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The increasing distribution area of zokor mounds weaken greenhouse gas uptakes by alpine meadows in the Qinghai–Tibetan Plateau

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ABSTRACT

The population of the plateau zokor (*Myospalax fontanierii*) rapidly increases on the degraded alpine meadows of Qinghai–Tibetan Plateau. The burrowing and feeding activities of plateau zokor exert huge effects on the plant community and soil properties. However, the possible effects on the production and consumption of greenhouse gases have not been investigated. To evaluate the effects, we measured the ecosystem respiration (Re), soil methane (CH_4) and nitrous oxide (N_2O) fluxes and the main soil, vegetation and environmental factors of zokor mounds of different excavation years (one-, two- and three to five-year, hereafter referred to as ZM1, ZM2 and ZM3–5) and surrounding control meadow (CM) in a typical *Kobresia humilis* meadow from July to November 2012. The cumulative Re, CH_4 uptake and N_2O emissions were 1.82 ± 0.28, 2.83 ± 0.48, 3.13 ± 0.13 and 3.91 ± 0.27 ton C ha^{-1}, 1.55 ± 0.27, 1.33 ± 0.15, 1.20 ± 0.16 and 1.02 ± 0.25 kg C ha^{-1} and 0.23 ± 0.02, 0.10 ± 0.04, 0.08 ± 0.01 and 0.07 ± 0.02 kg N ha^{-1} for ZM1, ZM2, ZM3–5 and CM, respectively. The soil CH_4 uptake and N_2O emission were stimulated and the Re was inhibited for ZM1, ZM2 and ZM3–5 as compared to the CM. If the distribution area of zokor mounds increased from 2% to 6%, the combined CO_2-equivalent of CH_4 and N_2O exchanges strengthened 3.2 times. Furthermore, the composition of plant community altered; the plant biomass, topsoil organic carbon content, temperature and moisture decreased; and the topsoil gas permeability, inorganic nitrogen and dissolved organic carbon contents increased on zokor mounds as compared to the CM ($P < 0.05$). The recovery process of the vegetation and soil organic carbon pools of zokor mounds requires many years (>10 years). In view of the loss of soil organic carbon and the stimulation of N_2O emission, the increasing distribution area of zokor mounds weaken the function of alpine meadows on the Qinghai–Tibetan Plateau as a greenhouse gas sink.

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1. Introduction

Designated "the third pole" of the earth, the Qinghai–Tibetan Plateau occupies approximately 25% of the total country area in China and has a typical plateau continental climate (Hu et al., 2010). Alpine meadows are one of the main ecosystem types on the Qinghai–Tibetan Plateau which accounts for nearly 35% of the entire plateau (Zhang and Liu, 2003; Cao et al., 2008; Zheng et al., 2012). The dominant plant species of alpine meadows include *Kobresia humilis*, *Carex parva*, *Kobresia tibetica*, *Potentilla fruticosa* and *Kobresia pygmaea* (Li et al., 2004). Because of the vast expanse and high fragility to environmental disturbances, alpine meadows of the Qinghai–Tibetan Plateau are not only regarded as a sensitive trigger of climate change in the Asian monsoon region, but also show pronounced feedbacks to human activities and climate change (Du et al., 2010; Hu et al., 2010; Jiang et al., 2010).

Over the past decades, the degradation of alpine meadows has rapidly increased as a result of over-grazing and intensive farming activities (Zhou et al., 2005; Harris, 2010). Rodents profit from the degradation of alpine meadows by domestic livestock, since degraded meadows provide favorable ecological conditions for their rapid reproduction and expansion (Shi, 1983; Bian et al., 1994). Meanwhile, the increasing number of rodents further accelerates the degradation of overgrazed alpine meadows and hampers a

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rehabilitation of alpine meadow ecosystem even if the grazing pressure is reduced (Shi, 1983; Zhou et al., 2005; Harris, 2010). Therefore high rodent abundance is regarded as an indicator rather than a cause of alpine meadow degradation on the Qinghai–Tibetan Plateau (Harris, 2010).

Plateau zokors (*Myospalax fontanierii*) are blind, subterranean and herbivorous rodents on the Qinghai–Tibetan Plateau with an average density of 15 animals per hectare (ranging from 10 to 25 animals ha^{-1}) (Zhang and Liu, 2003). Plateau zokors forage on plant belowground biomass at a depth of 3–20 cm. The intensive burrowing activity brings fresh topsoil to the surface and results in bare mounds on the ground (Gettinger, 1984; Reichman and Smith, 1985; Zhang and Liu, 2003). It is obvious that the foraging and burrowing activities of plateau zokor have significant effects on the alpine ecosystem, changing in plant diversity (Yoshihara et al., 2010) and altering of soil physical properties (Wilkinson et al., 2009). Following the disturbance of the original vegetation, the bare zokor mounds provide space and surface light for the weeds which are preferred by plateau zokors but poisonous and non-palatable for livestock (McDonough, 1974; Hobbs and Hobbs, 1987; Hobbs et al., 1988; Zhang and Liu, 2003; Zhang et al., 2003). The mounds on the surface created by plateau zokors increase the availability of nitrogen and phosphorous on the bare soil due to feces deposition. Mixing of subsoil with topsoil alters the soil texture and water-holding capacity and often results in reduced soil moisture and organic matter of mound soils (Wang and Fan, 1987; Wang et al., 2000; Zhang and Liu, 2003; Li et al., 2009). After years of occupation, burrowing and mound-building activities will result in large and distinct areas of grassland, in which the ecosystem processes (e.g., vegetation succession) might proceed at different rates as compared to unoccupied areas (Zhang et al., 2003).

Previous studies show that the alpine meadows of the Qinghai–Tibetan Plateau act as a sink for atmospheric methane (CH_4), and are weak source of nitrous oxide (N_2O) (Pei et al., 2003; Hirota et al., 2004; Cao et al., 2008; Du et al., 2008). The reported net ecosystem production (NEP) of alpine meadows is 1.21 ton C ha^{-1} yr^{-1} (Kato et al., 2006). Cao et al. (2008) observed that the alpine meadows on the Qinghai–Tibetan Plateau absorb approximately 1.62 kg C ha^{-1} yr^{-1} (CH_4). With regard to the N_2O, the work of Du et al. (2008) showed that *K. humilis* meadows emit approximately 1.88 kg N ha^{-1} yr^{-1}, with most emissions (57%) occurring in the growing season. The effects of excavation by plateau zokor on ecosystem respiration (Re), CH_4 uptake and N_2O emission have not yet been evaluated. Thus, the objectives of this study were to quantify the effects of the increased distribution area of zokor mounds on the Re, CH_4 uptake and N_2O emission in a typical *K. humilis* meadow. To identify major drivers of greenhouse gas exchange between the zokor mounds and the atmosphere, several soil and plant parameters were additionally monitored.

2. Materials and methods

2.1. Experimental site and field treatments

The experimental area (37°36′45″ N, 101°19′2″ E) was located on the south slope of a hill near the Haibei Alpine Meadow Ecosystem Research Station (HAMERS), in Qinghai, China. The vegetation of the experimental area (area: 80 ha, altitude: 3208–3259 m, slope: 9.4–11.1°) was covered by the *K. humilis* community, a herbaceous vegetation community with more than 40 species per square meter (Du et al., 2010). The dominant species were *K. humilis*, *Stipa aliena*, *Elymus nutans* and *Poa annua*. The companion species were *Stellera chamaejasme*, *Thermopsis lanceolata*, *Pedicularis kansuensis*, *Aster flaccidus*, *Gentiana aristata*, *Gentiana farreri*, *Gentianopsis paludosa*, *Gentiana straminea* and *Saussurea pulchra*. The soil of the *K. humilis* meadow was a Matti-Gryic Cambisol (Cao et al., 2008). The meadow has been used as a winter pasture since the 1960s. While grazing is not allowed in the period May to September, the stocking rate during daytime grazing from October to April is rather high with 0.9 yak and 5 Tibetan domestic sheep per hectare. The climate is typical plateau continental climate. The growing season typically begins in early May and ends in September (Li et al., 2004). The annual mean air temperature in this area was −1.3 °C from 1980 to 2012, with a maximum monthly mean of 12.5 °C in July and a minimum of −15.5 °C in January. From 1980 to 2012, the total annual precipitation varied from 325.6 to 850.4 mm, with a mean of 527.9 mm, of which 80% was concentrated during the growing season (data provided by the HAMERS of the Chinese Ecosystem Research Network).

The zokor mounds (2200–2800 mounds per hectare) were categorized into three types (one-, two- and three to five-year zokor mounds) depending on the year of excavation. The one- and two-year zokor mounds were excavated in April 2012 and 2011, respectively. The experiment was carried out on the south slope of a hill with three types of zokor mounds (one-, two-, three to five-year zokor mounds, hereafter referred to as ZM1, ZM2 and ZM3–5, respectively) and a control meadow (hereafter referred to as CM) in 2012. A transect with four measuring positions at different altitudes was established along the slope. Each position contained one replicate for each type of zokor mounds and control meadow and therefore four replicates were set up (Fig. 1).

2.2. Gas flux measurements

Fluxes of Re, CH_4 and N_2O were measured manually twice per week between 9th July and 26th November 2012 using a vented static, opaque chamber-gas chromatograph measuring system (Yao et al., 2009; Liu et al., 2010). The chambers (length × width × height: 50 × 50 × 40 cm) were equipped with digital platinum resistance thermometers (JM624, accuracy: ±0.1 °C, Jinming Instrument Co., Ltd., Tianjin, China) to monitor the air temperature inside the chamber after closure and were covered with styrofoam (thickness: 3 cm) and waterproof cloth to mitigate the temperature increase inside the chambers caused by solar radiation. The chambers were fixed gas-tight on stainless steel pedestals (length × width: 50 × 50 cm), which extended 30 and 15 cm into the soil for ZM1 and for ZM2, ZM3–5 and CM, respectively. Gas was simultaneously sampled with plastic stopcock-syringes at all replicate plots between 08:00 and 10:00 a.m. The fluxes detected in this period were similar to the diurnal averages (Cao et al., 2008; Du et al., 2010). The carbon dioxide (CO_2), CH_4 and N_2O concentrations of gas samples were analyzed within eight hours with a gas chromatograph system

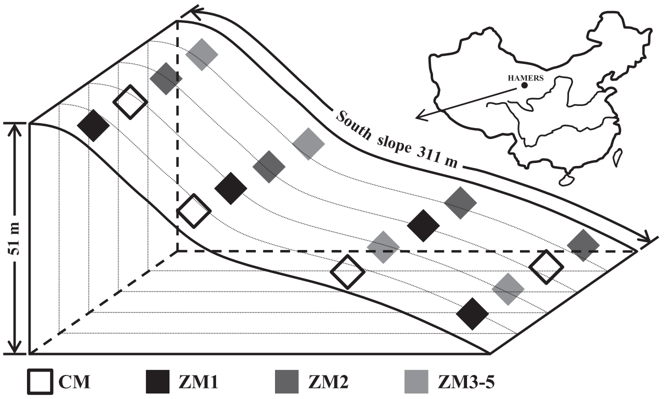

Fig. 1. The diagram of experimental design. The explanation of the legend codes is given in Table 1.

(GC, HP7890A, Agilent Technologies, Santa Clara, CA, USA) (Liu et al., 2012). No significant differences were detected in the CO_2, CH_4 and N_2O concentrations of gas samples stored in the plastic stopcock-syringes within 24 h. Calibration gas (485.5 ppm CO_2, 1.98 ppm CH_4 and 0.987 ppm N_2O in N_2, Beijing AP BAIF Gas Industry Co., Ltd., Beijing, China) was injected 3 times before and after 20 samples. The N_2O emissions from the no-fertilized alpine meadows are very weak (Du et al., 2010; Jiang et al., 2010). To decrease the detection limits of the measuring system and obtain enough valid fluxes, the sampling interval and chamber closure time were set to be 20 and 80 min, respectively. All fluxes were calculated from five concentrations of the gas sample based on a first order differential or linear equation and were temperature- and pressure-corrected (Liu et al., 2010, 2012). The non-linear calculation of fluxes could correct the suppression effects of gas accumulation on emissions inside the chambers. The detection limits of the CO_2, CH_4 and N_2O fluxes were estimated to be ± 0.9 mg C m^{-2} h^{-1}, ± 6.5 μg C m^{-2} h^{-1} and ± 2.5 μg N m^{-2} h^{-1} (within 68% confidence interval), respectively, for a chamber height of 40 cm, a chamber closure time of 80 min and a GC precision of 1.3 ppm, 10.0 ppb and 1.7 ppb for CO_2, CH_4 and N_2O, respectively.

2.3. Auxiliary measurements

Hourly meteorological data (air temperature, air pressure and precipitation) were obtained from the meteorological station at HAMERS (500 m distance from the experimental site). During gas sampling, the temperature of the chamber air and soil (5 cm depth) were simultaneously measured using digital thermometers (JM624). Topsoil moisture (0–6 cm depth) was manually measured daily. In case of frozen soil, soil moisture was determined gravimetrically, otherwise with a portable moisture probe (ML2x, ThetaKit, Delta-T Devices, Cambridge, UK). Water-filled pore space (WFPS) was calculated from volumetric water content and measured bulk density, using a theoretical particle density of 2.65 g cm^{-3}. At all gas sampling dates, topsoil samples (0–10 cm depth) from each type of zokor mounds and control meadow were taken and analyzed for soluble ammonium (NH_4^+), nitrate (NO_3^-) and dissolved organic carbon (DOC) contents. The soil was sieved (2 mm mesh), and 24.0 g of fresh soil was extracted with 100 ml of 1 M KCl-solution for inorganic nitrogen and de-ionized water for the DOC analysis (shaking for 1 h). The extracts for the DOC analysis were centrifuged for 20 min and filtrated with polyethersulfone membrane filters. The extracts were stored in 50 ml polyethylene terephthalate bottles at −18 °C for subsequent analysis with a continuous flow analyzer (San^{++} Continuous Flow Analyzer, Skalar Analytical B. V., the Netherlands). At the end of the growing season, aboveground biomass was collected by clipping the aboveground grass from three 50 × 50 cm replicates. It was oven-dried at 105 °C for 30 min and at 80 °C for 48 h, and then weighed. The soil organic carbon (SOC) and total nitrogen contents of soil profile (0–20, 20–40, 40–60, 60–80, 80–100 cm) were analyzed using the Potassium Dichromate Oxidation method and the Kjeldahl method after passing the soil through a 0.25 mm sieve. In addition, we measured the soil gas permeability of zokor mounds and control meadow three times in the field using an air permeability test system (PL-300, Eijkelkamp Agrisearch Equipment, The Netherlands).

2.4. Statistical analysis

The SPSS Statistics Client 16.0 (SPSS Inc., Chicago, USA) and Origin 8.0 (OriginLab Ltd., Guangzhou, China) software packages were used for the statistical data analysis. A general linear model for repeated measures was applied to analyze the significance of the differences in the Re, CH_4 and N_2O fluxes, soil temperature, WFPS, NH_4^+, NO_3^- and DOC contents between the zokor mounds and control meadow. Nonparametric tests of two independent samples (Mann–Whitney *U*-test) were used to analyze the differences in the aboveground biomass, soil texture, SOC, total nitrogen, bulk density and gas permeability between the zokor mounds and control meadow. Linear, non-linear or stepwise regression was used to identify the key regulators and describe the correlations between the environmental factors and fluxes.

3. Results

3.1. Meteorology, vegetation and soil

The daily mean air temperature (1.5 m) varied between −19.7 and 14.8 °C, with a mean of 3.3 °C. The soil temperature (5 cm depth) ranged from −8.9 to 18.2 °C and showed similar seasonal patterns for all types of zokor mounds and control meadow (Fig. 2a). The average soil temperature for the CM was higher than for the zokor mounds, particularly ZM1 and ZM2 ($P < 0.05$, Table 1). The total precipitation was 271.5 mm, of which 94% (253.9 mm) fell between July and September. The dynamic patterns of soil WFPS (0–6 cm depth) were regulated by precipitation (Fig. 2b). After strong or successive rain events between July and September, the soil WFPS of all types of zokor mounds and control meadow rapidly increased. The soil WFPS for the different types of zokor mounds were constantly low (<35%) from October to November because of the sparse precipitation. The mean soil WFPS for the CM was significantly higher than for ZM1, ZM2 or ZM3–5 ($P < 0.01$, Table 1).

The flora of zokor mounds clearly differed from the surrounding alpine meadow. Both the species diversity and plant biomass were reduced on zokor mounds as compared to the CM (Table 1). Because of the excavation and feeding activities of plateau zokor, there was almost no vegetation on ZM1. The dominant plant species on ZM2 and ZM3–5 were dicotyledons such as *Potentilla anserina*, *Elsholtzia densa*, *Lancea tibetica* and *Ajania tenuifolia*. In contrast, the gramineous herbages were more abundant for the CM. The aboveground biomass of ZM2 and ZM3–5 was only 14 and 58% of that for CM, respectively (Table 1).

No significant differences in pH, soil texture and total nitrogen content were detected between the zokor mounds and control meadow (Table 1). The topsoil (0–20 cm) SOC contents for the zokor mounds tended to be lower than for the CM, particularly in case of ZM2 ($P < 0.05$). However, the subsoil (20–40 cm) SOC

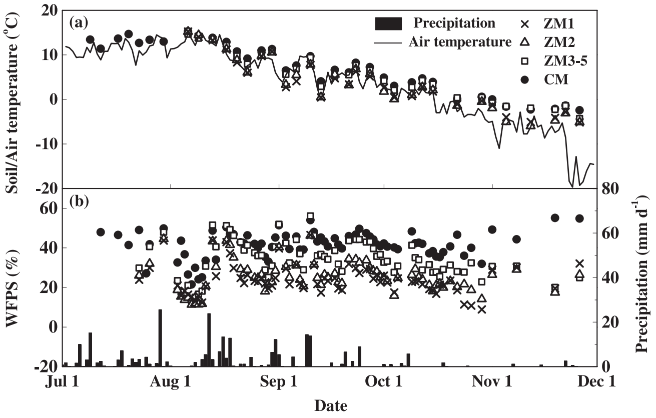

Fig. 2. (a) Air and soil temperature (5 cm depth), (b) water-filled pore spaces (WFPS; 0–6 cm depth) and daily precipitation during the experimental period. Each temperature or moisture data point is the average of four replicate observations, with standard errors not shown for figure clearance. The explanation of the legend codes is given in Table 1. The legend applies to both panels.

Table 1
The main characteristics of the zokor mounds and control meadow.

	ZM1[a]	ZM2	ZM3–5	CM
DPS[b]	Bare soil	*Potentilla anserina*, *Elsholtzia densa*	*Lancea tibetica*, *Ajania tenuifolia*	*Kobresia humilis* *Stipa aliena*, *Elymus nutans*
AB[c]	0^{A} (0.0)	41.5^{B} (0.7)	169.1^{C} (4.8)	293.3^{D} (21.1)
Texture[d]				
Sand	52.3 (2.1)	54.7 (2.8)	58.6 (5.0)	55.4 (3.5)
Silt	33.5 (1.0)	31.6 (1.7)	29.1 (2.9)	31.7 (2.0)
Clay	14.2 (1.2)	13.7 (1.4)	12.3 (2.2)	12.9 (1.6)
SOC[e]				
0–20 cm	6.6^{AB} (0.6)	5.8^{A} (0.9)	6.6^{AB} (1.3)	7.9^{B} (0.4)
20–40 cm	5.1^{A} (0.6)	3.8^{B} (0.4)	4.6^{AB} (1.2)	3.8^{B} (0.4)
40–60 cm	2.8 (0.4)	3.0 (0.8)	2.6 (0.7)	2.6 (0.7)
60–80 cm	1.8 (0.7)	1.9 (0.7)	2.4 (0.4)	1.9 (0.9)
80–100 cm	1.8^{AB} (0.5)	1.9^{A} (0.1)	1.2^{B} (0.2)	1.9^{A} (0.1)
TN[f]				
0–20 cm	0.60 (0.06)	0.61 (0.08)	0.59 (0.10)	0.68 (0.04)
20–40 cm	0.50 (0.06)	0.42 (0.04)	0.43 (0.09)	0.39 (0.04)
40–60 cm	0.29 (0.04)	0.29 (0.07)	0.26 (0.07)	0.26 (0.06)
60–80 cm	0.19 (0.07)	0.19 (0.07)	0.24 (0.03)	0.19 (0.09)
80–100 cm	0.18^{AB} (0.05)	0.19^{A} (0.001)	0.12^{B} (0.02)	0.19^{A} (0.01)
pH[g]	7.7 (0.4)	7.7 (0.4)	7.7 (0.4)	7.7 (0.4)
BD[h]	0.69^{A} (0.01)	0.81^{AB} (0.02)	0.90^{B} (0.06)	0.74^{AB} (0.04)
GP[i]	22.6^{A} (0.7)	19.9^{A} (0.7)	6.0^{B} (0.5)	1.4^{C} (0.2)
ST[j]	3.7^{A} (0.1)	3.7^{A} (0.1)	5.1^{AB} (0.1)	5.7^{B} (0.1)
WFPS[k]	24.1^{A} (0.9)	25.5^{A} (0.9)	34.0^{B} (1.1)	41.5^{C} (0.8)
NH_4^+[l]	4.3^{A} (0.1)	2.8^{B} (0.04)	2.4^{C} (0.04)	4.1^{A} (0.1)
NO_3^-	43.6^{A} (0.6)	19.0^{B} (0.3)	5.5^{C} (0.1)	2.2^{C} (0.1)
DOC	88.6^{A} (0.9)	77.1^{B} (0.7)	62.3^{C} (0.4)	69.8^{D} (0.9)

[a] ZM1, ZM2, ZM3–5 and CM: one-, two-, three to five-year zokor mounds and the control meadow.
[b] DPS: dominant plant species.
[c] AB: aboveground biomass (g dry matter m^{-2}).
[d] Sand, silt and clay: sand (0.02–2 mm), silt (0.002–0.02 mm) and clay (<0.002 mm) contents of the topsoil (%, 0–20 cm).
[e] SOC: soil organic carbon content (%).
[f] TN: total nitrogen content (%).
[g] pH: soil pH (0–10 cm).
[h] BD: bulk density (g cm^{-3}, 0–4 cm).
[i] GP: gas permeability (cm s^{-1}, 0–6 cm).
[j] ST: soil temperature (°C, 5 cm).
[k] WFPS: soil water-filled pore space (%, 0–6 cm).
[l] NH_4^+, NO_3^- and DOC: ammonium, nitrate and dissolved organic carbon contents of the soil (mg N kg^{-1} dry soil and mg C kg^{-1} dry soil, 0–10 cm). The values in parentheses indicate the standard error of three replicates. The different capital letter superscripts indicate significant differences at the level of $P < 0.05$.

contents obviously increased for ZM1 ($P < 0.05$) as compared to the CM. For the ZM2, the topsoil SOC content was significantly reduced by 27% as compared to the CM ($P < 0.05$), while the subsoil SOC content was similar. No significant differences in SOC of deeper layers (40–100 cm) were observed between the zokor mounds and control meadow. Both the total nitrogen and SOC contents decreased rapidly with the increase of soil depth. The topsoil (0–4 cm) bulk density for ZM1 was significantly lower than for ZM3–5 ($P < 0.05$). The topsoil (0–6 cm) gas permeability for the zokor mounds was obviously higher than for the CM. However, topsoil gas permeability tended to decrease with increasing age of zokor mounds (Table 1).

The soil NH_4^+ contents were constantly low (mainly <10 mg N kg^{-1} dry soil) and no significant seasonal pattern was detected for any zokor mounds or control meadow (Fig. 3a). The average soil NH_4^+ content for ZM1 was similar to that for the CM, but was significantly higher compared to that for ZM2 or ZM3–5 ($P < 0.01$). The soil NO_3^- contents varied from 0.1 to 141.7 mg N kg^{-1} dry soil. Highest values (>30 mg N kg^{-1} dry soil) were obtained for ZM1 and ZM2 in July and August (Fig. 3b). The mean NO_3^- contents for the zokor mounds were significantly higher than for the CM (Table 1). The soil DOC contents ranged from 28.5 to 173.1 mg C kg^{-1} dry soil, with no significant seasonal trend (Fig. 3c). The mean DOC contents significantly decreased with the increased age of the zokor mounds ($P < 0.05$, Table 1).

3.2. Re, CH_4 and N_2O fluxes

With the increase of aboveground biomass, the cumulative Re gradually increased from 1.82 ± 0.28 (mean ± s.e.) to 3.91 ± 0.27 ton C ha^{-1} for ZM1, ZM2, ZM3–5 and CM (Fig. 4b, Table 2). For all types of zokor mounds and control meadow, Re clearly decreased from July to November (Fig. 4a). Soil CH_4 uptake from the atmosphere was relatively high from July to mid of October and gradually declined thereafter (Fig. 4c). Heavy precipitation events significantly reduced CH_4 uptake for a few days during the period from July to mid-October. Though no significant difference in CH_4 uptake was detected between the zokor mounds and control meadow, the CH_4 uptake of zokor mound soil tended to be higher as compared to the soil of CM (Fig. 4d, Table 2). The cumulative CH_4 uptake for ZM1, ZM2 and ZM3–5 was 52, 30, 18% higher than for the CM, respectively (Table 2).

The N_2O fluxes ranged from −0.4 to 23.3 μg N m^{-2} h^{-1} and the negative values were within the threshold of the GC detection limit. All N_2O fluxes for the CM were <5.7 μg N m^{-2} h^{-1}, and no clear seasonal pattern could be observed. The N_2O emission was relatively high from July to August and constantly low (<5.9 μg N m^{-2} h^{-1}) from September to November for the zokor mounds (Fig. 4e). The cumulative N_2O emission was 0.23 ± 0.02 kg N ha^{-1} for ZM1, which was 3.3 times higher than for the CM ($P < 0.05$, Fig. 4f, Table 2).

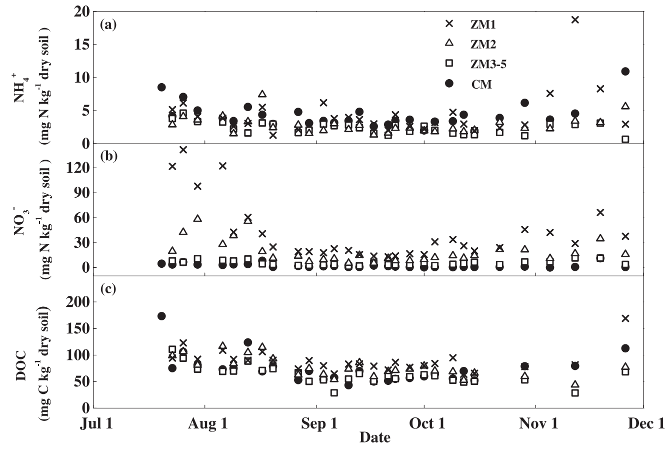

Fig. 3. (a) Ammonium (NH_4^+), (b) nitrate (NO_3^-) and (c) dissolved organic carbon (DOC) contents of the topsoil (0–10 cm depth). All data are the means of three replicates, with standard errors not shown for figure clearance. The frequency of DOC measurements was low in November, because of accidental sample loss. The explanation of the legend codes is given in Table 1. The legend applies to all subfigures.

3.3. *The effects of soil factors on the Re, CH_4 and N_2O fluxes*

Soil temperature was a major controlling factor for the seasonal variations of Re for all types of zokor mounds and control meadow. The correlations can be described by exponential models, in which the temperature sensitivity coefficient (Q_{10}) ranged from 2.9 to 5.5. Enhanced effects of DOC contents on Re were detected for ZM2, ZM3–5 and CM. Soil moisture, NH_4^+ and NO_3^- contents also selectively affected the fluctuations of the Re (Table 3). Soil WFPS significantly regulated the seasonal fluctuations of CH_4 fluxes for all types of zokor mounds and control meadow. An inhibiting effect of soil NH_4^+ contents on CH_4 uptake was observed for ZM2 (Table 3). Significant correlations between the N_2O emissions and soil temperature, NO_3^- and DOC contents were obtained for ZM1. The dependency of N_2O fluxes on soil temperature could be described by the Arrhenius equation with an apparent activation energy (E_a) of 67 kJ mol^{-1} and a Q_{10} of 2.8 for ZM1. Enhanced effects of soil WFPS, NH_4^+ and DOC contents on N_2O emissions were also observed for ZM3–5 and ZM2, respectively. Compared to the single factor analysis, the N_2O fluxes could be well described by the composite function of the Arrhenius and Michaelis–Menten equations for all observations when simultaneously accounting for the factors of soil temperature, WFPS and NO_3^- content. The fitted parameters of E_a and Q_{10} were estimated to be 21 kJ mol^{-1} and 1.3, respectively (Table 3). Furthermore, soil gas permeability (*GP*) and NO_3^- content (NO_3^-) significantly affected the cumulative CH_4 uptake (F_{CH_4}) and N_2O emissions (F_{N_2O}), respectively. These influences could be characterized by the following linear models:

$$F_{CH_4} = 0.02 \cdot GP + 1.02 \left(r^2 = 0.88, \quad n = 4, \quad P < 0.1\right) \tag{1}$$

$$F_{N_2O} = 0.004 \cdot NO_3^- + 0.05 \left(r^2 = 0.96, \ n = 4, \ P < 0.05\right) \tag{2}$$

4. Discussion

4.1. *The effects of zokor mounds on vegetation and soil*

In our study, plateau zokors not only fed on but also destroyed the plants above their mounds which resulted in the bare soil on the one-year zokor mounds. Even though the degraded vegetation

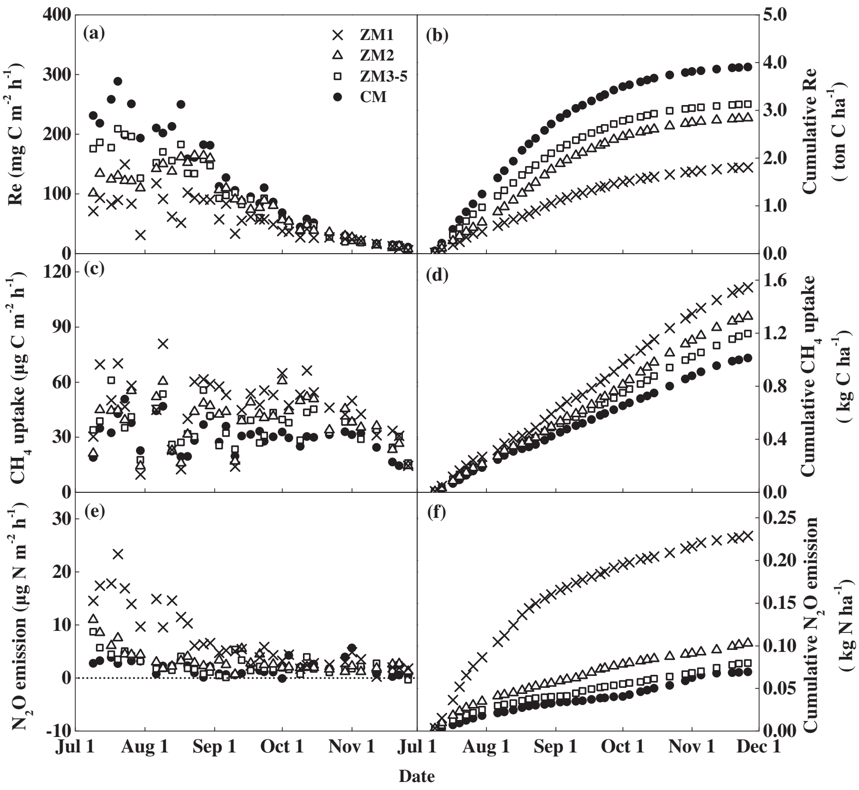

Fig. 4. (a, b) Daily mean and cumulative fluxes of ecosystem respiration (Re), (c, d) methane (CH_4) and (e, f) nitrous oxide (N_2O). Daily means are the average of four replicates, with standard errors not shown for figure clearance. The explanation of legend codes is given in Table 1. The legend applies to all subfigures.

Table 2

The minimum, maximum, balanced mean, averaged and cumulative ecosystem respiration (Re), methane (CH_4) uptake and nitrous oxide (N_2O) emissions for the zokor mounds and control meadow.

T[a]	Re					CH_4					N_2O				
	Min	Max	BM[b]	Ave	Cum[c]	Min	Max	BM	Ave	Cum	Min	Max	BM	Ave	Cum
	(mg C m^{-2} h^{-1})				(ton C ha^{-1})	(μg C m^{-2} h^{-1})				(kg C ha^{-1})	(μg N m^{-2} h^{-1})				(kg N ha^{-1})
ZM1	5.9	149.2	51.9 (1.1)	57.3 (5.7)	1.82^{A} (0.28)	9.7	80.9	39.6 (1.1)	46.5 (2.9)	1.55 (0.27)	0.3	23.3	5.3 (1.1)	7.4 (1.0)	0.23^{A} (0.02)
ZM2	7.7	164.3	63.5 (1.2)	88.6 (8.5)	2.83^{B} (0.48)	14.3	60.7	34.9 (1.1)	39.3 (2.1)	1.33 (0.15)	0.7	11.0	2.5 (1.1)	3.3 (0.4)	0.10^{B} (0.04)
ZM3–5	5.5	208.8	68.9 (1.2)	99.2 (10.9)	3.13^{B} (0.13)	15.9	61.0	31.9 (1.1)	35.6 (1.7)	1.20 (0.16)	−0.4	8.7	1.9 (1.1)	2.4 (0.3)	0.08^{B} (0.01)
CM	10.8	288.2	84.8 (1.2)	123.4 (14.2)	3.91^{B} (0.27)	14.4	50.8	25.1 (1.1)	30.0 (1.5)	1.02 (0.25)	−0.1	5.7	1.4 (1.1)	2.0 (0.2)	0.07^{B} (0.02)

[a] The definitions of the treatment codes are in the footnotes of Table 1.

[b] BM: the balanced mean which was calculated using the mean value of natural-logarithm-converted fluxes. The values in parentheses indicate standard error of four replicates.

[c] The different capital letter superscripts indicate significant differences at the level of $P < 0.05$.

began to recover on the two-year zokor mounds, the originally dominant perennial species (*K. humilis*, *S. aliena*, *E. nutans*, *P. annua*) were replaced by annual species (*P. anserina*, *E. densa*, *L. tibetica*, *A. tenuifolia*) due to the preference of plateau zokors. Thus, the abundance of forbs on zokor mounds was much higher than that of sedges or grasses. As for the vegetation recovery, both the plant biomass and composition of the plant community had not completely restored within five years in our experimental field. Zhang et al. (2003) also showed that the recovery process of vegetation on zokor mounds might take longer than 10 years.

The SOC contents of the top two layers of soil (0–20 and 20–40 cm) significantly reduced on the zokor mounds. Only for three to five-year old zokor mounds, could a trend towards recovery of original SOC contents be found. However, complete recovery of a degraded soil organic matter pool most likely required a very long period (>15 years) as Li et al. (2009) reported. The reduction in topsoil (0–20 cm) SOC contents on zokor mounds might be induced by three pathways: (a) the significant decrease in plant biomass which resulted in decreased carbon input into the soil; (b) the stimulation of organic carbon mineralization rate by improved

Table 3

The dependencies of Re, CH_4 and N_2O fluxes on soil temperature (*T*; 5 cm depth), soil water-filled pore space (*W*; 0–6 cm depth), and dissolved organic carbon (*DOC*) and inorganic nitrogen (NH_4^+, NO_3^-) substrate contents in the topsoil (0–10 cm depth).

Gas[a]	Method[b]	Factors[c]	T[d]	Equation[e]	n	r^2	P	Remarks[f]
Re	SF	*T*	ZM1	$F = \exp(24.5)\cdot\exp(-E_a/(R\cdot T_k))$; $F = 26.9\cdot\exp((\ln Q_{10}/10)\cdot T_c)$	29	0.63	<0.01	$E_a = 48$; $Q_{10} = 2.9$
	SF	*T*	ZM2	$F = \exp(27.3)\cdot\exp(-E_a/(R\cdot T_k))$; $F = 36.3\cdot\exp((\ln Q_{10}/10)\cdot T_c)$	29	0.73	<0.01	$E_a = 53$; $Q_{10} = 3.7$
	SF	*T*	ZM3–5	$F = \exp(35.3)\cdot\exp(-E_a/(R\cdot T_k))$; $F = 23.7\cdot\exp((\ln Q_{10}/10)\cdot T_c)$	29	0.86	<0.01	$E_a = 72$; $Q_{10} = 5.5$
	SF	*T*	CM	$F = \exp(40.9)\cdot\exp(-E_a/(R\cdot T_k))$; $F = 26.1\cdot\exp((\ln Q_{10}/10)\cdot T_c)$	36	0.92	<0.01	$E_a = 84$; $Q_{10} = 5.3$
	SF	*DOC*	ZM2	$F = 1.5\cdot DOC - 20.4$	25	0.35	<0.01	
	SF	*DOC*	ZM3–5	$F = 2.1\cdot DOC - 33.8$	25	0.43	<0.01	
	SF	*DOC*	CM	$F = 1.3\cdot DOC + 32.1$	26	0.21	<0.05	
	SF	NO_3^-	ZM1	$F = 0.4\cdot NO_3^- + 38.0$	28	0.19	<0.05	
	SF	NO_3^-	CM	$F = 14.0\cdot NO_3^- + 86.1$	29	0.20	<0.05	
	SF	NH_4^+	ZM3–5	$F = 33.8\cdot NH_4^+ + 11.6$	28	0.26	<0.01	
	SF	*W*	ZM3–5	$F = 250.5\cdot W + 2.3$	29	0.18	<0.05	
	MF	*T, W, DOC*	ZM3–5	$F = 2.2\cdot 10^6\cdot W\cdot DOC\cdot\exp(-E_a/(R\cdot T_k))$	22	0.32	<0.01	$E_a = 31$
	MF	*T, W, DOC*	CM	$F = 1.5\cdot 10^8\cdot W\cdot DOC\cdot\exp(-E_a/(R\cdot T_k))$	26	0.52	<0.01	$E_a = 41$
	MS	*T, DOC*, NO_3^-	CM	$F = 11.7\cdot T + 9.2\cdot NO_3^- + 0.5\cdot DOC - 19.1$	25	0.97	<0.01	
CH_4	SF	*W*	ZM1	$F = -113.3\cdot W + 77.3$	30	0.37	<0.01	
	SF	*W*	ZM2	$F = -83.2W + 63.3$	30	0.33	<0.01	
	SF	*W*	ZM3–5	$F = -41.2\cdot W + 49.6$	30	0.18	<0.05	
	SF	*W*	CM	$F = -89.4\cdot W + 70.4$	33	0.54	<0.01	
	SF	*T*	CM	$F = \exp(9.3)\cdot\exp(-E_a/(R\cdot T_k))$; $F = 24.7\cdot\exp((\ln Q_{10}/10)\cdot T_c)$	36	0.15	<0.05	$E_a = 14$; $Q_{10} = 1.2$
	SF	*DOC*	ZM1	$F = -0.3\cdot DOC + 76.9$	26	0.17	<0.05	
	SF	NH_4^+	ZM2	$F = -5.8\cdot NH_4^+ + 55.8$	29	0.31	<0.01	
	MS	*W, DOC*	ZM1	$F = -100.1\cdot W - 0.4\cdot DOC + 105.8$	22	0.58	<0.01	
	MS	*W*, NH_4^+	ZM2	$F = -77.8\cdot W - 4.5\cdot NH_4^+ + 75.1$	22	0.83	<0.01	
	MS	*T, W*	ZM3–5	$F = 1.0\cdot T - 65.6\cdot W + 53.3$	22	0.72	<0.01	
N_2O	SF	*DOC*	ZM1	$F = 0.2\cdot DOC - 13.0$	26	0.49	<0.01	
	SF	*DOC*	ZM2	$F = 0.03\cdot DOC + 0.7$	26	0.17	<0.05	
	SF	NO_3^-	ZM1	$F = 0.09\cdot NO_3^- + 2.4$	29	0.52	<0.01	
	SF	NH_4^+	ZM3–5	$F = 0.8\cdot NH_4^+ + 0.2$	29	0.26	<0.01	
	SF	*T*	ZM1	$F = \exp(30.1)\cdot\exp(-E_a/(R\cdot T_k))$; $F = 3.0\cdot\exp((\ln Q_{10}/10)\cdot T_c)$	29	0.80	<0.01	$E_a = 67$; $Q_{10} = 2.8$
	SF	*W*	ZM3–5	$F = 5.3\cdot\exp(-8.5\cdot W + 14.7\cdot W^2)$	30	0.21	<0.01	
	MF	*T, W, DOC*	ZM3–5	$F = 454.9\cdot W\cdot DOC/(23.7 + DOC)\cdot\exp(-E_a/(R\cdot T_k))$	22	0.13	<0.05	$E_a = 9.8$
	MF	*T, W*, NH_4^+	ZM3–5	$F = 21.7\cdot W\cdot NH_4^+/(1.6 + NH_4^+)\cdot\exp(-E_a/(R\cdot T_k))$	25	0.15	<0.05	$E_a = 2.1$
	MF	*T, W*, NO_3^-, *DOC*	ZM1	$F = 8.6\cdot 10^7\cdot W\cdot NO_3^-/(28.8 + NO_3^-)\cdot DOC/(112.3 + DOC)\cdot\exp(-E_a/(R\cdot T_k))$	20	0.65	<0.01	$E_a = 32$
	MF	*T, W*, NO_3^-	All	$F = 2.8\cdot 10^5\cdot W\cdot NO_3^-/(33.9 + NO_3^-)\cdot\exp(-E_a/(R\cdot T_k))$	104	0.34	<0.01	$E_a = 21$
				$F = \exp(0.02\cdot NO_3^- + 1.1\cdot W + 0.3)\cdot\exp((\ln Q_{10}/10)\cdot T_c)$		0.45		$Q_{10} = 1.3$

[a] The units of the Re, CH_4 and N_2O fluxes: mg C m^{-2} h^{-1}, μg C m^{-2} h^{-1} and μg N m^{-2} h^{-1}, respectively.

[b] SF, MF and MS: single factor, multiple factor and multiple stepwise regressions.

[c] The units for NH_4^+, NO_3^- and DOC: mg N kg^{-1} dry soil and mg C kg^{-1} dry soil.

[d] T: definitions of the treatment codes are in the footnotes of Table 1.

[e] T_k and T_c: soil temperature in Kelvin and centigrade, respectively; R: universal or molar gas constant (8.314 J mol^{-1} K^{-1}).

[f] E_a: apparent activation energy (kJ mol^{-1}). Q_{10}: temperature sensitivity coefficient.

soil aeration; (c) the mixing of topsoil with low SOC rich subsoil due to burrowing activity. The study of Kalbitz et al. (2000) showed that organic carbon mineralization was positively correlated to soil DOC contents. The significantly higher DOC contents on the one- and two-year zokor mounds indirectly showed the possibility of enhanced effects on organic carbon mineralization. Due to the opposite changes of topsoil and subsoil SOC contents for one-year zokor mounds and consistent changes for two-year zokor mounds (no SOC changes in the subsoil), the topsoil SOC loss of two-year zokor mounds can be used to quantify the soil organic pool degradation relative to the surrounding meadow. Zhang and Liu (2003) reported that the density of plateau zokor on the Qinghai–Tibetan Plateau ranged from 10 to 25 animals ha^{-1}. The average number of soil mounds created by each plateau zokor was 242 mounds yr^{-1}. The average soil mass of each zokor mound in the experimental region was approximately 4.23 kg dry soil (Wang et al., 1993). If the topsoil (0–20 cm) of zokor mounds loses 27% SOC after two years, as occurred in our case, the SOC loss rate was estimated to be 107.5–268.8 kg C ha^{-1} yr^{-1} (corresponding to 10 to 25 animals ha^{-1}). Therefore, the increasing distribution area of zokor mounds may exert a large and long-term effect on the SOC pool of alpine meadows on the Qinghai–Tibetan Plateau.

The topsoil bulk density of the one-year zokor mounds decreased due to the excavation activity, however, it gradually increased for older zokor mounds due to soil compaction caused by precipitation events and livestock trampling. The reductions of plant cover and aboveground biomass on zokor mounds enhanced soil heat loss by long-wave radiation, water infiltration and evapotranspiration. Therefore, soil temperature and moisture were significantly reduced on zokor mounds as compared to the surrounding alpine meadow. The decrease in soil moisture and possible improvement of pore spaces due to zokor excavation contributed to the significant increase of gas permeability on zokor mounds. The total nitrogen contents of topsoil tended to be lower in the zokor mounds than that in the surrounding meadow, which might have been induced by the reduction of plant nitrogen input. Plateau zokor excrement, the decomposition of dead plants, reduction of plant nitrogen absorption and possible stimulation of organic nitrogen mineralization collectively promoted soil inorganic nitrogen contents, particularly NO_3^- content, on zokor mounds.

4.2. The effects of zokor mounds on the Re, CH_4 and N_2O fluxes

Ecosystem respiration consists of plant autotrophic respiration and microbial heterotrophic respiration (Hu et al., 2008). Because there was no vegetation on ZM1, its ecosystem respiration was significantly lower as compared to the other sparse vegetated zokor mounds. The gradual increase of plant biomass and root exudates for ZM2, ZM3–5 and CM enhanced both plant autotrophic respiration and microbial heterotrophic respiration. Cumulative ecosystem respiration for ZM1, ZM2, ZM3–5 and CM gradually increased with increasing plant biomass. The seasonal variations of ecosystem respiration were driven by the soil temperature, which has been extensively reported as a primary controlling factor of ecosystem respiration (Fang and Moncrieff, 2001; Hu et al., 2008).

The CH_4 uptake by upland soil is a biological process governed by the availability of CH_4 and oxygen as well as the activity and quantity of methanotrophic bacteria in the soil profile (Liu et al., 2007). The improvements of soil gas permeability and aeration and the decrease of soil moisture on the zokor mounds facilitated the diffusion of atmospheric CH_4 and oxygen into the soil profile. The sufficient CH_4 and oxygen substrates for methanotrophic bacteria in zokor mounds enhanced atmospheric CH_4 uptake. In addition, the grasses in the alpine meadows are cold-tolerant mesophytes with well-developed aerenchyma, which facilitate the aerobic methane emission by plants. Cao et al. (2008) reported a strong methane emission at the rate of 19.7 ± 1.3 μg C m^{-2} h^{-1} for the grass community in the *K. humilis* meadow, which accounted for more than 50% of the bare soil uptake rate (38.1 μg C m^{-2} h^{-1}). Thus, the absence or weakness of plant CH_4 emissions on zokor mounds might also have contributed to the observed higher CH_4 uptake.

The improvements of soil aeration and gas permeability on zokor mounds enhanced the microbial nitrification, which might be the major process to produce N_2O in alpine meadows (Neff et al., 1994). The soil inorganic nitrogen content is considered a possible indicator of nitrification and denitrification rates, provided that soil temperature and moisture are no limiting factors (Ludwig et al., 2001). The significantly higher soil inorganic nitrogen and DOC contents possibly indicated higher nitrification and denitrification rates, which caused the obviously higher N_2O emissions on the zokor mounds. In our study, the observed N_2O fluxes in *K. humilis* meadow were much lower than previous results with average value 2.0 versus 19.1 μg N m^{-2} h^{-1} in the growing season (Du et al., 2008). For the previous studies, the samples were analyzed by the GC with an electron capture detector using nitrogen as the carrier gas. However, Zheng et al. (2008) reported a significant overestimation by using nitrogen as the carrier gas, especially at low concentrations, due to the positive correlation between CO_2 and the apparent N_2O concentrations in air samples.

If we consider the averaged fluxes from July to September and from October to November as the mean fluxes for the growing and dormant season, respectively, the annual cumulative CH_4 and N_2O exchanges were estimated to be −4.01 ± 0.07 and −2.53 ± 0.06 kg C ha^{-1} yr^{-1}, and 0.50 ± 0.01 and 0.18 ± 0.01 kg N ha^{-1} yr^{-1} for ZM1 and CM. The aggregate CO_2-equivalent of CH_4 and N_2O exchanges for ZM1 and CM corresponded to be 101.7 and −1.3 kg CO_2-equivalent ha^{-1} yr^{-1} using a global warming potential of 25 and 298 CO_2-equivalents for CH_4 and N_2O on the 100-year time horizon, respectively (Forster et al., 2007). If the distribution area of zokor mounds increased from 2% to 6% of total area (corresponding to 10 to 25 animals ha^{-1}), the CO_2-equivalent of CH_4 and N_2O exchanges by the alpine meadows changed from 1.1 to 4.6 kg CO_2-equivalent ha^{-1} yr^{-1}. In addition, the grazed alpine meadows normally uptake CO_2 (NEP: 2.9–7.1 ton CO_2 ha^{-1} yr^{-1}, Kato et al., 2006) without the consideration of aboveground biomass removal by livestock. However, the feeding and burrowing activities of plateau zokor destroyed the vegetation on the one-year zokor mounds and therefore the zokor mounds functioned as a strong CO_2 source (the cumulative emission was 6.7 ton CO_2 ha^{-1} from July to November). Obviously, the increased zokor population and mound area can rapidly weaken the function of alpine meadows as a greenhouse gas sink.

5. Conclusion

We investigated the ecosystem respiration, CH_4 uptake, N_2O emission and main soil, vegetation and environmental factors of plateau zokor mounds of different age in a typical *K. humilis* meadow on the Qinghai–Tibetan Plateau. Compared to the surrounding meadow, the vegetation composition changed and the ecosystem respiration, plant biomass, topsoil organic carbon content, temperature and moisture decreased and the CH_4 uptake, N_2O emission, topsoil gas permeability, inorganic nitrogen and dissolved organic carbon contents increased on the zokor mounds. The reduction of ecosystem respiration was primarily due to the weak autotrophic respiration of devastated vegetation on the zokor mounds. The enhanced CH_4 uptake and N_2O emission resulted from high gas permeability, the absence or weakness of plant CH_4

emissions, sufficient inorganic nitrogen and dissolved organic carbon supplies caused by the burrowing and feeding activities of the plateau zokor. The degradation of alpine meadows induced by overstocking provided favorable conditions for the rapid reproduction of plateau zokor. The enlarged area of zokor mounds decreased the greenhouse gas uptakes and resulted in the loss of soil organic carbon in the alpine meadows. Therefore, the intensive control of plateau zokor population by reducing the grazing intensity and the applications of rodenticide and mousetrap should be beneficial to the recovery of soil organic carbon and greenhouse gas uptakes by the alpine meadows on the Qinghai–Tibetan Plateau.

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