

1 **N deposition can accelerate the degradation succession from grasses- and sedges-**  
2 **dominated plant communities into forbs-dominated ones in overgrazed alpine**  
3 **grassland systems on Qinghai-Tibetan Plateau**

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23 **Running head:** N deposition accelerate overgrazing-induced degradation succession

24 **Abstract**

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25 Alpine grasslands are sensitive to grazing and atmospheric deposition of nitrogen (N). With the  
26 increase of N deposition, experimental investigations of the effects of grazing on alpine grassland  
27 vegetation with the background of N deposition are scarce.

28 In this study, we examined the effects of overgrazing and overgrazing with N deposition on eco-  
29 physiologies of alpine grassland plants at the functional group level. We found that both  
30 overgrazing and overgrazing with N deposition obviously changed species composition and the  
31 dominance of three plant functional groups (PFGs) in alpine meadow and alpine steppe.

32 Under overgrazing and overgrazing with N deposition treatment, forb tended to be predominant  
33 in the whole plant community, while grass and sedge dominance was obviously decreased. In  
34 addition, we found that the underlying eco-physiological processes that lead to forb-dominant  
35 were different under overgrazing and overgrazing with N deposition. Overgrazing with N  
36 deposition obviously tended to increase forb dominance both directly by selective herbivory and  
37 indirectly by enhancing forb photosynthetic capacity.

38 Our results suggested that long-term overgrazing with N deposition will lead to a more  
39 favorable living environment for forbs, making the grassland community of alpine grasslands on  
40 the Qinghai-Tibetan Plateau likely shift to forb-dominant in the future.

41 **Key words:** N deposition; overgrazing; plant functional groups; photosynthesis; respiration

## 42 **Introduction**

43 Livestock grazing is the primary land use of grasslands in the developing world where local  
44 livelihoods depend heavily on pastoralism (Sigcha *et al.*, 2018; Yu *et al.*, 2019; Dong *et al.*, 2020).  
45 Generally, sustainable grazing plays an important role in keeping the balance between livestock  
46 intakes and grassland productivity, especially in alpine regions (Fen *et al.*, 2010). In most previous  
47 studies, grazing usually leads to an obvious effect on grassland productivity, species composition

48 and structure of plant community (Zhang *et al.*, 2018). In recent decades, effect of overgrazing on  
49 grassland ecosystems has become a hot research topic in the Qinghai-Tibetan Plateau where the  
50 ecosystem is fairly sensitive to global change and human disturbance (Niu *et al.*, 2019; Dong *et*  
51 *al.*, 2020; Ji *et al.*, 2020). Though fencing has usually been regarded as one of the most effective  
52 ways to prevent grassland degradation (Wang *et al.*, 2011), light or moderate grazing is still  
53 considered beneficial to the health of grasslands (Quan *et al.*, 2015). However, little is known  
54 about the effects of overgrazing on plant compositions and eco-physiological processes of the  
55 alpine grasslands in the scenario of increasing N deposition.

56 As we know, N deposition is one of the key driver of global change (Bobbink *et al.*, 1998), and  
57 N deposition rate has been significantly increased for decades and predicted to continue in the  
58 future (Galloway *et al.*, 2004; Galloway *et al.*, 2008). In alpine grasslands, N deposition rate has  
59 increased to about 10 kg N ha<sup>-1</sup>yr<sup>-1</sup> in recent years (Zhu *et al.*, 2016). So far, many studies of N  
60 deposition effects on plants have been carried out worldwide. Both positive and negative effects of  
61 N deposition on grasslands are commonly reported (Van Der Wal *et al.*, 2003; Li *et al.*, 2018; Liu  
62 *et al.*, 2018). Nevertheless, the studies of joint effects of overgrazing and N deposition on plants  
63 are scarce. To date, we still know little about how would overgrazing with N deposition affect  
64 plants in alpine regions, especially in the perspective of plant functional traits to functional group  
65 composition.

66 Therefore, we believe that it warrant much attention to study the joint effects of overgrazing  
67 and N deposition, which could possibly give us a better understanding of plant response  
68 mechanism under joint effects of human disturbance and global change rather the sole effect of  
69 single driver. We hypothesized that: 1) Responses of different functional groups to overgrazing

70 and overgrazing with N deposition would be different. 2) Forbs would be dominant as all grass  
71 and sedge species in our study site are edible for herbivores, while most forbs are not edible or  
72 even poisonous to herbivores. 3) Overgrazing with N deposition would also promote the  
73 dominance of the forbs indirectly by increasing their photosynthetic capacity.

## 74 **Material and Methods**

### 75 **Study area**

76 The field experiment was conducted in alpine meadow locating at Xihai Town of Haiyan  
77 County (100°57'E,36°56'N, 3100 m ASL) and alpine steppe locating at Tiebujia Town of Gonghe  
78 County (99°35'N,37°02'E, 3270 m ASL) in Qinghai province, China. The alpine meadow is with  
79 clay soil and alpine steppe is with loam-clay soil. The mean annual temperature in alpine meadow  
80 is about 1.4 °C, the mean annual precipitation is about 330–370 mm and the annual evaporation is  
81 around 1400 mm. The mean annual temperature in alpine steppe is about 0 °C, the mean annual  
82 precipitation is about 377 mm, and the annual evaporation is about 1484 mm.

83 Fig.2

### 84 **Experimental design**

85 In 2012, the grassland with an area of 20m×20m in both two study sites (Fig.1) were fenced with  
86 iron fence (1.2m high), large herbivores such as yak and sheep were excluded from the fenced  
87 area. In 2018, three plots in the ungrazed area (2m by 5m) were chosen as the replication of  
88 control, In the area near the ungrazed area, three plots (2m by 5m) were randomly chosen for the  
89 replication of overgrazing, and other three plots (2m by 5m) were randomly chosen as the  
90 replication of overgrazing with N deposition. The grazed plots was overstocked by the free-  
91 ranging sheep from June to October over long term. In overgrazing with N deposition treatment,  
92 the plots were fertilized with ammonium nitrate (NH<sub>4</sub>NO<sub>3</sub>) in early May and July since 2018.

### 93 **Vegetation and soil sampling**

94 In early August (growing season) of 2018 and 2019, vegetation survey, plant and soil sampling  
95 were carried out. Vegetation in each plot were surveyed by using a randomly placed quadrat in the  
96 size of 1 m×1 m. The aboveground plant parts were harvested in a 0.5m ×0.5m sub-quadrat in  
97 each plot. After harvest, plant samples were oven dried at 65 °C for 24 hours to constant weight  
98 for the calculation of total AGB of community. We calculated the species dominance by using the  
99 equation of Dominance = (Relative abundance + Relative cover)/2. Soil cores (3.5 cm in diameter)  
100 collected from 0–20 cm depth were air dried at 70°C and sieved through a 0.15-mm mesh.  
101 Element analyzer (EA 3000, Italy) was used to measure soil total nitrogen (STN) and soil total  
102 carbon (STC) content. Soil available potassium (SAK) and available phosphorus (SAP) were  
103 measured using inductively coupled plasma spectrometers (ICP) (SPECTRO ARCOS EOP,  
104 Germany). Soil total phosphorus (STP) was measured using an ultraviolet spectrophotometer  
105 (Lambda 25) based on the Mo–Sb colorimetric method. Soil Ca, Mg, K, and S content were  
106 determined by atomic absorption spectrometry (AA-610S; Shimadzu, Kyoto, Japan). Soil  
107 ammonium nitrogen ( $\text{NH}_4^+$ ) and nitrate nitrogen ( $\text{NO}_3^-$ ) concentrations were measured using a  
108 continuous flow auto-analyzer (AACE, Germany).

### 109 **Photosynthesis and respiration measurement**

110 We measured the photosynthetic parameters of all plant species appeared in the study plots  
111 using a LI-6800 portable photosynthesis system (Li-Cor, Lincoln, NE, USA), between 9:30 am  
112 and 11:00 am in early August 2018 and early August 2019. Net photosynthesis rate ( $P_n$ ) of all  
113 plant species in the study plots were quickly surveyed and recorded. For each plot, three of each  
114 species with similar growth status were chosen as a replication. The  $\text{CO}_2$  concentration in the leaf

115 chamber was regulated by the LI-COR CO<sub>2</sub> injection system, which was set to 400  $\mu\text{mol mol}^{-1}$ . An  
116 irradiance of 1500  $\mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$  was achieved using a built-in LED lamp (red/blue).  
117 Temperature in the leaf chamber was maintained at approximately 25°C. The respiration rate was  
118 measured after the measurement of net photosynthetic rate with the irradiance of 0  $\mu\text{mol (photons)}$   
119  $\text{m}^{-2} \text{ s}^{-1}$ . The net photosynthetic rate and respiration rate of three PFGs was calculated by averaging  
120 the values of the key plants in each functional group (only species whose abundance  $\geq 3$  in each 1m  
121 by 1m quadrat were chosen for the final calculation of net photosynthetic rate and respiration rate  
122 of each functional groups).

### 123 **Statistical analysis**

124 One-way analysis of variance (ANOVA) was applied to test the difference of plant traits and  
125 soil properties of all plots. Dun-can's Multiple Range Test (Duncan) in analysis of variance  
126 (ANOVA) was used to test the effects of grazing and grazing with N deposition on plant  
127 photosynthesis and respiration. Principle component analysis (PCA) analysis was performed to  
128 determine the relationship between plant traits and soil properties. ANOVA analysis was carried  
129 out in SPSS22.0 and PCA analysis was carried out in R. In addition, structural equation model  
130 (SEM) was developed in AMOS 22.0 (Amos Development, Spring House, PA, USA) to identify  
131 the direct and indirect pathways that determine forb dominance under overgrazing and  
132 overgrazing with N deposition treatment.

### 133 **Results**

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#### 135 *Effects of overgrazing and overgrazing with N deposition on species composition*

136 Overgrazing and overgrazing with N deposition obviously affected species composition in both  
137 alpine meadow and alpine steppe, and both decreased the relative abundance of grass and sedge in

the whole plant community in 2018 and 2019 (Fig.2). Grass species such as *Leymus secalinus* was most heavily affected. However, overgrazing and overgrazing with N deposition showed no obviously uniform effects on the relative abundance of the only two sedge species: *Carex capillifolia* and *Carex melanantha*. The relative abundance of forbs such as *Stellera chamaejasme*, *Pedicularis kansuensis* and *Aconitum carmichaeli* etc., mostly the poisonous plants were obviously increased under overgrazing and overgrazing with N deposition. The PFG dominance of forbs over that of grasses and sedges tended to dominate the plant communities in the alpine meadow and the alpine steppe of 2018 and 2019 (Fig.3).

#### *Effects of overgrazing and overgrazing with N deposition on net photosynthetic rate of three PFGs*

The  $P_n$  of three functional groups (grass, sedge and forb) varied greatly under overgrazing and overgrazing with N deposition (Fig.4). In 2018,  $P_n$  of grass and forb in the alpine meadow and the alpine steppe were significantly increased under overgrazing and overgrazing with N deposition ( $P < 0.05$ ), while  $P_n$  of sedge was only significantly increased in the alpine steppe ( $P < 0.05$ ) (Fig.4a, 4b). In 2019,  $P_n$  of grass and forb in the alpine meadow showed similar variation with that in 2018 (Fig.4c), yet  $P_n$  of grass in the alpine steppe under the treatment of overgrazing with N deposition didn't show much significantly change compared with that under the treatment of ungrazing (Fig.4d,  $P > 0.05$ ).

#### *Effects of overgrazing and overgrazing with N deposition on respiration rate of three PFGs*

Overgrazing and overgrazing with N deposition had similar effect on the  $R_s$  of grass and forb (Fig.5).  $R_s$  of grass and forb in alpine meadow and alpine steppe were significantly increased under overgrazing and overgrazing with N deposition treatment (Fig.5a, 5b,  $P < 0.05$ ), while  $R_s$  of sedge showed no regular variation in the consecutive two years (Fig.5).

## *Relationship between plant eco-physiological characters and soil properties*

PCA analysis of plant traits and soil properties showed that PC1 and PC2 explained 59.7% of the variance (Fig. 6). Different treatments in the PCA analysis made clear separation. Overgrazing and overgrazing with N deposition obviously affected soil nutrients. Overall, forb dominance was positively related with soil nutrients such as STN, SAK, STK, STS, SAP, soil  $\text{NH}_4^+\text{-N}$  and soil  $\text{NO}_3^-\text{-N}$ . Among all soil properties, soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  variation had a higher weight in all variables. Other soil nutrients were positively correlated with these two variables. Forb dominance was positively related to plant  $P_n$ , while negatively related to grass and sedge dominance.

## *Path analysis under overgrazing and overgrazing with N deposition*

Two SEM models were successfully developed with the data collected under overgrazing and overgrazing with N deposition (Fig.7). Different pathways leading to the variance of forb dominance were observed. Overgrazing showed a direct positive effect on forb dominance, while overgrazing with N deposition induced significant effects on forb dominance through more complex indirect paths, except for direct positive effect. Overgrazing with N deposition had an indirectly positive influence on forb dominance through increasing soil nitrate nitrogen, which directly increased plant N uptake and enhanced photosynthetic capacity of forb, leading to increased forb dominance in the end. Additionally, overgrazing with N deposition directly enhanced respiration of forb, which in turn directly promoted photosynthetic capacity and finally elevated forb dominance. However, negative effects of enhanced soil nitrate nitrogen ( $\text{NO}_3^-\text{-N}$ ) on forb dominance under overgrazing with N deposition were also observed.

## **Discussion**

In general, overgrazing obviously causes some negative effects on plant community, such as decreasing vegetation cover, or breaking soil nutrient balance (Pasari *et al.*, 2014; Sun *et al.*, 2016;



Wang & Wesche 2016), which finally might cause land degradation (Yu *et al.*, 2019). However, positive effects such as compensatory growth and stimulating photosynthesis were also found (Mipam *et al.*, 2019; Zhang *et al.*, 2019b). Certainly, these phenomena were only appeared in light and moderate grazing condition (Pykälä *et al.*, 2005). As grazing has been a long-term human disturbance which is closely associated with local people's livelihood, many studies have focused on the grazing alone. In the era of global change, the effect of livestock overgrazing is simultaneously interacted with that of increasing N deposition on the alpine grasslands (mainly the alpine meadow and alpine steppe), the dominate ecosystems of the Qinghai-Tibetan Plateau (Dong and Sherman, 2015). Therefore, it is imperative to uncover the mechanisms that control the dynamics of plant communities of the alpine grasslands, if the livestock overgrazing and climate changes continue in the future.

#### *Overgrazing and overgrazing with N deposition change species composition*

Generally, grazing effects on plant species composition was usually more direct and principal (Pasari *et al.*, 2014), as herbivores were sensitive and selective to plants. In our study, plant compositions of both the alpine meadow and meadow steppe were significantly altered by overgrazing and overgrazing with N deposition, i.e., forb tended to be dominant in the plant communities. Relative abundance of poisonous forbs such as *Stellera chamaejasme*, *Pedicularis kansuensis* and *Aconitum carmichaeli* were much higher under overgrazing and overgrazing with N deposition treatments than that under ungrazing treatment, indicating that overgrazing and overgrazing with N deposition could lead to a favorable living environment for poisonous forbs (Wang *et al.*, 2019). Selective browsing by the overstocked herbivores might be a key factor that finally lead to the changes of species composition of alpine grassland plant community into forb-

dominated. Moreover, the forbs could be much competitive with the decrease of plant species of other functional groups, as the decrease of plant density will certainly lead to increase of light penetration for forbs, which will definitely in turn improve their photosynthesis.

In contrast to sole overgrazing, overgrazing with N deposition could directly promote the positive effect of photosynthesis and the negative effects of nitrate nitrogen ( $\text{NO}_3^-$ -N) on forb dominance. Positive effects of selective browsing and increasing photosynthesis associated with soil total nitrogen and nitrate nitrogen ( $\text{NO}_3^-$ -N) may suppress the negative effects of nitrate nitrogen ( $\text{NO}_3^-$ -N) on forb dominance, leading to a higher forb dominance under overgrazing with N deposition treatment than that under overgrazing treatment alone. This may be explained by that low N deposition ( $8\text{kgNha}^{-1}\text{yr}^{-1}$ ) could supply N resource and bring beneficial effects on forbs in this N-limited ecosystem, even more pronounced in the overgrazed alpine grasslands.

#### *Overgrazing and overgrazing with N deposition influence carbon gain and loss of three PFGs*

It is well known that photosynthesis and respiration are the two most important physiological processes that determine carbon gain and loss in plants (Zhong *et al.*, 2019). Generally, photosynthesis can affect carbon gain by absorbing atmospheric  $\text{CO}_2$  and changing it into organic matter which is the ultimate source of energy for almost all organisms, while respiration is the energy center, which can provides adenosine triphosphate (ATP) and carbon skeletons (Sperlich *et al.*, 2016). The trade-off between photosynthesis and respiration can actually determine plant fitness. Grass and forbs showed much higher net photosynthetic rate and respiration rate under overgrazing and overgrazing with N deposition treatments in contrast to the control, indicating that both drivers will promote carbon gain and loss process of grass and forb. However, the variation of net photosynthetic rate and respiration rate in sedges was not obviously consistent

with other two functional groups, suggesting that uncertainty existed for the plant functional group of sedges. It might be attributed to a much lower sampling for the sedges, because only two sedge species were recorded in our study site. In general, grazing can remove plant aboveground parts, and introduce more light, which could definitely increase plant light use efficiency in photosynthesis. However, grazing-induced disturbance such as the behavior of trampling and eating could also cause mechanical injury which in turn accelerate plants respiration process, making plants consume more energy for their self-healing (Kurtz *et al.*, 2016).

*N deposition deepens grazing effect on plants by more N resource supply*

Grazing-induced plant residue is the main resource of organic matter input into soil (Zhang *et al.*, 2019a). In addition, livestock urine and faeces are an important path that returns most chemical elements to the soil, which accelerates nutrients cycling of grassland ecosystems (Naeth *et al.*, 1991; Stark *et al.*, 2000). Typically, soil nutrients balance is definitely an important factor affecting plants (Fransen *et al.*, 2001; Zhang *et al.*, 2019a). In our study, we found that soil available N played an important role in changing the plant eco-physiological traits in the overgrazing habitats. This is the evidence to support the fact that plant N uptake is usually an important physiological indicator to reflect plant fitness (Ariz *et al.*, 2015). It seemed that N deposition brought more N resource for overgrazed plots, showing “gain effect” on plant photosynthesis. As we know, N is usually a limiting element in alpine regions (Simpson *et al.*, 2019), thus N deposition could provide more N resource for plant. In our study, overgrazing with N deposition could significantly change soil properties, both directly and indirectly leading to the variations of plant composition. Additionally, overgrazing with N deposition can also indirectly enhance the photosynthesis of alpine grasslands plants whose habitat is usually N-limited (Zong *et*

*al.*, 2016), as the plant photosynthesis can be promoted by plant N uptake when soil N is adequate (Graaf *et al.* 2005). Our synthesized paper shows that livestock grazing and nitrogen deposition can change the plant productivity, diversity, soil physics and soil biochemistry of the alpine grasslands, though the findings about the effects of these two drivers remained controversial due to various data sources, different research methodologies, diverse study sites and times (Dong *et al.*, 2020). Confidently, we drawn conclusion from reviewing hundreds of literatures that overgrazing can lead to declined productivity, biodiversity loss and soil deterioration of the alpine grasslands, and nitrogen deposition can result in soil acidification and eutrophication, which is harmful for alpine grassland health and stability (Dong *et al.*, 2020). With increased yearly atmospheric N deposition in alpine regions in the future (Zhang *et al.*, 2020), our results suggest that future N deposition will worsen overgrazing effects on the alpine grassland health and stability.

## **Conclusions**

Two types of the alpine grasslands (alpine meadow and alpine steppe) showed similar responses of plant traits and vegetation community to both overgrazing and overgrazing with N deposition according to our consecutive two-year observation. Overgrazing and overgrazing with N deposition both tended to shift the grass- or sedge-dominated alpine grasslands into forb-dominated ones. The underlying mechanism associated with overgrazing with N deposition was more complex than that associated with sole grazing. Apart from direct effects of selective browsing, overgrazing with N deposition could also enhance forb-dominance through increasing forb photosynthesis due to increased available N resource for forb growth. Overgrazing-induced disturbance enhanced forb carbon loss, which in turn promoted forb photosynthesis for more

carbon gain, thus to enhance its competence among the three PFGs. Indirect pathways of increasing forb dominance in the alpine grassland plant communities under overgrazing with N deposition was much more obvious than the sole overgrazing. Urgent actions are called for mitigating the accelerated shifts of alpine grasslands primarily dominated by grasses and sedges into degraded ones dominated by poisonous forbs with the couplings of continuous overgrazing and increasing N deposition on the Qinghai-Tibetan Plateau in the future.

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### **Data Availability Statement**

The datasets generated for this study are available on request to the corresponding author.

### **Conflict of Interest Statement**

No conflict of interest exists in the submission of this manuscript, and the manuscript is approved by all authors for publication.

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