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Mowing and topography effects on microorganisms and nitrogen transformation processes responsible for nitrous oxide emissions in semi-arid grassland of Inner Mongolia

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Abstract
Purpose Few studies have been done to investigate the impact of mowing on N_2O emissions and the abundance of functional microbial genes, especially in sloping landscapes. This study aims to explore the impact of mowing on key N_2O-producing processes under different topographical conditions in a semi-arid grassland.
Materials and methods Soil samples were collected from a semiarid grassland ecosystem in Xilingol region, Inner Mongolia, where long-term management practices including non-mowing and mowing in flat and sloping blocks were conducted. We then determined (1) soil moisture, total carbon (TC) and nitrogen (TN), and mineral N (NH_4^+-N and NO_3^--N) content; (2) the potential N_2O emission from nitrification (N_{N2O}) and from denitrification (D_{N2O}) and potential N_2 emission (D_{N2}); and (3) the gene abundance of ammonia-oxidizing archaea *(AOA)* and ammonia-oxidizing bacteria (*AOB*), the *narG* (nitrate reductase) gene, and *nosZ* (nitrous oxide reductase) gene.
Results and discussion Soil moisture and potential N_2O emission from nitrification and denitrification were significantly lower in sloping than in flat conditions, whereas the TC, TN, NH_4^+-N, NO_3^--N content, gene abundance of *AOA*, *AOB*, *narG*, and *nosZ* showed no difference between flat and sloping conditions. Mowing significantly decreased the gene abundance of *AOA*, *AOB*, *narG* in both flat and sloping areas, and significantly decreased potential N_2O emissions, especially in sloping areas.
Conclusions The potential N_2O emission was significantly lower on sloping than flat grassland. Mowing significantly decreased the potential N_2O emissions, especially on sloping grassland. Our results suggest that topographical conditions should be incorporated into methods for estimating N_2O emission and land management practices in semiarid grassland.

Keywords Microbial functional groups · Mowing · N_2O emission potential · Slope

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1 Introduction

Nitrous oxide (N_2O) emissions contribute to global warming and to the catalytic depletion of the ozone layer (IPCC 2007). They are mainly produced in soils by microbial nitrification denitrification (Zumft 1997). Temperate grasslands are the major sources of atmospheric N_2O (Oenema et al. 2007), and mowing for hay is an important land-use type in grassland regions. Much evidence has suggested that mowing or hay-harvesting could significantly reduce carbon (C) and nitrogen (N) deposits below ground, resulting in substrate limitation to soil-inhabiting microbes, particularly in nutrient-limited environments (Wan et al. 2002). Mowing leads to changes in the size of the root system and thus causes the death and decay of the roots and nodules, followed by decomposition, mineralization of nitrogen (Sørensen et al. 2008), nitrification, and denitrification (Pan et al. 2016) related to N_2O emissions.

N_2O production and reduction depend on both the abundance of specific groups of soil microbes, such as *AOA*, *AOB*, *narG* genes, etc. (Wrage et al. 2001; Canfield et al. 2010), and on a range of soil abiotic factors, like soil pH, C, N, and water content (Wallenstein et al. 2006), which regulate their activity. Abiotic influences on N_2O production in grassland are well understood and have been extensively reviewed (e.g., Saggar et al. 2004 and Luo et al. 2010. More recently, there has been a greater focus on the role of microbial functional groups in N_2O emissions from soil (Chen et al. 2014; Zhong et al. 2014; Keil et al. 2015). Chen et al. (2014) showed that *AOA* abundance decreased significantly with mowing, while the effect of mowing on *AOB* abundance varies seasonally in Inner Mongolia grasslands; Keil et al. (2015) also showed increased potential N_2O emissions and denitrification gene abundance under mowing, but this was a combined effect of mowing, fertilization, and grazing, making it impossible to confirm effect of mowing alone. However, no information is available on how mowing affects soil microbial functional potentials of N cycles in grasslands under different topographical conditions.

The northern grasslands of China are mainly used for stock raising, and a large part of this region is sloping (Yao 2005). The effect of mowing on the soil ecosystems varies in flat or sloping grasslands (Luo et al. 2013). Previous works investigating N cycling components, for example, N_2O flux (Letica et al. 2010; Luo et al. 2013; Zhong et al. 2014), N leaching (Parfitt et al. 2009), and urine and dung deposition patterns (Betteridge et al. 2010) under varied topography, were mainly conducted in humid climate in New Zealand or European grassland. Little work has focused on the mechanisms driving the variation in N_2O production processes in sloping landscapes in semi-arid grasslands.

The Inner Mongolian grassland is one of the best-known rangelands in the eastern part of the Eurasian steppe (Wang 2004). In recent decades, with the rapid increase in livestock numbers, pastoralists prepare increasingly more hay by mowing the natural grassland, which has induced a series of grassland degradations (Li et al. 2008) and altered N_2O emissions (Zhang et al. 2015). However, there has been little research on the impact of mowing on N_2O emissions and the abundance of functional microbial genes in grassland, especially in sloping landscapes. The aim of this study is to explore the impact of mowing on key soil characteristics and microbial functional gene abundance known to regulate N_2O production under different topographical conditions in the semi-arid grassland.

2 Materials and methods

2.1 Experimental site

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43° 38′ N, 116° 42′ E) of the Chinese Academy of Sciences, which is located in the Xilin River Basin of Inner Mongolia, China (Bai et al. 2004). The topography consists of low rolling hills, with an elevation ranging from 1200 m to 1280 m above sea level. The mean annual precipitation is 346.1 mm, with about 60–80% falling as rainfall in the growing season (April to September). The mean annual temperature is 0.3 °C. The soil is classified as dark chestnut (Calcic Chernozem, according to ISSS Working Group RB, 1998). *Stipa grandis* (perennial bunchgrass) and *Leymus chinensis* (perennial rhizomatous grass) are the two dominant species of the native grassland vegetation in the study area, which together account for 60–80% of total aboveground biomass. The experimental area had been used for sheep grazing until 2003, when the experiment was established, and in order to have an equal starting point, the whole area was cut to 3–5 cm stubble height at the end of the 2004 growing season.

Our experimental site, which covers a total area of 128 ha, was established in 2005 with a split–split plot in a random complete block design. The 128-ha area was first divided topographically into two blocks (sloping and flat, with the slope class about 3–4°), and each block was divided into different management treatments (traditional grazing treatments, mixed treatments [each plot alternated year on year between mowing and grazing], and mowing treatments). In this study, we selected two topography types (slope and flat) with two mowing treatments (non-mowing and mowing), a total of four 2 ha units. The mowing treatment was one-cut haying in mid-August every year (2–3 cm above the ground).

2.2 Sampling procedures and parameters

Sampling was done in mid-August 2014, corresponding to peak biomass in the growing season. Five 5 m × 5 m sampling sub-plots were established randomly along a diagonal line in each of the 4 plots. Within each soil sample plot, five soil cores (5 cm in diameter) were collected and combined from 0 to 10 cm as one sample. Soil samples were then passed through a 2 mm sieve and stored at 4 °C in the laboratory until further use. Sub-samples of fresh soil were stored at − 20 °C for DNA extraction.

2.3 Chemical and microbial functional gene analyses

Soil NH_4^+ and NO_3^- concentrations were determined in 2 M KCl extracts using a LACHAT Quickchem Automated Ion Analyzer (FIA Star 5010 Analyzer; Tecator). Gravimetric soil moisture content was determined by oven-drying at 105 °C for 24 h. Total soil C content was analyzed using the H_2SO_4-$K_2Cr_2O_7$ oxidation method (Nelson et al. 1996). Total N content was analyzed using the Kjeldahl acid-digestion method with an auto-analyzer (Foss Inc., Hillerød, Sweden). DNA was extracted from 0.3 g of frozen soil using a MoBio Powersoil™ DNA Isolation Kit (San Diego, CA, USA) following the manufacturer's instructions and stored at − 80 °C until further required. The abundance of *AOA*, *AOB*, *narG*, and *nosZ* genes was quantified in triplicate by real-time PCR using an iCycler IQ (Biorad). The real-time PCR mixture contained 2 ng of undiluted soil DNA, 5 pmol of primers (Table 1), and 2 × SYBR Green iCycler iQ mixtures (Bio-Rad, US) in a total of 25-ml reaction volumes.

2.4 Incubation experiment to measure N_2O emission potential from nitrification and denitrification

The incubation experiment was performed in a 250-ml flask with 40 g (dry weight) of sieved moist field soil. The headspace inside the flask was set with three acetylene (C_2H_2) partial pressures: 0, 10 Pa, and 10 K Pa, each with three replicates (Hergoualc'h et al. 2007). Each flask was sealed with an airtight rubber lid and incubated at temperatures and moisture levels similar to those recorded in the field. Gas samples of 1 ml from the headspace of the flasks were taken at 0, 1, and 7 days and analyzed for N_2O concentration using a gas chromatograph (Agilent 7890 GC USA) equipped with a ^{63}Ni-electron capture detector operating with a column.

The N_2O emission potential from nitrification was estimated from the difference in headspace N_2O concentration between flasks without C_2H_2 and those with 10 Pa C_2H_2. The N_2O emission potential evolved by denitrification was estimated from the headspace N_2O concentration in the flasks with C_2H_2 at 10 Pa. The N_2 emission potential evolved by denitrification was estimated by the headspace N_2O concentration difference between the flasks with C_2H_2 at 10 KPa and those with C_2H_2 at 10 Pa. The 10 k Pa C_2H_2 concentration inhibits the reduction of N_2O to N_2 (Klemedtsson et al. 1988; Webster and Hopkins 1996).

2.5 Statistical analysis

For the controlled experiment, the statistical significance of the effects of mowing, topography, and their interaction on all data was tested with a two-way SAS ANOVA analysis (SAS Institute, version 9). Significant differences were tested using Duncan's multiple-range test at the level of 0.05.

3 Results

3.1 Soil properties

Soil moisture content varied from 7 to 10% (*w*/*w*) (Table 2). Soil moisture content was significantly lower with mowing than non-mowing treatment ($P < 0.01$), and significantly lower on the slope than on the flat ($P = 0.04$), but there was no interaction effect between mowing treatments and topography ($P = 0.49$). Soil pH varied from 6.98 to 7.15, with no significant differences for treatment or topography (Tables 2 and 3).

The TN and TC content of soils were significantly lower (TN: $P = 0.01$; TC: $P < 0.01$) only with mowing rather than non-mowing treatment; there were no differences between flat and slope and no interaction effects between mowing treatments and topography (Tables 2 and 3).

The NH_4^+-N content showed no differences between the various conditions (Tables 2 and 3). However, the NO_3^--N content was significantly lower with mowing than non-mowing ($P = 0.04$), again with no difference between flat and slope. No interaction was observed between mowing treatments and topography for soil NO_3^--N (Tables 2 and 3).

3.2 Microbial functional genes

The *AOA*, *AOB*, and *narG* genes were significantly less abundant under mowing than non-mowing treatment (*AOA*: $P = 0.02$, *AOB*: $P < 0.01$, Fig. 1a, b), but none showed any difference between flat and slope (both $P > 0.05$). The *nosZ* gene abundance was not significantly affected by mowing or topography (data not shown).

3.3 N_2O production potential from nitrification and denitrification

The N_2O emission potential from nitrification (N_{N2O}) and denitrification (D_{N2O}) and nitrogen gas from denitrification (D_{N2}) were significantly lower under mowing than non-mowing treatment (N_{N2O}: $P < 0.01$, D_{N2O}: $P = 0.02$, D_{N2}: $P < 0.01$; Fig. 2); N_{N2O} and D_{N2} were also significantly lower on the slope than on the flat (N_{N2O}: $P = 0.03$, D_{N2}: $P = 0.01$), whereas D_{N2O} was only marginally lower on sloping than flat blocks (D_{N2O}: $P = 0.10$). No interaction effects were observed between mowing treatments and topography.

4 Discussion

Many studies have reported greater N_2O emission or emission potential in low sloping landscapes due to higher C and N substrates or soil water, but low sloping areas generally constitute a small percentage of the whole sloping pasture, while in medium or high sloping areas, usually N_2O emission was

Table 1 Enzymes encoded by functional genes measured in this study, and thermal conditions and primer sequences used in qPCR

Functional gene	Enzyme	Annealing time and temperature	Elongation time and temperature	Primer	Primer sequence	Reference
Bacterial amoA	Ammonia monooxygenase	55 °C, 30 s	72 °C, 45 s	amoA1F,	GGG GTT TCT ACT GGT GGT	Rotthauwe et al. 1997
				amoA2R	CCC CTC KGS AAA GCC TTC TTC	
Archaeal amoA	Ammonia monooxygenase	55 °C, 30 s	72 °C, 45 s	CrenamoA23F, CrenamoA616R	ATGG TCTGGCTWAGACG GCCATCCATCTGTA TGTCCA	Francis et al. 2005
narG[a]	Nitrate reductase	58 °C, 30 s	72 °C, 30 s	narGG-F,	TAY GTS GGG CAG GAR AAA CTG	López-Gutiérrez et al. 2004
				narGG-R	CGT AGA AGA AGC TGG TGC TGT T	
nosZ[b]	Nitrous oxide	60 °C, 30 s	72 °C, 30 s	nosZ2F,	CGC RAC GGC AAS AAG GTS MSS GT	Henry et al. 2006
	reductase			nosZ2R	CAK RTG CAK SGC RTG GCA GAA	

[a] Touch down starting at 63 °C temperature decrease of 1 °C per cycle for 6 cycles

[b] Touch down starting at 65 °C temperature decrease of 1 °C per cycle for 6 cycles

lower (Letica et al. 2006; Hoogendoorn et al. 2008; Zhong et al. 2016). Therefore, N_2O emission on sloping areas is generally lower than that on flat areas, because nutrition and water aggregates through rain runoff and water infiltration in medium or high slope areas cause lower soil fertility compared with flat areas. Our results were consistent with this: N_{N2O}, D_{N2O}, and D_{N2} were all lower in sloping compared with flat areas (Fig. 2), but in sloping areas, this was mainly caused by soil moisture. In our study, there were no differences between sloping and flat areas in C and N substrates or the abundance of key functional microbial groups; only soil moisture was significantly lower in sloping areas (Tables 2 and 3; Figs. 1 and 2), which suggested that soil moisture was the main factors affecting the N_2O-producing process. This is not surprising; in our result, the correlation analysis also showed that soil moisture had stronger correlation with the N_{N2O} or D_{N2O} compared with other soil factors or the abundance of key functional microbial groups (Table S1, Electronic Supplementary Material); since in the Inner Mongolian grasslands, N_2O production also has proved to be regulated mainly by changes in soil moisture (Bai et al. 2000; Zhong et al. 2014). In sloping areas, the soil has higher infiltration capacities with more sand and reduced water availability (Hook and Burke 2000), leading to a lower potential N_2O emission.

We found that mowing significantly decreased the abundance of key functional microbial groups responsible for nitrification and denitrification processes and decreased the N_{N2O} and D_{N2O} in soils, suggesting that mowing has significant effect on N_2O production. In humid-climate grassland, mowing can increase potential N_2O emissions due to fertilization following the mowing, or it can have a positive impact on plant and soil microbial species and number, increasing the rates of N and C cycling under relatively good soil moisture conditions (Patra et al. 2006; Keil et al. 2015). However, in semi-arid grassland, mowing may have a negative impact on plant diversity, as few species are able to bear such a degree of disturbance (Mariotte et al. 2013). It also leads to less input of

Table 2 Gravimetric soil moisture content, pH, TC, TN, NH_4^+-N, and NO_3^--Nin semiarid grassland. Values are means ± 1 s.e.m (*n*=3)

Treatments	Flat		Slope	
	Non-mowing	Mowing	Non-mowing	Mowing
Soil moisture (%)	9.75 ± 0.24	8.69 ± 0.18	9.36 ± 0.05	7.64 ± 0.14
pH	7.09 ± 0.13	7.05 ± 0.14	7.15 ± 0.15	6.98 ± 0.03
TC (g kg^{-1})	11.04 ± 0.56	8.92 ± 0.80	11.43 ± 0.69	8.95 ± 0.60
TN (g kg^{-1})	1.43 ± 0.06	1.21 ± 0.05	1.32 ± 0.08	1.13 ± 0.07
NH_4^+-N (mg kg^{-1})	13.06 ± 1.86	10.59 ± 0.66	11.20 ± 4.06	8.43 ± 0.59
NO_3^--N (mg kg^{-1})	6.45 ± 0.94	3.25 ± 0.40	5.33 ± 1.08	3.87 ± 1.17

Values are means ± 1 s.e.m. (*n* = 3)

Table 3 Results (*P* value) from two-way ANOVA for the effects of mowing treatments (M), topography (T), and their interaction (T × M) on soil moisture, pH, TC, TN, NH_4^+-N, and NO_3^--N in semiarid grassland. Values are means ± 1 s.e.m (*n*=3)

Factor	Soil moisture	pH	TC	TN	NH_4^+-N	NO_3^--N
M	*< 0.01*	0.42	*< 0.01*	*0.01*	0.28	*0.03*
T	*0.04*	0.95	0.76	0.19	0.40	0.80
T × M	0.49	0.65	0.79	0.91	0.95	0.38

Values are means ± 1 s.e.m. (*n* = 3)

labile C and N into the soil for roots and microorganisms, as a result of the removal of hay from plots (Han et al. 2012). Our study shows that mowing significantly decreases soil moisture, as well as TC, TN, and NO_3^--N concentration (Tables 2 and 3). All these soil factor changes caused the reduced abundance of genes *AOA*, *AOB*, and *narG* (Fig. 1) and thus lower levels of potential N_2O emission under mowing (Fig. 2).

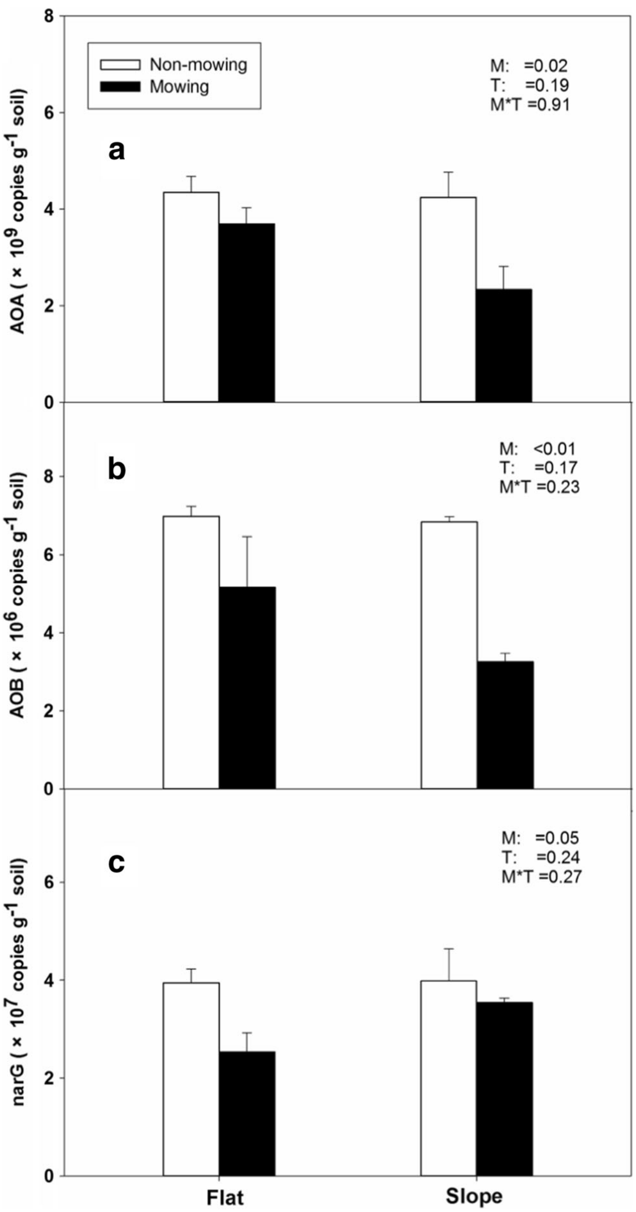

Fig. 1 Soil *AOA* (**a**), *AOB* (**b**), and *narG* (**c**) gene copies in semiarid grassland; *M* mowing treatment (non-mowing and mowing); *T* topography (flat and slope). Values are means ± 1 s.e.m. (*n* = 3)

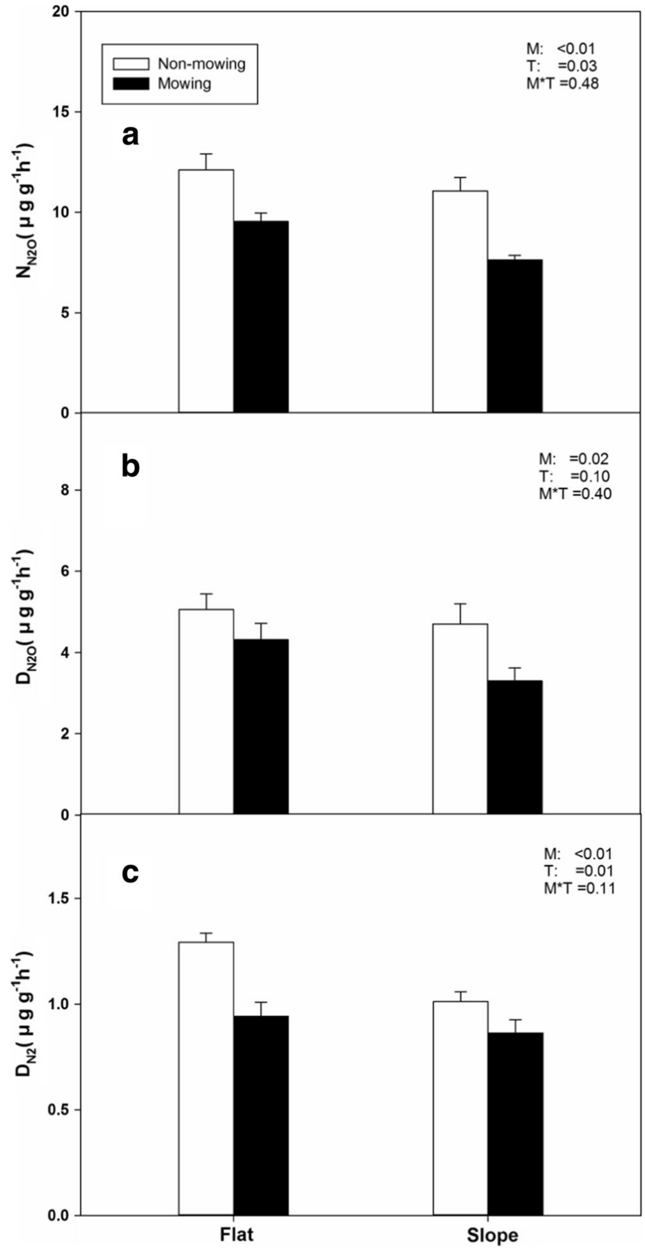

Fig. 2 Soil N_{N2O} (**a**), D_{N2O} (**b**), and D_{N2} (**c**) in mid-August 2014 in semiarid grassland. *M* mowing treatments (non-mowing and mowing); *T* topography (flat and slope). Values are means ± 1 s.e.m. (*n* = 3)

Management and topography are both relevant drivers of N_2O emission in grassland, confirming results from other management types (e.g., grazing, fertilization) (Han et al. 2012; Luo et al. 2013). However, our results did not show any conclusive evidence of interactive effects of mowing and topography on N_2O production potentials in the Inner Mongolian grassland (Fig. 2). The N_2O production potential showed the same trend in response to mowing on the slope as on the flat, but in sloping area, the response to mowing on N_2O production potentials appeared to be more sensitive to changes. This may be related to higher soil infiltration capacity in slope than in flat land (Hook and Burke 2000); on the other hand, high sensitivity of soil physio-chemical and biological properties to mowing is also related to the loss of soil nutrients with mowing that results in lower C and N cycling rates (Zhong et al. 2016). Our study also showed greater reduction in soil moisture and gene abundance of *AOA* and *AOB* under mowing on sloping land (Table 2 and Fig. 1). The high sensitivity of soil moisture and microbial function genes' response to mowing in sloping areas caused a greater reduction in potential N_2O production in these areas.

However, *narG* gene abundance shows a different trend under mowing from that of D_{N2O} on the flat and on the slope (Fig. 1c and Fig. 2c). Two possible reasons may help explain the different trend between *narG* gene abundance and D_{N2O} observed in this study: (1) gene abundance cannot provide information on real-time process rates since such rates are dependent on environmental conditions (Petersen et al. 2012); (2) soil NO_3^--N concentration is the substrate of *narG*; our result showed the gene abundance of *narG* had significant positive correlation with soil NO_3^--N but not with soil moisture (Table S1, Electronic Supplementary Material); it indicates that the abundance of *narG* is mainly affected by soil substrate concentration instead of soil moisture. The *nosZ* gene abundance shows no difference under any of the conditions, which is consistent with Zhong et al. (2014) and agrees with findings from grassland ecosystems (Chroňáková et al. 2009) in which soil was not strongly affected by environmental changes.

5 Conclusions

In conclusion, potential N_2O emission was significantly lower in sloping than in flat grassland chiefly because of the lower soil moisture in sloping areas. Mowing significantly decreases potential N_2O emissions, especially on slopes, and sloping grassland is more sensitive to human activities than flat. Our results suggest that estimating N_2O emission and choosing land management practices in semiarid grassland should consider topography.

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