Grazing increases litter decomposition rate but decreases nitrogen release rate in an alpine meadow

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Abstract. Litter decomposition and N release are the key processes that strongly determine the nutrient cycling at the soil-plant interface; however, how these processes are affected by grazing or grazing exclusion in the alpine grassland ecosystems on the Qinghai-Tibetan Plateau (QTP) is poorly understood. So far few studies have simultaneously investigated the influence of both litter quality and incubation site on litter decomposition and N release. Moreover, previous studies on the QTP investigating how grazing exclusion influences plant abundance and biodiversity usually lasted for many years, and the short-term effects have rarely been reported. This work studied the short-term (6 month) effects of grazing and grazing exclusion on plant community composition (i.e., plant species presented) and litter quality, and long-term (27 – 33 month) effects on soil chemical characteristics and mixed litter decomposition and N release on the QTP. Our results demonstrate that: (1) shorter term grazing exclusion had no effect on plant community composition but increased plant palatability and total litter biomass; (2) grazing resulted in higher N and C content in litter; and (3) grazing accelerated litter decomposition, while grazing exclusion promoted N release from litter and increased soil organic carbon. In addition, incubation site had significantly more impact than did litter quality on litter decomposition and N release, while litter quality affected decomposition in the early stages. This study provides insights into the mechanisms behind the nutrient cycling in alpine ecosystems. We suggest that periodic grazing and grazing exclusion is beneficial in grassland management on the QTP.

1 Introduction

The Qinghai-Tibetan Plateau (QTP) represents an important eco-region in China (Wen et al., 2010), in which alpine grasslands cover more than 85 % of total area and are regarded as the major land unit of natural pastures in China (Dong et al., 2010). However, the grassland systems in this region have suffered from severe degradation driven by a range of factors including climate change, overgrazing, over-cultivation and poor management (Han et al., 2008; Li et al., 2009; Wu et al., 2009; Feng et al., 2010; Wu et al., 2010), and with the degraded land area increasing at 1.2-7.44 % per year (Ma et al., 2007). Since the 1990's, the restoration of degraded grasslands has attracted considerable attention (Kang et al., 2007; Han et al., 2008), and some efforts has recently been directed towards grassland restoration and maintenance by increasing aboveground plant abundance (Niu et al., 2009) and biodiversity (Wu et al., 2009; Niu et al., 2010), and improving soil organic matter content and nutrient availability (Cao et al., 2004; Wu et al., 2010; Sun et al., 2011). It is well known that grazing may change the vegetation community structure, soil structure and nutrient cycling processes, and that such changes have important consequential impacts on the structure and functioning of the ecosystem as a whole. However, litter decomposition and N release, the key factors regulating the nutrient cycle and availability at the soil-plant interface through grazing (Carrera and Bertiller, 2013), are as yet litter studies in these alpine ecosystems (Luo et al., 2010; Zhu et al., 2016).

Herbivore grazing may induce short-term ecophysiological changes in plant tissues which in turn may translate into litter quality changes, and long-term shifts in plant community composition. At the short-term ecophysiological level, grazing may promote the plant species producing high-quality litter (Holland and Detling, 1990; Sirotnak and Huntly, 2000; Olofsson and Oksanen, 2002; Semmartin et al., 2004, 2008); because the consuming of plant tissues by herbivores may favour the grazed species with a higher re-growth rate and greater nutrient contents in plant tissues due to the higher nutrient uptake (see Holland and Detling, 1990; Olofsson and

Oksanen, 2002; Semmartin et al., 2008). At the long-term community level, selective foliar grazing may alter the competitive interactions and recruitment patterns of plant species, which may change their abundance and life form structure (Bardgett and Wardle, 2003; Semmartin et al., 2008; Wu et al., 2009; Niu et al., 2010). For instance, herbivores preferentially feed on the most palatable plants (e.g., species with high nutrient and low fibre contents), which may promote dominance of unpalatable species (Garibaldi et al., 2007), resulting in the high inputs of low-quality litter to soil and thus a reduction of decomposition rate, nutrient availability and nutrient cycling (Ritchie and Knops, 1998; Moretto et al., 2001; Olofsson and Oksanen, 2002). Therefore, litter in grassland subject to long-term grazing may decompose more slowly. However, some studies demonstrate that grazing *per se* may accelerate litter decomposition by modifying site conditions for litter turnover through physical changes in the soil by herbivore activities, such as trampling and urine/dung deposition (Takar et al., 1990; Fahnestock and Knapp, 1994; Semmartin et al., 2008; Luo et al., 2010; Liang et al., 2018). Empirical evidence of variance in litter quality input and decomposition caused by grazing is still subject to debate (Garibaldi et al., 2007).

It is often assumed that higher nutrient content in plant tissue usually results in faster litter decomposition, and in higher nutrient mineralization and availability in soil (Olofsson and Oksanen, 2002). At the ecosystem scale, the chemical characteristics of plant litter, for example the carbon:nitrogen ratios (C:N) and/or nitrogen and lignin content, are often regarded as the indicators of litter quality (Aerts, 1997; Strickland et al., 2009). Many studies have demonstrated a positive correlation between litter decomposition rate and litter N content, or a negative relationship between litter decomposition rate and initial litter lignin content and C:N or lignin:N ratios ratios (e.g., Wardle et al., 2002; Aerts et al., 2003; Semmartin et al., 2004; Garibaldi et al., 2007; Luo et al., 2010; Vaieretti et al., 2013).

In addition to litter quality (its chemical composition), two further factors controlling litter decomposition are the climate (mainly temperature and humidity) and decomposing organisms (their abundance and activity)

(Coûteaux et al., 1995; Aerts, 1997; Semmartin et al., 2004; Keeler et al., 2009; Berg and McClaugherty, 2014; Zhu et al., 2016). Climate usually regulates decomposition processes at global and regional scales (Coûteaux et al., 1995; Silver and Miya, 2001), but microbial activity regulates decomposition processes through soil temperature and moisture effects (modified by grazing) at a local scale (Coûteaux et al., 1995; De Santo et al., 1993; Luo et al., 2010; Orsborne and Macauley, 1988). Generally, climatic influence dominates litter quality and decomposer activity in areas where weather conditions are unfavourable (Coûteaux et al., 1995), due to the dependence of decomposer activity on microclimate (De Santo et al., 1993). Under favourable conditions, litter quality may largely prevail as the regulator and remain important until the late decomposition stages (Coûteaux et al., 1995). However, specific temperature and moisture conditions and litter quality may interact strongly and thus the rate of litter decomposition is difficult to predict.

Most studies evaluating the effect of grazing on litter decomposition usually focus on forest, grassland or crop ecosystems in temperate areas (e.g., Aber and Melillo, 1980; Berg and Staaf, 1981; Luo et al., 2010; McCurdy et al., 2013), largely ignoring those in the alpine zones. On the QTP, previous studies prove that long-term grazing exclusion (> 2 years) may promote plant abundance and biodiversity (Niu et al., 2009, 2010; Wu et al., 2009, 2010); however, exclusion may limit the efficient use of grassland. By contrast, the short-term effect of grazing exclusion is seldom studied. Other previous studies have focused on the dominant species only (e.g., Wu et al., 2009; Luo et al., 2010) and this approach provides less insight into the nature of nutrient cycling in the grasslands than work on mixed litter (Zhu et al., 2016; this study). Moreover, few studies have simultaneously investigated how both litter quality and incubation site affect litter decomposition (e.g., Luo et al. 2010; Zhu et al. 2016; Liang et al. 2018). In this study, we examined the short-term effect (6 month) of grazing and grazing exclusion on plant community composition and litter quality and their longer-term effect on mixed litter decomposition and N release (27 month) and soil chemical characteristics (33 month). Based on the above, this research aimed to test three hypotheses: (1) short-term grazing exclusion does not change plant community composition and litter quality (i.e., nutrient content as N and biomass of palatable plant species), (2) grazing may accelerate litter decomposition and N release and thus increase soil organic carbon and N, and (3) litter quality has less effect on litter decomposition and N release compared to incubation site. Results of the present study may improve our understanding of nutrient cycling in alpine regions in general, and this study may also further provide knowledge relevant to the development of strategies for restoring the degraded grasslands on the QTP in particular.

2 Materials and methods

2.1 Experimental site

This study site was an alpine meadow on the eastern QTP, Northwestern, SW China (N33°59′, E102°00′, altitude 3,500 m above sea level). The mean annual temperature is 1.2 °C, ranging from –10 °C in January to 11.7 °C in July, with approximately 270 days with frost per year. The mean annual precipitation over the last 35 years, occurring mainly during the short and cool summer is 620 mm (Niu et al., 2010). The years during this study (i.e., 2009 – 2012) were climatically typical (Sun et al., 2015; Supplemental Fig. 1).

The grassland selected for experiments was > 9 ha in area (including 6 ha of experimental plots and 3 ha buffer areas) and regularly used for Tibetan sheep and yak grazing during the grazing season (May – October). The slopes at the site are less than 5 %, typical of the gently undulating topography of the region. The soil properties in the experimental plots were similar after a long-term grazing history with the same grazing pattern. The soil type at the experiment site is an alpine meadow soil, similar to the Mat-Cryic Cambisols (Wu et al., 2010).

2.2 Litter composition and quality

To measure the annual litter composition and determine whether plants could recover without grazing, three grazing (GP, 100 m × 200 m) and three grazing exclusion paddocks (GEP, 30 m × 20 m) were established when all aboveground plants were dormant in October 2009. Grazing in GP started with an optimal moderate stocking rate of 4 Tibetan sheep/ha from April 2010. The mean body weight of sheep was about 38 kg when used for the experiment. Before grazing started, 20 quadrats (0.5 m × 0.5 m) identified by GPS coordinates were randomly established within the GP or GEP, and litter was cleared soon after the establishment of quadrats. In October 2010, we collected all plant litter from each quadrat of the GP and GEP for two purposes: (1) measurement of litter composition and quality in this experiment, and (2) measurement of litter decomposition and N release in the next experiment. Three sampling methods [i.e., half alongside, half along diagonal, and two sub-quarters (0.25 m × 0.25 m) along diagonal; see Supplemental Fig. 2] were designed to minimize the sample variance caused by the uneven litter distribution and to ensure the similar composition and quality of litter used for this and the next experiment.

To measure the litter composition, litter of different species collected from each quarter was identified. After litter species identification, litter was separated into two groups of contrasting palatability to the Tibetan sheep (Niu et al., 2009, 2010; Wu et al., 2009; see Supplementary Table 1): (1) palatable species - preferred and desirable species, and (2) unpalatable species - undesirable and toxic species. To measure the dry biomass, the palatable and unpalatable litter was separately oven-dried at 60 °C for 48 h and then weighed.

To measure the quality of litter collected from GP (GP-litter treatment) or from GEP (GEP-litter treatment), the palatable and unpalatable litter from a quarter was mixed again, then ground and stored in a zip-lock bag with 10 g per bag for a quality test. There were six replicates for each treatment. The contents of lignin, cellulose and hemicellulose were measured as descripted by van Soest et al. (1991). Organic carbon concentration (C) was measured by the $K_2Cr_2O_7$-H_2SO_4 oxidation method of Walkley-Black (Nelson and Sommers, 1996). The total Kjeldahl nitrogen (N) and total phosphorus (P) were analyzed using a FIAstar 5000 flow injection analyzer (Foss

Tecator, Högnäs, Sweden) (Chen et al., 2016). We also calculated the ratios of C:N, lignin:N, cellulose:N and hemicellulose:N.

We also examined the effects of grazing and grazing exclusion on soil characteristics. We randomly collected five soil samples in each experimental paddock (n=30 in total) from the 0 – 10 cm depth using a bucket auger (10 cm in diameter) in October of 2010, 2011 and 2012. The same methods used to test litter quality (i.e., Nelson and Sommers, 1996; Chen et al., 2016) were applied to estimate the soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (TP).

2.3 Litter decomposition and N release

In this experiment, we included four treatments: (1) GP-GP, litter of all species was collected from and incubated in the GP; (2) GEP-GEP, litter of all species was collected from and incubated in the GEP; (3) GP-GEP, litter of all species was collected from the GP but incubated in the GEP; (4) GEP-GP, litter of all species was collected from the GEP but incubated in the GP. Treatments 1 and 2 were designated "in situ" incubation treatments, while treatments 3 and 4 were designated "across" grazing category incubation treatments, and these were included to improve understanding of the "home-field advantage" effect on litter deposition (John et al., 2011).

For each sample soil particles attached to the litter were cleaned off with a soft brush, and samples were air-dried for three days. Dry litter collected from each quadrat was cut to ≈ 5 cm length and 10 g litter was packed into a nylon litter-bag (15 cm × 20 cm with mesh size of 0.35 mm) (Cornelissen, 1996), which should have prevented any loss of material and had no effect on litter decomposition (Cornelissen et al., 1999). On 20th Oct 2010, the packed litter was incubated above the soil surface by fastening to the ground surface with four steel stakes to prevent removal by sheep and small animals (Vaieretti et al., 2013), such as the plateau pika *Ochotona curzoniae* (Hodgson). For each treatment, 24 litter-bags were incubated with 20 cm apart from each other to reduce the mutual interference. Three litter bags from each treatment were retrieved after incubation periods of 56, 141, 247, 391, 444, 582, 695 or 799 days (i.e., on 15th December 2010, 10th March, 24th June and 4th September 2011, and 7st January, 24th May, 14th September and 27th December 2012, respectively). There were a total of 96 litter-bags used in this experiment. Retrieved litter was brought back to the laboratory, cleaned by removing any extraneous material attached, and then weighed after being oven-dried at 60 ºC for 48 h. Samples were ground and stored in a zip-lock bag for further chemical analyses as mentioned above. We estimated the litter decomposition and N release as the percentage of dry weight lost during each incubation period (Cornelissen et al., 1999; Vaieretti et al., 2013).

2.4 Statistical analyses

A goodness-of-fit test (Shapiro-Wilk test, Univariate Procedure) was used to test the normality of data before mean comparison using analysis of variance (ANOVA, GLM Procedure). All data were normally distributed. Data on the initial chemical characteristics of litter (Table 1) were analyzed using ANOVA followed by Tukey’s Studentized multiple range test. Data on the biomass of palatable or unpalatable species and that on the total biomass between GP and GEP were also analyzed using ANOVA, while for GP or GEP the difference in litter biomass between the palatable and unpalatable species was compared by paired-t test (TTEST Procedure) (Fig. 1). Data on the final proportion of litter biomass or N remaining (Fig. 4), litter quality (content of organic carbon, nitrogen, phosphorous and other chemical characteristics of litter) (Table 1), and soil SOC, TN and TP (Fig. 2) were analyzed using ANOVA followed by least significant difference test (LSD test) for multiple comparisons.

The decomposition rate (k, $g \cdot 10\ g^{-1} \cdot day^{-1}$) of litter biomass during the incubation period (Table 2) was assessed using a negative exponential model according to Swift et al. (1979): $y = a{*}e^{-(t*k)}$, where y is the dry biomass of litter remaining in the litter bags at time t (days), a is the initial litter biomass (i.e., 10 g in this study).

The difference in decomposition rate between treatments was compared according to Julious (2004), i.e. there is deemed to be no significant difference in decomposition rate if their 83.4 % CL overlap. The decomposition rate and 83.4 % CI were estimated by fitting the negative exponential model to a nonlinear least square regression model (NLIN Procedure).

A multivariate regression model (GLM Procedure) employed by Vaieretti et al. (2013) was applied to quantify the effect of incubation site and litter quality (the two independent factors) on the final litter decomposition or N release (the dependent factor) (Table 3): litter decomposition or N release = Site + Quality + Site×Quality + ϵ, where 'Site' is the paddock category where the litter was incubated (i.e., incubation site: GP and GEP), 'Quality' is the litter quality reflecting the sources where the litter was collected from (i.e., GP and GEP), and ϵ is the model error. The proportional contribution of incubation site, litter quality and their interaction to variability of litter decomposition or N release was calculated as the sum of squares for each of the terms, divided by the total sum of squares. The Type I sum of squares was used because of the balanced design of this experiment. All analyses were done using SAS 9.3 (SAS Institute Inc., Cary, NC, USA). The rejection level for H_0 was set at $\alpha < 0.05$. Values of the means (± SE) are presented in Figs. 1-4.

3 Results

3.1 Litter composition and quality and soil property

Fifty-five plant species (mostly forbs and grasses along with several legumes and sedges) were identified, and all were found in both GP and GEP, except *Gentiana macrophylla* Pallas, which was only found in the GP (Supplemental Table 1). However, even though the annual litter biomass of unpalatable species in both GP and GEP was similar (ANOVA: $F_{1,38} = 3.43$, $P = 0.0717$), litter biomass of palatable species was significantly greater in the GEP than in the GP (ANOVA: $F_{1,38} = 75.32$, $P < 0.0001$), and this difference contributed significantly more to the total litter biomass in the GEP than in the GP (ANOVA: $F_{1,38} = 114.66$, $P < 0.0001$) (Fig. 1). The litter biomass was not significantly different between palatable and unpalatable species in the GP (Paired-t test: $t_{19} = 0.96$, $P = 0.3510$); however, in the GEP, litter biomass of palatable species was significantly greater than that of unpalatable species (Paired-t test: $t_{19} = 7.17$, $P < 0.0001$) (Fig. 1).

GP-litter had significantly higher C and N but significantly lower hemicellulose and hemicellulose:N than GEP-litter (Table 1). Although other quality characteristics were lower in GP-litter than in GEP-litter, the differences were not significant (Table 1).

The concentrations of soil TN and TP were not significantly different between the GP and GE for any year (LSD = 0.0002 - 0.0015 and 0.0003 - 0.0004 for TN and TP, respectively; $P > 0.05$) (Fig. 2a-b). Similarly, there was no significant difference in SOC concentration between the GP and GE in 2010 and 2011 (LSD = 0.0169 and 0.0111 for 2010 and 2011, respectively; $P > 0.05$), while in 2012 SOC was significantly higher in GEP than in GP (LSD = 0.0138, $P = 0.0279$) (Fig. 2c).

3.2 Litter decomposition

The proportion of litter biomass remaining continuously decreased with incubation duration and litter decomposed faster in the first year (i.e., 44.6, 38.5, 41.46 and 31.6 % decomposition in GP-GP, GEP-GEP, GEP-GP and GP-GEP, respectively) than in the second year (i.e., 18.8, 24.1, 27.6 and 23.4 % decomposition in GP-GP, GEP-GEP, GEP-GP and GP-GEP, respectively) (Fig. 3a). As shown in Table 2, the decomposition rate (*k*) of litter incubated in GP was significantly higher than that in GEP (non-overlap of 83.4 % CL), i.e., for the “in situ” treatments *k* in GP-GP > *k* in GEP-GEP and for the “across” treatments *k* in GEP-GP > *k* GP-GEP. The final proportion of litter biomass remaining was significantly lower in GP-GP and GEP-GP than in GP-GEP (LSD = 2.51, $P < 0.0001$) (Fig. 4a).

3.3 N release

Generally, the percentage of total N release did not change during the first winter when temperature was < 0 °C, except that it increased during the incubation period of December 2010 and March 2011 (first winter) in the treatment GEP-GP (Fig. 3b). From January in the second winter (2012), the percentage of total N remaining decreased steadily until the end of the experiment (Fig. 3b). The final proportion of total N remaining was significantly higher in GEP-GP and significantly lower in GEP-GEP and GP-GEP (LSD test: LSD = 5.36, P = 0.0002) (Fig. 4b).

3.4 Contribution of incubation site and litter quality to litter decomposition and N release

The multivariate regression model indicates that both incubation site and litter quality significantly affected litter decomposition and N release (Table 3). Incubation site contributed respectively near 25 % and 50 % more to litter decomposition and N release than did litter quality (Table 3). Furthermore, the model predicts that GP resulted in significantly greater litter decomposition (8.13 %) but significantly lower N release (9.73 %) than did GEP ($F_{1,8}$ = 62.48 and 57.49 for litter decomposition and N release, respectively; P < 0.0001). Results show that GEP-litter decomposed significantly faster (2.5 %) but released N significantly more slowly (9.27 %) than GP-litter ($F_{1,8}$ = 34.99 and 15.80 for litter decomposition and N release, respectively; P < 0.01).

A significant interaction between incubation site and litter quality for litter decomposition was found ($F_{2,8}$ = 7.10, P = 0.0286), i.e., litter collected from GEP but incubated in GP decomposed significantly faster (also see Fig. 4a). However, the interaction between incubation site and litter quality on N release was not significant ($F_{2,8}$ = 2.76, P = 0.1350).

4 Discussion

4.1 Litter Composition and Quality

Grazing or grazing exclusion of herbivores may indirectly alter the species composition and functioning of grasslands by inducing shifts in plant competitive interactions and recruitment patterns, and thus changes in species abundance and life form structure (Bardgett and Wardle, 2003; Garibaldi et al., 2007; Semmartin et al., 2008; Wu et al., 2009; Niu et al., 2010; Chaneton, 2011). However, our results indicate that herbivore grazing or grazing exclusion did not alter plant community composition in terms of species inventory, as species found in the GEP mostly also occurred in the GP. On the QTP, species composition is grazing-intensity-dependent (Niu et al. 2010; Sun et al., 2011) and/or grazing exclusion-period-dependant (Wu et al., 2009). Thus our results imply that a stocking rate of 4 Tibetan sheep/ha in the GP or a short period of grazing exclusion (i.e., from April to October) in the GEP did not change the species composition.

However, our results show that herbivore grazing significantly altered species composition in terms of species abundance or palatability with significantly less palatable as well as total litter produced in the GP compared to the GEP (Fig. 1). The low biomass of palatable species in GP may be attributed to the more palatable species (mostly the grasses and sedges, see Supplemental Table 1) on the QTP being taller (Sun et al., 2011), and therefore more accessible to herbivore grazing, in addition to being more likely to be grazed by preferential grazing. Through these two mechanisms, the biomass of palatable species in the GP would subsequently be reduced. Results of this study indicate that grazing exclusion for a short period may allow the recovery of palatable species in the alpine meadows. However, there was no significant difference in the litter biomass of unpalatable species between the GP and GEP (Fig. 1), which provides evidence against the assumption that removing the canopy of palatable species may allow the intra- and inter-specific competition for light which ultimately favours the establishment of short, less-palatable species (Sternberg et al., 2000; Pavlů et al., 2008; Wu et al., 2009; Sun et al., 2011).

It is generally accepted that litter quality is usually determined by the levels of various chemical compounds such as soluble C, N and P, as well as lignin or lignin:N ratio, and litter of high quality usually has higher N content but lower lignin and lignin:N ratio (e.g., Aerts, 1997; Olofsson and Oksanen, 2002; Wardle et al., 2002; Garibaldi et al., 2007; Strickland et al., 2009). In this study, grazing might have improved litter quality at least to some extent by significantly increasing the N content and potentially reducing the hemicellulose content and C:N, lignin:N, cellulose:N and hemicellulose:N ratios (Table 1). Therefore, our results align with previous studies that have indicated grazing may promote litter quality due to the high nutrient uptake (e.g., Sirotnak and Huntly, 2000; Olofsson and Oksanen, 2002; Semmartin et al., 2004).

4.2 Litter decomposition

For a given climatic region, the ecological processes of litter decomposition are regulated by incubation microenvironment (i.e., grazing/grazing exclusion and soil property in this study) and litter quality. Our results suggest that herbivore grazing played a major role in litter decomposition on the QTP. Firstly many studies have demonstrated that litter quality is one of the most important factors affecting the litter decomposition, and litter with higher N content but lower lignin and lignin:N ratio will decompose faster (Aerts, 1997; Olofsson and Oksanen, 2002; Wardle et al., 2002; Garibaldi et al., 2007; Strickland et al., 2009). Therefore, it may be expected that regardless of incubation site, GP-litter that had significantly higher N content should decompose faster than GEP-litter. However, evidence for this expectation was only detected for the “in situ” incubation treatments (i.e., greater decomposition rate in GP-GP than in GEP-GEP), while for the “across” incubation treatments opposite results were found (i.e., greater decomposition rate in GEP-GP than in GP-GEP) (Table 2 and Fig. 4a). Our experimental site is located at high altitude with a low mean annual temperature of 1.2 °C; hence the activity of decomposers may be inhibited during the cold seasons (Coûteaux et al., 1995). Therefore, litter quality may not be a good predictor of litter decomposability in cold temperate regions (Aerts, 1997), where climate is more important than litter quality in the regulation of litter decomposition (Coûteaux et al., 1995). On the QTP, decomposition rate (k = 1.04 × 10^{-3} - 1.34 × 10^{-3} g·10 g^{-1}·day^{-1} in Table 2, i.e. k = 0.38 - 0.48 g·g^{-1}·$year^{-1}$) was much lower than that of the global mean (k ≈ 0.75 g·g^{-1}·$year^{-1}$) with similar latitudes (N30° - 40°) (Zhang et al., 2008).

Additionally, incubation site had significantly greater effect on litter decomposition (≈ 25%) than did litter quality (Table 3), and regardless of litter quality, litter decomposed faster in GP (19.9 % for GP-litter and 11.8 % for GEP-litter) than in GEP (Fig. 4a; Table 2). This may be attributed to the effect of herbivore grazing activity, which modifies the incubation site conditions for litter turnover (Takar et al., 1990; Fahnestock and Knapp, 1994; Semmartin et al., 2008; Luo et al., 2010; Liang et al., 2018). Our results further demonstrate that regardless of incubation site and litter quality, litter decomposed faster in the first year (31.6 – 44.6 % decomposition) than in the second year (18.8 – 27.6 % decomposition) (Fig. 3a). Berg (2014) and Berg and McClaugherty (2014) have stated that litter decomposition rate varies at different stages. In the early stages of decomposition litter mass is lost rapidly via the leaching of soluble compounds, while in the later stages decomposition can even cease after only recalcitrant litter compounds remain (Berg 2014; Berg and McClaugherty 2014). Therefore, litter quality regulates decomposition processes mainly in the early stages of decomposition (Berg and McClaugherty, 2014), which is supported by our results, i.e., when incubated in GP in the first year, the percentage decomposition of GP-litter (44.6 %) was higher than that of GEP-litter (41.5 %). However, we could not reject the above conclusion that incubation site is the dominant factor affecting litter decomposition over litter quality, as in the first year litter always decomposed faster in GP (i.e., 44.6 % in GP-GP and 41.5 % in GEP-GP) than in GEP (i.e., 38.5 % in GEP-GEP and 31.6 % in GP-GEP) (Fig. 3a). These data also imply that a home-field advantage is detected only for GP-litter during the first year of incubation (i.e., percentage decomposition 44.6 % in GP-GP > 31.6 % in GP-GEP) with no evidence for GEP-litter (i.e., percentage decomposition 38.5 % in GEP-GEP < 41.5 % in GEP-GP).

In a long-term (9 year) study on the QTP, Wu et al. (2009) reported that grazing exclusion favors the increase of soil total nitrogen, soil organic matter, soil organic carbon, soil microbial biomass carbon and soil carbon storage. It is intersting that in the present study, only soil organic carbon (SOC) significantly increased after three-years grazing exclusion (Fig. 2). The increase in SOC in GEP may be because grazing exclusion prevents the reduction of removal of palatable litter by the herbivores (Fig. 1), and the organic C locked within plant tissues may be returned to the soil during litter decomposition instead (Bardgett and Wardle, 2003; Wu et al., 2009). Holland and Detling (1990) and Ågren et al. (1999) stated that increasing carbon availability in soil may promote decomposer growth and activity even at low nitrogen concentrations. However, the expected results, i.e. significantly higher litter decomposition rate caused by the possible increasing decomposer mass and/or activity in the grazing exclusion grasslands (Wu et al., 2009), were not observed in the GEP in this study (Table 2, Fig. 4a). Thus during a relatively short period the soil properties are unlikely to be significantly changed through grazing or grazing exclusion, and thus limited duration grazing events have a smaller effect on litter decomposition under cool environments on the QTP, than in experiments conducted in warmer climates.

4.3 N release

N release is a more complex process, compared to litter decomposition. N release may involve any one or both processes of N immobilization and N mineralization, where the former results in the accumulation of N in the litter and the latter causes the release of N from the litter (Manzoni et al., 2008). Swift et al. (1979) and Berg and McClaugherty (2014) reported that the biological decomposition of litter is mainly carried out by microbial decomposers, which *per se* have a higher N:C ratio compared with most litter types. This property of decomposers creates a high N demand for decomposer growth (Manzoni et al., 2008). Results show that regardless of litter quality or source, N remaining was significantly higher when litter was incubated in GP than in GEP (Fig. 4b). Bosatta and Balesdent, (1996) and Manzoni et al. (2008), a promising candidate mechanism may be that the faster decomposition rate of litter in GP increases the utilization of C by the decomposers which in turn increases the N:C ratio in litter; when N:C ratio is high, large amounts of mineral N are immobilized, increasing the N concentration in litter. This mechanism may also account for the dynamics of N release over the incubation period (Fig. 3b). For instance, decomposer activity resulted in continuous C consumption and litter decomposition (March – June 2011), while high N:C ratio due to decomposition progress induced the release of accumulated N (June – August 2011). The inverse pattern of N release and litter decomposition found in this study (Fig. 4) is frequently reported (e.g., Aber and Melillo, 1980; Fahey et al., 1991; Gallardo and Merino, 1992).

It is not surprising that because both litter decomposition and N release are regulated by decomposers synchronously, incubation site also had a significantly greater effect (≈ 50%) on N release as on litter decomposition (Table 3) than did litter quality, indicating the latter is not a good predictor on litter N release in the cold temperate region (Aerts, 1997).

5 Conclusion

Results of our study are not completely consistent with previously proposed hypotheses. On the cold QTP, short-term grazing exclusion did not promote species abundance but increases plant palatability and total litter biomass. Grazing improves litter quality through higher N content but lower hemicellulose and hemicellulose:N ratio. Grazing significantly accelerated litter decomposition, while grazing exclusion promoted N release and increased SOC. Although litter quality may affect decomposition at the early stages, incubation site had significantly more impact on both litter decomposition and N release. The different effects of grazing and grazing exclusion functioning on the grassland ecosystems may have implications in the management of alpine meadows on the

QTP. For example, periodic grazing and grazing exclusion may be a good option which allows plant recovery and promotes nutrient cycling, and thus contributes to the restoration of degraded grasslands.

Author contributions. YS and FH designed the experiments, YS, ZW and SH Chang performed research and collected data. XZH and YS analysed data and prepared the manuscript, and all authors contributed to the writing.

Competing interests. The authors declare that they have no conflict of interest.

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Table titles

Table 1. Initial chemical characteristics (mean ± SE) of litter collected grazing paddocks (GP-litter) and grazing exclusion paddocks (GEP-litter). Unit of chemical characteristics is mg/g litter for C, N, P, lignin, cellulose and hemicellulose. Different letters in each row indicate significant difference (ANOVA: $P < 0.05$).

Table 2. Litter decay rate (k, $g \cdot 10\ g^{-1} \cdot day^{-1}$) in different incubation environments. GP-GP, mixed litter was collected from grazing paddocks (GP) and incubated in GP; GEP-GEP, mixed litter was collected from grazing exclusion paddocks (GEP) and incubated in GEP; GEP-GP, mixed litter was collected from GEP and incubated in GP; GP-GEP, mixed litter was collected from GP and incubated in GEP. k values followed by different letters are significantly different (non-overlap of 83.4 % CL). The R^2, F and P are estimated from the negative exponential model of Swift et al. (1979).

Table 3. Contribution (%) of incubation site (Site: GP, grazing paddocks; GEP, grazing exclusion paddocks) and litter quality (Quality: GP-litter, mixed litter collected from grazing paddocks; GEP-litter, mixed litter collected form grazing exclusion paddocks) to litter decomposition and N release.

Supplemental table title

Table S1. The list of all species in grazing and grazing exclusion paddocks (Niu et al., 2009, 2010; Wu et al., 2009).

Figure captions

Figure 1. Mean (± SE) annual biomass of litter collected from grazing paddocks (GP) and grazing exclusion paddocks (GEP). For each category, columns with different letters are significantly different (ANOVA: $P < 0.05$).

Figure 2. Mean (± SE) soil total nitrogen (TN) (**a**), soil total phosphorous (TP) (**b**), and soil organic carbon (SOC) (**c**) between the grazing paddocks (GP) and grazing exclusion paddocks (GEP). Significant difference was only found between GP and GEP for SOC in 2012 (LSD test: $P < 0.05$).

Figure 3. Dynamics (mean ± SE) of litter decomposition (**a**) and N lease (**b**) on the QTP. GP-GP, mixed litter was collected from grazing paddocks (GP) and incubated in GP; GEP-GEP, mixed litter was collected from grazing exclusion paddocks (GEP) and incubated in GEP; GEP-GP, mixed litter was collected from GEP and incubated in GP; GP-GEP, mixed litter was collected from GP and incubated in GEP. Grey lines under months indicate the mean air temperatures < 0 ºC.

Figure 4. Percentage of litter mass (**a**) and total N remaining (**b**) at the end of experiments. GP-GP, mixed litter was collected from grazing paddocks (GP) and incubated in GP; GEP-GEP, mixed litter was collected from grazing exclusion paddocks (GEP) and incubated in GEP; GEP-GP, mixed litter was collected from GEP and incubated in GP; GP-GEP, mixed litter was collected from GP and incubated in GEP. Vertical bars are the least significant different (LSD) values. Columns with the different letters are significantly different (LSD test: $P < 0.05$).

Supplemental figure captions

Figure S1. Mean temperature (ºC) and total precipitation (mm) during experiments.

Figure S2. Field sampling methods: (**a**) half alongside, (**b**) half along diagonal, (**c**) two sub-quarters along diagonal, and (**d**) additional quarter for supplementary litter collection to make up 20 g in quarter **a**, **b** or **c**.