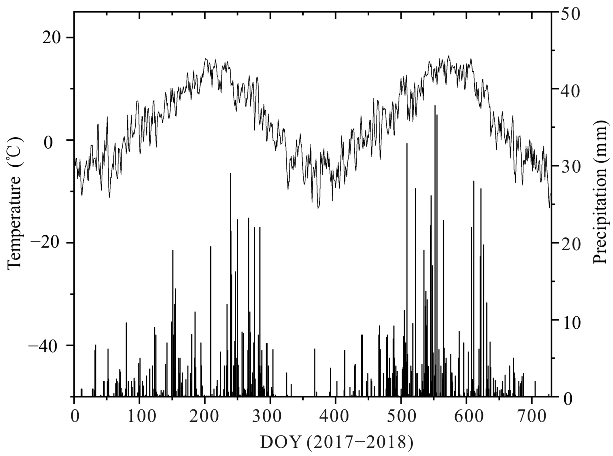

Fig. 1 Variations in precipitation and temperature in the study area (2015–2016)

grasslands, dry grasslands and deserts have been developed along the representative landscape degradation gradients (Wang et al., 2016b).

2.2 Field sampling, and plant/soil samples analysis

In August 2017, an experiment was conducted in the Zoige Plateau. The sampled sites were established along natural degradation land in Waqie Village of Hongyuan County (the experimental plot is approximately 500 m in length and 200 m in width). We selected nine typical degraded alpine meadows with different degraded degrees which were divided into nine degradation gradients ranging from potentially to severely degraded based on vegetation coverage, plant community structure, and other factors (Ma et al., 2002). The degraded grasslands of these nine gradients had similar climatic, topographic and pedological conditions. Along the degradation gradients, the vegetation shifted from being a primary community dominated by graminoids to a secondary community dominated by forbs and annual weeds, and the soil shifted from loam to sandy loam. Arabic numerals (from 1 to 9) were used to label sites having degradation rates from least to worst. There are three sample plots (approximately 50 m × 20 m) in each degradation gradient. Three sub-plots (1 m × 1 m) were randomly selected in each plot for sampling.

Aboveground biomass (AGB) and belowground biomass (BGB) were harvested from three sub-plots (1 m × 1 m). AGB was determined by clipping the plants at ground level and oven-drying the plants at 65℃ until a constant weight was achieved (Liu et al., 2014a). BGB was collected from the 0–30 cm soil depth, where most BGB occurred (Li et al., 2011). BGB was obtained from the blocks using 5-cm diameter soil cores, and the blocks were then soaked in water to remove the residual soil via a 0.5 mm sieve and then dried at 65℃ to a constant weight. Simultaneously, soil samples (from the 0–30 cm soil depth) were collected from three replicate soil profiles to determine soil properties. After being air-dried and sieved (2 mm mesh), the soil samples were carefully handpicked to extract the surface organic materials and fine roots for soil chemical properties analysis. Each mixed soil sample was separated into two parts. One sub-sample was oven-dried at 105℃ to a constant weight for measuring soil physical properties (SWC and soil bulk density, SBD) (Liu et al., 2014b). The other part was used to analyse soil chemical properties, including pH, soil organic carbon (SOC), soil total nitrogen (STN), soil available nitrogen (SAN), soil total phosphorus (STP), and soil available phosphorus (SAP). The soil pH value was measured using the potentiometric method (pH 700). SOC was determined using the $K_2Cr_2O_7$ volumetric method (external heating method). STN was determined using the vario MACRO cube method. SAN was determined using the continuous alkali-hydrolysed reduction-diffusion method (Wang et al., 2014). STP was determined using the molybdate colorimetric test after perchloric acid digestion (Cao et al., 2013), and SAP was determined using the Olsen method (Olsen et al., 1954). All indicators of soil properties were determined following standard protocols (Bao, 2000).

2.3 Data analysis

All statistical analyses and plotting were conducted using the packages of R version 3.3.2 (R Development Core Team, 2016). The data were analysed using the following four steps. First, the relationships of pH, SOC, STN, SAN, STP, SAP, SWC, SBD, AGB and BGB with the degradation gradients were generated using linear regression via the *ggplot2 package*. Second, classification and regression tree analysis (CART) was used to screen out the main variables that influenced vegetation biomass via the *rpart package*, which identified the key variables that significantly influenced the response variables (Sun et al., 2013). Third, linear regression in *SigmaPlot* for Windows version 14.0 (Systat Software, Inc., Chicago, IL, USA) was used to generate the relationships of plant biomass (AGB and BGB) with soil properties in different degradation gradients. Finally, structural equation modelling (SEM) was conducted to explicitly evaluate both direct and indirect impacts of these screened soil factors on AGB and BGB.

3 Results

3.1 Variations of vegetation biomass and soil properties

Remarkable variations of both AGB and BGB were observed among all degradation gradients (Fig. 2). The minimum mean value of 20.28 g/m^2 of AGB was found at the site worst affected by degradation (site 9), compared with the least affected site (site 2), which had a maximum mean value of 129.66 g/m^2. Similarly, BGB represented an decreasing trend from 1 to 9. Relatively low values of BGB were observed at sites 8 and 9, with mean values of 0.59 g/m^2 and 1.01 g/m^2, respectively.

As shown in Fig. 3, significant changes of all the soil properties (SWC, SBD, SOC, pH, STN, STP, SAP and SAN) were observed along the degradation gradients ($P < 0.01$). Increases in SBD and pH were observed along the gradients, ranging from 1.08 to 1.49 g/cm^3 and 4.89 to 6.93, respectively (Figs. 3B and C). In contrast, SWC, SOC, STP, STN, SAN and SAP decreased along the degradation gradient. From site 1 to 9, SWC and SOC decreased from 20.7% to 5.3% and from 22.7 g/kg to 3.4 g/kg, respectively (Figs. 3A and D). The maximum value of STN was 2.4 g/kg, which appeared in the most lightly degraded site (site 1), and the minimum values of STP and SAP were observed in the severely degraded site (site 9) with the values of 0.39 g/kg and 7.69 mg/kg, respectively (Fig. 3).

3.2 Soil properties affect AGB and BGB

As shown in Fig. 4A, the CART model indicated that AGB was mainly influenced by SWC, SBD, SOC, STN, and pH. In particular, SBD was the most important indicator for AGB when SWC > 8.9%. For the second tree (Fig. 4B), three critical environmental factors, including SAN, SOC and pH, had significant influences on BGB. Moreover, the analysis indicated that pH and SOC were most closely associated with large-scale variations in AGB when SAN < 224.5 mg/kg.

The regression analyses revealed that plant biomass had significant negative relationships with SBD and pH and were notably positively related to SWC, SOC, STN, STP, SAN and SAP ($P < 0.05$) (Fig. 5). The R^2 values of SWC with AGB and BGB were 0.23 and 0.29, respectively (Fig. 5A), which were much lower than those of plant biomass with other soil properties.

3.3 SEM explains the direct/indirect/total effects

Soil properties explained 50.6% and 58.8% variations of the AGB and BGB, respectively (Fig. 6). Obviously, the direct path coefficients from SWC were 0.57 and 0.52 for AGB and BGB, respectively. The total standardized

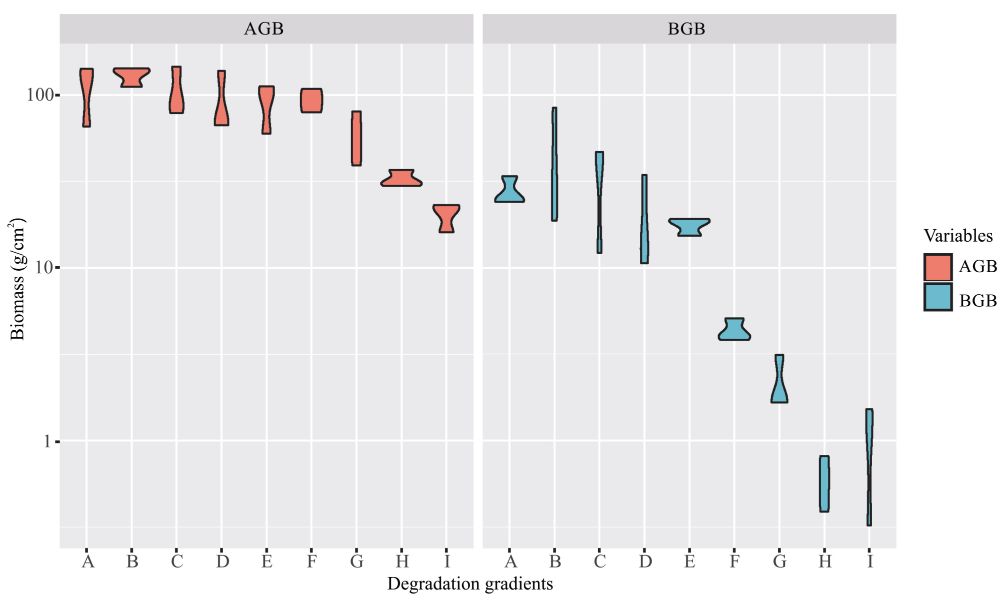

Fig. 2 Variation of vegetation biomass (AGB and BGB) along the degradation gradients

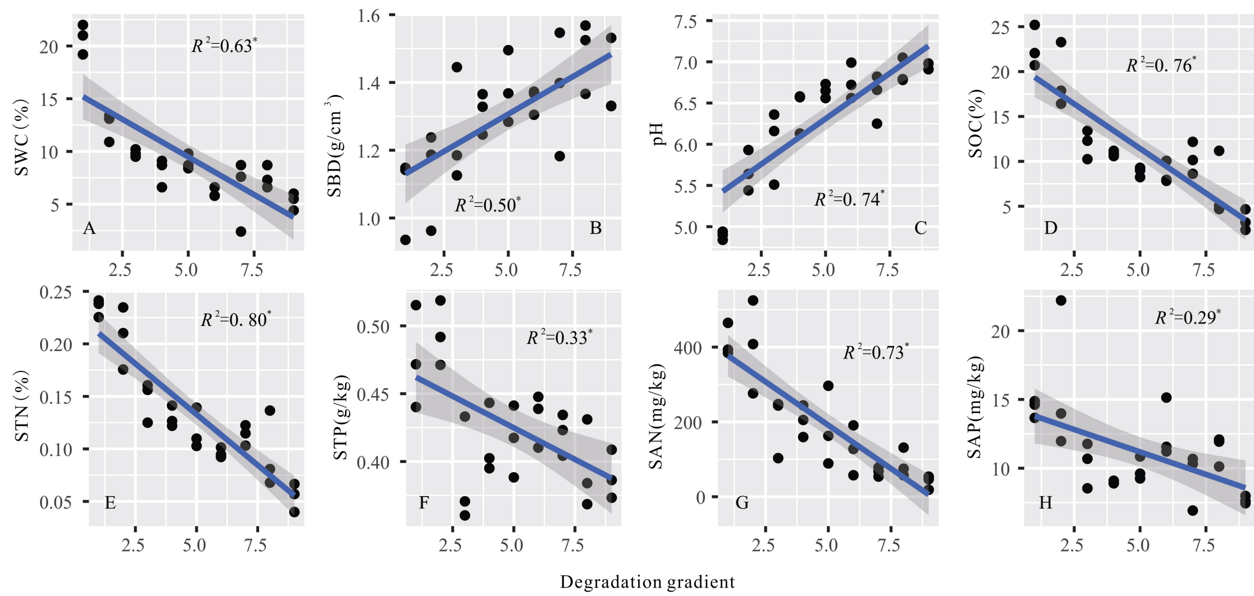

Fig. 3 Variations of soil physical (i.e., SWC, A and SBD, B) and chemical properties (i.e., pH, C; SOC, D; STN, E; STP, F; SAN, G and SAP, H) along the degradation gradients. SWC, SBD, SOC, STN, STP, SAN, and SAP are soil water content, soil bulk density, soil organic carbon, soil total nitrogen, soil total phosphorus, soil available nitrogen, and soil available phosphorous, respectively. * indicates a significant difference (P < 0.05)

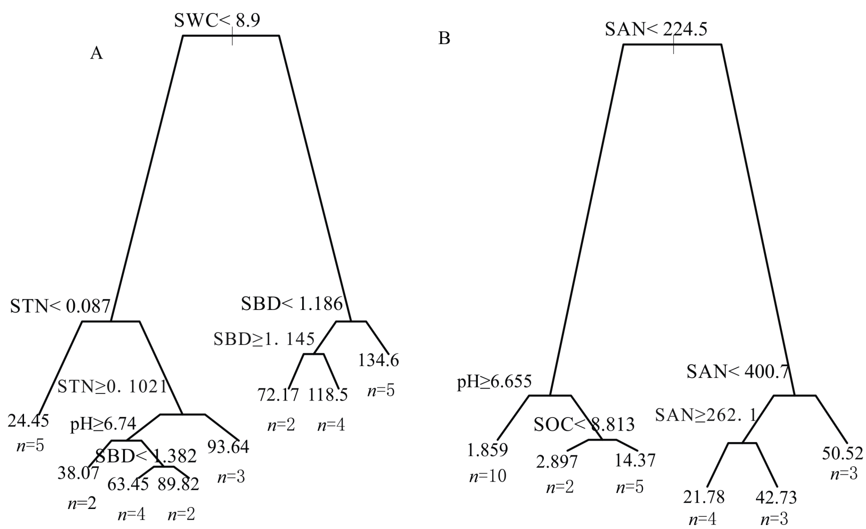

Fig. 4 CART analysis of the relationships between soil indicators and vegetation biomass along the degradation gradients. The critical soil factors were screened in panels A (AGB) and B (BGB). Branches are labelled with criteria used to segregate data. Values in terminal nodes show mean vegetation biomass of sites grouped within the cluster. n = number of plots in the category. SWC, SBD, SOC, and SAN are soil water content, soil bulk density, soil organic carbon, and soil available phosphorous, respectively.

coefficients of SWC to other soil variables, i.e., STN, SBD, pH, SAN and SOC, were 0.85, –0.67, –0.91, 0.81 and 0.85, respectively. SOC also played important roles in the system. The total standardized coefficients of SOC to STN, pH, and SAN were 0.88, 0.81 and 0.81, respectively. The direct effects of SOC on ABG and BGB were more than 0.7. In addition, the SEM showed that almost all soil factors had a positive effect on AGB and BGB, while SBD had a slightly negative effect on AGB (path coefficient = –0.08) and pH inhibited the growth of BGB (path coefficient = –0.31).

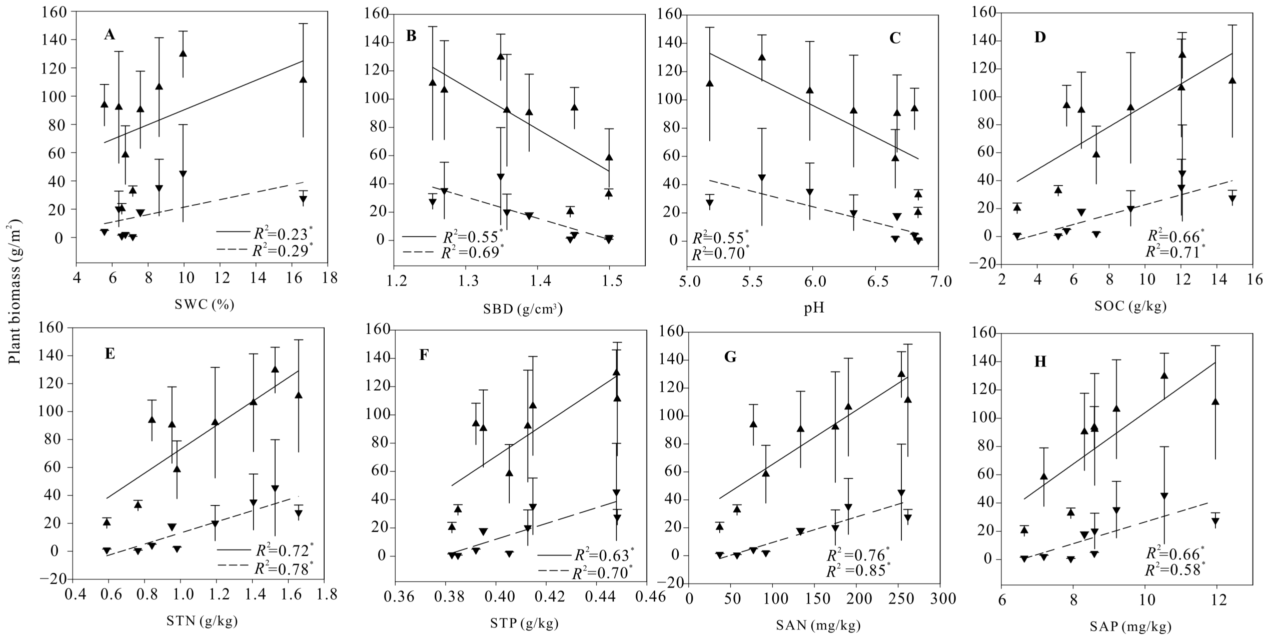

Fig. 5 Patterns of the relationship between plant biomass and soil properties. SWC, SBD, SOC, STN, STP, SAN, and SAP represent soil water content, soil bulk density, soil organic carbon, soil total nitrogen, soil total phosphorus, soil available nitrogen, and soil available phosphorous, respectively. * indicate significant difference ($P < 0.05$)

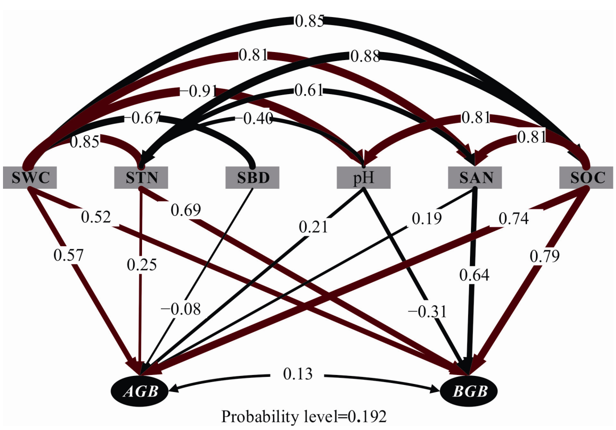

Fig. 6 Analysing the direct and indirect effects among variables by SEM. The standardized coefficients are listed on each significant path, the covariance is listed on the double-headed arrow between AGB and BGB, and the standardized coefficients of the red shadow contain the indirect path, while the others do not. The thickness of the solid single-headed arrows reflects the magnitude of the standardized SEM coefficients. All designations are the same as in previous figures

4 Discussion

4.1 Dynamics of vegetation biomass and soil properties along the degraded gradients

Vegetation biomass and soil properties all exhibited large variations along the degraded gradients; AGB and BGB decreased from 141.79 to 16.07 g/m^2 and from 84.29 to 0.32 g/m^2, respectively. The mean values of AGB (81.63 g/m^2) and BGB (17.15 g/m^2) in the present study were found to be lower than that in China's grasslands, which were estimated at 104.8 g/m^2 and 570.2 g/m^2, respectively (Yang et al., 2010). This finding may be due to the degradation-induced decreases in AGB and BGB. Additionally, in the present study, BGB was lower than AGB across the study area; BGB was approximately 0.2 times less than AGB. By contrast, BGB was far larger than AGB in grassland ecosystems (Ma et al., 2008, Liu et al., 2014a). This indicated that the vegetation biomass of degraded grasslands was allocated more to aboveground than belowground parts in the humid zone of Zoige, where rainfall is sufficient for plant growth and plants do not need many roots to compete for water. Additionally, previous studies have revealed that degradation causes decreases in clay content but increases in silt content, which results in loose soils (Strudley et al., 2008). The lower BGB is also for the most part due to the degradation-induced cohesionless soil, which restrains root growth.

Soil properties also showed significant variations along the degradation gradients, and it was very interesting to note that soil pH was a sensitive indicator for degradation. Similar research has reported that degradation was induced by the significant impact of soil pH and that a possible explanation of this discovery could be that the soil structure would become fragile at a higher soil pH level (Jobbágy and Jackson 2003; Berthrong et al., 2009). Additionally, comparatively obvious trends along the degradation gradients emerged for the other soil chemical and physical elements. In our study, the mean values of 9.47%, 11.42 g/kg, 1.3 g/kg, 0.42 g/kg and 1.31 g/cm^3 for SWC, SOC, STN, STP and SBD, respectively, were lower than those of arid and semi-arid zones (Liu et al., 2014a). Moreover, SWC and STN had significantly negative correlations with degradation gradients. Some studies have indicated that soil nitrogen cycling may be accelerated by the increase in soil water availability (Lü et al., 2014; Van Groenigen et al., 2014). Therefore, the inseparable effects of SWC and STN, or even of all the soil indicators, are seen in the process of grassland degradation.

The biomass allocation provided the basis for understanding the response or adaptive strategies of plants to environmental stress (Sun et al., 2014). Our results indicated that the plants will not develop larger root systems if soil resources are limited, which conflicts with the functional equilibrium hypothesis (optimal partitioning) that plants reduce the proportion of AGB and allocate more photosynthetic products to BGB to adapt to relatively arid and barren soil environments (McConnaughay and Coleman, 1999). Due to the biomass allocation pattern revealing the plant life history and life span (Sun and Wang, 2016), trade-offs between biomass partitioning between aboveground and belowground are driven by both external 'environmental filtering' and internal adaptation strategies (Sun et al., 2018). It has been concluded that extreme cold and short growing periods may cause unique plants (Sun et al., 2014) and that the extremely high elevation grassland plants preferentially invest in structures for persistence (K-strategy) rather than maximizing carbon gain belowground (Patty et al., 2010).

4.2 Response mechanism of vegetation biomass and soil properties to the degradation gradients

SWC and soil nutrients played important roles in the dynamics of AGB and BGB (Figs. 5 and 6), and biomass thus declined with the development of degradation (Zhang et al., 2010), which was determined by the decreased availability of soil moisture and soil nutrients (Fig. 3). Lower SWC inhibited the growth of alpine meadow vegetation that had shallow root systems (Xue et al., 2009). Additionally, the lower SWC influenced the plant absorption and the utilization of soil nutrients. It was also found that SWC has a significant positive correlation with SOC, STN and SAN. Moreover, soil carbon and nitrogen were the main factors that influenced AGB and BGB (Fig. 4), and the biomass allocation between AGB and BGB increased with soil nitrogen (Ma et al., 2017) and organic carbon gradients across the alpine grassland (Sun and Wang, 2016). It has been found that soil nutrients loss does not only result in deteriorative vegetation features but also has a distinct impact on the alteration of soil C and N storage via the deep modification of biogeochemical cycles (Lu et al., 2014a).

It has been concluded that SWC is an important driving force in regulating ecosystem functioning by influencing soil nutrient availability and regulating plant growth in alpine grassland ecosystems (Wang et al., 2016a). As a positive feedback, the vegetation biomass can be enhanced by more litter input that improves soil conditions and nutrients that result from more plant biomass in well water and heat conditions (Liu et al., 2014a, b). Notably, the correlations of SWC with AGB and BGB were relatively less significant than those of other soil properties, including SBD, pH, SOC, STN, STP, SAN, and SAP (Fig. 5), which did not agree with previous researchers who demonstrated that SWC is a dominant environmental factor driving plant biomass (Yan et al., 2013). In the Zoige region, the high precipitation (approximately 700 mm, Fig. 1), which mostly occurs in the peak growing season, provides abundant water for plant growth (Chen et al., 2016), and the main limiting factor of plant growth is thus not SWC in this humid area. We implied that vegetation cover and community production in most alpine grassland of the Zoige region also hinted that human activities (livestock grazing) had greater impact on degraded grassland. Additionally, the dry and cold climates in winter and spring (precipitation generally occurred from May to August, Fig. 1) were mainly responsible for the expansion of degraded grassland (Hu et al., 2012).

5 Conclusions

In the current study, AGB and BGB decreased with the increasing gradients of degradation, and soil properties produced a similar change, with the exceptions of SBD and pH. The linkages between SWC and soil nutrients with the growth dynamic of vegetation biomass were complicated, and these soil factors considerably influence biomass dynamics. SWC is not the primary limiting factor of plant growth in the humid Zoige region. Our results can provide guidance to restore and improve the quality of degraded alpine grassland on the Tibetan Plateau. However, our experiment was carried out at a particular site with sequential degradation gradients, and the dynamics of soil-plant interacted relationships in response to grassland degradation might exhibit large differences in different grassland types. Therefore, we will carry out a transect survey in degraded alpine grasslands on a spatial scale to explore the change rules in subsequent research.

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