



Spatial and Seasonal CH₄ Flux in the Littoral Zone of Miyun Reservoir near Beijing: The Effects of Water Level and Its Fluctuation

Meng Yang¹, Xuemeng Geng¹, John Grace², Cai Lu¹, Yi Zhu¹, Yan Zhou¹, Guangchun Lei^{1*}

¹ School of Nature Conservation, Beijing Forestry University, Beijing, China, ² School of Geosciences, The University of Edinburgh, Edinburgh, United Kingdom

Abstract

Wetlands, and especially their littoral zones, are considered to be CH₄ emissions hotspots. The recent creation of reservoirs has caused a rapid increase in the area of the world's littoral zones. To investigate the effects of water depth and water level fluctuation on CH₄ fluxes, and how these are coupled with vegetation and nutrients, we used static closed chamber and gas chromatography techniques to measure CH₄ fluxes in the littoral zone of a large reservoir near Beijing, China, from November 2011 to October 2012. We found that CH₄ flux decreased significantly along a transect from open water to dry land, from 3.1 mg m⁻² h⁻¹ at the deep water site to approximately 1.3 mg m⁻² h⁻¹ at the shallow water site, and less than 0.01 mg m⁻² h⁻¹ in the non-flooded area. Water level influenced CH₄ flux by affecting soil properties including soil redox potential, soil carbon and nitrogen, and bulk density. The largest emission of all was from the seasonally flooded site after a flooding event (up to 21.1 mg m⁻² h⁻¹), which may have been caused by vegetation decomposition. Submerged sites had greater emissions, while the driest site had lower emissions. Immediately after the monthly measurements had been made, we removed the aboveground vegetation to enable an assessment of the gas transportation per unit of biomass. Removal of biomass decreased emissions by up to 53%. These results indicated the dominant effect of water depth on CH₄ flux through effects of soil conditions, plant species composition and distribution. This study suggests that temporally flooded wetlands, including littoral zones, contribute significantly to the global CH₄ burden. However, the current challenge is to capture their spatial extent and temporal variation in the fluxes.

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* E-mail: guangchun.lei@foxmail.com

Introduction

Methane is the second most important contributor to total greenhouse gas emissions, with a Global Warming Potential of 25 over a 100-year time-span [1]. Wetlands are considered to be the most important CH₄ source, thought to account for 24–39% of the total global emission of CH₄, albeit with a large degree of uncertainty [2]. Reservoirs are an important type of wetland, whose combined area across the globe has increased in recent years to now occupy approximately 5 × 10⁵ km², which is 1/3 the size of all natural lakes [3]. One reason for the large development of reservoirs is their potential as a clean energy source, although uncertainties in their methane emissions have led some scientists to question whether they are as clean as people believe [4]. Several authors have insisted that the subject of greenhouse gas emissions from reservoirs requires more scientific study [5–7]. The Ministry of Water Resources of the People's Republic of China has stated that China has over 80,000 reservoirs, large and small [8]. However, work in China on their greenhouse gas emissions, and the extent to which these reservoirs contribute to total emissions, is limited [9].

The littoral zone of reservoirs features fast and complicated material cycles and is reported to be a hotspot for CH₄ emissions [10,11]. Furthermore, there are indications from elsewhere about

the importance of the littoral zone: for example, in boreal systems, where about 70% of total CH₄ emissions comes from the littoral zone, even though its area is no more than 24% of the total wetland area [12]. Water depth and its diurnal and seasonal fluctuations are thought to be the main drivers determining the characteristics of the littoral habitat, including plant species composition and distribution, soil conditions, and CH₄ flux [11,13–16]. However, the interaction between water level fluctuation, CH₄ production, transportation, and emissions is still not fully understood [17,18], especially the effect of dynamic water fluctuation coupling with vegetation and nutrients [19,20]. The rate of change of the water table, as distinguished from just differences in the water table, is known to be a major environmental factor controlling the CH₄ flux [21].

In summary, studies of the CH₄ flux from the littoral zone are essential for evaluating the atmospheric and climatic impacts of reservoirs as energy sources, as well as for a better understanding of the biogeochemical mechanism of CH₄ flux. Research on the mechanisms of how the water level and its fluctuations influence CH₄ flux is an important foundation for related work aimed at modeling and controlling carbon loss through ecosystem management. In this context, we report the seasonal and monthly variation of CH₄ flux of the littoral zone of Miyun Reservoir,

Beijing, China. We hypothesized that water depth and water level fluctuation would be the main factors driving the CH₄ flux variability, together with soil and vegetation.

Materials and Methods

This study was authorized by Beijing North Miyun Reservoir Eco-agriculture Co. Ltd. It did not harm any protected species, and thus no ethics committee was required to authorize the work. All data used in this paper were collected in the field by the research team, and the raw data are available upon request from the senior author. No data were downloaded from publicly available resources, and thus no permission was required.

Study area

The research was carried out at Miyun Reservoir (40°29'N, 116°50'E), which is located in the northern mountainous area near Beijing, China. It was built in 1960 with a maximum water area of 188 km². Its catchment is characterized by warm temperate semi-humid monsoonal climate with an annual average air temperature of 10.5°C, maximum air temperature of 38°C, and a minimum of -18°C. The reservoir is normally covered by ice from the middle of November to the end of March. The growing season is from April to November. The annual average precipitation is close to 600 mm, of which 80% is concentrated from July to August [22]. The annual change in the water level is 1–5 m because of rainfall and water supply for domestic use. The area between the highest and lowest water level from 1984 to 2005 was 84 km² [23]. In the summer of 2012, when the work was carried out, continuous heavy rain in July caused a sudden water level increase of one meter, and part of the littoral vegetation was inundated.

We divided the littoral zone into five areas based on water level (Figure 1). Sites were selected ranging from locations in open water to the dry area on higher ground, to provide five contrasting environments: (i) deep water area (DW); (ii) shallow water area (SW); (iii) seasonal (August and September) flooded area (SF); (iv) 'seasonally flooded control' (SFC) area, which was 500 m away from SF, had the same plant species and similar soil carbon/nitrogen content as SF, but escaped the flood in August and September because of its 1-m-higher elevation; and (v) permanent non-flooded area (NF). Details of the water depths in each of these areas are shown in Figure 2B. Three typical plant communities in each area were selected, and Table 1 shows the dominant species in different seasons in all zones. For more details on biomass and soil, see Figures 2 and 3.

CH₄ flux measurements

Methane flux was measured in November 2011, then May, July, August, September and October 2012. The experiment of three plots at site SFC was carried out just after the flooding and during the time when the water level dropped from August to October 2012. In order to reduce uncertainty in the average daily flux, sampling to capture any diurnal variation was performed at three-hourly intervals (local time: 6, 9, 12, 15, 18, 21 and 24 h). Each plot had four replicates located within three meters from each other. To eliminate disturbance to the soil, wooden access platforms were built.

The static opaque chamber technique was used to determine the CH₄ flux [24]. The chambers were made of stainless steel (volume: 125 L; surface area: 0.25 m²) and covered with polyethylene foam to avoid any warming effect inside the chamber. An internal chamber (volume: 200 L; surface area: 0.25 m²) could be added if plants were tall. Two fans were built

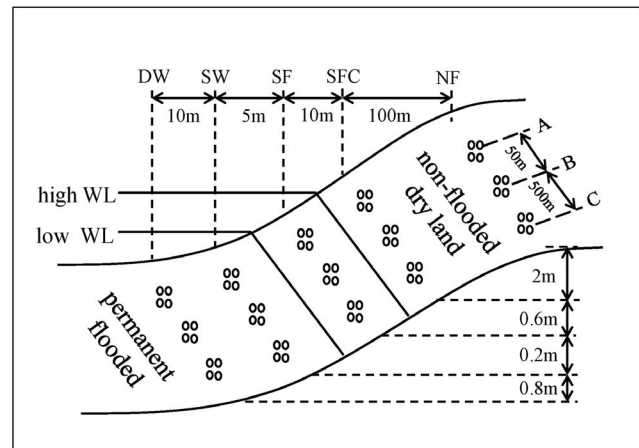


Figure 1. Experimental design. WL: water level. The sites are grouped at different heights. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site. A, B and C denote samples from different vegetation types within each height band (see Table 1 for information on plant species). There were four replicates in each case, repeatedly sampled six times (also repeatedly sampled seven times in a day) in the year. For more details on water depth and other environmental parameters, see Figures 2 and 3.
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into the chamber for air mixing. Four gas samples (200 mL each) were taken using 100-mL polypropylene syringes at 15-min intervals over a 45-min period after enclosure, and stored in 500-mL plastic and aluminum membrane gas sampling bags. The concentration of CH₄ was analyzed within one week by gas chromatography (7890A, Agilent, California, USA) equipped with a flame ionization detector (FID). Gases were separated with a column (3 m, 3.2 mm) packed with Porpak Q (80/100 mesh). The temperatures of the oven, injector, and detector were 70°C, 20°C, and 200°C, respectively. The flow rate of the carrier gas (N₂) was 25 mL min⁻¹. Standard CH₄ gas (2.03 ppm in air, China National Research Center for Certified Reference Materials, China) was used for precision verification for CH₄ concentrations. The coefficient of variation was below 1%. The flux of CH₄ was calculated following Chen et al. [25]. In order to determine the effect of aboveground vegetation on flux, one more flux measurement was taken at 9 am the following day (after seven times sampling for diurnal variation), with aboveground plant material removed. Chambers were reset into new positions near the old positions each sampling month. All positions at each site were within an area of 20 m², but not so close to each other to cause artifacts in the data through (for example) changes in the local hydrology.

Environmental factors

In order to analyze the effects of environmental parameters on fluxes, the following factors were taken into account: water level, dissolved oxygen (DO) in water, soil total carbon (TC) and nitrogen (TN), soil bulk density, biomass, and air temperature.

Water level was measured after gas sampling at DW, SW and SF (when SF had standing water in August and September 2012). At site SF (when there was no standing water in November 2011, May, July and October 2012) and SFC, a 1-m PVC tube was inserted vertically into the soil under the chamber after all monthly gas sampling was complete, allowing two hours for the water level to equilibrate before measuring the level. The water table of site NF was calculated according to the elevation measured by a

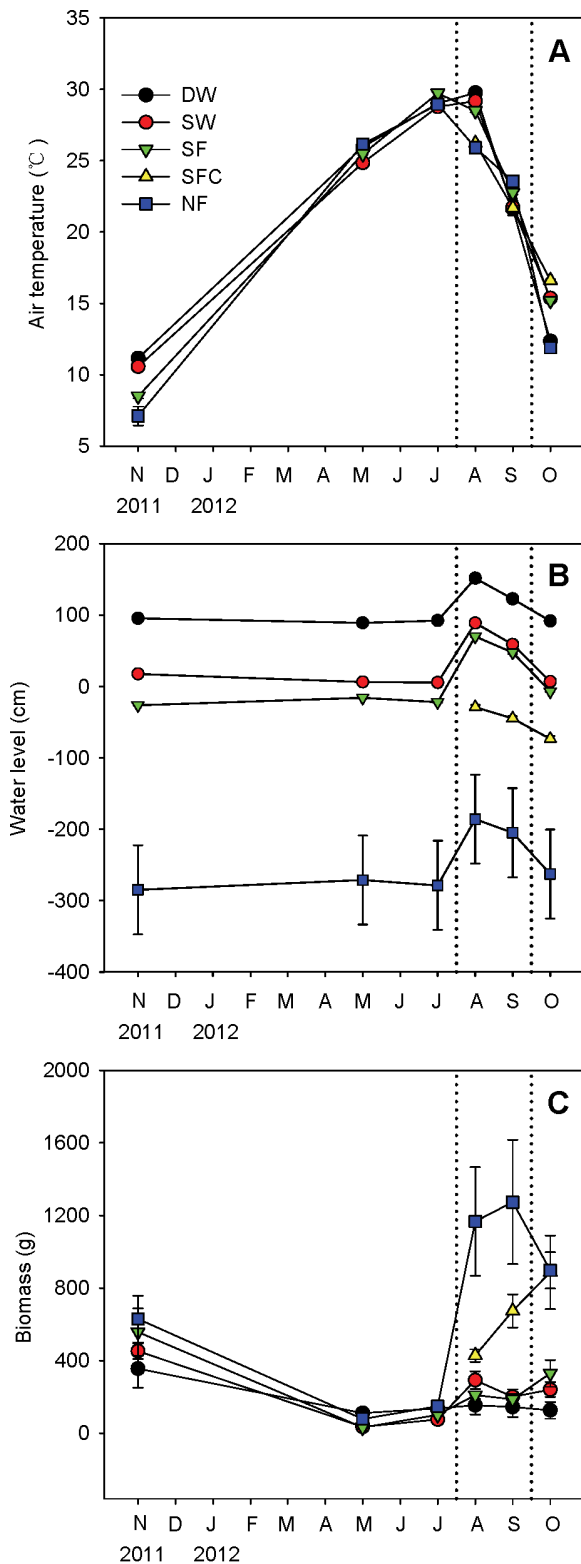


Figure 2. Monthly variation of air temperature, water level and biomass of each site. Days between dotted lines was the high water level period and thus the seasonally flooded site (SF) was under water. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site. A negative value of water level indicates the ground water depth. Error bars represent SE. doi:10.1371/journal.pone.0094275.g002

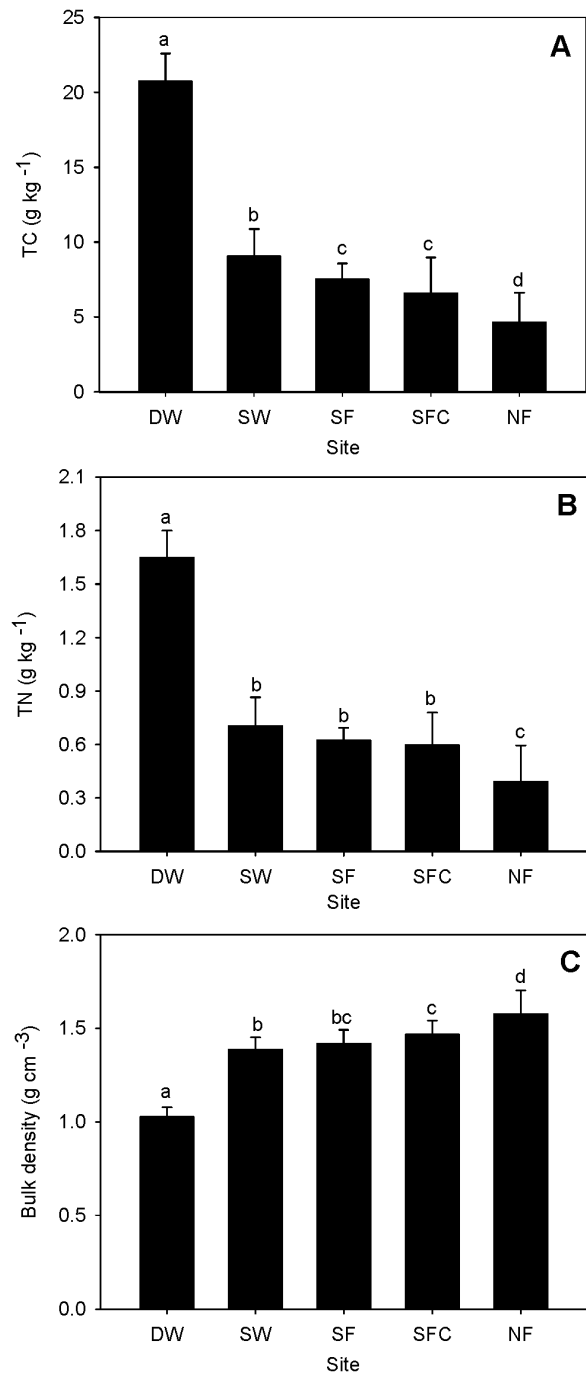


Figure 3. Soil properties (mean \pm SE) of each site. Bars with different letters indicate a significant difference at $p < 0.05$. TC: total carbon, TN: total nitrogen. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site. doi:10.1371/journal.pone.0094275.g003

Global Navigation Satellite System receiver (BLH-L90, Daheng International, China). DO in water was measured during the gas sampling by a handheld multi-parameter meter (Professional Plus, YSI, USA), after flooding.

Soil samples at site DW, SW, SF and NF were collected from three different layers (0–10 cm, 10–20 cm, and 20–30 cm below ground) at each replicate location in November 2011, except site SFC in October 2012. After air-drying and grinding (passing

Table 1. Dominant plant species at each plot in different months.

Site	Nov 2011	May 2012	Jul 2012	Aug 2012	Sep 2012	Oct 2012
DW	A <i>Echinochloa olonum</i> ^{AE}	<i>Myriophyllum</i> sp.		<i>Trapa</i> ^{AE} sp.		
	B no vegetation					
	C <i>Typha angustifolia</i> ^{AE}					
SW	A <i>Xanthium sibiricum</i> ^E	<i>Scirpus planiculmis</i> ^{AE}		<i>Echinochloa colonum</i> ^{AE}		
	B <i>Setaria viridis</i> ^E	<i>Bidens pilosa</i> ^E		<i>Echinochloa colonum</i> ^{AE}		
	C <i>Zea mays</i> ^E	<i>Polygonum lapathifolium</i> ^E				<i>Typha angustifolia</i> ^{AE}
SF	A <i>Xanthium sibiricum</i>	<i>Cirsium setosum</i>		<i>Cirsium setosum</i> ^E		<i>Cirsium setosum</i>
	B <i>Setaria viridis</i>	<i>Hemarthria altissima</i>		<i>Hemarthria altissima</i> ^E		<i>Hemarthria altissima</i>
	C <i>Zea mays</i>	<i>Polygonum lapathifolium</i>		<i>Polygonum lapathifolium</i> ^E		<i>Polygonum lapathifolium</i>
SFC	A #			<i>Cirsium setosum</i>		
	B #			<i>Hemarthria altissima</i>		
	C #			<i>Zea mays</i>		
NF	A <i>Xanthium sibiricum</i>					
	B <i>Setaria viridis</i>	<i>Artemisia argyi</i>				
	C <i>Zea mays</i>					

indicates no data;

DW: deep water site, SW: shallow water site, SF: seasonally flooded site, SFC: 'control site' for seasonally flooded site, NF: non-flooded site;

A, B, C indicates sample plot with different vegetation;

Species with aerenchyma are denoted ^A, species that are emergent are denoted ^E.

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through a 100 mesh sieve), TC and TN were analyzed using an elemental analyzer (vario MACRO cube, Elementar, Germany). Soil bulk density was measured following Chinese national standards NY/T 1121.4-2006 [26].

To determine which species had aerenchyma tissues, thin hand sections were made of roots and stems (photomicrographs were made). The aboveground biomass of every replicate in the chamber was weighed after drying at 80°C to constant mass.

Diurnal air temperature was measured by a digital thermometer (JM624, Jiming, China) at the start and end of each gas sampling at every plot.

Statistical analysis

Reported daily fluxes were obtained by averaging the means of the three-hourly values. To estimate how much CH₄ was transported by vegetation and to calculate the differences between species, plant-mediated flux was estimated on the basis of the difference between the flux before and after vegetation removal. We followed Kankaala et al. [27] to derive a mass-based plant transport index, PTI:

$$PTI = \frac{AF}{B} = \frac{\text{flux with aboveground vegetation} - \text{flux without aboveground vegetation}}{\text{biomass}}$$

The Kruskal–Wallis H test was used to test for spatial difference of flux and the Mann–Whitney U test for further multiple comparisons. Spatial differences of soil properties were analyzed with one-way ANOVA, and then LSD for multiple comparisons. A log₁₀ transformation was used to show the correlation between water depth and CH₄ flux. A value of 0.5 was added to the flux data before transformation to make sure that all of the data were positive. Spearman analyses were used for correlations between

flux and environmental factors. All the analyses above were performed using IBM SPSS Statistics (19.0, IBM, USA). Charts were made using SigmaPlot (11.0, SYSTAT, USA).

Results

Spatial and seasonal variation of CH₄ flux

CH₄ fluxes at the five sites showed significant differences (n = 324, p < 0.05; Figure 4). CH₄ fluxes at permanently flooded sites, both the deep and shallow water sites (DW: 3.1 ± 0.5 mg m⁻² h⁻¹; SW: 1.3 ± 0.2 mg m⁻² h⁻¹), and the seasonally flooded site (2.1 ± 0.4 mg m⁻² h⁻¹) were significantly higher than non-flooded sites. The seasonally flooded site SF, which was flooded for two months, emitted higher (1.6 times) CH₄ than the permanent flooded site SW with shallow water. The seasonally flooded site SF was dramatically higher than its control site, SFC (the flux was 247 times higher). Although the never-flooded site NF presented as a weak sink (-2.7 ± 9.2 10⁻³ mg m⁻² h⁻¹), while site SFC was a weak source (8.7 ± 8.9 10⁻³ mg m⁻² h⁻¹), there was no significant difference between them (n = 144, p > 0.05). The average CH₄ emission from all the flooded sites (DW, SW and SF) was about 1120 times higher than the non-flooded sites (SFC and NF).

There were different seasonal patterns among different sites (Figure 5). CH₄ flux at site DW and SW continuously increased from November 2011 to August 2012, and thereafter decreased gradually. CH₄ flux at site SF increased slightly from November 2011 to July 2012. After flooding it rose sharply (from 0.05 mg m⁻² h⁻¹ to 6.4 mg m⁻² h⁻¹) to a high peak, and then remained the highest emitter among all sites until the autumn. The seasonal pattern of site NF was totally contrary to sites DW, SW and SF; although the amplitude of flux was narrow. It decreased from autumn to the following summer, and then increased gently. CH₄ flux at site SFC was as low as site SF before it was flooded.

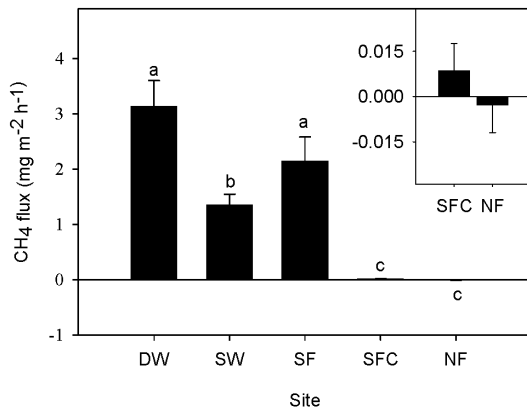


Figure 4. CH₄ flux (mean ± SE) at different sites. Bars with different letters indicate a significant difference at $p < 0.05$. Positive values of flux indicate a CH₄ source. Inset in the top right-hand corner shows SFC and NF on a different scale. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site. doi:10.1371/journal.pone.0094275.g004

Effects of environmental factors

Considering all the cases where the water depth was 2 m or less, the water depth was positively correlated with CH₄ flux ($n = 324$, $p < 0.01$; Table 2). When there was standing water (water depth > 0 cm; Figure 6), the habitat always emitted more CH₄ than when there was no standing water (water depth < 0 cm).

Soil properties varied according to the zone: TC and TN were highest at site DW and lowest at site NF, while bulk density showed an opposite trend ($n = 60$, $p < 0.05$; Figure 3). Soil TC and TN were positively correlated with flux at all sites ($n = 324$, $p < 0.01$; Table 2), as well as individually at sites DW and SFC ($n = 72$, $p < 0.01$). Bulk density was negatively correlated with flux at the whole-site scale ($n = 324$, $p < 0.01$; Table 2), and no significant correlations were found at separate sites ($n = 72$, $p > 0.05$).

There were large differences in CH₄ flux before and after the removal of aboveground vegetation at all sites (Figure 7). After vegetation removal, fluxes at sites DW and SW decreased by approximately 50% (47% and 53%, respectively), while the contribution of transportation at site SF was much smaller (6%). For the two emergent sites, SFC and NF, where fluxes were very small, opposite patterns were found. After the plants were removed, emissions at site SFC increased, while at site NF they decreased. The plant transportation index differed among the five sites and 14 plots (Figure 8). It showed seasonal variation, with the highest transportation efficiency found in spring or summer at most of the sites.

CH₄ emissions showed different patterns with different plant species after flooding at site SF (Figure 9). High CH₄ emissions (from $9.6 \text{ mg m}^{-2} \text{ h}^{-1}$ to $21.1 \text{ mg m}^{-2} \text{ h}^{-1}$; average: $14.2 \pm 2.5 \text{ mg m}^{-2} \text{ h}^{-1}$) were recorded at the plot with *Cirsium setosum* after the flooding (August; flooded for 20 days), which was 6.8 and 5.1 times higher than the site with *Polygonum lapathifolium* (from $1.6 \text{ mg m}^{-2} \text{ h}^{-1}$ to $2.6 \text{ mg m}^{-2} \text{ h}^{-1}$; average: $2.1 \pm 0.2 \text{ mg m}^{-2} \text{ h}^{-1}$) and *Hemarthria altissima* (from $2 \text{ mg m}^{-2} \text{ h}^{-1}$ to $4.1 \text{ mg m}^{-2} \text{ h}^{-1}$; average: $2.8 \pm 0.5 \text{ mg m}^{-2} \text{ h}^{-1}$), respectively. At the same time, the lowest water DO (30%–33%) was observed at the plot with *C. setosum* when the flux was the highest. Water DO was negatively correlated with flux at all flooded sites (DW: $n = 72$, $p < 0.01$; SW: $n = 72$, $p < 0.01$; SF: $n = 24$, $p < 0.01$; Table 2).

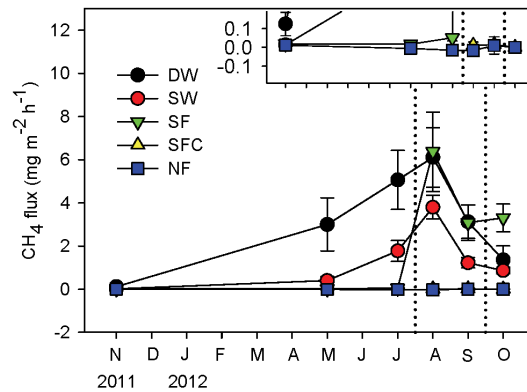


Figure 5. Monthly variation of CH₄ flux (mean ± SE) at different sites. A positive value of flux indicates a CH₄ source. Inset in the top right-hand corner shows SFC and NF on a different scale. Days between dotted lines was the high water level period and thus the seasonally flooded site (SF) was under water. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site. doi:10.1371/journal.pone.0094275.g005

The vegetation biomass began to increase in July and peaked in September to October (Figure 2C). There was a significantly negative correlation ($n = 324$, $p < 0.01$; Table 2) between flux and biomass when all sites were taken as a whole. However significantly positive correlations were observed at sites DW and SF ($n = 72$, $p < 0.01$; $n = 72$, $p < 0.05$). No significant correlations were found at the other three sites ($n = 72$, $p > 0.05$).

Air temperature positively correlated with CH₄ flux at sites DW and SW ($n = 72$, $p < 0.01$; Table 2), but was negatively correlated at site NF ($n = 72$, $p < 0.05$). No significant correlations were observed at sites SF and SFC ($n = 72$, $p > 0.05$; $n = 36$, $p > 0.05$).

Discussion

High CH₄ emissions from the littoral zone

The average CH₄ emission rate ($1.3 \text{ mg m}^{-2} \text{ h}^{-1}$) from the littoral zone of Miyun Reservoir was 6.5 times higher than the flux from the open water area ($0.2 \text{ mg m}^{-2} \text{ h}^{-1}$) [28]. The low emissions from open water are similar to those from reservoirs at higher or lower latitudes, but in those cases the littoral zone has not been investigated [29,30]. Reservoirs differ enormously in the percentage of their area that can be deemed 'littoral'. In the case

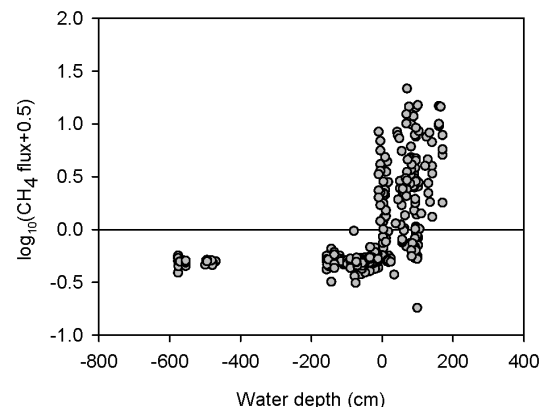


Figure 6. Relationship between water depth and CH₄ flux. doi:10.1371/journal.pone.0094275.g006

Table 2. Correlation coefficient *R* between CH₄ flux and environmental parameters.

Site	Water level	Soil TC	Soil TN	Soil bulk density	Biomass	Water DO	Air temperature
all sites	0.75**(324)	0.62**(324)	0.56**(324)	-0.53**(324)	-0.26**(324)	-0.28**(168)	0.25**(324)
DW	0.38**(72)	0.45**(72)	0.43**(72)	-0.02(72)	0.42**(72)	-0.31**(72)	0.63**(72)
SW	0.42**(72)	-0.06(72)	-0.05(72)	-0.03(72)	0.08(72)	-0.32**(72)	0.65**(72)
SF	0.74**(72)	0.19(72)	0.12(72)	0.07(72)	0.24*(72)	-0.51*(24)	0.08(72)
SFC	0.47**(36)	0.57**(36)	0.57**(36)	0.24(36)	-0.31(36)	#	0.10(36)
NF	-0.02(72)	-0.14(72)	-0.15(72)	0.05(72)	-0.03(72)	#	-0.28*(72)

indicates no data;

Numbers in () indicate the sample size;

TC: total carbon, TN: total nitrogen, DO: dissolved oxygen;

** indicates significant correlation ($P < 0.01$), * indicates significant correlation ($P < 0.05$).

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of Miyun, in the period from 1984 to 2005, the average area of the water surface was $103 \pm 15 \text{ km}^2$, while its annual difference was $9.5 \pm 2 \text{ km}^2$ [23]. Although the seasonally flooded area is as high as 8.5% of the total area of the reservoir, it explains how the littoral component of emissions is as much as 40% of the total. The high level of emissions from the littoral zone emphasizes its status as a methane hotspot in this case, but not all reservoirs will have a littoral zone comprising such a high percentage of the total. Although the present study involving 15 typical habitats, there are still uncertainties in the estimation because of high spatiotemporal flux variation and environmental heterogeneity, as demonstrated by the complex effects of plant, soil and temperature on fluxes found in this research. Furthermore, the dynamics of the littoral zone exacerbates the uncertainty. Nevertheless, emissions from the littoral zone are likely to form a substantial part of the reservoir's methane budget, and deserve further research [10,31].

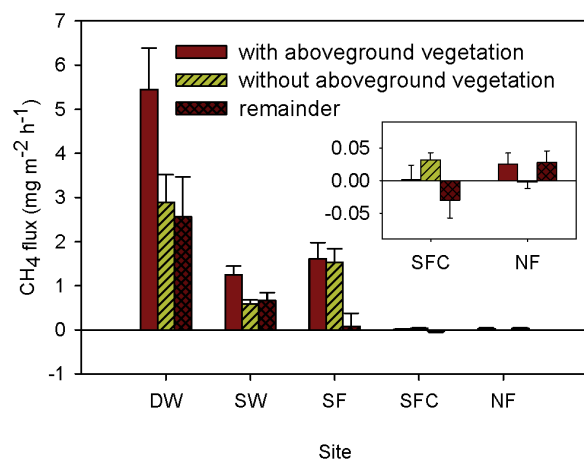


Figure 7. Contribution of aboveground plants to CH₄ flux (mean \pm SE) of each site. A positive value of flux indicate a CH₄ source. A positive remainder means methane is transported from the vegetation to the atmosphere. Inset in the right-hand center shows SFC and NF on a different scale. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site.

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Water level fluctuation and increased CH₄ emissions from the littoral zone

After 20 days of flooding, CH₄ emissions from site SF increased sharply to the highest level among all sites, and this high rate lasted to October (Figure 5). In contrast, a decreasing of CH₄ emissions was reported at a site in Finland and was explained by diminished plant-mediated transportation and decreased carbon supply from growing plants to the rhizosphere after plants were totally submerged [16]. In another study, different patterns were shown when flooding occurred in different seasons; CH₄ emissions were negligible after flooding in autumn or winter, but increased sharply after flooding in summer [32]. Based on the present work, we suggest that anaerobic plant decomposition, which apparently occurred at site SF after flooding, is the main reason for high emissions. Elsewhere, it has been shown to be the cause of CH₄ loss from tropical reservoirs [33]. Our situation was similar, but one in which the effect was more rapid due to the herbaceous environment.

Different fluxes among flood-tolerant and -intolerant plants were observed. In the case of the flood-intolerant *C. setosum*, flooding caused a sharp increase in emissions, but for the flood-tolerant *P. lapathifolium* and *H. altissima*, under the same water depth, no sharp increase was seen. This phenomenon might be the reason for the difference between the aforementioned research in Finland and that of our own; their research was carried out at places where *Carex* is the main vegetation, which does not rot immediately after flooding [16]. Different responses of plant species to flooding help to explain the spatial variation, and this could represent a potential approach to reducing methane emissions, i.e., through careful vegetation management.

The lowest water DO found in the plots with flood-intolerant species (Figure 9) may be the result of oxygen consumption during plant tissue decomposition [34]. Variations in CH₄ emissions have sometimes been attributed to variations in methane oxidation [35]. The observed negative relationship between DO and CH₄ flux (Table 2) asserts the importance of available DO and plant decomposition on CH₄ loss. A dramatic rise in CH₄ emissions appeared when the DO fell to approximately 30%, suggesting that 30% might be the lower bound of usable DO concentration for methanotrophs. However, more work on this aspect is needed, since CH₄ oxidation is a complex process affected by many factors, including microorganisms, temperature, water content, and redox potential [36,37]. It is therefore probable that the DO threshold will vary across different habitat types.

It is conceivable that wetlands featuring a littoral zone constituting a relatively large proportion of the total area, as well

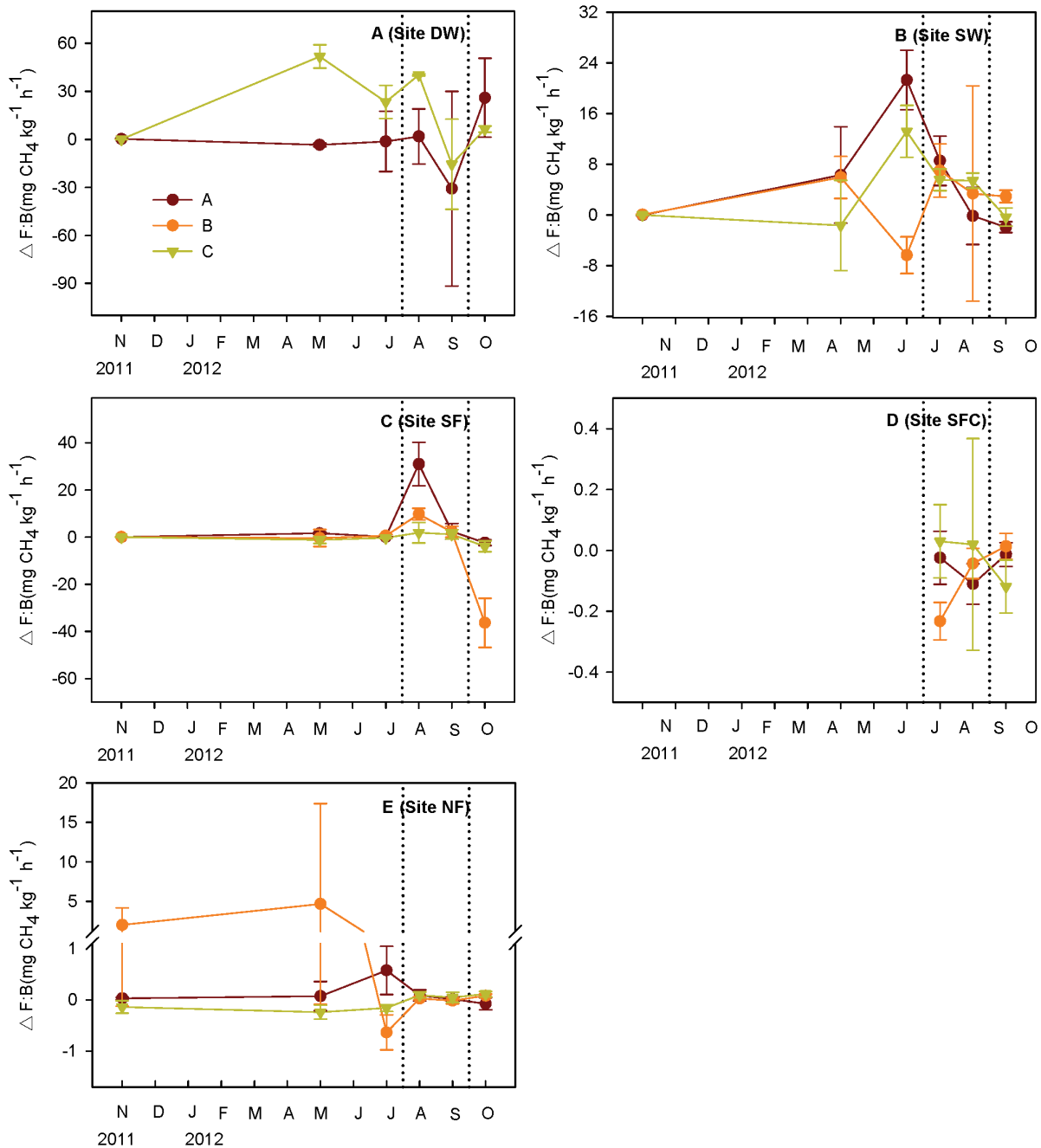


Figure 8. Above-ground plant transport index (mean \pm SE). ΔF ($\text{mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$) is the flux with vegetation minus the flux without vegetation, i.e. the flux of methane that can be attributed to the presence of the vegetation. B (kg m^{-2}) is biomass. A positive flux means methane is transported from the vegetation to the atmosphere. Days between dotted lines was the high water level period and thus the seasonally flooded site (SF) was under water. DW: deep water site; SW: shallow water site; SF: seasonally flooded site; SFC: 'control site' for the seasonally flooded site; NF: non-flooded site.

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as frequent water level fluctuations, might produce especially high emissions when the majority of the plant community comprises flood-intolerant species. It is further conceivable that climatic variability, i.e., an increased risk of flood and drought [38], will exacerbate methane production because of CH₄ emissions caused by unusual water level fluctuations, and those associated with re-flooding. For example, these conditions occurred in China after an extreme drought in 2010–2011, which caused the drying out of numerous lakes, giving them the appearance of grasslands,

exemplified by a well-documented case at the largest freshwater lake in China, Poyang, which has an area of 3,150 km² [39].

Effects of water depth on the flux through soil and plants

Water depth determines soil and plant conditions, which in turn influence CH₄ flux through different mechanisms. However, we found these effects to be sometimes limited by the water depth itself.

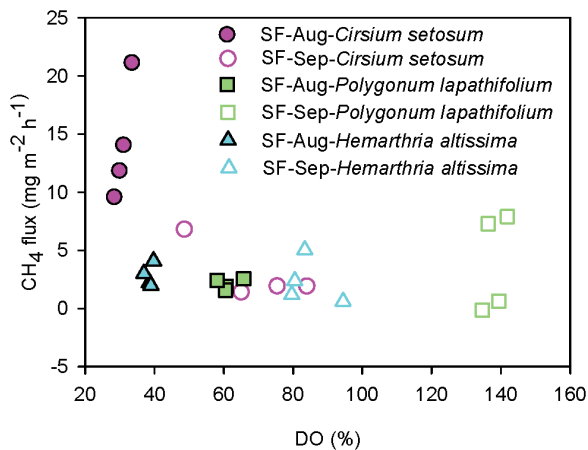


Figure 9. Relationship between dissolved oxygen (DO) of water and flux of the seasonally flooded site (SF).
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Flooding decreases the soil redox potential [40–42], which affects both methanogenesis activity and gas transfer through plant tissues [43]. Besides, the anaerobic conditions inhibit aerobic respiration and thus allow more organic matter accumulation [44,45], which was the likely reason for the soil nutrients pattern found in our research (Figure 3). Carbon and nitrogen compounds form the substrate for CH₄ production [46,47]. Positive correlations are usually observed between soil nutrients and CH₄ emissions [48,49]. However, the insignificant correlations at SW, SF and NF suggested that the effect of soil nutrients was sometimes weak, and even dominated by other factors. A similar result has also been shown at a grassland site in Germany, where flux was found to be positively correlated with soil moisture but not nitrogen fertilizer application from 0 to 450 kg N ha⁻¹ yr⁻¹ [50]. High accumulation rates of organic matter forms a soil that has a low bulk density [51] and high porosity [52], which might accelerate CH₄ diffusion in soil pores, leading to methane release [53]. Our results agree with the literature, showing that the water level influenced CH₄ production through the soil redox potential and availability of organic substrates.

Plants are another important reason for the spatial pattern of flux. An apparent interspecific difference in the plant-mediated flux was found at site DW (Figure 8A), i.e., the flux transported by emergent plants was much higher than that of totally submerged plants. Higher emissions from emergent plants have also been observed at a Qinghai–Tibetan Plateau wetland, although they did not reduce the flux through the water surface [54]. Emergent macrophytes with a well-developed vascular system and with aerenchyma can be an important pathway for CH₄ transportation from sediment to atmosphere [55]. Although submerged plants have also developed aerenchyma, even a thin film of water over

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the leaves and stems might inhibit gas release from plant tissues since the diffusive velocity of gases in water is much slower than in air, by a factor of 10⁴ [56]. In such cases, emissions will be suppressed until the time when ebullition begins. Further interpretation in this regard came from a study in which it was found that CH₄ emissions in a sedge-dominated zone decreased significantly, when the flood level was high enough to submerge the venting structures of the plants [16].

Much variation in plant-mediated CH₄ emissions among the five sites was observed (Figure 7), decreasing by 99% along the water depth gradient from water to dry land. Around 50% of the CH₄ emissions was transported by plant tissues at the permanently flooded sites (DW and SW), as was also found in a marsh with *Spartina alterniflora* [57]. Plant-mediated fluxes from the same species growing under different water depths were different, e.g., sites SF and SFC (Figures 9C and 9D). This shows that, although the transportation ability was different among plant species, it was nevertheless highly dependent on flooding.

Besides the spatial pattern, plant development is also considered as an explanation for the seasonal variation of CH₄ flux. There were positive correlations between flux and the biomass of sites DW and SF (Table 2). Gas transportation through aerenchyma is the most likely explanation [55,57]. Besides, we also calculated methane flux per kilogram of biomass as an index of transportation efficiency (Figure 8). The arched patterns of plant transportation at sites DW and SW suggest that vegetation activity might be correlated with plant transportation capacity [58–60]; and the high level of emissions in summer were caused not only by the high biomass, but were also influenced by the high transpiration rate of vegetation (methane dissolved in plant water can be transported from soil to the leaves, and hence reach the atmosphere). The interaction between biomass and transportation efficiency might be a reason for the lack of correlation between biomass and emissions at sites SW, SFC and NF (Table 2). Taking all sites as a whole, a negative correlation between flux and biomass was observed (Table 2), but this relationship is affected by the fact that the lowest CH₄ emissions and highest biomass were found at the driest site.

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Author Contributions

Conceived and designed the experiments: GL MY Y. Zhou CL. Performed the experiments: MY XG CL Y. Zhu. Analyzed the data: MY JG XG. Contributed reagents/materials/analysis tools: GL MY XG Y. Zhu CL. Wrote the paper: MY JG CL.

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