

Greenhouse gas emissions as influenced by wetland vegetation degradation along a moisture gradient on the eastern Qinghai-Tibet Plateau of North-West China

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Abstract Vegetation loss and plant diversity decline in wetlands affect carbon and nitrogen cycling and consequently influence gas fluxes. Although extensive grazing by livestock and climate change have caused significant physical degradation of wetlands on the Qinghai-Tibet Plateau (QTP), and created a clear drainage gradient, the impact on greenhouse gas (GHG) emissions associated with this change has rarely been reported. A 3-year study (2013–2015) was conducted to examine the effect of vegetation change and seasonality on ecosystem respiration, methane (CH₄) and nitrous oxide (N₂O) fluxes in four classes of wetlands with distinct magnitudes of vegetation degradation: healthy vegetation (HV), slightly degraded (SD), moderately degraded, and heavily degraded (HD). We used the dark static chamber-chromatography method to measure the gas fluxes. Highly degraded wetlands were larger C and GHG

sources than HV, despite lower methane emissions, due to the loss of gross primary production. SD and HD exhibited the highest cumulative mean annual ecosystem respiration and N₂O emissions, respectively. Ecosystem respiration and CH₄ fluxes were much higher during the growing seasons than in the non-growing seasons. Ecosystem respiration and N₂O fluxes were positively correlated with soil and air temperatures. This points at a potential effect of global warming on GHG emissions from the QTP wetlands. Top soil (0–20 cm) moisture content significantly correlated positively with CH₄ fluxes. Vegetation loss led to a reduced C uptake and increased global warming potential. Therefore, we recommend soil conservation measures and reduced livestock grazing in the wetlands in order to conserve their role as carbon sinks.

Keywords Climate change · Wetland vegetation degradation · Plant diversity decline · Greenhouse gas · Atmosphere

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Introduction

Wetlands are very important ecosystems with ideal conditions for capturing and storing carbon from the atmosphere (Mitsch et al. 2013). One-third of the global soil carbon pool is stored in wetlands (Khatri 2014). Although wetlands occupy less than 10% of the

global land surface (Khatri 2014), they provide diverse beneficial services. One significant function of wetlands is climate change mitigation through the regulation of atmospheric concentrations of carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) (Song et al. 2009). Alpine wetland meadows exhibit high carbon sequestration potential due to high soil organic content and low decomposition (Zhao et al. 2010). However, increased temperature and intensified livestock grazing have caused widespread degradation of alpine wetlands (Gao and Li 2016; Wu et al. 2017), which may provide conditions to reverse this trend, leading to overall carbon loss.

The Qinghai Tibet Plateau (QTP) extends over 2.5 million km² and is the highest plateau in the world (Cao et al. 2004). Wetlands cover about 50,000 km² of the QTP (Zhao 1999). The QTP has received recognition worldwide due to its biodiversity and ecological significance. Specifically, the Gahai Lake Wetland which is located on the Zoige Plateau at the eastern edge of the QTP, covers an area of 5.78×10^4 ha and has been included in the Ramsar List of Wetlands of International Importance in early 2011 (Sun et al. 2014). However, almost all wetlands on the QTP are being used for livestock grazing (Hirota et al. 2005). Furthermore, in many areas of the Plateau, wetlands are experiencing large-scale degradation, shrinkage and transformation because of increasing threats from human activity and a highly variable climate (Hirota et al. 2005; Nie and Li, 2011). Wet meadows are ecosystems which are abundant on the QTP and account for 70% of the Gansu Gahai wetland Nature Reserve (Ma et al. 2015). They serve as valuable source of livestock feed due to their high nutrition levels (Gao and Li 2016). With the need to raise livestock to meet a surging population, there has been overgrazing on the QTP. Grazing intensity on the QTP increased from 82.3×10^4 sheep ha⁻¹ year⁻¹ in the 1950s to 306.7×10^4 sheep ha⁻¹ year⁻¹ in 2005, i.e., 64.4% higher than the theoretical grazing capacity of this ecosystem (Li et al. 2008), which resulted in significant vegetation loss (Gao and Li 2016). Overgrazing triggers degradation of wet meadows primarily through vegetation loss, which if not checked, is then exposed to rodent attack, erosion and freeze–thaw cycles, leading to complete denudation (Gao 2016). Overgrazing depletes grass root nutrient levels causing incomplete root development and premature seeds that lack the vigor to rejuvenate (Chen 2005). As reported

by Liu and Chen (2000), the QTP has also experienced a warming climate for over 30 years. Mean annual temperature increased at a rate of 0.16 °C per decade between 1955 and 1996 (Wu et al. 2017). This resulted in drier conditions and a shift from wet meadows to grassland meadows, followed by moderately degraded meadows and ultimately sandy meadows at severely deteriorating sites (Wu et al. 2017).

Little information is available on the effects of the magnitude of wetland vegetation degradation and season on the three most important greenhouse gases (GHGs) in North-West China. Previous studies on the QTP did not address the three GHGs and were mostly conducted during growing seasons (Hirota et al. 2005; Hu et al. 2010; Lin et al. 2015). Some continuous studies covering growing and non-growing seasons (Li et al. 2015) have been conducted in the QTP but these studies were not conducted in the wet meadows. Furthermore, in previous studies degraded wetlands were often considered as a single homogeneous entity. Wetland vegetation degradation, however, occurs slowly and undergoes several changes at various stages. Previous work in the wet meadows of the QTP categorized these wetlands into (1) healthy vegetation (HV), (2) slightly degraded vegetation (SD), (3) moderately degraded vegetation (MD), and (4) heavily degraded vegetation (HD) (Ma et al. 2015). Vegetation cover, plant species composition, soil water content (SWC), soil organic carbon (SOC), soil total and available nitrogen, and soil physical properties were the indicators used to classify wetland vegetation degradation. A similar approach was used by Gao et al. (2011) and Gao (2016). Furthermore, another study in the Maduo county on the QTP assessed the effectiveness of the indicators employed in classifying wetland degradation into four levels as above and concluded that vegetation cover and SWC were the most effective indicators though not perfect, especially in same wetland types (Gao et al. 2013). Wetlands at each magnitude of vegetation degradation exhibit distinct physico-chemical and biological properties. These physico-chemical and biological properties associated with each vegetation degradation class may also influence greenhouse gas fluxes.

The present study assessed the influence of the magnitude of wetland vegetation degradation on GHG fluxes and on temporal variations in the wet meadows of the eastern QTP. This study will provide preliminary data for large scale and long term modeling of

ecosystem-atmosphere gas exchange processes in the context of future climate and land use changes. The specific objectives of this study were: (1) to determine the annual, growing and non-growing season ecosystem respiration, CH₄ and N₂O fluxes in the classified wet meadows; (2) to assess the inter-annual and seasonal variations of ecosystem respiration, CH₄ and N₂O fluxes at various degradation stages; (3) to identify the controlling factors and mechanisms of GHG fluxes and their interactions at various stages of wetland vegetation degradation; and (4) to estimate the ecosystem carbon balance and global warming potential (GWP) of GHG fluxes in the wetlands.

Materials and methods

Study area description

The field experiment was conducted in Gansu Gahai Wetlands Nature Reserve (34°16'N, 102°26'E), located on the eastern Qinghai-Tibet Plateau (Fig. 1). The altitude of the Reserve is between 3430 and 4300 m above sea level. The Gahai Lake Wetland covers an area of 5.78×10^4 ha, with alpine lakes, peat lands and wet meadows accounting for 0.67×10^4 ha, 1.04×10^4 ha, and 4.07×10^4 ha, respectively (Ma et al. 2015). There is a difference in vegetation between the various stages of degradation in the wet meadows. The region is characterized by cold Qinghai-Tibetan climatic conditions. According to the Luqu weather data obtained from China Meteorological Data Sharing Service System (<http://data.cma.cn/data/weatherBk.html>), from 1981 to 2010, mean annual precipitation was 592.6 mm, with 80% occurring in the growing season (May–September) and only 20% occurring during the non-growing season (October–April). In the non-growing season, the climate is cold and the freezing period extends from October to April which inhibits plant growth and leads to withered vegetation. The annual average temperature is 2.9 °C, with the lowest monthly mean of – 8.5 °C in January and a highest monthly mean of 12.9 °C in July. Monthly temperature data of the Gahai station for 2013 and 2014 ranged between – 26.2 °C in February 2014 to 26.2 °C in September 2013 as indicated in online resource 1 (ESM 1). The soil type on the site is meadow soil with a sandy loam texture within the 0–20 cm and clayey in the

20–55 cm profile (Liu and Ma 1997). Details of the soil physico-chemical properties are summarized in Table 1.

In a previous study, we conducted a vegetation survey of the dominant species, species composition, aboveground biomass, height and coverage of community in this research area (Ma et al. 2015). Based on these data, four degradation grades were confirmed and their characteristics are summarized in Table 2. Soil samples in the categorized wetlands were simultaneously collected at the end of the growing season (late September 2013).

Experimental design

Four 10 × 10 m plots were randomly marked within each degradation category in April 2013. Within each plot four square boxes (length × width × height = 0.5 m × 0.5 m × 0.2 m) serving as collars to support the sampling chamber were inserted directly into the soil. The top 5 cm were left exposed above the soil surface and the collars were kept in place for the duration of the experiment. The four wetland vegetation degradation classes were continuously surveyed from May 2013 to September 2015. Gas flux measurements were conducted once per week during the growing seasons (May–September) and once per month during the non-growing seasons (October–April) with the exception of 2 winter months (January 2014 and February 2015) when samples were not collected due to extremely cold weather conditions.

Gas flux measurements

The static dark chamber and gas chromatography (GC) technique was used to measure ecosystem respiration, CH₄, and N₂O fluxes. The gas flux measurements were conducted in quadruplicate and the mean value was calculated and analyzed. During sampling, an open bottom stainless steel chamber (50 cm × 50 cm × 50 cm, equipped with two fans at the top powered by 12v batteries to mix the air inside the chamber) with a rubber seal strip pasted on the open bottom part and placed over the collar to ensure tightness. Air samples (five in total) were drawn from inside the chamber right after chamber closure (T₀) and every 10 min thereafter over a 40 min period using 100 ml gas-tight polypropylene syringes equipped with three-way stopcocks. The drawn

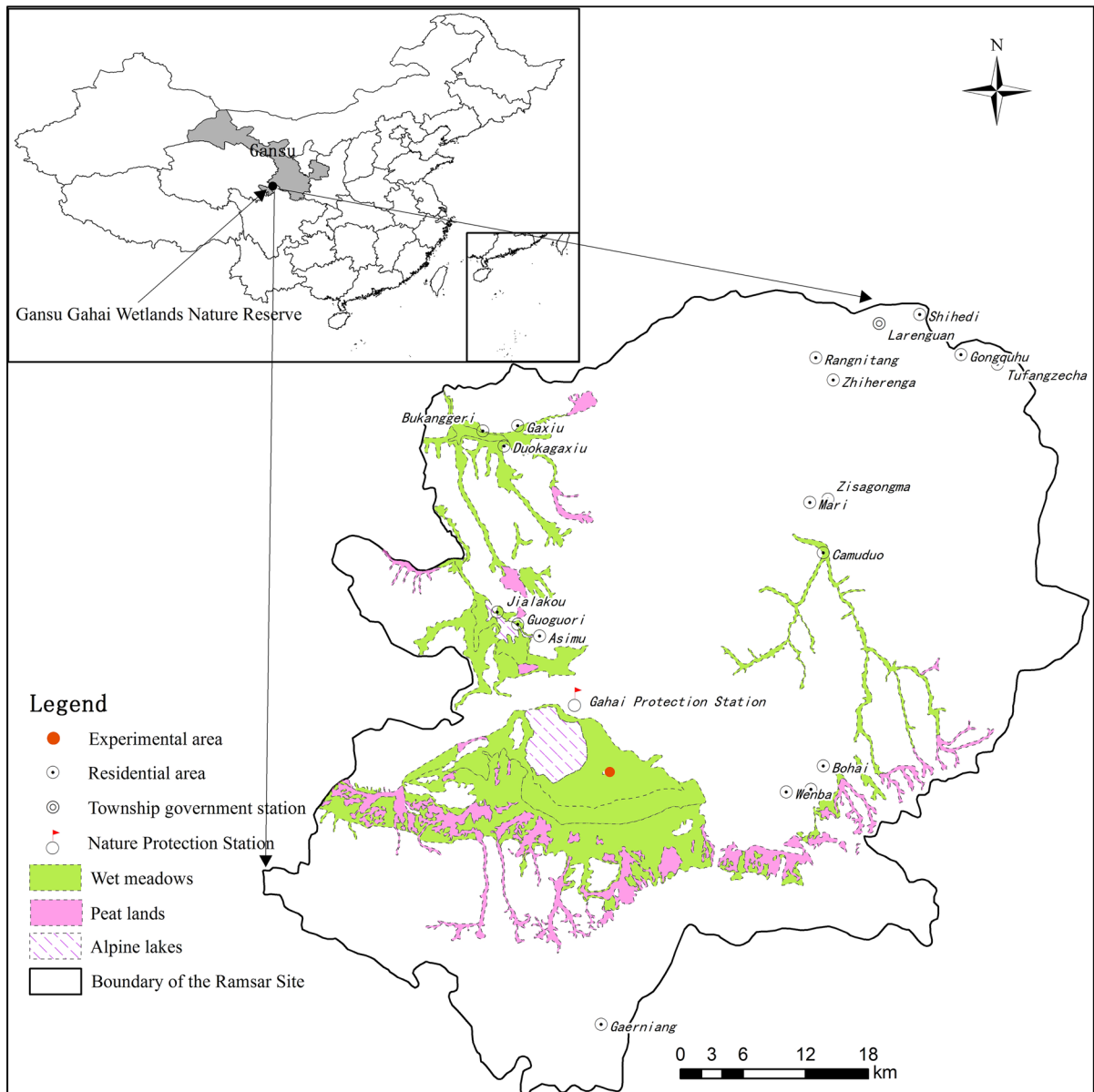


Fig. 1 Study site within the Gansu Gahai National Nature Reserve

sample was then injected into polyethylene coated aluminum bags via a rubber tube connected to the valve. Gas sampling usually occurred between 9 am and 12 pm. Fluxes measured within this period were found to be representative of the daily average flux on the plateau (Lin et al. 2009). Gas samples were immediately taken to the laboratory and analyzed within 3 days after sampling. A GC system (Agilent 4890D, Agilent Technologies, Wilmington, Delaware, USA) was used to measure the concentration of gases

in the air samples using the method described by Wang and Wang (2003). Details of the methods and description of the GC system can be found in online resource 2 (ESM2). The data was analyzed in Microsoft Excel (2007) and by conducting linear regression of the five or four sample concentrations against time. For Ecosystem respiration if correlation yielded an $r^2 \geq 0.80$ or $r^2 \geq 0.90$ for five and four samples respectively, then the slope (dC/dt) was used to calculate the flux, otherwise the sample results were

Table 1 Physicochemical properties of soil (0–60 cm depth) in the experimental sites

Plots ^a	pH	BD g cm ⁻³	SOM g kg ⁻¹	TN g kg ⁻¹	TP g kg ⁻¹	T K g kg ⁻¹	C/N
HV	7.92 ± 0.04	0.36 ± 0.01	65.82 ± 13.64	2.13 ± 1.01	1.48 ± 0.51	6.03 ± 0.41	17.11 ± 2.79
SD	7.79 ± 0.06	0.39 ± 0.02	65.45 ± 9.67	1.88 ± 0.66	1.29 ± 0.30	6.02 ± 0.44	20.69 ± 2.76
MD	7.77 ± 0.08	0.61 ± 0.05	54.39 ± 10.66	1.64 ± 0.92	1.17 ± 0.08	5.74 ± 0.26	19.66 ± 3.85
HD	7.76 ± 0.06	0.56 ± 0.03	53.63 ± 10.66	1.63 ± 0.63	1.15 ± 0.22	5.58 ± 0.42	17.49 ± 3.44

^aHV means wetland with healthy vegetation, SD means slightly degraded vegetation, MD means moderately degraded vegetation; and HD means heavily degraded vegetation. The values are presented as mean ± standard deviation. The same applies to the tables below. (BD bulk density, SOM soil organic matter, TN total nitrogen, TP total phosphorus, TK total potassium, C/N carbon nitrogen ratio)

Table 2 Aboveground biomass, dominant and associate plant species in the experimental sites

Plots	Dominant species	Coverage (%)	Height (cm)	Aboveground biomass (dry matter) (g m ⁻²)
HV	<i>Kobresia tibetica</i> + <i>Potentilla anserine</i> + <i>Poa annua</i>	96.25 ± 5.32	16.71 ± 2.98	355.90 ± 174.64
SD	<i>Carex</i> sp. + <i>Artemisia frigida</i> Willd. + <i>Oxy tropis</i> sp.	86.347.36	13.02 ± 2.24	293.02 ± 143.93
MD	<i>Artemisia sacrorum</i> .var. <i>messerschmidtiana</i> + <i>Kobresia capilifolia</i>	45.33 ± 13.34	7.43 ± 0.97	185.73 ± 134.90
HD	Only little <i>Artemisia frigida</i> Willd. and <i>Polygonum viviparum</i>			

rejected. For CH₄ and N₂O, all sample results were accepted because of the high variability but low value of CH₄ and N₂O flux rates. Fluxes were then computed using Eq. 1 (Song et al. 2009). The flux detectable limits were 0.062 mg m⁻² h⁻¹, 6.89 mg m⁻² h⁻¹ and 0.027 μg m⁻² h⁻¹ for CH₄, CO₂ and N₂O respectively.

$$F = \frac{dC}{dt} \cdot \frac{M}{V_0} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T} \cdot H \quad (1)$$

where dC/dt is the rate of concentration change; M is the molar mass; P is the atmospheric pressure of the sampling site; T is the thermodynamic temperature of air in the chamber at the sampling time; V_0 , P_0 , and T_0 are the molar volume, atmospheric pressure, and thermodynamic temperature under standard conditions, respectively; and H is the chamber height over the soil surface.

Measurements of environmental parameters

Chamber temperature and soil temperatures at 0, 5, 10 and 20 cm depths (T_{soil}) were measured with a portable digital thermometer (JM624, Jinming Instrument Co., Tianjing, China). Soil water content (SWC) at 10 cm depth was monitored using a soil moisture content analyzer (QS-SFY (RS232), Qiang Sheng

Manufacturing Center of Analysis Instruments, Beijing, China). Measurements were conducted concurrently with gas sampling. Additionally, ambient air temperature and precipitation data (logging interval: every 60 min) from 2013 to 2015 were taken from a local climate station located at the Nature Reserve.

Measurement of Aboveground net primary production (ANPP)

The aboveground plant biomass (APB) was measured at the end of September in 2013 and 2014. The plants in demarcated areas within the plots (0.5 m × 0.5 m) representing the four vegetation degradation categories were cut near the ground surface. All of the samples (in triplicate) were oven-dried to constant mass at 80 °C, and weighed. There were no grazing activities during the growing seasons, and therefore we considered APB in September 2013 and 2014 to be representative of ANPP (Zhu et al. 2015a, b).

Calculation of cumulative ecosystem respiration, CH₄ and N₂O fluxes

Based on measurements from May 2013 to September 2015 in both growing and non-growing seasons, we calculated annual/seasonal ecosystem respiration,

CH₄ and N₂O fluxes using Eq. 2 below. The average annual fluxes were calculated by using the data measured in 2013–2014 and 2014–2015 due to unavailable data for the non-growing season of 2015–2016.

$$\text{Sum} = \sum_{i=1}^n \left(\frac{F_i + F_{i+1}}{2} \right) \times 24 \times (D_{i+1} - D_i) \quad (2)$$

F_i and F_{i+1} denote ecosystem respiration, N₂O and CH₄ fluxes for previous and current day ($\text{mg m}^{-2} \text{h}^{-1}$) respectively; D_i and D_{i+1} are previous and current sampling days, respectively.

Calculation of ecosystem carbon fluxes and GWP

In order to obtain the net ecosystem fluxes, we used biomass measurements from September 2013 and 2014, the end of the growing season, and ecosystem respiration as well as CH₄ fluxes for growing and non-growing seasons to calculate net fluxes and the cumulative contribution to global warming. In alpine meadows, the proportion of ANPP/NPP (net primary production) was found to be 0.135 (Yang et al. 2010). Zhang et al. (2009) also found that ratio of NPP to gross primary production (GPP) was 0.54 in herbaceous plants. Tian et al. (2003) found that carbon content of herbaceous plants was 52.18% of the total biomass. Based on these references, we estimated the annual net flux of carbon ($F(C)$) using Eq. (3) (Sheng et al. 2015):

$$\begin{aligned} F(C) &= -F(\text{GPP}-C) + F(\text{CO}_2-C) + F(\text{CH}_4-C) \\ &= -F(\text{GPP}-C) + F(\text{CO}_2) \times \frac{12}{44} + F(\text{CH}_4) \times \frac{12}{16} \end{aligned} \quad (3)$$

where $-F(\text{GPP}-C)$ is the annual total amount of carbon absorbed by plants; $F(\text{CO}_2)$ is the total annual ecosystem respiration, $F(\text{CO}_2-C)$ is the carbon of $F(\text{CO}_2)$, $F(\text{CH}_4)$ is the total annual CH₄ emissions, and $F(\text{CH}_4-C)$ is the carbon of $F(\text{CH}_4)$.

In order to evaluate the GWP of carbon emissions and absorptions, CH₄ fluxes were converted to CO₂-equivalents using a GWP factor of 32 (100-year time horizon) as proposed by Neubauer and Magonigal (2015) and added to the respective ecosystem respiration values. It was assumed that N₂O fluxes were too low (Fig. 2c) to cause significant change to the

cumulative GWP in this study, and they were therefore ignored in its calculation. The annual CO₂equivalent flux (CO₂e) from the wetland was calculated using Eq. (4):

$$\begin{aligned} F(\text{CO}_2\text{e}) &= -F(\text{GPP}-\text{CO}_2) + F(\text{CO}_2) + F(\text{CH}_4-\text{CO}_2\text{e}) \\ &= -F(\text{GPP}-C) \times \frac{44}{12} + F(\text{CO}_2) + F(\text{CH}_4) \times 32 \end{aligned} \quad (4)$$

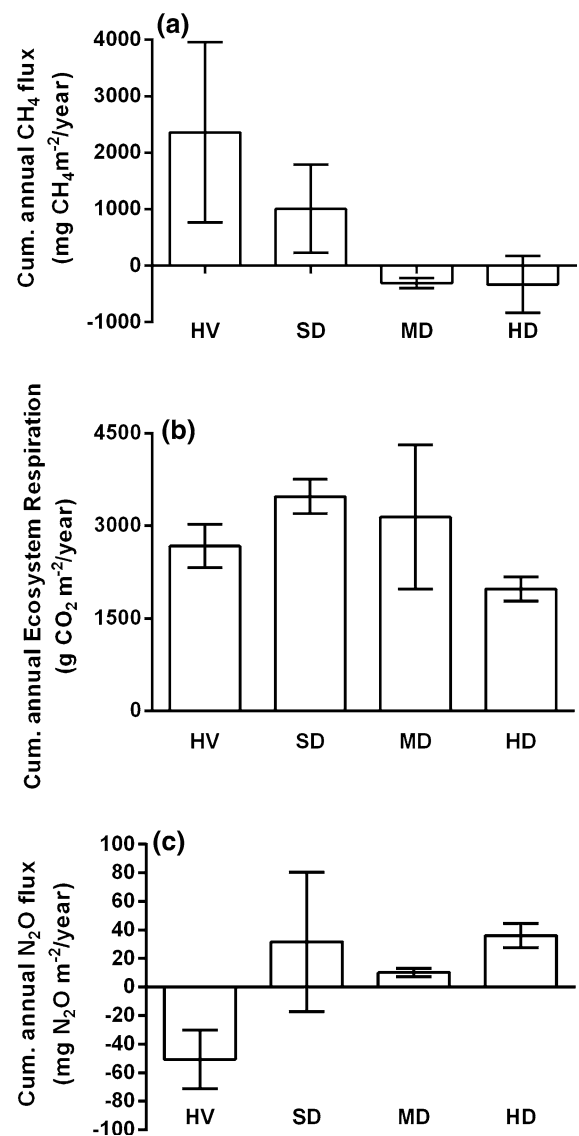


Fig. 2 Average annual cumulative fluxes of ecosystem respiration, CH₄ and N₂O in wetlands of different magnitudes of vegetation degradation

Statistical analysis

The Q_{10} function (Maier and Kress 2000) was also used to express the temperature sensitivity of ecosystem respiration (ER) as

$$ER = \alpha \exp(\beta T) \quad (5)$$

$$Q_{10} = \exp(10\beta) \quad (6)$$

where ER and T represent ecosystem respiration and soil temperature during the study period, respectively, and α and β denote fitting parameters.

One way analysis of variance (ANOVA) was employed to assess the variation of gas fluxes due to wetland vegetation degradation. All statistical analyses were conducted using SPSS version 22 for Windows 10. A further statistical test (the paired *t* test) was used to evaluate differences in annual gas budgets among the four wetland vegetation degradation classes. Duncan's multiple range test was used to determine differences between treatment means. A two-tailed Pearson correlation and regression analysis was used to identify significant correlations between environmental variables and CH_4 , N_2O fluxes and ecosystem respiration.

Results

GHG Fluxes across different magnitudes of vegetation degradation in the wetland

Different magnitudes of vegetation degradation in the wetland influenced GHG fluxes. Annually, the average CH_4 emission in HV was 2360.46 ± 1595.19 mg CH_4 m^{-2} $year^{-1}$ for the two complete years studied (2013–2014 and 2014–2015) (Fig. 2a), which was higher compared to the other degradation stages. SD also acted as a net source of CH_4 , however, it exhibited a significant reduction in emissions of up to 43% compared to HV (Fig. 2a) whilst MD and HD acted as net sinks of CH_4 (Fig. 2a). One-way ANOVA analyses showed that mean CH_4 fluxes in HV were significantly higher than those of MD and HD ($P < 0.05$) but not statistically different from SD (Table 3).

Ecosystem respiration varied significantly for all four wetland vegetation degradation classes during the 2 year study period (2013–2014 and 2014–2015) (Fig. 2b). HV respired 2676.14 ± 351.04 g

CO_2 m^{-2} , which was lower than SD (3475.41 ± 278.59 g CO_2 m^{-2} $year^{-1}$) and MD (3144.68 ± 1164.80 g CO_2 m^{-2} $year^{-1}$) (Fig. 2b). However, ecosystem respiration in HD (1981.39 ± 197.30 g CO_2 m^{-2} $year^{-1}$) was lower than HV. Annual average ecosystem respiration for all wetland vegetation degradation classes was 502.91 ± 378.66 mg CO_2 m^{-2} h^{-1} . Ecosystem respiration in the growing season months ranged from 280.48 to 1227.14 mg CO_2 m^{-2} h^{-1} , which was much higher than those in the non-growing season (Fig. 3).

For N_2O fluxes, HV served as a net sink of N_2O (-50.74 ± 20.53 mg N_2O m^{-2} $year^{-1}$) while SD, MD, and HD wetlands emitted 31.69 ± 48.85 mg N_2O m^{-2} $year^{-1}$, 10.3 ± 3.01 mg N_2O m^{-2} $year^{-1}$, and 36.04 ± 8.48 mg N_2O m^{-2} $year^{-1}$, respectively (Fig. 2c). However, for the growing seasons observed in this study, HV, SD, and HD served as sources of N_2O while MD acted as a weak sink (Table 3). Mean N_2O fluxes in the growing season among the four vegetation classes were not statistically different ($P > 0.05$). In the non-growing season, there was uptake of N_2O in HV (Fig. 3, Table 3) and therefore HV served as a net sink (Fig. 2c). SD, MD and HD acted as net sources of N_2O in the non-growing season.

Interannual changes of ecosystem respiration, CH_4 , and N_2O fluxes

During the test, the exchanges of CH_4 and N_2O between wetlands and the atmosphere and ecosystem respiration varied significantly year by year (Fig. 4). The annual fluxes of CH_4 , N_2O and ecosystem respiration for all four wetland vegetation degradation classes were higher in 2013 than in 2014 and 2015. The magnitude of annual flux varied so much that it even changed from sink to source; for example, the CH_4 flux for HD was negative in 2013–2014, but positive in 2014–2015; The SD wetland changed from an N_2O source to an N_2O sink releasing 66.23 ± 8.32 mg N_2O m^{-2} $year^{-1}$ in 2013–2014 but consuming 2.85 ± 6.72 mg N_2O m^{-2} $year^{-1}$ in 2014–2015 (Table 3).

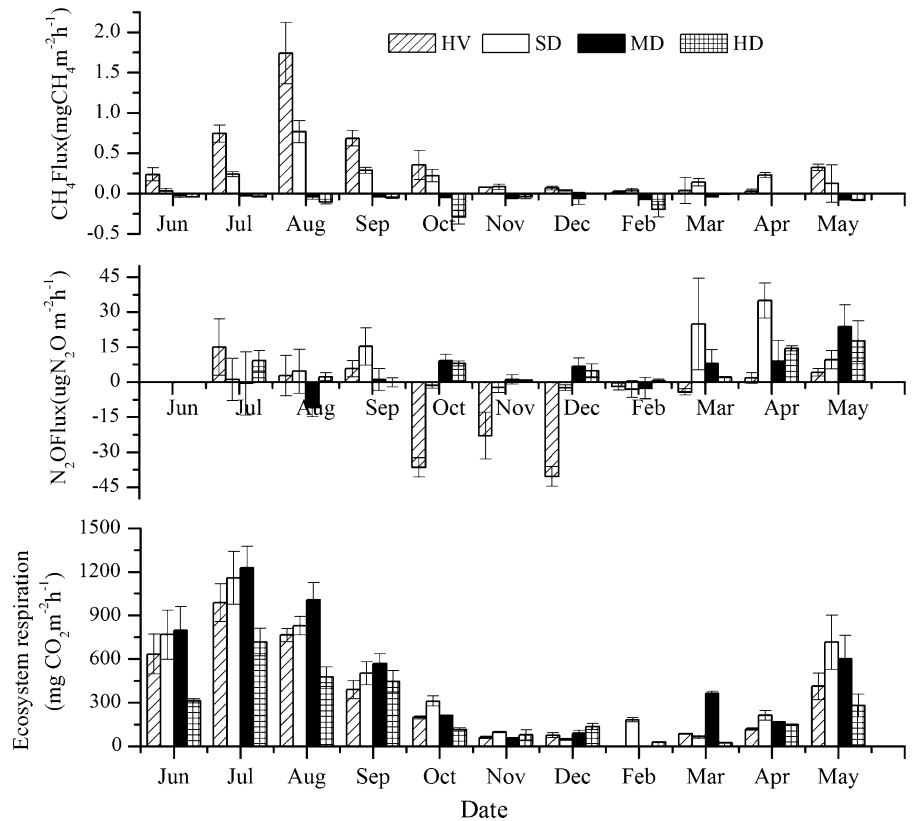
The fluxes from different years had a greater difference in the same season (Table 3). In the growing season, MD absorbed CH_4 in 2013, however, in 2014 and 2015, it emitted CH_4 . Similarly, HD had a negative CH_4 flux in 2013 but a positive CH_4 flux in 2014. The trend changed to negative again in 2015. In the non-

Table 3 Cumulative ecosystem respiration, CH₄, and N₂O fluxes from wetlands of different vegetation degradation during the non-growing and growing seasons in 2013–2015

Year	Treatment	Non-growing season (cumulative)			Growing season (cumulative)		
		CH ₄ (mg CH ₄ m ⁻²)	Ecosystem respiration (g CO ₂ m ⁻²)	N ₂ O (mg N ₂ O m ⁻²)	CH ₄ (mg CH ₄ m ⁻²)	CO ₂ (g CO ₂ m ⁻²)	N ₂ O (mg N ₂ O m ⁻²)
2013–2014	HV	464.07 ± 36.69	461.44 ± 198.31	- 88.60 ± 9.22	3024.36 ± 273.60	2462.92 ± 221.63	23.35 ± 1.27
	SD	372.17 ± 19.09	772.05 ± 135.94	42.79 ± 1.46	1187.27 ± 209.41	2900.35 ± 126.67	23.44 ± 5.95
	MD	- 239.90 ± 25.75	773.35 ± 179.28	26.42 ± 3.26	- 132.44 ± 21.74	3194.96 ± 266.39	- 13.95 ± 2.56
2014–2015	HD	- 467.97 ± 38.09	439.88 ± 156.32	25.79 ± 2.46	- 220.47 ± 23.45	1681.02 ± 108.28	16.24 ± 1.28
	HV	285.97 ± 259.98	411.49 ± 37.34	- 39.18 ± 55.40	946.52 ± 310.31	2016.42 ± 358.63	2.96 ± 1.62
	SD	171.06 ± 15.13	527.80 ± 48.45	1.12 ± 0.58	285.76 ± 143.06	2750.62 ± 266.06	- 3.97 ± 9.94
2015–2016	MD	- 284.08 ± 27.71	745.44 ± 153.28	8.47 ± 1.26	42.75 ± 5.96	1575.60 ± 105.69	- 0.26 ± 0.10
	HD	- 219.00 ± 16.68	410.36 ± 40.26	- 3.10 ± 0.56	247.77 ± 20.35	1431.52 ± 106.32	33.14 ± 2.25
	HV	-	-	-	267.98 ± 67.08	1068.56 ± 115.71	9.35 ± 0.94
2013–2016*	SD	-	-	-	239.43 ± 160.89	880.80 ± 34.48	6.69 ± 2.32
	MD	-	-	-	24.79 ± 5.78	1357.5 ± 125.71	- 0.38 ± 0.20
	HD	-	-	-	- 134.63 ± 10.68	1185.34 ± 89.63	1.16 ± 0.39
2013–2016*	HV	375.02 ± 89.05a	436.47 ± 24.97a	- 63.89 ± 24.71a	1412.95 ± 829.17a	1849.30 ± 411.09a	11.89 ± 6.02a
	CV(%)	33.58	8.09	54.69	101.64	38.50	87.72
	SD	271.62 ± 100.55a	649.92 ± 122.12a	21.95 ± 20.83b	570.82 ± 308.51a	2177.26 ± 649.66a	8.72 ± 7.97a
2013–2016*	CV(%)	52.35	26.57	134.21	93.61	51.68	158.49
	MD	- 216.90 ± 22.09b	759.40 ± 13.96b	17.44 ± 8.98a	- 21.63 ± 55.64b	2042.69 ± 579.56a	- 4.86 ± 4.54a
	CV(%)	14.40	2.06	72.76	445.58	49.14	161.93
2013–2016*	HD	- 343.40 ± 124.48b	425.12 ± 14.76a	11.34 ± 14.44 a	- 35.78 ± 143.92b	1432.63 ± 143.09a	16.84 ± 9.24 a
	CV(%)	51.27	4.91	180.16	699.70	17.30	95.01

Different letters within the same column indicate statistical differences in variable means among treatments over the 2013–2015 seasons by the Duncan's multiple range test ($P < 0.05$). Non-growing season gas emissions in 2015–2016 were not collected

Fig. 3 Monthly values of CH_4 and N_2O fluxes (mean \pm std) along wetland vegetation degradation gradient. Vertical bars represent standard deviation



growing season, HD emitted N_2O in 2013, but absorption N_2O in 2014. The magnitudes of flux changes were also significant: in the growing season, CH_4 flux from HV in 2013 was 3.2 and 11.3 times higher than in 2014 and 2015, respectively; in SD, fluxes of CH_4 in 2013 were 4.2 and 5 times higher than in 2014 and 2015, respectively. In MD, CH_4 fluxes were 3 and 5 times higher in 2013 than in 2014 and 2015 respectively while N_2O flux from MD in 2013 was more than 53 and 36 times the fluxes in 2014 and 2015, respectively. In the non-growing season, the change of magnitude of the flux by year was relatively small. CH_4 flux in 2013–2014 was only 1–2.5 times higher than in 2014–2015.

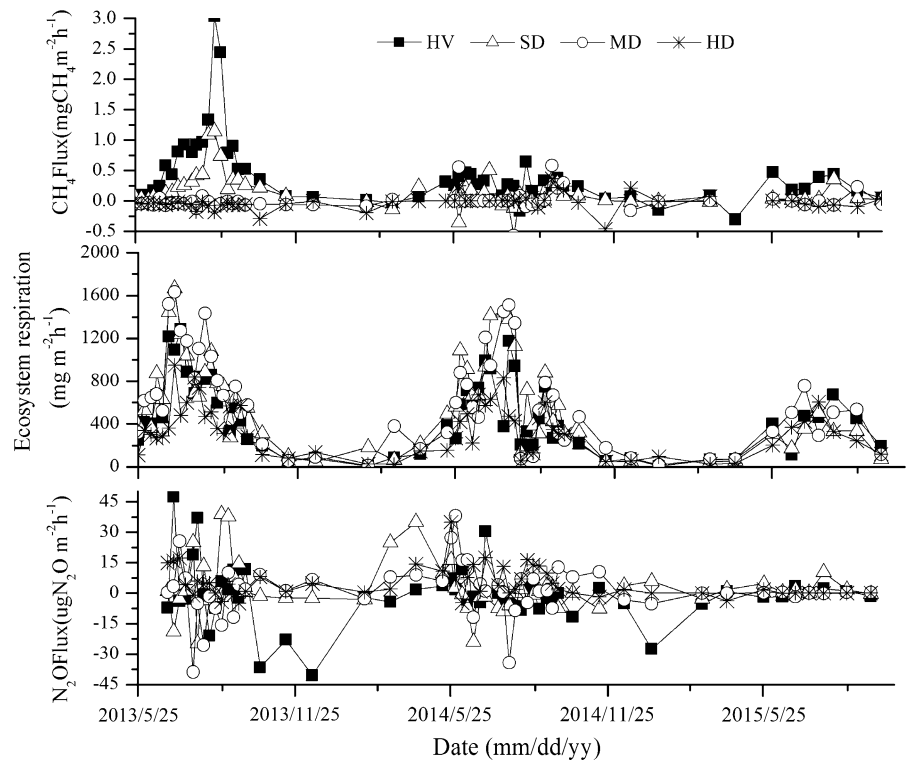
To quantify the interannual variation of gas fluxes in growing and non-growing seasons, we took the coefficient of variance (CV) as the index. In the growing season, CH_4 exchange between HD and the atmosphere was the most variable with a CV of 699.7% while ecosystem respiration from HD had the lowest variation with a CV of 17.3%. In the non-growing season, the highest CV was observed for N_2O flux in HD (180.2%) and the lowest CV was observed

for ecosystem respiration in MD (2.1%) (Table 3). Ecosystem respiration showed the lowest variability in both seasons for the entire study period.

Seasonal variations of ecosystem respiration, CH_4 , and N_2O fluxes

There were clear seasonal variations in greenhouse budget for all four different wetland vegetation degradation classes (Figs. 3, 4). The majority of the gas releases occurred in growing seasons, but the gas emissions were relatively low in the non-growing season. Higher emissions of CH_4 occurred in the growing season with cumulative fluxes of $1412.95 \pm 829.17 \text{ mg CH}_4 \text{ m}^{-2}$ and $570.82 \pm 308.51 \text{ mg CH}_4 \text{ m}^{-2}$ for HV and SD, respectively. Comparatively, in the non-growing season, cumulative fluxes were $375.02 \pm 89.05 \text{ mg CH}_4 \text{ m}^{-2}$ and $271.62 \pm 100.55 \text{ mg CH}_4 \text{ m}^{-2}$ for HV and SD, respectively. MD and HD recorded negative values of CH_4 indicating uptake both in the growing season ($-21.63 \pm 55.64 \text{ mg CH}_4 \text{ m}^{-2}$ and $-35.78 \pm 143.92 \text{ mg CH}_4 \text{ m}^{-2}$ for MD and HD

Fig. 4 Interannual variations of ecosystem respiration, CH₄ and N₂O fluxes in four wetland vegetation degradation classes (2013 to 2015)



respectively) and non-growing season ($-216.90 \pm 22.09 \text{ mgCH}_4 \text{ m}^{-2}$ and $-343.40 \pm 124.48 \text{ mg CH}_4 \text{ m}^{-2}$ for MD and HD respectively). There was higher uptake in the non-growing season than the growing season. For both seasons, HV and SD wetlands were sources of CH₄ while MD and HD wetlands were CH₄ sinks.

Ecosystem respiration was higher in the growing seasons for all wetland vegetation degradation classes with values ranging between $880.80 \pm 34.48 \text{ g CO}_2 \text{ m}^{-2}$ and $3194.96 \pm 266.39 \text{ g CO}_2 \text{ m}^{-2}$. Only 25% of ecosystem respiration occurred in the non-growing season (Table 3). HV wetlands served as N₂O sources during the growing season but acted as sinks in the non-growing season. All wetland vegetation degradation classes acted as sources of N₂O in both seasons except for MD which was a sink in the growing season ($-4.86 \pm 4.54 \text{ mg N}_2\text{O m}^{-2}$). Peak emission of CH₄ occurred in the peak of the growing season in the month of August while peak ecosystem respiration happened in July (Fig. 3). For N₂O, peak emissions occurred in April in SD while relatively higher uptake

rates occurred in HV between October and December (Fig. 3).

Aboveground net primary production (ANPP)

Vegetation degradation significantly decreased ANPP (Fig. 5) ($P < 0.05$). In this study, there were very few plants in HD, and therefore we ignored its ANPP. In 2013, ANPP in MD and SD reduced by 41.36% and 17.64% respectively compared with HV. Similarly, in 2014, ANPP reductions were 61.13% and 17.71% in MD and SD respectively. In 2013, ANPP in both HV and MD were significantly higher than in MD, however, in 2014 while ANPP in HV was still significantly higher than in MD, ANPP in SD though higher, did not show any significance compared with MD.

Net carbon flux and global warming potential (GWP)

The annual net carbon flux ($F(C)$) and its CO₂ equivalent (GWP) in 2013 and 2014 are shown in

Fig. 5 Aboveground Net Primary Production (ANPP) in four wetland vegetation degradation classes

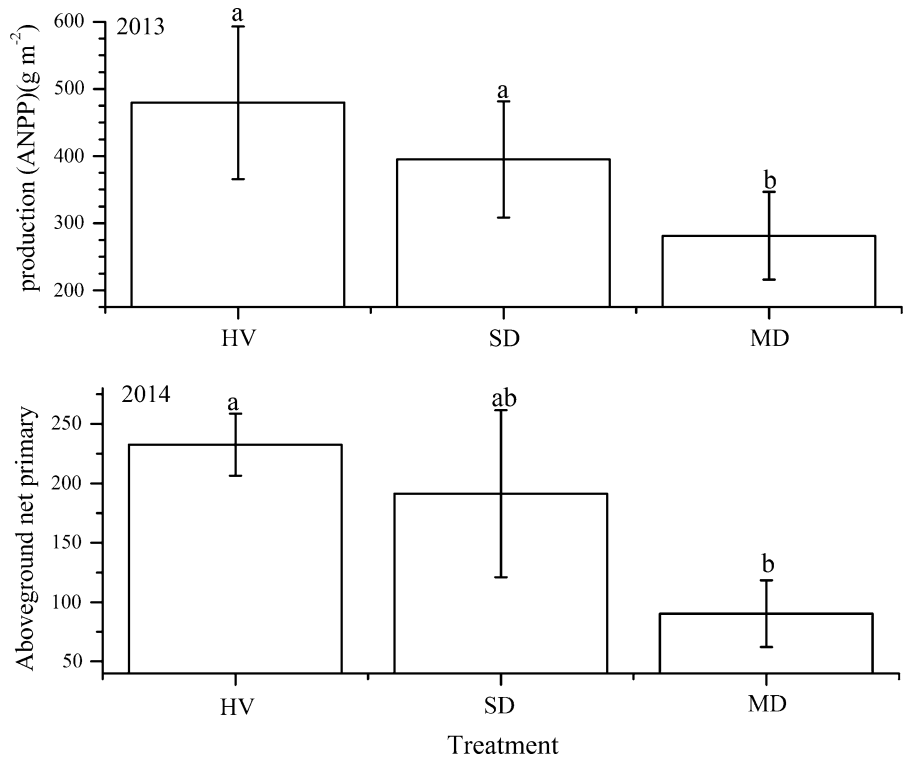


Table 4. There was a reduction in C uptake along the vegetation and moisture gradient with highly vegetated and moister soils exhibiting a net cooling effect. HV exhibited high uptake of C and a higher global cooling effect compared to SD and MD while HD showed a net global warming effect. Negative values in HV, SD and MD indicated net C uptake while a positive value in HD indicated net C emissions. However, there was a reduction in net C uptake in HV, SD, and MD in 2014–2015 compared with 2013–2014. Total climate cooling potential were ranked in the order of HV > SD > MD; while climate warming potential was exhibited in HD.

Discussions

Effect of environmental variables on variations of GHG fluxes

Temperature, soil moisture and ANPP were considered as the influencing factors on CH₄ and N₂O fluxes, and ecosystem respiration (Song et al. 2009; Zhu et al.

2015a, b) though with seasonal variations. Olefeldt et al. (2013) emphasized that temperature and moisture were the main controls on CH₄ emissions in the permafrost region, and their effects were interactive and exhibited different predominance according to ecosystem characteristics. In this study, no significant relationship was found between CH₄ and soil temperature (5–20 cm) in the growing season. However, in the non-growing season, there were significant positive correlations for all wetland vegetation degradation classes except SD, which had a significant negative correlation with soil temperature at 10 cm depth. Surface temperature (0 cm) had no significant relationship with CH₄ flux except in MD in the non-growing season (Table 5). There were also highly significant positive correlations between soil water content (SWC) at 10 cm soil depth and CH₄ flux in HV and SD in the growing season ($P < 0.01$). In the non-growing season however, SWC was significantly correlated with SD ($P < 0.05$). These results suggested that SWC rather than soil temperature could explain the seasonal variation in CH₄ emissions in the study area. Soil moisture drawdown significantly decreased

Table 4 CO₂-equivalent greenhouse gas fluxes in four wetland vegetation degradation categories

Year	Treatment	$-F(\text{GPP-C})$ (kg m ⁻² year ⁻¹)	$F(\text{CO}_2\text{-C})$ (kg m ⁻² year ⁻¹)	$F(\text{CH}_4\text{-C})$ (kg m ⁻² year ⁻¹)	$F(\text{C})$ (kg m ⁻² year ⁻¹)	$F(\text{CO}_2\text{e})$ (kg m ⁻² year ⁻¹)
2013–2014	HV	- 3.4314 ± 0.8130	0.7976 ± 0.1027	0.0026 ± 0.0002	- 2.6312 ± 1.2376	- 9.5457 ± 1.4562
	SD	- 2.8258 ± 0.6201	1.0016 ± 0.1319	0.0012 ± 0.0001	- 1.8231 ± 0.9523	- 6.6390 ± 1.2030
	MD	- 2.0122 ± 0.4676	1.0823 ± 0.1425	- 0.0003 ± 0.0001	- 0.9302 ± 0.6232	- 3.4216 ± 0.7036
	HD	-	0.5784 ± 0.0705	- 0.0005 ± 0.0001	0.5779 ± 0.0704	2.0989 ± 0.0608
2014–2015	HV	- 1.6635 ± 0.1871	0.6622 ± 0.1860	0.0009 ± 0.0002	- 1.0005 ± 0.2532	- 3.6323 ± 0.2846
	SD	- 1.3688 ± 0.5033	0.8941 ± 0.0739	0.0003 ± 0.0001	- 0.4744 ± 0.5253	- 1.7261 ± 0.5536
	MD	- 0.6466 ± 0.2031	0.6330 ± 0.0826	- 0.0002 ± 0.0001	- 0.0137 ± 0.2031	- 0.0574 ± 0.2054
	HD	-	0.5023 ± 0.0652	0.0001 ± 0.0001	0.5024 ± 0.0653	1.8428 ± 0.0657

Negative values of $F(\text{C})$ show net carbon storage, while positive $F(\text{C})$ values indicate net carbon emission. More negative CO_{2e} values reflect climate cooling effects, and more positive values reflect climate warming effects

CH₄ emissions that may be attributed to a number of causes. First, soil moisture drawdown can make soil less anaerobic, decreasing CH₄ production by methanogens (Dijkstra et al. 2012). Second, soil moisture drawdown in turn affects temperature sensitivity of the soil and organic carbon decomposition in the soil, both of which slow CH₄ production (Craine and Gelderman 2011). Third, soil moisture drawdown could alter vegetation communities, especially in aerenchymatous plants, leading to lower CH₄ emissions (Yang et al. 2014).

Most often, soil temperature is the dominant environmental control on wetland CO₂ fluxes (Liu et al. 2015; Zhu et al. 2015a, b). Activity of microorganisms is generally temperature-dependent in wetland. Warm air and soil temperatures can stimulate biological activity and consequently increase CO₂ fluxes. It was a clear evident in our study that there were significant positive correlations ($P < 0.01$) between ecosystem respiration and almost all soil temperatures for almost all degradation classes in the growing season (Table 5). Our study also indicated that there was positive correlation between ecosystem respiration and soil temperature ($P < 0.05$) except HD in the non-growing season (Table 5). In HV, SD, and MD wetlands, ecosystem respiration showed very strong positive correlations with near surface temperatures ($T_{0\text{cm}}$ and $T_{5\text{cm}}$) compared to deep soil temperatures (Table 5). This may be attributed to the organic-mineral structure of the covered soil. The total carbon and nitrogen contents usually decreased with depth in this study area (Huang et al. 2014), which indicated more active decomposition and exchange of matter and energy in the surface soil layer (Deppe et al. 2010). However, no correlation was found between ecosystem respiration and SWC in either season for all degradation gradients apart from HD which indicated a strong positive correlation in the non-growing season. These result suggested that soil temperature were the main control on ecosystem respiration. This is consistent with the dominant temperature effect shown by other reports (Zhu et al. 2015a, b).

The Q_{10} is commonly used to express the temperature sensitivity of ecosystem respiration (Zhu et al. 2015a, b). The temperature sensitivity (Q_{10} value) of ecosystem respiration assessed in this study (Table 6, 7) revealed that SD and HV wetlands were most sensitive to temperature changes in the both seasons.

Table 5 Pearson Correlations (2-tailed) between environmental factors and GHG fluxes in different vegetation degradation stages in growing and non-growing seasons

Indicators	HV			SD			MD			HD		
	CH ₄	ER	N ₂ O	CH ₄	ER	N ₂ O	CH ₄	ER	N ₂ O	CH ₄	ER	N ₂ O
Growing season												
T _{soil-5 cm}	0.135	0.663**	0.146	0.003	0.781**	-0.401*	-0.113	0.727**	-0.111	-0.169	0.428**	0.365*
T _{soil-10 cm}	0.196	0.612**	0.12	0.076	0.757**	-0.377*	-0.103	0.703**	-0.114	-0.172	0.433**	0.364*
T _{soil-20cm}	0.159	0.255	0.005	0.165	0.697**	-0.28	-0.111	0.495**	-0.122	-0.202	0.460**	0.356*
T _{soil-0 cm}	0.092	0.655**	0.163	-0.046	0.685**	-0.436**	-0.161	0.727**	-0.125	-0.165	0.368*	0.375*
T _{chamber}	0.028	0.686**	0.361*	-0.159	0.655**	-0.420**	-0.048	0.644**	-0.035	-0.041	0.346*	0.353*
T _{air}	0.107	0.627**	0.128	-0.023	0.609**	-0.347*	-0.188	0.720**	-0.131	-0.162	0.370*	0.384*
SWC _{0-10 cm}	0.528**	0.17	0.137	0.501**	0.294	0.185	0.058	0.06	0.061	0.01	0.192	0.087
Non-growing season												
T _{soil-5 cm}	0.672*	0.835**	0.165	0.163	0.549	0.405	0.906*	0.736*	0.493	0.494	0.573	0.515
T _{soil-10 cm}	0.837*	0.871*	-0.116	-0.902*	0.464	-0.271	0.974	0.412	-0.039	0.906**	0.647	0.403
T _{soil-20cm}	0.790*	0.652	-0.483	-0.814	0.535	-0.703	0.998*	0.303	-0.197	0.864*	0.551	0.231
T _{soil-0 m}	0.513	0.777**	0.457	0.276	0.703**	0.421	0.639*	0.700**	0.503	0.255	0.393	0.432
T _{chamber}	0.377	0.736**	0.577*	0.182	0.545*	0.514*	0.515	0.751**	0.611*	0.317	0.36	0.371
T _{air}	0.495	0.747**	0.463	0.301	0.603*	0.393	0.646*	0.686**	0.468	0.244	0.359	0.389
SWC _{0-10 cm}	0.296	0.183	-0.062	0.866*	0.577	-0.396	0.373	0.655	0.524	0.358	0.920**	0.595

“**” indicates significance at $P < 0.01$; “*” indicates significance at $P < 0.05$. The same applies to the tables below. ER means ecosystem respiration

Table 6 Regression equations and Q_{10} values between temperature and ecosystem respiration (ER) at the four sites in growing season

Temperature	HV	SD	MD	HD
T_{air}	ER, R^2 $y = 150.72e^{(0.096T)}$ 0.326	$y = 143.94e^{(0.098T)}$ 0.250	$y = 138.55e^{(0.096T)}$ 0.290	$y = 194.46e^{(0.038T)}$ 0.063
$T_{soil-0\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 139.05e^{(0.101T)}$ 0.355	2.66 $y = 114.73e^{(0.115T)}$ 0.315	2.61 $y = 113.26e^{(0.106T)}$ 0.311	1.46 $y = 200.46e^{(0.036T)}$ 0.060
$T_{soil-5\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 120.96e^{(0.113T)}$ 0.384	3.16 $y = 73.44e^{(0.148T)}$ 0.488	2.89 $y = 115.34e^{(0.106T)}$ 0.328	1.43 $y = 74.46e^{(0.085T)}$ 0.329
$T_{soil-10\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 120.58e^{(0.116T)}$ 0.327	4.39 $y = 79.75e^{(0.147T)}$ 0.455	2.89 $y = 131.63e^{(0.101T)}$ 0.289	2.34 $y = 171.38e^{(0.045T)}$ 0.102
$T_{soil-20\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 405.10e^{(0.019T)}$ 0.011	4.35 $y = 79.72e^{(0.153T)}$ 0.375	2.75 $y = 234.89e^{(0.064T)}$ 0.167	1.57 $y = 161.29e^{(0.053T)}$ 0.126
	Q_{10} value, Sig.	0.010	0.022*	1.70 0.008**

Table 7 Regression equations and Q_{10} values between temperature and ecosystem respiration (ER) at the four sites in non-growing season

Temperature	HV	SD	MD	HD
T_{air}	ER, R^2 $y = 54.89e^{(0.148T)}$ 0.665	$y = 87.16e^{(0.076T)}$ 0.296	$y = 46.63e^{(0.127T)}$ 0.576	$y = 62.81e^{(0.027T)}$ 0.045
$T_{soil-0\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 55.19e^{(0.143T)}$ 0.683	2.14 $y = 89.86e^{(0.056T)}$ 0.339	3.56 $y = 44.30e^{(0.131T)}$ 0.590	1.31 $y = 60.63e^{(0.031T)}$ 0.061
$T_{soil-5\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 50.35e^{(0.193T)}$ 0.947	1.75 $y = 158.42e^{(0.052T)}$ 0.204	3.71 $y = 40.92e^{(0.156T)}$ 0.688	1.36 $y = 56.34e^{(0.058T)}$ 0.239
$T_{soil-10\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 52.97e^{(0.228T)}$ 0.929	1.68 $y = 203.55e^{(0.060T)}$ 0.249	4.76 $y = 169.65e^{(0.049T)}$ 0.195	1.79 $y = 54.13e^{(0.084T)}$ 0.535
$T_{soil-20\text{ cm}}$	Q_{10} value, Sig. ER, R^2 $y = 59.72e^{(0.229T)}$ 0.634	1.82 $y = 168.17e^{(0.090T)}$ 0.390	1.63 $y = 184.05e^{(0.046T)}$ 0.123	2.32 $y = 58.21e^{(0.085T)}$ 0.446
	Q_{10} value, Sig.	0.073	0.146	2.34 0.100

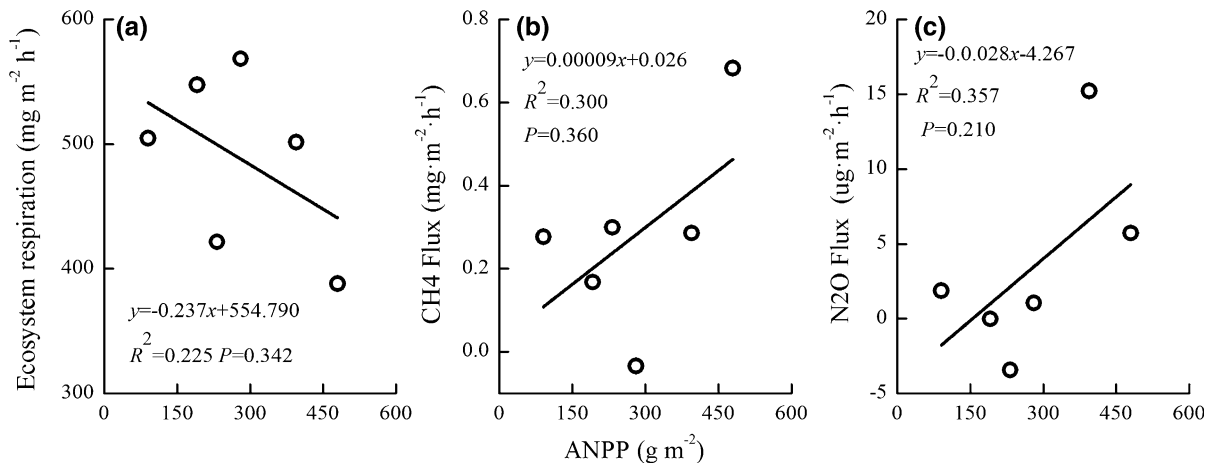


Fig. 6 Relationships between ecosystem respiration, CH₄, and N₂O fluxes and ANPP. Biomass and GHG data were for September 2013 and 2014

Q₁₀ values in the non-growing season (1.31–9.87) (Table 7) were higher than those of the growing season (1.21–4.62), particularly in HV (Table 6). The clear differences in the Q₁₀ values between the four sites and the two seasons suggested that there was substantial spatial–temporal variation influenced by varied environmental conditions. Hence, further studies should pay more attention to the temperature sensitivity under controlled conditions.

There were several factors influencing N₂O fluxes, including temperatures and SWC (Table 5). However, in different seasons, the N₂O fluxes were related to these factors differently. In the growing season, the N₂O flux was significantly negatively correlated with T_{air}, and soil temperature at all depths in the SD, but significantly positively correlated in HD. However, in the non-growing season N₂O flux was significantly correlated with only chamber temperature for all degradation classes except HD. Given that various factors determine N₂O emissions, positive and negative influences, such as air temperature, would offset each other, leading to a minimal overall net effect (Dijkstra et al. 2012). In contrast, there was no significant correlation with SWC (0–10 cm) for any vegetation degradation classes in either season (Table 5). Though there was no significant relation between SWC and N₂O emissions, we still considered that seasonal and inter-annual variations of N₂O emissions was related to the temporal dynamics of soil water content. A study by Beringer et al. (2013)

demonstrated an increase in nitrifying rates as a function of soil moisture content from 15 to 75%. However, the N₂O production were very minimal at soil moisture content either dry (< 60%) or wet (> 80%). Soil moisture contents at all study sites ranged from 9% to 55% over observation times. This may explain our results which showed a weak positive correlation between the N₂O flux and topsoil (0–10 cm) moisture.

In the growing season, the ANPP was an important variable influencing ecosystem respiration, CH₄, and N₂O fluxes in all wetland vegetation degradation classes, excluding HD (Fig. 6). Ecosystem respiration was negatively correlated with ANPP and accounted for 22.5% of ecosystem respiration variations (Fig. 6a). Vegetation degradation may destroy the SOC balance, thus exposing a large amount of SOC, which is oxidized into CO₂ and passes to the atmosphere (Cao et al. 2012). Therefore, vegetation degraded state of wetlands led to the increased respiration rates. Moreover, the soils of wetland in vegetation degradation state with lower ANPP and plant biodiversity were more sensitive to changes in air temperature, leading to the higher respiration rates and carbon mineralization (Wang et al. 2010). We also found that there were positive correlations between ANPP and CH₄ and N₂O fluxes (Fig. 6b, c). ANPP explained about 30% and 35.7% of CH₄ and N₂O flux variations, respectively. Our results were consistent with the previous findings (Zhu et al. 2015a, b),

possibly because the transport of plant aerenchyma of CH_4 and N_2O was reduced with decreasing ANPP (Sheng et al. 2015).

Effect of wetland vegetation degradation on GHGs

Effect of wetland vegetation degradation on CH_4 flux

In the present study, moderately degraded (MD) and heavily degraded (HD) wetlands acted as CH_4 sinks in the wet meadows of the eastern QTP. Monthly fluxes ranged between -0.03 ± 0.02 and $-0.10 \pm 0.03 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ (Fig. 3). These fluxes were consistent with previous studies in a forest ecosystem in China by Mo et al. (2005) who reported CH_4 uptake rates between $-0.05 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ and $-0.15 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$. In grazed alpine steppe in the QTP, Wei et al. (2012) reported mean CH_4 uptake rates of $-0.06 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ and $-0.07 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$. HV and SD acted as sources of CH_4 with emission rates between 0.03 ± 0.02 to $1.74 \pm 0.38 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$.

Figure 3, which were also in the range of a study by Liu et al. (2015) in a permafrost region in North-East China, where an average emission rate of $0.14 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ was recorded. CH_4 emissions generally decreased with degradation which is characterized by moisture loss which is consistent with previous studies (Song et al. 2009). These decreases could be attributed to the lower moisture (ESM 4) because methane producing archaea require anaerobic conditions typically found in wet soils, and the drier degraded sites may therefore limit methane production. In the present study, there was significant positive correlation ($P < 0.01$) between soil moisture and CH_4 emissions in HV and SD in the growing seasons (Table 5) which further confirms that increased soil moisture conditions resulted in increased CH_4 emissions. This also confirms findings by Werner et al. (2006) and Curry (2007). Soils with higher water filled pore space (WFPS) due to higher moisture limits diffusion of atmospheric CH_4 into the soil medium resulting in lower uptake or even emission from highly moist soils (Wu et al. 2010). There was reduced uptake in the growing season compared to the non-growing season (Table 3) which may also be attributed to seasonality of soil moisture conditions. Apart from soil moisture reduction, vegetation loss may also cause changes in soil properties such as bulk density (Li et al. 2015).

These changes in soil properties and soil moisture stress due to vegetation degradation (online resource 3) coupled with already moisture stressed conditions in the non-growing season, could increase CH_4 uptake capacity of vegetation degraded wetlands (Werner et al. 2006).

Lower biomass from degraded wetlands (Table 2 and Fig. 5) could also reduce CH_4 emissions due to lower capacity of vascular transportation of CH_4 from wetlands into the atmosphere (Zhang et al. 2007). Additionally, lower biomass reduces substrate and root exudate supply consequently reducing methanogenesis and leading to lower production of CH_4 (Bai et al. 2018). Figure 4 and Table 3 show clear seasonal variations in CH_4 fluxes. Higher emissions were recorded in HV and SD in the growing season than in the non-growing season whilst in MD and HD higher uptakes of CH_4 occurred in the non-growing season. Mean CH_4 emissions in the growing season (0.745 ± 0.635 and $0.240 \pm 0.300 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for HV and SD, respectively) were higher than those measured during the non-growing season (0.082 ± 0.097 , $0.059 \pm 0.103 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ for HV and SD, respectively), with peak emissions observed in August, which is the peak of the growing season (Fig. 3). A similar observation was reported in wetlands in the Sanjiang Plain (Song et al. 2009). For HV and SD, higher biomass and plant diversity (Table 2 and Fig. 5) coupled with higher moisture conditions in the growing season account for higher emissions of CH_4 .

Effect of wetland vegetation degradation on ecosystem respiration

Throughout the study period, the average ecosystem respiration from the wetlands with plant communities (HV, MD, and SD) was $557.17 \pm 403.61 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$. This value is close to a previous study by Jiang et al. (2010) in the alpine meadows on the QTP but higher than that reported in the alpine steppe on the central Tibetan Plateau ($132.7 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) (Wei et al. 2014) and in a permafrost area in North-East China ($403.47 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) (Liu et al. 2015). Ecosystem respiration increased with wetland vegetation degradation with higher emissions in SD and MD than in HV in both seasons. Higher ecosystem respiration in SD and MD could be attributed to temperature increase due to vegetation loss (Zhu et al.

2015a, b). Temperature increase often results in higher decomposition of stored carbon (Juszczak et al. 2012; Zhu et al. 2015a, b). There were strong significant correlations between temperature and ecosystem respiration (Table 5), which explains the influence of temperature on ecosystem respiration. Our findings also indicated that ecosystem respiration increased with temperature (Table 5) for all three wetland vegetation categories (HV, SD and MD).

Effect of wetland vegetation degradation on N₂O flux

For a 2-year period (2013–2014 and 2014–2015), HV acted as a net sink of N₂O while all degraded wetlands acted as net sources, however, cumulative fluxes of N₂O were very small in all wetland vegetation categories (Fig. 2c). Healthy vegetation experienced reduced N₂O emissions as result of lower denitrification in non-degraded vegetation (Yeboah et al. 2016) thus lower N₂O emissions. Higher biomass in HV may have played a vital role in lower N₂O efflux in this experiment. In an experiment involving bare soil and vegetated soil mesocosms, Saarnio et al. (2013) elucidated that plants in the vegetated soils compete with microbes for nitrogen, increasing N-uptake which resulted in lower N₂O efflux compared with bare soil. Congruently, Zhang et al. (2012) indicated that higher yields of rice and maize resulted in reduced soil N₂O efflux. Furthermore, lower flux in the non-growing season (Fig. 3, 4) contributed to HV being a net sink of N₂O. The extreme cold conditions during this period may have limited denitrification rates and caused higher uptake in HV. Denitrification is highest during wet and warm conditions. More so, higher moisture in HV could reduce oxygen availability hence reduced N₂O emission (Tauchnitz et al. 2008). The highest emissions come from HD which was also consistent with previous studies (Hu et al. 2010; Li et al. 2015; Zhu et al. 2015a, b), and researchers have posited that livestock grazing enhances N₂O emission due to soil compaction (Rafique et al. 2011) and nutrient deposition by the grazing livestock (Pendall et al. 2010).

Effect of wetland vegetation degradation on the overall C balance and GWP

In the four wetland vegetation degradation sites, HV wetlands indicated greater carbon sink potential than

SD and MD wetlands, while HD was a net carbon source (Table 4). Wetland net carbon sink capacity was largely due to the dominance of net ecosystem fluxes by GPP (Table 4). Therefore, vegetation (Table 2) was an important factor influencing wetland carbon balance in Gahai. Excluding HD in the correlation analysis, as no ANPP was observed there, ecosystem respiration negatively correlated with ANPP (Fig. 6a).

The GWP in HV which had negative values which were 1.44 and 2.79 times higher than that of SD and MD respectively in 2013–2014, and 2.10 and 63.28 times in 2014–2015 (Table 4) indicating higher carbon absorption and climate cooling effects in the healthy vegetation wetland. However, HD wetlands had positive values of CO₂e, indicating that HD wetlands had been converted into carbon sources and increased climate warming. In 2014–2015, global cooling effect of HV compared to MD rose from 2.71 times in 2013–2014 to 46.65 times indicating that further loss in ANPP (Fig. 5) could draw MD closer to a net GHG source. Carbon absorptions in HV, SD and MD in 2013–2014 were higher than in 2014–2015. This was also attributed to higher GPP in 2013–2014 than in 2014–2015 (Table 4).

Our study suggested that the net exchange of CO₂ between wetland ecosystems and the atmosphere was dominated by GPP, since CH₄ fluxes remained relatively lower. Further research is required to quantify photosynthesis, autotrophic respiration, litterfall, and plant mortality to give more insight into the carbon balance of the alpine wetlands (Tian et al. 2011).

Conclusion

On the basis of 3-years of continuous observation of CH₄, ecosystem respiration, and N₂O fluxes as well as carbon budget estimation in the wet meadows under different magnitudes of vegetation degradation on the Qinghai-Tibet Plateau, we conclude that vegetation degradation significantly reduced carbon uptake of grassland ecosystems and increased global warming potential but may cause a reduction in CH₄ flux and slight influence on N₂O flux. Furthermore, response of GHGs to degradation also depends on the magnitude of vegetation degradation and associated changes in SOC, bulk density and soil moisture in the

wetland. For all wetland types, in the growing season, CH₄ flux showed the strongest interannual variation, followed by N₂O flux but in the non-growing season, N₂O fluxes varied the most, followed by CH₄ fluxes. Ecosystem respiration fluxes showed the weakest interannual variations. Generally, the wetlands tended to have high emissions of CH₄ and ecosystem respiration in the peak growing season of alpine wetland plants (July and August) than in the early growing season of alpine plants (May) and the non-growing season of alpine plants (October to April). However, seasonal variations of N₂O fluxes were more complicated especially in the degraded wetlands; showing no clear seasonal trends during the observation. Our study also showed that temperature was the most dominant factor affecting ecosystem respiration and N₂O fluxes, but soil moisture mostly controlled the variations of CH₄ flux. We recommend conservation measures and biodiversity protection such as reduced livestock grazing and erosion control measures in order to reduce the impact of wetland vegetation degradation on radiative forcing.

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