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Nitrogen addition stimulated compensatory growth responses to clipping defoliation in a Northern Tibetan alpine meadow

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Abstract

Grazing and clipping defoliation are the most important human disturbances in natural grasslands. Compensatory growth is a common response to clipping defoliation, which is of great significance for forage production and livestock husbandry development. However, how clipping intensity affects plant compensatory growth and how nitrogen (N) addition regulates this response in alpine ecosystems are still unclear. A manipulative experiment including two clipping intensities (light and heavy) crossed with N addition was conducted in an alpine meadow ecosystem to examine the effects of how N addition regulated plant compensatory growth induced by clipping defoliation. Selective clipping was used to simulate animal feeding, that is, only grasses and sedges were clipped. Under the N addition treatment, the relative growth rate of grasses and total biomass after clipping were significantly higher than those under the no N addition treatment. The total community biomass showed over-compensatory growth in light clipping under N addition treatment, while it showed equal-compensatory growth under the other treatments. The over-compensatory growth in light clipping under the N addition treatments mainly resulted from the stimulated growth of grasses. Regression analysis showed that the relative growth rate and biomass of grasses were positively correlated with soil inorganic N content, but increasing N availability was not conducive to the growth of sedges and other forbs. Divergent responses of different plant functional groups to clipping and N addition would lead to changes in community structure and functioning. Both community biomass and compensatory growth tended to increase first and then reach a stable state with the increase in soil N availability. Our results show that although light clipping could largely stimulate forage production under N addition, excessive clipping cannot lead to a continuous increase in compensatory growth of plant biomass, even under N addition conditions, in this semiarid alpine meadow ecosystem.

KEYWORDS
clipping defoliation, compensatory growth, nitrogen addition, plant production, relative growth rate

1 | INTRODUCTION

Clipping defoliation, which is defined as partial or entire defoliation of plants, is one of the most important human disturbances in natural grassland ecosystems, and also the main measure affecting the structure and function of grassland ecosystems (Bagchi & Ritchie, 2010; Tuffa, Hoag, & Treydte, 2017; Wei et al., 2016; Zhao, Chen, & Lin, 2008). Clipping defoliation can inhibit plant growth by injuring plant normal tissues and organs (Leriche et al., 2003; Ward, 2016); on the other hand, clipping defoliation can stimulate plant growth by removing the apices and aging tissues of plants (Leriche et al., 2003; Liu et al., 2012). Compared with the control, optimized clipping intensity can eliminate plant redundancy growth and increase plant net primary production (Liu et al., 2012; Siddappaji, Scholes, Bohn, & Paige, 2013). Selective feeding by animals has direct effects on plants, and the feeding behaviors can affect the interactive relationships among different plant species and substantially affect plant community structure.

Plant compensatory growth after clipping defoliation is a common phenomenon in natural grasslands. Belsky (1986) argued that plant compensatory growth is a positive response to mechanical damage, and a certain degree of leaf removal or animal feeding is beneficial to plant growth. When the sum of biomass loss by clipping defoliation and the regenerated biomass is larger than undisturbed natural grasslands, plants show over-compensatory growth; when plant material removal is detrimental to plant growth, the sum of plant regenerated biomass and biomass loss is less than undisturbed natural grasslands, and plants show under-compensatory growth; when clipping defoliation does not have any significant effect on total community biomass accumulation, plants show equal-compensatory growth (Belsky, 1986). Optimized grazing theory demonstrated that moderate intensity can cause plants to recover quickly by promoting forage tillers and strengthening photosynthetic capacity, resulting in equal- or over-compensatory growth (McNaughton, 1983; Siddappaji et al., 2013). However, excessive clipping defoliation can decrease the photosynthetic capacity of plant leaves, cause difficulty in stimulating plant growth and often lead to an under-compensatory growth pattern (Ferraro & Oesterheld, 2002; Herrero-Jáuregui, Schmitz, & Pineda, 2016; McNaughton, 1983). Until now, there has been a lack of research on the effects of clipping defoliation and its intensity on the compensatory growth of alpine plants.

At present, there are many studies on the mechanism of plant over-compensation after clipping defoliation (Belsky, 1986; Ferraro & Oesterheld, 2002; McNaughton, 1979). It is generally thought that clipping defoliation can produce more tillers (Heckathorn & Delucia, 1996; Werger et al., 2002) or change resource allocation patterns by stimulating plant photosynthesis to promote plant growth (Herrero-Jáuregui et al., 2016). In addition to the impacts of clipping intensity on forage compensatory growth, resource availability is also one of the important factors that affect plant compensatory growth (Sun, Ma, & Lu, 2018; Sun et al., 2014; Tuffa et al., 2017; Zhao et al., 2008). Soil nutrient availability can directly affect plant biomass production and root growth patterns (Sun, Cheng, & Fan, 2013; Sun & Wang, 2016), and the determination of plant nutrient contents is fundamental for rangeland management (Arzani, Sour, & Motamedi, 2012; Stevens & Gowing, 2014; Sun & Wang, 2016), as livestock development is generally limited by forage nutritional yield (Abdala-Roberts, Parra-Tabla, Campbell, & Mooney, 2014; Ren et al., 2016). Due to the harsh climate on the plateau, plant growth in alpine ecosystems is severely restricted by soil nutrient availability, so alpine plants are more sensitive to exogenous nutrient inputs (Bowman, Gartner, Holland, & Wiedermann, 2006; Bowman, Murgel, Blett, & Porter, 2012; Zong et al., 2016). Therefore, alpine ecosystems may respond differently than other ecosystems to nutrient input after clipping defoliation. As important grassland use and management activities, the impacts of clipping defoliation under global climate change are regulated by other factors, such as nitrogen (N) deposition patterns.

Alpine grassland is the main ecosystem type on the Tibetan Plateau, and clipping is one of the main methods of grassland utilization. As an important measure in understanding plant compensatory growth, studies on the regulation of different clipping intensities and N addition are of great significance to forage production and animal husbandry development on the Tibetan Plateau. Our objective was to evaluate whether and how clipping intensity affected compensatory growth of alpine grasslands and how N addition regulated the response of the compensatory growth to clipping defoliation. We conducted a manipulative experiment including different clipping intensities (light and heavy) and N addition in an alpine meadow ecosystem. We hypothesized that (a) the effects of light clipping defoliation on plant biomass compensatory growth were higher than heavy clipping defoliation (regardless of N addition); (b) the compensatory effects of clipping defoliation on plant growth (regardless of clipping defoliation intensity) were greater under N addition than no N addition treatment.

2 | MATERIALS AND METHODS

2.1 | Study site description

This study was conducted at the Damxung grassland station (91°05′E, 30°29′N) in Damxung County, Tibet Autonomous Region, China. The altitude is 4,333 m above sea level, and the climate is semiarid continental. The mean annual temperature is 1.3°C, and the mean annual precipitation is 477 mm, 85% of which mainly occurs during the growing season (from June to August) (Shi et al., 2006; Zong et al., 2014). The soil is classified as meadow soil with sandy loam, with a depth of approximately 0.3–0.5 m (Shi et al., 2006) and soil bulk density being 1.29 g/cm^3. Detailed soil properties can be found in Zong et al. (2014). The vegetation type is classified as alpine meadow ecosystem, with a community cover approximately 30%–50%. The dominant species are *Kobresia pygmaea* C.B. Clarke var. *pygmaea*, *Carex montis-everestii*, and *Stipa capillacea* Keng. In addition, the alpine meadow in this region has been invaded by *Anaphalis xylorhiza* due to overgrazing in recent decades. The atmospheric N deposition rate is approximately 10 kg N ha^{-1} year^{-1} at this site (Zong et al., 2016).

2.2 | Experimental design

An area of 20 m × 20 m alpine meadow was selected for the N fertilization and clipping experiment in July 2010, and the same treatments were conducted in every growing season from then on. A split-plot design with a randomized block was used for the N addition and clipping experiment, with N addition as the main plots and clipping as the subplots. We established four blocks, and two

3 m × 3 m split plots were setup in each block. The two plots in each block were assigned randomly for control and N addition, with an N addition rate of 40 kg N ha^{-1} year^{-1}. This N addition rate is roughly equal to 4 times of the current levels of N deposition (10 kg N ha^{-1} year^{-1}) (Lü & Tian, 2007; Zong et al., 2016) and corresponds to the projected atmospheric deposition in this region by the year of 2050 (Galloway et al., 2004). Two-meter aisles were left as buffer areas between the adjacent plots.

In each no N or N addition plot, four 1 m × 1 m subplots were established: light clipping (LC), heavy clipping (HC), permanent retained plot and nonclipping plot (NC) (Figure 1). Thus, in the no N addition plots, there were the NC, LC and HC treatments, and in the N addition plots, there were the N, N+LC and N+HC treatments. We clipped the plots twice in early June and late July in 2017. Plants were manually clipped to heights of approximately 5 cm and 0–0.5 cm above the ground with scissors in the LC and HC treatments according to the light and heavy grazing intensity outside the fence, respectively. In addition, only species with palatable edibility for livestock were clipped, including grass and sedge functional groups. Plant aboveground materials clipped in early June and late July were collected, oven-dried at 65°C for over 48 hr and weighed to determine the aboveground biomass removed by the clipping treatments.

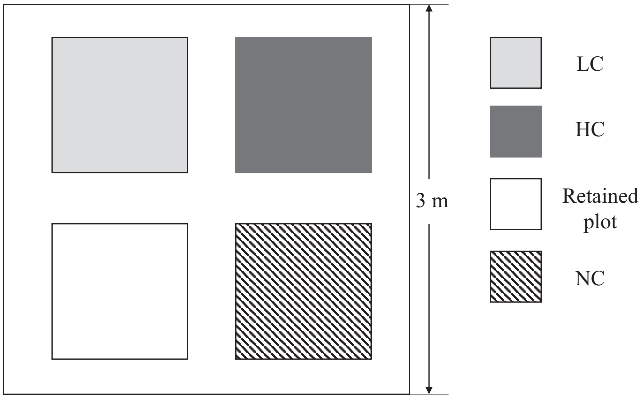

FIGURE 1 Experimental design in each treatment plot. NC, LC and HC indicate no, light and heavy clipping treatments, respectively. The retained plot indicates permanently preserved plot with no sampling treatment

Nitrogen was sprayed as aqueous NH_4NO_3 solution (18 L in each plot) in early June and early August each year, twice during each growing season. Water addition accompanied by N fertilizer represented a 6-mm precipitation increase, approximately 1.2% of the annual precipitation, which is well within the magnitude of inter-annual variations (Zong et al., 2014). The same amount of water was also added to the no N addition plots.

2.3 | Measurement of plant production and soil properties

In the peak growing season in mid-August, plant aboveground materials were collected at the ground level in a 50 cm × 50 cm quadrat, oven-dried at 65°C for over 48 hr and weighed to determine the community aboveground biomass. Dry matter weight was calculated and expressed by per square meter as aboveground net primary productivity. Five soil cores were randomly sampled in each quadrat using an auger (3.8 cm in diameter, 0–15 cm in depth) after plant material collection. Five soil cores were mixed as a composite sample and immediately passed through a 2-mm sieve to remove plant roots, gravel and stones. NO_3^--N and NH_4^+-N in soil samples were extracted using 2.0 mol/L KCl solution, filtered and analyzed by a continuous flow analyzer (AA3; SEAL Analytical, Norderstedt, Germany).

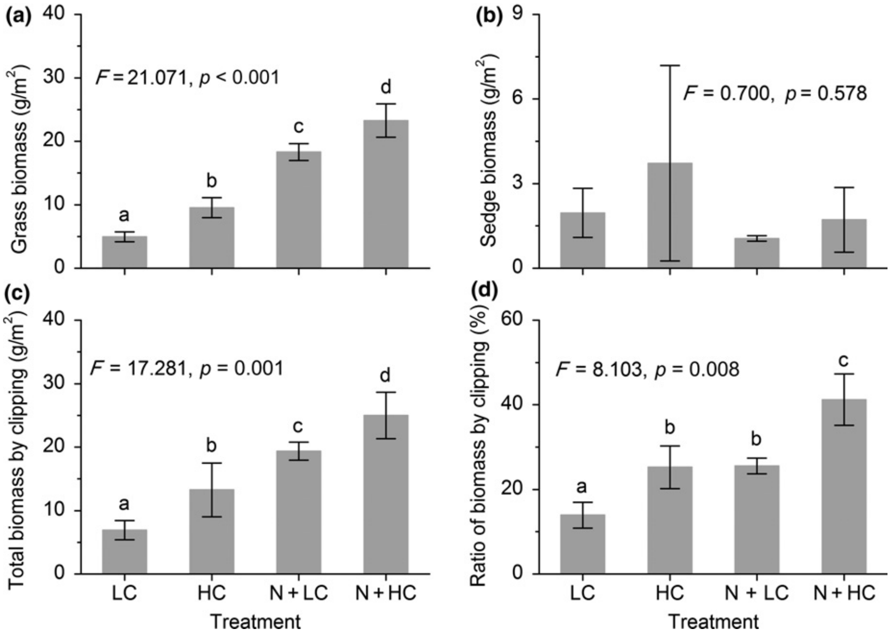

FIGURE 2 Aboveground biomass removed by clipping treatment. (a–c) It represent grasses, sedges and their total biomass, respectively. (d) It represents the ratio of the clipped biomass to total community biomass. Different lowercase letters mean significant differences among these treatments. LC and HC represent light and heavy clipping treatments under no N addition, respectively, and N+LC and N+HC represent light and heavy treatments under N addition, respectively. The same treatment definitions are represented in the following figures

2.4 | Data calculation and statistical analysis

The relative growth rate (RGR) indicates the relative growth rate of plant aboveground biomass after clipping defoliation. The RGR refers to the ratio of aboveground biomass (AGB_R) regeneration to the days between the two clipping treatments.

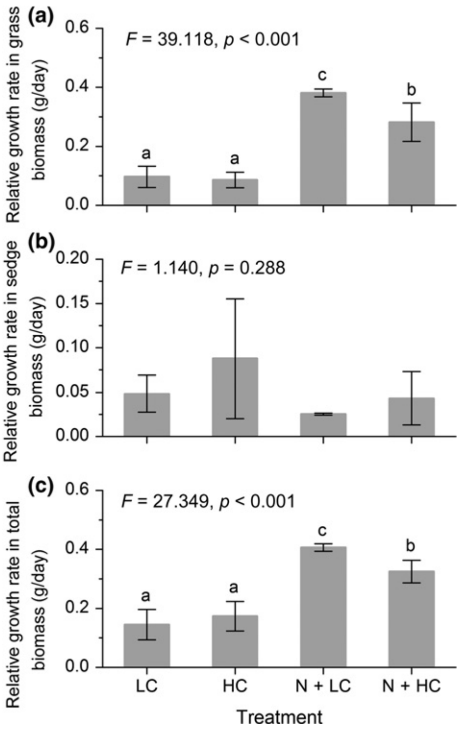

FIGURE 3 Relative growth rate of aboveground biomass under different clipping treatments. (a–c) It represent grasses, sedges and their total biomass, respectively. Different lowercase letters indicate significant differences among these treatments. LC and HC represent light and heavy clipping treatments under no N addition, respectively, and N + LC and N + HC represent light and heavy treatments under N addition, respectively

$$RGR = AGB_R/t$$

The AGB_R refers to the aboveground biomass regenerated between early June and late July in 2017 and harvested in late July in 2017. The t refers to the days between two clipping treatments.

The compensation index (CI) is generally used to measure the degree of plant compensatory growth, and always refers as the ratio to the sum of aboveground biomass removed by clipping defoliation and biomass harvested in the peak growing season to aboveground biomass in no N addition and nonclipping treatment. The equation is as follows (Belsky, 1986):

$$CI = G/C$$

G refers to the sum of aboveground biomass removed by clipping defoliation and biomass harvested in the peak growing season, and C refers to aboveground biomass in no N addition and nonclipped treatment.

Statistical analysis was conducted using the SPSS 16.0 software package (SPSS, Chicago, IL, USA). Two-factor analysis of variance (ANOVA) followed by Tukey's multiple comparisons was used to detect the effects of clipping defoliation and N addition on grasses, sedges, total biomass (grasses and sedges) and the ratio of clipped biomass to total biomass. We also used two-factor ANOVA followed by Tukey's HSD test to analyze the RGR of aboveground biomass, the CI in different plant functional groups and the overall community, as well as soil inorganic N content under the different clipping defoliation treatments. Linear regression analysis was used to analyze the relationships between aboveground biomass in different plant functional groups and soil inorganic N content, while noncurve regression analysis was used to analyze the relationships among the total aboveground biomass, CI and soil inorganic N content. The statistical significance of all analyses was set at $P < 0.05$.

Structure equation modeling (SEM) was used to evaluate the direct and indirect effects of different variables on total aboveground biomass. Based on the theoretical knowledge of the factors

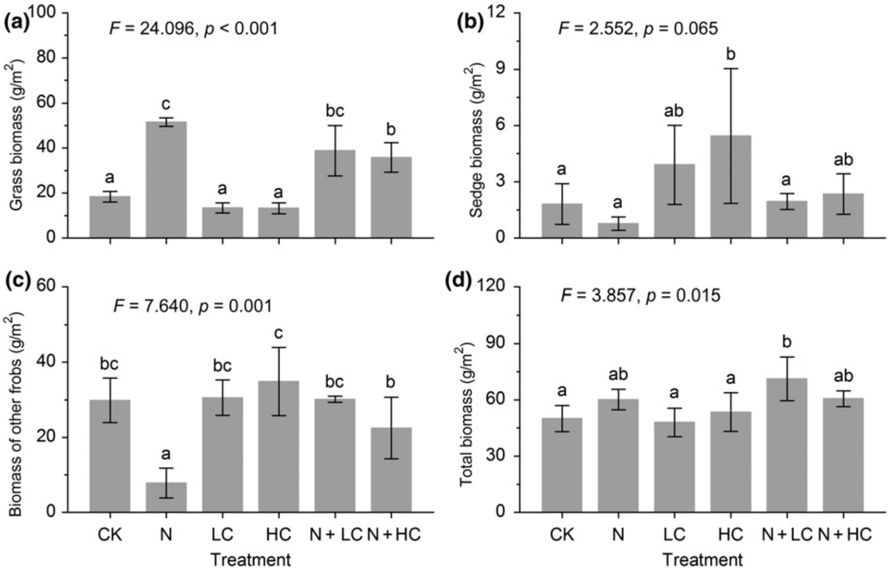

FIGURE 4 Total biomass (removed by clipping and harvested in the peak growing season) of grasses, sedges and the overall community. CK represents the no N addition and nonclipping treatment. (a-d) It represent grasses, sedges, other forbs and total community. LC and HC represent light and heavy clipping treatments under no N addition, respectively, and N + LC and N + HC represent light and heavy treatments under N addition, respectively

controlling community biomass, a path model was developed to evaluate the interactive relationships between soil inorganic N content, the RGR, compensatory index and total aboveground biomass. The adequacy of this model was evaluated by the chi-squared test and Akaike information criterion (AIC). Nonsignificant chi-squared tests ($P > 0.05$) and a low AIC value suggested that the model could be accepted as a potential explanation of the observed covariance structure (Grace, 2006). Based on the AIC values, nonsignificant pathways were removed to improve the model adequacy. Eventually, the final model was relatively strong: $\chi^2 = 3.187$, probability level = 0.074. The SEM analysis was conducted by Amos 17.0 (SPSS Inc.).

3 | RESULTS

3.1 | Aboveground biomass removed by clipping and the RGR

Grasses and total aboveground biomass (grasses and sedges) removed by HC were significantly higher than those removed in the LC treatment (Figure 2a,c). However, regardless of clipping intensity, the grasses and total biomass removed by clipping were significantly higher in the N treatment than in the no N addition treatment (Figure 2a,c). The results showed that sedge biomass removed by clipping defoliation showed no significant differences among treatments (Figure 2b).

The proportion of the clipped biomass to total biomass in the HC treatment was 25.2% and 41.2% in no N and N addition treatments, respectively, which was significantly higher than in the LC treatment (13.9% and 25.5%) (Figure 2d). However, the proportion of the clipped grass biomass to total biomass in the HC treatment was 72.9% and 65.3% in the no N and N addition treatments, respectively, significantly higher than in LC (37.8% and 50.0%). Meanwhile, the proportion of the clipped sedge biomass to total in HC was 58.8% and 66.3% in no N and N addition treatments, respectively, which was significantly higher than in the LC treatment (48.5% and 58.6%). Therefore, the light and heavy intensity clipping mainly referred to grasses and sedges.

The RGR of grass and total biomass showed the same trends under clipping defoliation (Figure 3a,c). Under the N addition treatment, the RGR of grass and total biomass after clipping defoliation were significantly higher than those under the no N addition treatment (Figure 3a,c). Under the no N addition treatment, there was no significant difference in the RGR of grass and total biomass between the LC and HC treatments (Figure 3a,c). Under the N addition treatment, the RGR of grass and total biomass in the LC treatment were significantly higher than those in the HC treatment (Figure 3a,c). The RGR of sedges showed no difference under the different clipping defoliation treatments (Figure 3b).

3.2 | Aboveground biomass in different plant functional groups and the overall community

N addition significantly increased grass biomass (removed by clipping and harvested in the peak growing season) (Figure 4a). Under the no N addition treatment, clipping defoliation promoted the growth of sedges (Figure 4b), but had no effect on the overall biomass (Figure 4d). Under the N addition treatment, clipping defoliation significantly increased grass biomass (Figure 4a). In addition, the N+LC treatment significantly increased the total community biomass. Therefore, the effect of the N+LC treatment on community biomass was mainly due to the promotion of grass growth.

3.3 | Compensation index in different plant functional groups and the overall community

Compared with the control, both the N+LC and N+HC treatments led to over-compensatory growth of grasses, while these two clipping defoliation treatments led to equal-compensatory growth of grasses under the no N addition treatment (Figure 5a). Regardless of N addition or not, sedges showed equal-compensatory growth

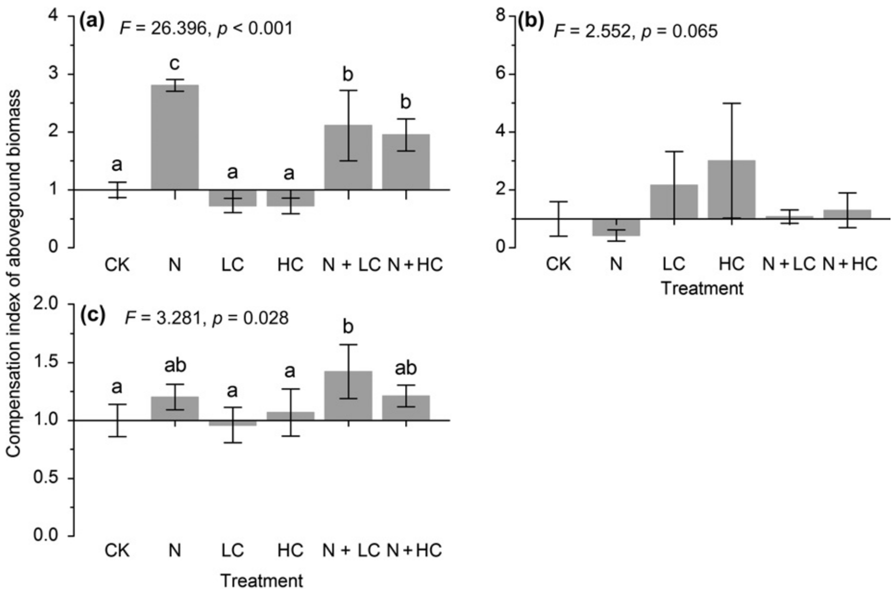

FIGURE 5 Compensation index in different plant functional groups and the overall community. (a–c) It represent grasses, sedges and the overall community, respectively. CK represents the no N addition and nonclipping treatment. LC and HC represent light and heavy clipping treatments under no N addition, respectively, and N + LC and N + HC represent light and heavy treatments under N addition, respectively

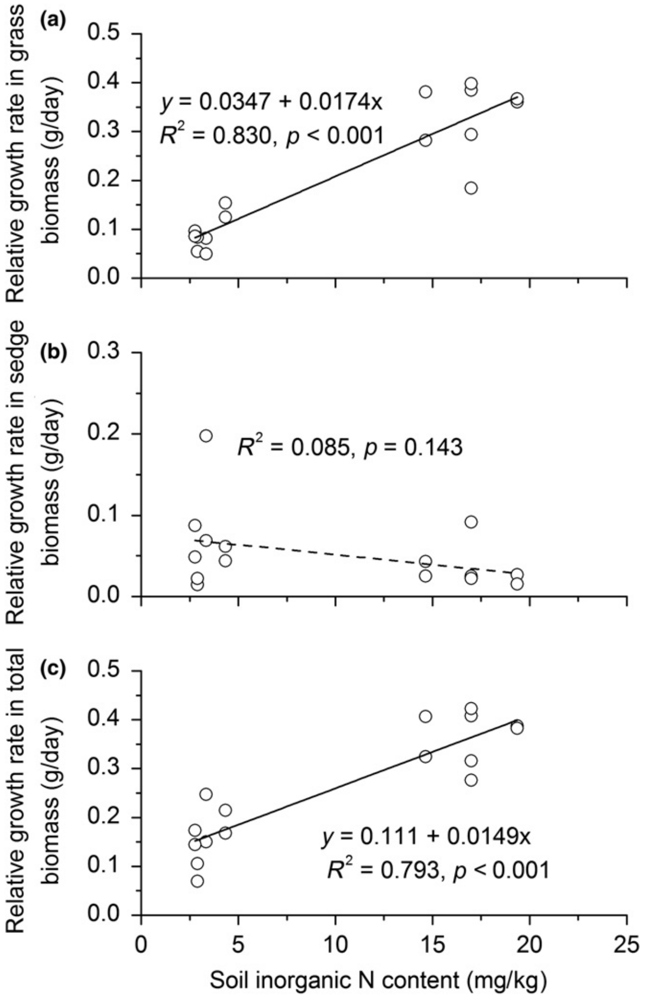

FIGURE 6 The dependence of relative growth rate on soil inorganic N content. (a–c) It represent grasses, sedges and the total community, respectively

pattern under the light and heavy clipping defoliation treatments (Figure 5b,c). Compared with the control, the total community biomass showed an over-compensatory growth pattern in the N+LC treatment, while it showed an equal-compensatory growth pattern under the LC, HC and N+HC treatments (Figure 5d).

3.4 | Factors regulating the RGR and plant compensatory growth

Regardless of clipping or not, N addition significantly increased soil N content, while clipping alone had no significant effects (Figure S1). Regression analysis showed that the RGR of grasses and total aboveground biomass were linearly correlated with soil inorganic N content (Figure 6a,c), while the RGR of sedges had no pronounced relationship with soil inorganic N content (Figure 6b).

Grass biomass increased linearly with the increase in soil inorganic N content (Figure 7a), but the increasing N availability was not conducive to the growth of sedges (Figure 7b). Both community biomass and compensatory growth tended to increase rapidly and then tended to be stable with the increase in soil N availability (Figure 7c, d), which indicates that high N addition cannot lead to a continuous increase in community biomass.

The SEM analysis was further used to evaluate the relationships between these interactive variables and total aboveground biomass (Figure 8). The final model was strong with $\chi^2 = 3.187$. The chi-square test showed that our hypothesized path analysis model can be accepted as a potential explanation of the observed covariance matrix ($P = 0.074$). Soil inorganic N content not only had direct effects on total aboveground biomass (Figure 8, $R^2 = 0.16$) but also had indirect effects on total aboveground biomass through affecting RGR ($R^2 = 0.90$) and CI ($R^2 = 0.64$). The RGR had a direct effect on total aboveground biomass ($R^2 = 0.25$), and the effect of CI was also

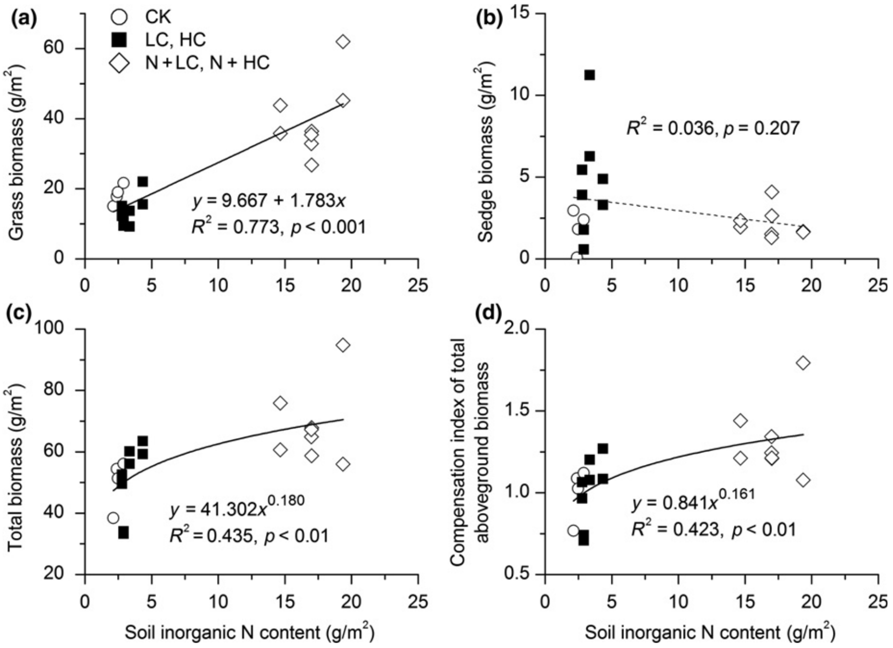

FIGURE 7 The dependence of plant compensatory growth on soil inorganic N content. (a–d) It represent biomass of grasses, sedges and the overall community as well as the compensatory index of the total community, respectively

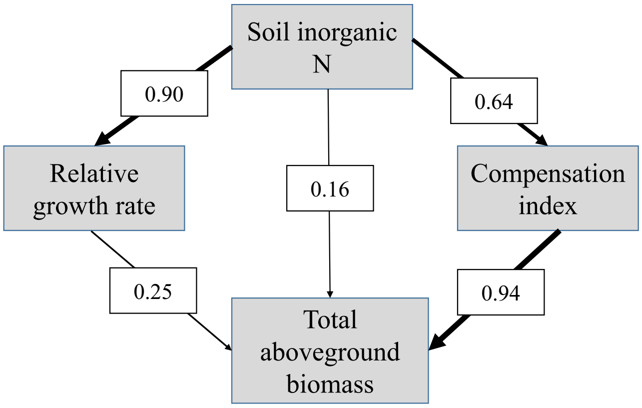

FIGURE 8 Structural equation model analysis for total aboveground biomass. The thickness of the solid arrows reflects the magnitude of the standardized SEM coefficients. Standardized coefficients are listed on each significant path. The SEM model used in this analysis was χ^2 = 3.187, probability level = 0.074

significant (R^2 = 0.94). The results demonstrate that soil nutrient content not only directly affects community biomass but also indirectly affects community biomass through compensatory growth.

4 | DISCUSSION

4.1 | Effects of clipping defoliation on plant compensatory growth

Clipping defoliation is typically used to simulate grazing effects. Generally, there are three main processes associated with grazing impacts on ecosystems: plant tissue removal, animal trampling and excrement input (Malo & Suarez, 1996). Both clipping defoliation can change community structure and ecosystem functioning (Li et al., 2015). To some extent, the effect of clipping defoliation is similar to biomass removal by animal grazing, but is less selective and more spatially uniform (Herrero-Jáuregui et al., 2016). Therefore, grazing is not completely replicated by clipping defoliation because the effects of livestock trampling and excrement deposition cannot be taken into consideration. However, previous studies also showed that there were some similarities between clipping defoliation and grazing on plant morphological plasticity, the sensitivity of plant traits and the trade-offs for plant allocation to stems or leaves, which can diminish leaf traits, stem traits and whole plant traits compared with plants under undefoliated treatments (Li et al., 2015).

Plant compensatory growth after clipping defoliation depends on the clipping defoliation intensities and plant tolerance to mechanical damage. Previous studies have shown that moderate clipping defoliation intensity can promote plant over-compensatory growth, but when clipping defoliation intensity is too heavy, plants generally show under-compensatory growth (Herrero-Jáuregui et al., 2016; McNaughton, 1983; Tuffa et al., 2017). Our results did not support our first hypothesis. This study showed that regardless of functional group (grasses or sedges) or overall total community, aboveground biomass showed equal-compensatory growth under both the light and heavy clipping treatments. This is not consistent with the results of Zhao et al. (2008). They reported that, as a grass species, *Leymus chinensis* showed over-compensatory growth when exposed to light and moderate clipping defoliation (removal of 20% and 40% biomass, respectively), while severe clipping (removal of 80% biomass) led to under-compensatory growth. The light and heavy clipping treatments in our study mainly referred to grasses and sedges. We only clipped these two functional groups to the height of 5 cm and 0–0.5 cm above ground level in the light and heavy clipping treatments, respectively. The clipping treatment removed 13.9% and 25.3% of aboveground biomass from total plant community in these two clipping treatments, respectively. The intensity was similar to the light and moderate clipping treatments in Zhao et al. (2008). In addition, we also found that the RGR of aboveground biomass was not significantly different between the LC and HC treatments. Thus, that is why these inconsistent results occurred.

This result also supports the optimization hypothesis proposed by McNaughton (1979), which states that grasslands have an optimal level of utilization. Under the moderate level, the pastures recover rapidly, reach the maximum net primary productivity and show equal- or over-compensatory growth patterns. With the increase in intensity thereafter, net community primary productivity gradually decreases. The RGR means the relative growth rate of plant aboveground biomass after clipping defoliation and also reflects the rate of compensatory growth caused by clipping defoliation. If the clipping intensity is relatively moderate, the RGR should be higher. However, if the clipping intensity is too heavy and excessive, the RGR will be very slow and the growth may even stop. The distribution of plant biomass reflects the trade-off of resource allocation after clipping defoliation, and its tolerant strategy to grazing to a certain extent. This study mainly focused on the effects of clipping defoliation on community aboveground biomass, instead of studying the impact of clipping defoliation on plant biomass allocation. This research topic needs to be deeply explored in future studies.

4.2 | The impact of N addition regulation on clipping defoliation effects

Many studies have shown that plant compensatory growth patterns and soil nutrient availability are closely linked (Tuffa et al., 2017; Zhao et al., 2008). The present study showed that our second hypothesis was partly supported by our results. In this present study, we found that total community biomass showed over-compensatory growth in the N+LC treatment compared with the control, while it showed equal-compensatory growth under the LC, HC and N+HC treatments (Figure 5). N addition compensated the nutrient limits required compensatory plant growth, increased aboveground biomass and enhanced plant compensatory growth. In the N+HC treatment, plants showed equal-compensatory growth. The positive effects of fertilization on compensatory growth of aboveground biomass cannot offset the negative effects of heavy clipping defoliation. This is consistent with the results of other studies (Grogan & Zamin, 2018; Stevens & Gowing, 2014; Ward, 2016). Therefore, the effects of N addition on the compensatory growth of the plant community also depend on clipping intensity. In addition to the effects of clipping defoliation and N addition on plant biomass, another study in an alpine meadow showed that both grazing and N addition had negative effects on plant species richness, while the effects of fertilization on plant species richness were masked by grazing in the combined treatment (Li et al. 2017).

Differences in plant responses to herbivory are the result of different factors, such as the type of plant parts removed (e.g., leaves, buds and flowers), herbivory intensity, neighborhood effects and resource availability (Peters, Cleland, Mooney, & Field, 2006; Ren et al., 2016; Sun et al., 2018). Different functional groups may respond differently to these factors (Stevens & Gowing, 2014; van Staalduinen & Anten, 2005), and a clear understanding of how these factors interact is necessary for exploring the effects of herbivory on plant communities at the functional group level and for the sustainable development of grazed or clipped ecosystems. Compared with the control, both the N+LC and N+HC treatments led to over-compensatory growth of grass biomass, while these two clipping treatments led to equal-compensatory growth of grass biomass under no N addition treatment (Figure 5). Meanwhile, these treatments also led to equal-compensatory growth of sedges. Thus, the over-compensatory growth of community biomass was mainly due to the stimulation of grass growth.

Generally, previous studies showed that rhizomatous grasses are nitrophilous and better adapted to high N availability (Bai et al., 2010; Zong et al., 2016). As faster-growing and tall plant species, grasses are in the upper part of the community canopy and outcompete with other species for light (Hautier, Niklaus, & Hector, 2009). Furthermore, with fibrous root systems, grasses have a stronger ability to compete for soil water and nutrient resources (Yang, Ren, Zhou, & He, 2014; Zong et al., 2016). Recent studies also reported that the absorption capacities of soil organic N and nitrate in the grasses *Poa pratensis* and *Stipa aliena* are greater than those of other plant species in an alpine ecosystem, as shown in an in situ ^{15}N isotope labeling experiment (Wang et al., 2012). The high compensatory growth capacity and biomass increase ability of grasses, as a palatable forage species, are beneficial for the restoration of degraded grasslands, as well as the development of livestock husbandry. In addition, these different compensatory growth abilities among plant functional groups also can result in community structure changes.

5 | CONCLUSIONS

To our knowledge, this is the first study to evaluate the effects of clipping intensity and N addition on plant compensatory growth in natural semiarid alpine meadows. The most significant promotion of compensatory growth in community biomass occurred in light clipping defoliation under the N addition treatment, and this compensatory growth mainly resulted from the stimulation growth of grasses. These divergent responses of plant functional groups to clipping defoliation and N addition would lead to changes in community structure and function. As the alpine meadow is the most important pasture on the Qinghai-Tibetan Plateau, the evaluation of the compensatory growth of plant production is of great significance for livestock husbandry development. Additionally, the results also infer that grazing activity is essential for the sustainable use of alpine pastures, but should be controlled at an appropriate intensity. Continuous nutrient input is important for the maintenance of forage production in alpine grasslands.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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