

Physicochemical controls of diffusive methane fluxes in the Okavango Delta, Botswana

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Abstract Atmospheric methane (CH₄) is one of the three key greenhouse gases (GHGs) driving global climate change. The atmospheric concentration of CH₄ has increased by about 150 % above pre-industrial levels of 400–700 ppb due to anthropogenic activities. Although tropical wetlands account for 50–60 % of the global wetland CH₄ emissions, the biogeochemistry of these wetlands, including controls of CH₄ emissions from the systems, is poorly understood compared to temperate wetlands. This has resulted in large inter-model variations of the magnitude and distribution of CH₄ emission estimates from these tropical wetlands. A recent study in the Okavango Delta, Botswana, estimated diffusive CH₄ flux at 1.8 ± 0.2 Tg year⁻¹, accounting for 2.8 ± 0.3 % of the total CH₄ emission from tropical wetlands. In this paper we present an assessment of relationships between diffusive CH₄ flux rates and physicochemical variables in the overlying water column to identify and understand regulatory variables for the diffusive CH₄ fluxes in the Delta. The results show that diffusive CH₄ flux rates from the Delta seem to be controlled by a combination of physicochemical variables. Although site specific fluxes seem to be controlled

by different combinations of factors, temperature was the primary predictor of CH₄ flux rates at almost all the sampled habitats and sites in the Delta. Most physicochemical variables, especially in the permanent swamps, were correlated with temperature implying that their regulatory effect on diffusive CH₄ fluxes could be modified by climate change feedback as well.

Keywords Okavango · Wetland · Methane flux · Carbon cycling

Introduction

Atmospheric carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) trap infrared radiation emitted from the earth's surface, thereby serving as key greenhouse gases (GHGs) which drive climate change. The atmospheric concentrations of these GHGs have increased by about 40, 150 and 20 %, respectively, above pre-industrial levels due to anthropogenic activities. For instance, analysis of ice core records representing the last 650 kyear B.P. showed that CH₄ concentrations in the earth's atmosphere varied between 400 and 700 ppb only, but increased significantly during the post-industrial-revolution era to a global average concentration of 1,775 ppb in 2005 (Spahni et al. 2005). At the current concentration of 1,803 ppb, CH₄ is the second most abundant GHG in the atmosphere after CO₂ at 391 ppm (IPCC 2013). Despite its relatively trace concentrations in the

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atmosphere, CH₄ accounts for between 15 and 20 % of the total radiative forcing caused by anthropogenic GHGs (Chen and Prinn 2006; Tang et al. 2014). This has happened because the absorption potential of CH₄ for infrared radiation is 25 times higher than that of CO₂ at a mole to mole ratio (Lashof and Ahuja 1990; Lelieveld et al. 1998), such that its rapid increase in the atmosphere is of serious concern to atmospheric chemistry and global warming.

Atmospheric CH₄ originates from biogenic and abiotic (non-biogenic) sources. While abiotic sources include fossil fuel (natural gas, petroleum and coal) burning, biomass burning and geological (geothermal and volcanic) sources, biogenic sources, which collectively account for more than 70 % of the total global CH₄ emission of 503–610 Tg year⁻¹, include wetlands, rice agriculture, ruminant animals, landfill and termites (Denman et al. 2007). Wetlands, because of their anaerobic conditions, high organic matter content and large areal coverage of $\sim 5.3 \times 10^6$ km² (Matthews and Fung 1987), constitute the largest biogenic source of CH₄ in the world contributing between 100 and 231 Tg CH₄ year⁻¹ (Denman et al. 2007). According to Bartlett and Harriss (1993) and Cao et al. (1996b), tropical wetlands release about 60 % of the total wetland emissions.

CH₄ emissions from wetlands are generally ecosystem specific with large spatial and temporal variations controlled by climatic and soil environments. While most temperate wetlands have been extensively assessed for CH₄ emissions, very few studies have been conducted in tropical wetlands including the Okavango Delta in northwestern Botswana (Nahlik and Mitsch 2011). An extrapolation of recent direct flux measurements using static chambers by Gondwe and Masamba (2014) estimated high diffusive CH₄ emissions from the Okavango Delta (1.8 ± 0.2 Tg year⁻¹) which account for 2.8 ± 0.3 % of total global emission of 65 Tg year⁻¹ for tropical wetlands. However, the study did not assess the factors driving diffusive CH₄ emissions in the Delta. An adequate understanding of the factors and processes controlling CH₄ emissions in wetlands in general is crucial for upscaling (spatial and temporal) of empirical point measurements and bottom-up process-based modeling of CH₄ fluxes.

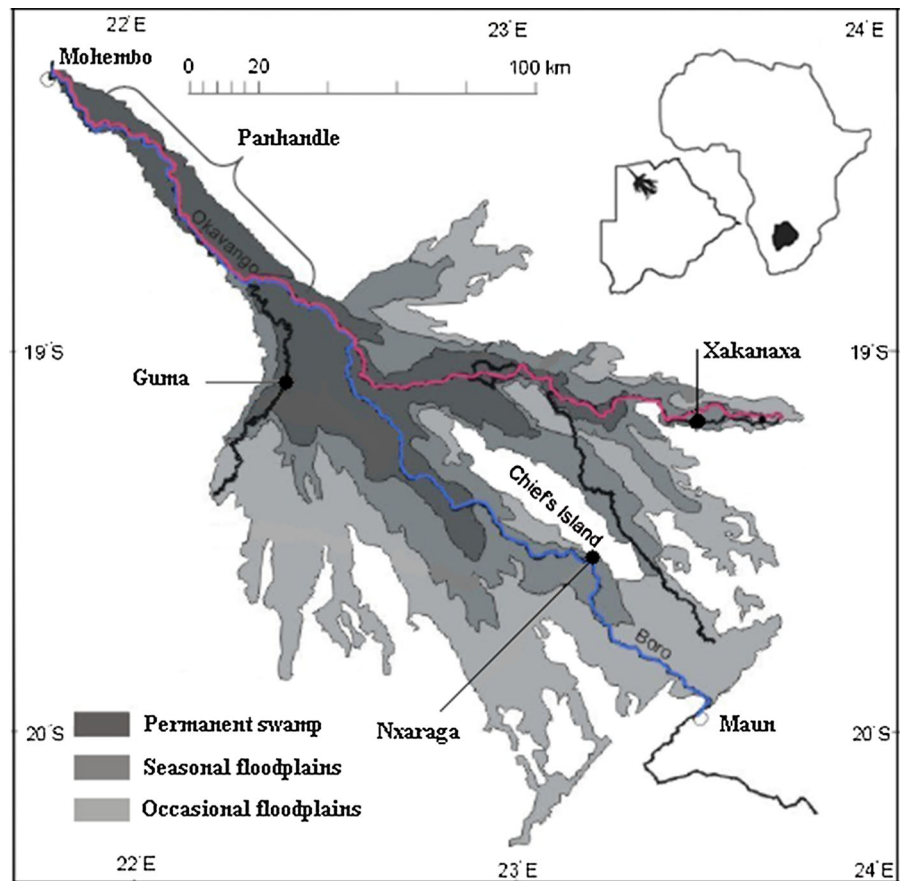
The objectives of the current study were (1) to assess the physicochemical factors controlling diffusive CH₄ emissions in the Okavango Delta and (2) to assess potential climate change feedbacks on CH₄ fluxes in the Delta.

Materials and methods

Study area—the Okavango Delta

The Okavango Delta is a large flood-pulsed inland alluvial wetland characterised by a very low level of anthropogenic transformation in semi-arid north-western Botswana (18°–20°S, 22°–24°E; Fig. 1). At almost 22,000 km², the Okavango Delta is one of the world's largest inland Deltas (Gumbrecht et al. 2004). The Delta's hydrology is dominated by seasonal pulsed inflows of runoff water which vary between 6.0×10^9 and 16.4×10^9 m³ year⁻¹ (mean of 10.1×10^9 m³ year⁻¹), supplied by the Cuito and Cubango Rivers from 1,300 mm year⁻¹ summer rains which fall between November and March in the subtropical Central Angolan highlands (Gumbrecht et al. 2004; Milzow et al. 2009). The two rivers join downstream near the Angola-Namibia boundary to form the Okavango River which proceeds across the Namibia's Zambezi Region into a narrow depression known as the Panhandle in Botswana. At the southern lower end of the Panhandle, the Okavango River divides into several distributary channels which disperse water across a generally flat (1:3,550; Gumbrecht et al. 2001) fault-bounded fan-shaped system of about 6,000 km² of permanently inundated swamp and a further 6,000–12,000 km² of seasonally (3–6 months) inundated swamps. The total area seasonally inundated in the Delta depends on prevailing floods and local precipitation over the Delta (Gieske 1997). Some of the main distributaries of the Okavango River include the Magwegqana or Selinda spillway (which under high inflow conditions may form a hydraulic connection with the adjacent Linyati River and further to the Zambezi system), the westerly Thaoge River which drains into Lake Ngami, and the central Nqoga River which branches downstream into the Jao-Boro and Maunachira-Khwai River systems (Gieske 1997). The Delta receives summer rainfall of about 490 mm year⁻¹ (6×10^9 m³ year⁻¹) in form of short thunderstorms between November and March each year (McCarthy et al. 1998). Air temperatures in the Delta region are relatively high throughout the year with summer and winter temperatures averaging ~ 35 and ~ 25 °C, respectively, which cause high potential evapotranspiration estimated at 2,172 mm year⁻¹ (McCarthy 2006). Several studies have estimated that 96–98 % of the inflow and rainfall to the Delta is lost to evapotranspiration as a consequence of the semi-arid climate, while

Fig. 1 Map of the Okavango Delta showing sampling sites—Guma in the permanent swamp and Nxaraga and Xakanaxa in the seasonal swamps. From Gondwe and Masamba (2014)



surface and groundwater outflows contribute the remainder.

Due to the Delta's low topographic gradient and dense vegetation, the flow rate of the flood water in the Delta is significantly reduced such that the water takes 4–5 months to traverse the 250 km distance from the apex at Mohembo to the distal end near Maun (Ramberg et al. 2006). As the flood water flows down the distributary channels from permanent to seasonal swamps, it leaks through the permeable vegetated channel banks to flood riparian swamps which are generally 50 cm lower than the water surface in channels. In response to the annual flood pulse, water levels in the permanent and seasonal swamps in the Delta fluctuate by approximately 20 and 100 cm, respectively, every year (McCarthy and Ellery 1994).

Study sites and habitats

The study sites and habitats which were sampled for determination of diffusive CH₄ flux rates and

physicochemical variables which potentially influence the flux rates are described in detail in Gondwe and Masamba (2014). Briefly, the study was conducted at Guma in the permanent swamp and at Nxaraga and Xakanaxa in the seasonal swamps (Fig. 1). Guma is fed by the westerly Thaoge channel and, like the rest of the permanent swamp, the area is dominated by thick stands of *Cyperus papyrus* and *Phragmites australis* and *P. mauritanius* species. The Xakanaxa area is fed by the extension of the main channel, the Nqoga-Maunachira, and is dominated by the hydrophytic grass *Miscanthus junceus*. Nxaraga characterises the seasonally flooded parts of the Delta; it receives flood pulses from the Jao-Boro system. The floodplains sampled there are co-dominated by two large sedge species, *Cyperus articulatus* and *Schoenoplectus corymbosus*. At each study site, water and gaseous sample collection and in situ physicochemical measurements were conducted over open waters (1–4 m depth) at the middle of distributary channels, floodplains and lagoons (Table 1), which represent the

Table 1 Correlation coefficients between physicochemical variables (diffusive CH₄ flux rate (Ln[CH₄]), turbidity, electrical conductivity (EC), dissolved oxygen (DO), temperature (Temp), dissolved organic carbon (DOC) and pH measured at Guma, Nxaraga and Xakanaxa

Ln[CH₄] is the natural logarithm of diffusive CH₄ flux rate (mg CH₄ m⁻² h⁻¹) while * and ** indicate significant correlations at $p \leq 0.004$ and between 0.01 and 0.05 (i.e., $0.01 \leq p \leq 0.05$), respectively

	Ln[CH ₄]	Turbidity	EC	DO	Temp	DOC	pH
Guma							
Ln[CH ₄]	1.000						
Turbidity	0.903*	1.000					
EC	0.860*	0.934*	1.000				
DO	-0.761*	-0.650*	-0.645*	1.000			
Temp	0.774*	0.798*	0.856*	-0.678*	1.000		
DOC	0.747*	0.762*	0.718*	-0.629*	0.618*	1.000	
pH	-0.156	-0.071	-0.070	0.195	0.067	-0.080	1.000
Nxaraga							
Ln[CH ₄]	1.000						
Turbidity	0.539*	1.000					
EC	-0.009	0.336**	1.000				
DO	-0.430*	-0.222	0.247**	1.000			
Temp	0.150	0.390**	-0.008	0.019	1.000		
DOC	-0.141	0.051	-0.006	0.184	0.676*	1.000	
pH	0.766*	0.591*	0.136	-0.319**	0.153	0.068	1.000
Xakanaxa							
Ln[CH ₄]	1.000						
Turbidity	-0.169	1.000					
EC	0.173	-0.467*	1.000				
DO	-0.122	-0.005	-0.428*	1.000			
Temp	0.559*	0.242	-0.125	-0.128	1.000		
DOC	0.047	0.036	0.208	-0.278**	-0.061	1.000	
pH	-0.004	0.160	-0.035	0.161	0.317**	-0.074	1.000

major inundated habitats in the Delta. While diffusive CH₄ fluxes occur from all inundated wetland habitats (vegetated and non-vegetated), the open water surface was chosen in order to eliminate contamination from gas bubble ebullition and advective transport through hydrophilic vegetation. According to Chanton and Dacey (1991) and Wassmann et al. (1992), CH₄ emission rates from ebullition and advective pathways are generally significantly higher than diffusive fluxes, which make it difficult to isolate diffusive fluxes from measurements done in these areas.

Physicochemical parameters in surface water

At each sampling point, in situ measurements of surface water temperature (°C) and electrical conductivity (EC, $\mu\text{S cm}^{-1}$), dissolved oxygen (DO, mg L^{-1}) and pH were done using, respectively, Cond 330i/SET, Oxi 330i/SET and pH 340i/SET portable field meters by Wissenschaftlich-Technische Werkstätten (WTW), Germany. Water turbidity (NTU) was measured using

a TN-100 turbidimeter by Eutech Instruments, Singapore. Water samples for estimation of dissolved organic carbon (DOC, mg L^{-1}) were collected from below the water surface at all sampled habitats and filtered through 0.45 μm GF/C filters into clean acid-washed polyethylene bottles which were stored at 4 °C until analysis. Estimation of DOC in the filtered water samples was done according to Mladenov et al. (2005) and Mackay et al. (2011) by measuring ultra-violet (UV) absorbance at 280 nm wavelength on the Lambda 20 Perkin Elmer UV/VIS Spectrometer at the Okavango Research Institute, Maun, Botswana.

Diffusive methane fluxes

Diffusive CH₄ fluxes were measured using two static chambers which were deployed simultaneously on the water surface for 40 minutes in the morning (between 07:30–10:00 h), mid-day (11:00–14:00 h) and evening (16:00–18:30 h) at the middle of distributary channels, floodplains and lagoons at Guma, Nxaraga and

Xakanaxa study sites (Fig. 1). Further details about headspace collection from the static chambers and subsequent CH_4 analysis at the Okavango Research Institute, Maun, Botswana using a Buck Scientific Model 310 Gas Chromatograph fitted with a flame ionization detector (FID), have been provided in Gondwe and Masamba (2014). A total of 359 CH_4 flux measurements were made once every 2 months over a one-year study period between December 2010 and January 2012, approximately 1 % of which were rejected for poor coefficients ($r^2 < 0.8400$; Gondwe and Masamba 2014) of linear regression between diffusive CH_4 concentrations and static chamber deployment time (40 min).

Data analysis

Scatter plots between physicochemical variables (temperature, EC, DO, pH, DOC and turbidity) of the water column and diffusive CH_4 flux rates were prepared using Sigmaplot 8.0 software by Systat Software Inc, San Jose, CA, USA. We also tested whether diffusive CH_4 flux rates in the Okavango Delta were dependent on the physicochemical variables mentioned above using a stepwise multiple regression analysis in IBM SPSS Statistics version 21 software at alpha level of significance of 0.05.

Results

Temporal and spatial variations in temperature, EC, pH, turbidity, DO and DOC in surface waters in

channel, floodplain and lagoon habitats at Guma, Nxaraga and Xakanaxa study sites have been presented and discussed in Gondwe and Masamba (2014).

Correlation between DOC and other physicochemical variables

DOC concentrations in habitats (channel, floodplain and lagoon) at Guma increased with water temperature (Fig. 2a), EC (Fig. 2g) and turbidity (Fig. 2j) levels but decreased with dissolved oxygen (Fig. 2d) and, although weakly, pH (Fig. 2m; $r^2 = 0.1675$). Unlike at Guma, DOC concentrations at Nxaraga were only correlated with EC (Fig. 2h; $r^2 = 0.7219$, $p < 0.0001$). At Xakanaxa the correlation of DOC with temperature was the poorest at r^2 of 0.0613 (Fig. 2c) compared to the rest of the physicochemical parameters (r^2 between 0.4380 and 0.5721). DO (Fig. 2f), turbidity (Fig. 2l), and pH (Fig. 2o) were generally inversely correlated with DOC levels in the water column at Xakanaxa while EC showed a positive correlation with DOC levels both at Nxaraga and Xakanaxa as at Guma (Fig. 2g–i).

Diffusive CH_4 fluxes

As with DOC concentrations, diffusive CH_4 fluxes at the three studied habitats (channel, floodplain and lagoon) at Guma increased exponentially as water temperature, EC, turbidity and DOC increased during the study period (Figs. 3a,d, 4d, 5d, respectively). While water temperature (Fig. 3a–c) and

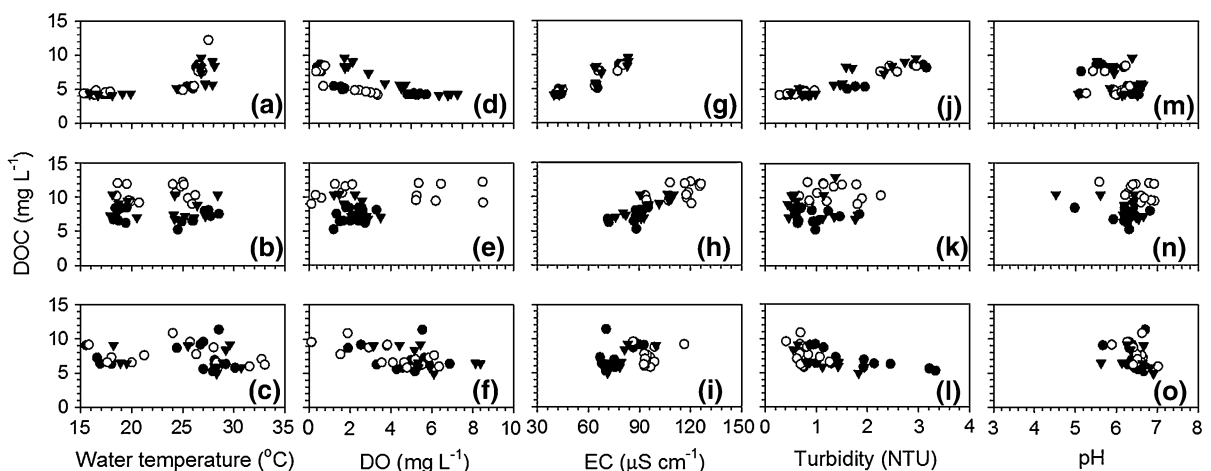


Fig. 2 Relationship between dissolved organic carbon (DOC) and temperature, DO, EC, turbidity and pH in surface waters in channels, floodplains and lagoons at Guma (a, d, g, j, m), Nxaraga (b, e, h, k, n) and Xakanaxa (c, f, i, l, o) study sites

Fig. 3 Relationship between diffusive CH_4 flux rates and water temperature and electrical conductivity (EC) in channels, floodplains and lagoons at Guma (a, d), Nxaraga (b, e) and Xakanaxa (c, f) study sites

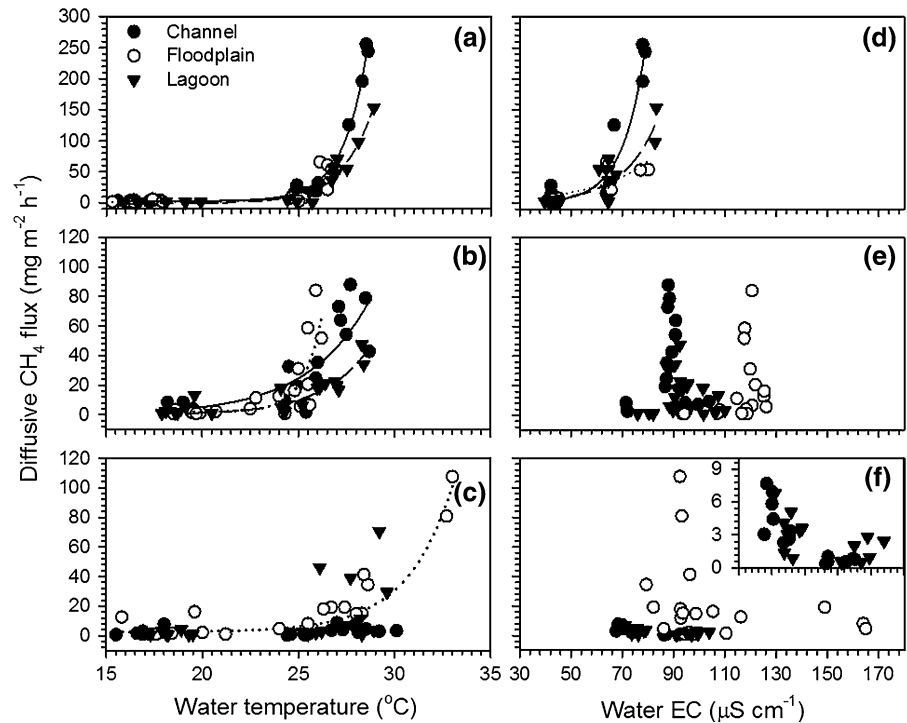
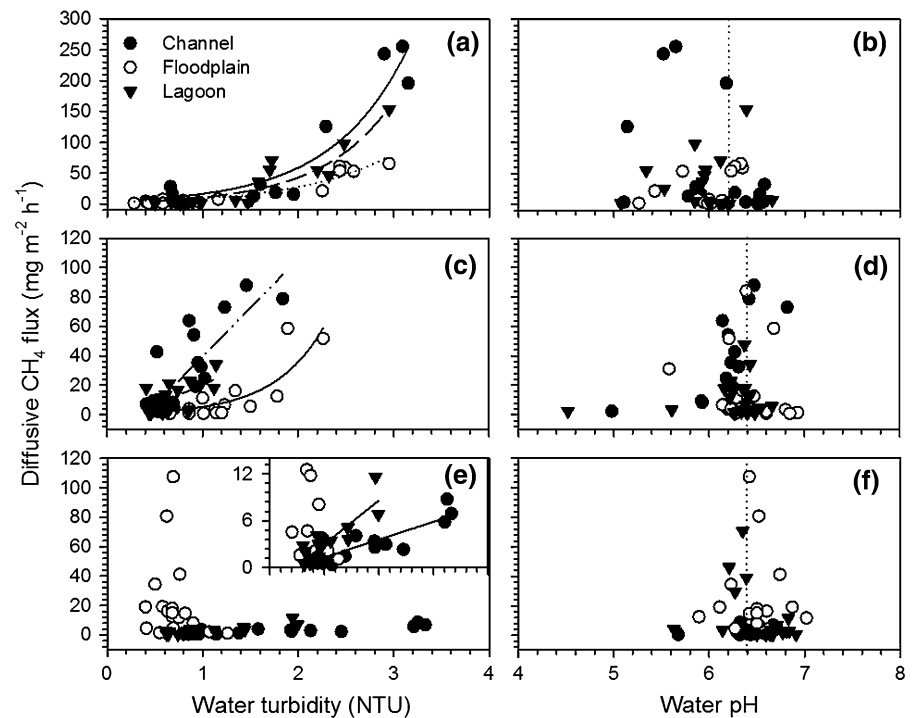


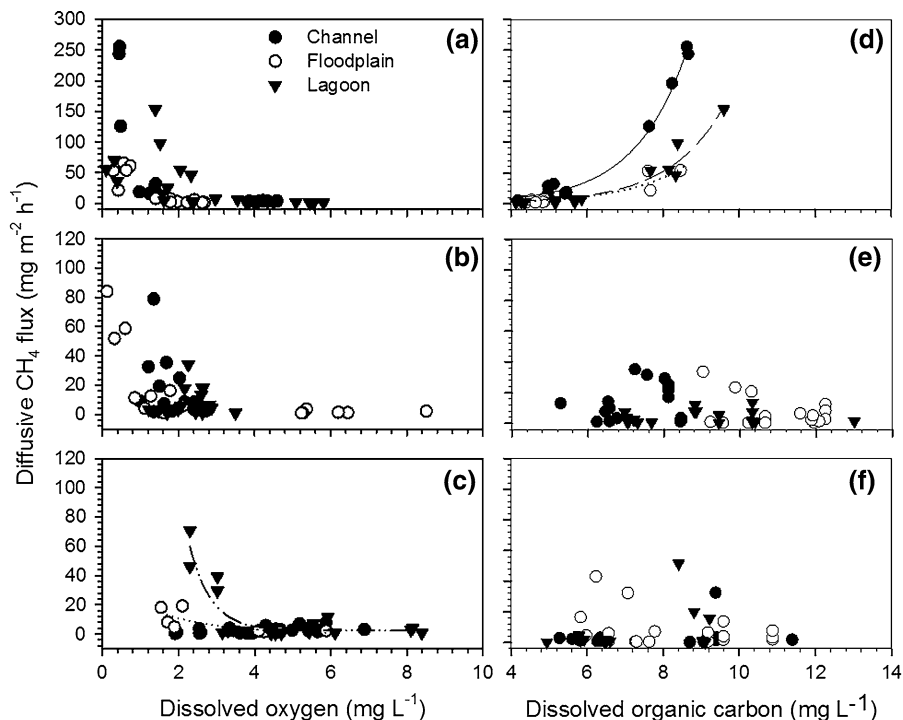
Fig. 4 Relationship between diffusive CH_4 flux rates and water turbidity and pH in channels, floodplains and lagoons at Guma (a, d), Nxaraga (b, e) and Xakanaxa (c, f) study sites. Dotted vertical lines in b, d and f panels indicate pH values at which maximum diffusive CH_4 flux rates were observed at Guma, Nxaraga and Xakanaxa, respectively



turbidity (Fig. 4a–c) generally showed the same relationship with diffusive CH_4 fluxes at Nxaraga and Xakanaxa as at Guma, EC did not (Fig. 3d–f).

At Nxaraga for instance, diffusive CH_4 fluxes peaked at an EC of $90 \mu\text{S cm}^{-1}$ in the channel and lagoon and at $120 \mu\text{S cm}^{-1}$ in the floodplain

Fig. 5 Relationship between diffusive CH_4 flux rates and dissolved oxygen and dissolved organic carbon in channels, floodplains and lagoons at Guma (a, d), Nxaraga (b, e) and Xakanaxa (c, f) study sites



(Fig. 3e) while at Xakanaxa fluxes decreased with increasing EC, especially in the channel and lagoon (Fig. 3f, insert). As expected, diffusive CH_4 fluxes decreased as the concentration of DO (mg L^{-1}) in the water column increased at Guma, Nxaraga and Xakanaxa (Fig. 5a–c). DO did not show any relationship with diffusive CH_4 emission rates from the lagoon at Nxaraga (Fig. 5b) and channel at Xakanaxa (Fig. 5c). As noted above, water pH did not vary significantly over the duration of the study at all the sites and habitats sampled and consequently did not show any significant relationship with diffusive CH_4 emission rates from all habitats at Guma, Nxaraga and Xakanaxa (Fig. 4d–f). Figure 4d–f suggest that maximum diffusive CH_4 flux rates in the Delta occur at pH of about 6.4 at Nxaraga and Xakanaxa in the seasonal swamp but at slightly acidic pH of 6.0 at Guma in the permanent swamp.

DOC and diffusive CH_4 fluxes

Although DOC concentrations and diffusive CH_4 fluxes tended to be influenced by the same physicochemical variables especially at Guma and Xakanaxa (Gondwe and Masamba 2014), there was no correlation between

the two variables in the seasonal swamps at Nxaraga and Xakanaxa (Fig. 5e, f). In contrast, diffusive CH_4 fluxes increased exponentially with DOC in all habitats in the permanent swamp at Guma (Fig. 5d).

The equations of correlation, including coefficients of determination (r^2) and p values, between selected variables have been provided in Tables 3 and 4 in the Appendix.

Multiple regression analysis of CH_4 fluxes and physicochemical variables

Pearson correlation analysis revealed that at Guma (even at habitat level), log transformed diffusive CH_4 fluxes were significantly ($p < 0.001$) correlated with DOC, EC, DO, turbidity and temperature, but not with pH (Table 1). Furthermore all the physicochemical measurements were significantly ($p < 0.001$) correlated with each other but not with pH (Table 1). However, only turbidity and DO collectively explained about 87 % of the variations in pooled (all three habitats) diffusive CH_4 fluxes at Guma (Table 2). While DOC explained over 90 % of the variations in CH_4 fluxes from Guma channel and lagoon, turbidity explained over 95 % of the CH_4 fluxes from the floodplain there (Table 2). While log

Table 2 Unstandardized coefficients of predictors of diffusive CH₄ fluxes from channel, floodplain and lagoon habitats in the permanent swamp (PS) at Guma (GUM) and seasonal swamps (SS) at Njaraga (NXA) and Xakanaxa (XAK) using stepwise multiple regression analysis

	All habitats	Channel	Floodplain	Lagoon
PS + SS	0.191Temp - 0.238DO - 0.594pH + 2.030 (0.536, <0.0001)	0.119Temp - 0.384DO + 0.592 (0.410, <0.0001)	0.226Temp - 0.159DO + 0.444Turb - 3.085 (0.787, <0.0001)	0.158Temp + 0.636Turb - 0.781pH - 0.179DO + 2.679 (0.598, <0.0001)
PS-GUM	1.363Turb - 0.305DO + 1.087 (0.868, <0.0001)	0.131Temp + 0.691DOC - 3.936 (0.978, <0.0001)	1.626Turb - 0.197 (0.948, <0.0001)	0.875DOC - 3.397 (0.904, <0.0001)
SS-NXA + XAK	0.176Temp - 0.153DO + 0.015EC - 3.160 (0.442, <0.0001)	0.187Temp - 0.588Turb - 1.686 (0.286, 0.010)	0.232Temp - 1.422pH - 0.153DO + 6.935 (0.794, <0.0001)	0.207Temp - 0.987pH + 2.767 (0.422, 0.001)
NXA	0.271Temp - 0.154DO - 3.733 (0.625, <0.0001)	0.297Temp - 0.149DOC - 3.049 (0.879, <0.0001)	0.473Temp - 8.817 (0.797, <0.0001)	0.209Temp - 3.180 (0.465, 0.005)
XAK	0.165Temp - 0.498Turb - 1.858 (0.412, <0.0001)	1.959pH - 11.446 (0.409, 0.014)	0.244Temp - 2.740pH + 14.116 (0.853, <0.0001)	0.195Temp - 3.531 (0.357, 0.004)

Numbers in brackets are coefficients of determination (r^2) and ANOVA significance levels (p value), respectively, for the models predicting diffusive CH₄ fluxes. Temp temperature, Turb turbidity, DO dissolved oxygen and EC electrical conductivity

transformed CH₄ fluxes were significantly ($p < 0.001$) correlated with turbidity, DO and pH at Njaraga, they were only with temperature at Xakanaxa (Table 1). Physicochemical parameters were generally infrequently significantly correlated at Njaraga and Xakanaxa study sites. At Njaraga and Xakanaxa, temperature explained between 31 and 80 % of the variations in diffusive CH₄ fluxes from channels, floodplains and lagoons (Table 2).

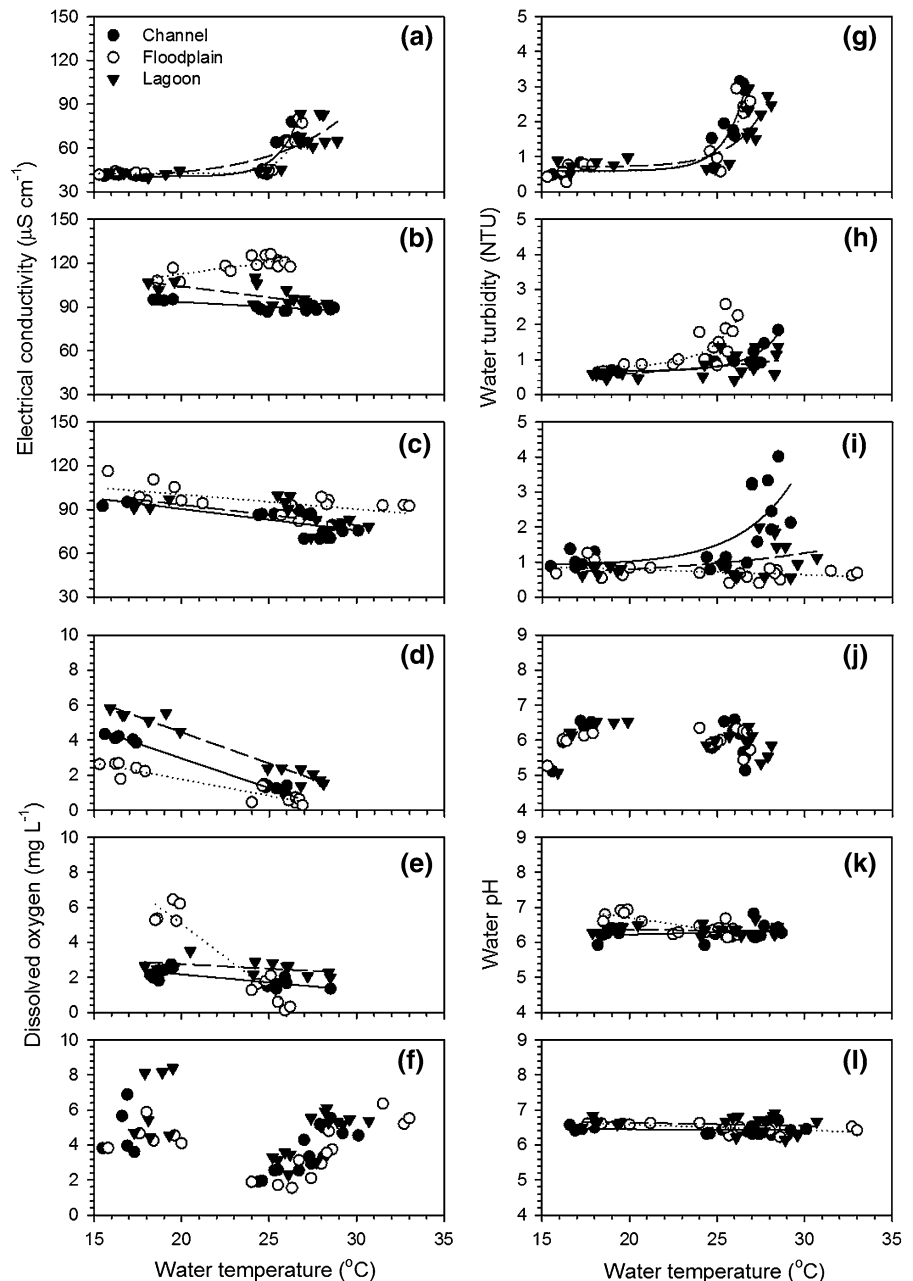
Climate change feedback on diffusive CH₄ fluxes

This study also attempted to understand how rising water temperatures due to global warming could affect diffusive CH₄ fluxes from the delta by affecting other physicochemical factors important for CH₄ fluxes. During the period of this study, the water temperature at Guma, Njaraga and Xakanaxa varied between 15 and 33 °C (Gondwe and Masamba 2014). While the concentration of DO decreased linearly with water temperature as expected at Guma and Njaraga, EC, turbidity and pH showed different trends across the study sites (Fig. 6). Turbidity generally increased exponentially with water temperature across all the three study sites except in the floodplain at Xakanaxa where it decreased linearly as water temperature increased during the study period (Fig. 6g–i). EC exponentially increased with water temperature at Guma (Fig. 6a) but it decreased again linearly at Njaraga and Xakanaxa (Fig. 6b, c). pH was not affected by temperature (Fig. 6j–l).

Discussion

The amount of CH₄ emitted from any given wetland is determined by the balance between CH₄ production in anoxic soils and CH₄ oxidation by methanotrophs at the anoxic/oxic interface and within the rhizosphere of vegetation (Cao et al. 1996a; Bridgham et al. 2013). Several studies have shown positive correlation between CH₄ fluxes and its concentrations in the sediment pore water and in overlying water. It has also been shown that most CH₄ production occurs in the top 10 cm of the soil (Crozier et al. 1995). Consequently significant correlations between CH₄ fluxes and environmental variables in the soil or sediments have been reported by many studies (e.g., Segers 1998). The current study attempted to determine how

Fig. 6 Relationship between temperature and electrical conductivity (a–c), dissolved oxygen (d–f), turbidity (g–i) and pH (j–l) in surface waters in channels, floodplains and lagoons at Guma (a, g, d, j), Nxaraga (b, h, e, k) and Xakanaxa (c, i, f, l) study sites



physicochemical variables in the water column affect diffusive CH_4 fluxes from the Okavango Delta. This is important because in the Okavango Delta, as in many other wetlands globally, frequent monitoring of environmental variables is done in the water column, not in the sediments where most of the CH_4 production occurs. As such the existence of strong and significant relationship(s) between one or more environmental variables and CH_4 flux rates can be easily used to

model changes in CH_4 fluxes over time, providing a monitoring proxy. The goal of the study was to understand how climate change may ultimately affect CH_4 fluxes from the Delta through feedback processes.

While we did not measure the physicochemical variables in the sediments, we assume that due to the shallow nature of the water column in the Okavango Delta, values of some of the variable (especially temperature, DO and pH) in the relatively aerobic

surface sediment layer (i.e., at the water-soil interface which can vary between a few mm to 2 cm Reddy et al. 2000) are likely to be closely related to values of the same in the water column, which were measured.

Dissolved organic carbon (DOC)

DOC, depending on its quantity and quality, may serve as an important source of substrates for CH₄ production in flooded soils (Lu et al. 2000). It has been observed that once anaerobic soil conditions have been met, substrate (DOC) supply (quality and quantity) may principally regulate methanogenesis (Bergman et al. 1998; Megonigal et al. 2004). For instance, Bergman et al. (1998) stimulated CH₄ production by amending peat soils with glucose which improved the quality and quantity of the carbon source. In their study CH₄ production increased as amended glucose concentration increased from 0.1 μM to 10 mM. In the current study CH₄ emissions increased exponentially with DOC concentrations at Guma which suggests that most of the DOC in the permanent swamp was readily metabolized into simple substrates for CH₄ production. The explanation here could be that the conducive reducing conditions and dense vegetation in the permanent swamp promoted high root exudation and rapid anaerobic fermentation of plant litter by a consortium of specialized obligate anaerobes which, compared to aerobic degradation, produce simple substrates for methanogenesis (Bergman et al. 1998). While fresh root exudates generally contain 50–80 % labile DOC (Marschner 1995), further bacterial hydrolysis produces more simple derivatives including acetate, H₂ and CO₂ which are the favorable substrates for methanogenesis (Yavitt et al. 1987). It is also important to note that the permanent swamp in the Okavango Delta is primarily dominated by giant sedges such as *Cyprus papyrus* which, due to their complex rhizoid system, have been reported to release more root exudates into the anaerobic sediments than other wetland vegetation. For instance Lupascu et al. (2012) reported a 40-fold higher CH₄ production rate in sedge-dominated (*Eriophorum angustiforum*) peat than in mires dominated by *Sphagnum* which contain less developed rhizoid systems (Galand et al. 2005).

Although DOC concentrations were higher at Nxaraga and Xakanaxa than at Guma (Gondwe and

Masamba 2014; also see Cawley et al. 2012), the DOC was not significantly correlated with diffusive CH₄ fluxes at the seasonal swamp sites. The poor correlation could be explained by findings from several studies (e.g., Mladenov et al. 2005, 2007; Cawley et al. 2012) which suggest that DOC concentrations observed in the seasonal swamps in the Delta are mobilized primarily from surrounding woodland/terrestrial vegetation and therefore tend to be highly refractory for methanogenic use. For instance, Cawley et al. (2012) observed that water samples in the seasonal floodplains, with three-times higher DOC levels than in the permanent swamp, displayed increasing SUVA₂₅₄ (specific UV absorbance at 254 nm normalized for DOC concentration) values indicating high percent aromaticity of DOC molecules commonly found in terrestrially- and soil-derived dissolved organic matter (DOM). This interpretation of SUVA₂₅₄ data is according to Weishaar et al. (2003) who observed a strong correlation ($r^2 = 0.97$) between SUVA₂₅₄ (L mg C⁻¹ m⁻¹) values and percent aromaticity measured by ¹³C-NMR. Generally humic substances make up the aromatic fraction of DOC in aquatic ecosystems (Weishaar et al. 2003). Since the current study and that by Gondwe and Masamba (2014) did not characterize the estimated DOC concentrations at the study sites into labile and non-labile proportions, the relationship between CH₄ emissions and DOC could not be evaluated further. It can however be postulated that a similar relationship to that observed in the permanent swamp is likely to be observed between CH₄ emission and the labile DOC proportions at study sites such as Nxaraga and Xakanaxa in the seasonal swamp as well.

Furthermore it has been shown that humic rich DOM, such as that observed in the seasonal swamps in the Delta, can suppress methanogenesis by acting as alternative electron acceptors in the anaerobic oxidation of fermentation products (Segers 1998; Heitmann et al. 2007). Although humic substances in DOM have been widely accepted as potential electron acceptors (Lovley et al. 1996), their ability to regulate methanogenesis in wetland habitats has only recently been studied.

Although DOC was correlated with diffusive CH₄ fluxes in the permanent swamp, it did not seem to limit

flux rates except in the lagoon where it explained over 90 % of the variation in the diffusive fluxes (Table 2).

Temperature

The observation that diffusive CH₄ fluxes at Guma, Nxaraga and Xakanaxa generally increased with water temperature (Fig. 3a–c) is consistent with results from previous studies (Dunfield et al. 1993; Westermann 1993). The in situ exponential relationships seen in Fig. 3a–c have previously been observed between CH₄ fluxes and temperature in laboratory experiments using peatland cores (Daulat and Clymo 1998). While CH₄ production and emission in wetland ecosystems generally increase with temperature between 2 and 40 °C (Sawyer and King 1993; Westermann 1993; Christensen et al. 2003), most isolated methanogens show optimum growth in the 30–40 °C range (Le Mer and Roger 2001; Whalen 2005). In the current study in the Okavango Delta, methanogenic activity indicated by diffusive CH₄ fluxes also increased as water temperature increased from 15 °C in winter (June–August) to about 33 °C in January (See Fig. 2 in Gondwe and Masamba 2014). Generally warmer temperatures enhance both CH₄ production and emission by stimulating metabolic activity of both methanogens and various syntrophic bacteria involved in the decomposition of organic matter to methanogenic substrates (Cao et al. 1996a). Temperature also increases net primary production up to a point (Wetzel 2001) and carbon rhizodeposition which, as noted above, is an important source of substrates for CH₄ production. However, a similar positive correlation has also been observed between temperature and microbial CH₄ oxidation in aerobic soil layers and rhizosphere. Nevertheless, while some studies have reported a strong dependence of the oxidation process on temperature (van Winden et al. 2012), others suggest a weak sensitivity of CH₄ oxidation to temperature variations (Whalen 2005). Since net CH₄ emission is determined by the balance between production and oxidation, the current study in the Okavango Delta suggests that CH₄ production increased more than its oxidation rate as evidenced by higher diffusive fluxes as temperature increased from winter to summer time.

Pearson correlation analysis revealed that temperature was a primary predictor of CH₄ flux rates at almost all the sampled habitats and sites in the Delta

(Table 2). The relationship between temperature and diffusive CH₄ fluxes (Table 2) however tended to be modified by other site-specific physicochemical factors such as the quality of DOC which in turn was influenced by spatial variations in vegetation composition and flood regime (see Gondwe and Masamba 2014).

Turbidity

Diffusive CH₄ fluxes generally increased as water turbidity increased in all the studied habitats except in the floodplain at Xakanaxa (Fig. 4a–c). This positive correlation is partly due to reduced oxidation of CH₄ as it diffuses to the water surface caused by low photosynthetic O₂ production by phytoplankton and submerged aquatic vegetation as turbidity increased (Abril et al. 2007). These results concur with King (1990) who studied CH₄ flux from wetland sediment cores overlain by an algal mat and water and reported lower CH₄ fluxes from cores under light which was attributed to increased CH₄ oxidation due to increased photosynthetic O₂ production by the algal mat. According to Kerr (1995) a 5 NTU increase in turbidity in clear-water ecosystems can reduce primary productivity by 3–13 % or more. This is partly because aquatic vegetation absorbs light energy for photosynthesis in the same region of the light spectrum where suspended sediments reflect light. These findings emphasize on the role of O₂ availability as one of the main factors limiting CH₄ emission through oxidation by methanotrophs in aquatic systems (Le Mer and Roger 2001).

On the other hand, high turbidity may also enhance CH₄ oxidation by methanotrophs attached to the suspended particles (Middelburg et al. 2002; Abril et al. 2007). A significant negative correlation between turbidity and dissolved CH₄ concentrations was first reported by Abril et al. (2007) in Garonne and Dordogne tidal rivers, France. In the study CH₄ concentrations in the water column dropped significantly despite prevailing conducive conditions for methanogenesis. This probably explains the decreasing CH₄ emissions in the floodplain at Xakanaxa as turbidity increased (Fig. 4c).

Turbidity was also positively correlated with DOC at Guma (Fig. 2j). This was also expected since DOC was positively correlated with diffusive CH₄ emissions at the same study site. No trend was however

observed between DOC and turbidity at Nxaraga (Fig. 2k) which could be due to frequent disturbance of the water column from wildlife. At Xakanaxa DOC decreased as water turbidity increased (Fig. 2l) which could be due to oxidation of the DOC by bacteria attached to suspended material and/or adsorption of DOC to suspended material.

Dissolved oxygen

The observed negative correlations between DO and diffusive CH₄ fluxes (Fig. 5a, c, e) and DOC (Fig. 2d, f) in the Okavango Delta are likely due to loss of DOC and most importantly diffusive CH₄ to methanotrophy in the water column and surface sediments (Epp and Chanton 1993; Denier van der Gon and Neue 1996). It has been shown that in the presence of DO, methanotrophs can significantly lower CH₄ fluxes from aquatic ecosystems through oxidation of between 55 and 85 % of diffusive CH₄ in oxic water columns, sediments and plant rhizospheres (Happell et al. 1993). This is why aquatic ecosystems colonized by algal mats and submerged aquatic plants tend to show lowest CH₄ flux rates during daylight when CH₄ oxidation rates are highest due to photosynthetic O₂ production (King 1990; Heilman and Carlton 2001). Variations in DO availability in aquatic systems can also be affected by temperature since the solubility of gases in water generally increases as water temperature decreases (e.g., minimum of 15 °C in winter and maximum of 33 °C in summer). Variations in CH₄ oxidation due to variations in DO availability partly explain the seasonal variations in diffusive CH₄ fluxes in the Delta observed by Gondwe and Masamba (2014). However, lower diffusive CH₄ fluxes during winter can also be directly associated with reduced methanogenesis at lower temperatures.

However, DO availability in sediments through gradient diffusion or plant aerenchyma can inhibit methanogenesis as it stimulates methanotrophy. CH₄ production is generally favored in environments with low concentrations of alternative electron acceptors such as NO₃⁻, Mn⁴⁺, Fe³⁺, SO₄²⁻ and O₂. The presence of the alternative electron acceptors enhances competition for common substrates (H₂ and acetate) between methanogens and various bacteria thereby lowering CH₄ production. However, the sequential reduction of the alternative electron acceptors by various aerobic and anaerobic bacteria helps to create strong reducing

conditions ($E_h < -300$ mV) required for methanogenesis (Conrad 1996). In addition to the competition for substrates, the metabolic products of some of the electron acceptors, particularly O₂ and NO₃⁻, have toxic effects on methanogens. A rapid and irreversible degradation of some cofactors such as Coenzyme F₄₂₀ critical in the physiology of methanogens, has been reported by Schönheit et al. (1981). More O₂-sensitive features of methanogens which include some enzymes and key cofactors for methanogenesis have been identified (Jarrell 1985). The sensitivity of methanogens to O₂ is in part believed to be caused by hydroxyl radicals (OH⁻), singlet oxygen (¹O₂) and superoxide ions (O₂⁻) which form when O₂ interacts with cells and media (Jarrell 1985; White 2000). Consequently CH₄ production is significantly inhibited in the presence of all electron acceptors except CO₂. In contrast, aerobes and other O₂ tolerant microorganisms contain detoxifying enzymes which convert O₂ radicals and hydrogen peroxide to molecular oxygen and water.

Electrical conductivity (EC)

EC is commonly used to estimate salinity, which is the sum concentration of all the ionic constituents dissolved in a water sample. Salinity has been shown to have a strong influence on water chemistry in wetland ecosystems. For instance, the solubility of O₂ in water is partly dependent on the salinity (or EC) of the water such that as salinity increases, the solubility of O₂ decreases (Copeland 1967). The salinity-O₂ solubility relationship has major implications for several processes such as CH₄ emissions by controlling CH₄ oxidation to CO₂ as it diffuses through oxic layers to the atmosphere. In the current study, DOC concentrations and CH₄ flux rates increased exponentially as EC increased at Guma which could be explained by suppressed aerobic oxidation of both DOC and diffusive CH₄ as DO decreased in the water column due to increasing EC. As already noted, EC in the Okavango Delta was generally lower in the permanent swamp but was almost twice as much in the seasonal swamps due to evaporative effect (Mackay et al. 2011; Gondwe and Masamba 2014). Although DOC concentrations increased with EC at Xakanaxa and Nxaraga, diffusive CH₄ flux rates decreased exponentially with EC at Xakanaxa, while no correlation was observed at Nxaraga. Since both O₂ solubility and aerobic oxidation of diffusive CH₄ are generally

inversely related to EC, the negative correlation and lack of it between EC and diffusive CH₄ fluxes at Xakanaxa and Nxrara, respectively basically shows that other processes probably influenced CH₄ production and/or diffusive fluxes more than EC in the seasonal swamps. Such processes might include sulphate, nitrate, iron and organic matter reductions (Pester et al. 2012). Sulfate, nitrate and iron reductions have all been associated with anaerobic oxidation of CH₄ in different freshwater systems (Eller et al. 2005; Niemann et al. 2009; Crowe et al. 2011). Concentrations of nitrate (Mackay et al. 2011) and humic substances have been shown to increase with distance from the Panhandle to the distal ends of the Okavango Delta. In contrast, sulfate concentrations are much lower at $0.35 \pm 0.60 \text{ mg L}^{-1}$ across the Delta (Mackay et al. 2011). However, several wetlands with naturally occurring low sulfate concentrations (see Pester et al. 2012 and references therein) have repeatedly displayed high bacterial sulphate reduction (BSR) rates which could suppress CH₄ production in these systems (Muyzer and Stams 2008). If we assume that BSR does occur at a high rate in the Delta as observed in other wetlands, then suppression of CH₄ production by BSR is likely to be stronger in the seasonal swamps where water temperatures are generally higher. Furthermore, the low sulfate pools can be rapidly replenished in the seasonal swamps through aerobic sulfur-oxidation during annual flood recession (Prietzel et al. 2009), around oxic plant rhizospheres (Liesack et al. 2000), and through chemical oxidation of H₂S to thiosulfate facilitated by high concentrations of humic substances which act as alternative electron acceptors in dissolved organic matter (Heitmann and Blodau 2006). Of more importance to the poor EC-diffusive CH₄ flux correlations observed at Xakanaxa and Nxrara could be the anaerobic oxidation of CH₄ during BSR which has been shown to be a very important process in anoxic sediments in marine (Knittel and Boetius 2009) and some freshwater systems.

pH

The pH plays an important role in the microbial degradation of organic matter in wetland ecosystems (Sawyer and King 1993; Ye et al. 2012). It has repeatedly been demonstrated that decomposition of organic matter is distinctly slower under acidic and alkaline than in neutral pH conditions (Neue 1989; Moran et al. 1989).

For instance, Moran et al. (1989) reported 85 % organic matter decomposition in Georgia salt marsh (pH = 7.0) just after 2 months, but only 35 % decomposition was observed after 12 months in the acidic Okefenokee freshwater swamp (pH = 3.6–4.2) in USA. Manipulation of the pH to neutral levels increased decomposition rates by 2–3 fold in the freshwater swamp (Benner et al. 1985). It has been suggested that pH affects decomposition rates probably by altering microbial community structure in terms of the microbial composition, density as well as activity (Bergman et al. 1998). Although methanogens have been isolated from habitats at various pH levels, methanogenesis is generally higher under neutral pH than under acidic or alkaline conditions (Ye et al. 2012). This could partly be due to inadequate supply of methanogenic substrates caused by suppressed fermentation rates at non-neutral pH levels. In contrast, menatrophs have been observed to be pH insensitive (Segers 1998).

In the current study pH varied widely between 4.52 and 7.02, with a mean pH of 6.27. The pH at which maximum diffusive CH₄ emission was observed in the Delta was slightly acidic at around 6.23 (Fig. 4d–f), but still agrees with previous studies (e.g., Jones et al. 1987) which have suggested that most methanogens show pH optima near neutrality. The optimum pH for CH₄ emission observed in this study is slightly higher than that (pH = 5.5) observed by Ye et al. (2012) in some peatlands in the Upper Peninsula of Michigan, USA. While the correlation between pH and diffusive CH₄ fluxes was only significant at Nxrara (Table 1), it was observed to be a strong predictor of diffusive CH₄ fluxes in the channel and floodplain habitats at Xakanaxa (Table 2). Analysis of pooled data from all the study sites and habitats showed that pH, temperature and DO were the only important predictors of diffusive CH₄ fluxes in the Delta (Table 2). As with diffusive CH₄ fluxes, pH correlations with DOC and temperature at site level were generally not significant (Table 1). This could be due to complex interactions of various factors which control carbon mineralization under natural in situ environments. The complex nature of factors controlling decomposition processes in natural environments has also been demonstrated by Benner et al. (1985) who even after neutralizing acidic sediments from Okefenokee swamps, observed lower decomposition rates than rates observed in naturally neutral sediments from Sapelo salt marsh which were sampled simultaneously for comparison.

Diffusive CH₄ fluxes and potential climate change feedbacks

It has been widely documented that CH₄ contributes to the greenhouse effect which, due to increasing concentrations of GHGs in the atmosphere, continues to enhance climate change. CH₄ accounts for 15–20 % of the total anthropogenic GHG radiative forcing (Chen and Prinn 2006; Tang et al. 2014). This study has shown that, in a feedback process, increasing local as well as global temperatures can enhance CH₄ fluxes in the Okavango Delta. Temperature was the most important predictor of diffusive CH₄ fluxes at local (site specific) as well as at large scale (Delta) (Table 2; Fig. 3a–c). Although the effect of temperature on DOC in the seasonal swamps was obscured by DOC inputs from terrestrial sources, DOC increased exponentially with temperature in the permanent swamp at Guma (Fig. 2a). Similarly, EC and turbidity levels increased exponentially as DO decreased with water temperature at Guma (Fig. 6a, d, g). As has been shown in this paper, these temperature-dependent physicochemical parameters in turn have direct effect on both DOC levels and diffusive CH₄ fluxes (Fig. 2–5).

Conclusion

Results presented in this study suggest that some physicochemical variables measured in the water column could be used for predicting patterns and trends in diffusive CH₄ fluxes from the Okavango Delta. This is an important finding in that, unlike the alternative laborious approach of analyzing discrete sediment samples to understand diffusive CH₄ fluxes,

physicochemical variables which provide the same information can be easily measured in the water column using portable field meters making monitoring of diffusive CH₄ fluxes in the Okavango Delta relatively cheaper. The results further show that diffusive CH₄ fluxes from the Okavango Delta seem to be controlled by a combination of physicochemical variables. While site specific fluxes showed different combinations of factors, temperature was the primary predictor of CH₄ flux rates at almost all the sampled habitats and sites in the Delta. Most physicochemical variables, especially in the permanent swamp, were correlated with temperature implying that their regulatory effect on diffusive CH₄ fluxes could be modified by climate change feedback as well. However, more research is needed to adequately understand the relationship between climate change and CH₄ emission in the Delta.

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Appendix

See Tables 3 and 4

Table 3 Curve fit parameters between diffusive CH₄ flux (mg CH₄ m⁻² h⁻¹; Y-variable) and water temperature (°C), EC (μS cm⁻¹), turbidity (NTU), DO (mg L⁻¹) and pH data in the Okavango Delta (see Figs. 3–5)

Site/Habitat	X-variable	Equation	Rsqr	p value
Guma				
Channel	Temperature	$f = 2.2407 + 2.01 \times 10^{-7} e^{0.6322x}$	0.9228	<0.0001
Floodplain	Temperature	$f = 1.4603 + 1.0023 \times 10^{-5} e^{0.4781x}$	0.8984	<0.0001
Lagoon	Temperature	$f = 0.9357 + 0.0023e^{0.2759x}$	0.9041	<0.0001
Nxaraga				
Channel	Temperature	$f = 0.0110e^{0.3087x}$	0.7081	<0.0001
Floodplain	Temperature	$f = 2.0480 + 8.070 \times 10^{-11} e^{1.0456x}$	0.6213	0.0007
Lagoon	Temperature	$f = 0.0004e^{0.4041x}$	0.8144	<0.0001

Table 3 continued

Site/Habitat	X-variable	Equation	Rsqr	<i>p</i> value
Xakanaxa Floodplain	Temperature	$f = 3.4973 + 0.0022e^{0.3238x}$	0.9215	<0.0001
Guma Channel	EC	$f = 0.0329e^{0.1131x}$	0.9279	<0.0001
Floodplain	EC	$f = 1.6964e^{0.0461x}$	0.6191	0.0005
Lagoon	EC	$f = 0.2615e^{0.0745x}$	0.7941	<0.0001
Guma Channel	Turbidity	$f = -15.2826 + 9.4031e^{1.0615x}$	0.9070	<0.0001
Floodplain	Turbidity	$f = -19.8966 + 15.3109e^{0.6101x}$	0.9176	<0.0001
Lagoon	Turbidity	$f = -17.1902 + 9.0613e^{0.9898x}$	0.8815	<0.0001
Nxaraga Channel	Turbidity	$f = -26.6001 + 66.2423x$	0.6725	<0.0001
Floodplain	Turbidity	$f = -10.8382 + 4.1067e^{1.2420x}$	0.7407	<0.0001
Lagoon	Turbidity	$f = -8.0301 + 28.5337x$	0.4142	0.0071
Xakanaxa Channel	Turbidity	$f = -1.0137 + 2.2879x$	0.7241	<0.0001
Lagoon	Turbidity	$f = -2.6734 + 5.6285x$	0.7495	<0.0001
Guma Channel	DO	$f = 11.9845 + 467804e^{-17.1097x}$	0.9735	<0.0001
Floodplain	DO	$f = -22.9694 + 96.8298e^{-0.5758x}$	0.7684	0.0002
Lagoon	DO	$f = -67.7953 + 141.6766e^{-0.1438x}$	0.3755	0.0183
Nxaraga Floodplain	DO	$f = 5.8026 + 90.9774e^{-1.6427x}$	0.5056	<0.0001
Xakanaxa Floodplain	DO	$f = 38.1295e^{-0.6353x}$	0.5648	0.0316
Lagoon	DO	$f = 2.3105 + 3374.4575e^{-1.7722x}$	0.8059	<0.0001
Guma Channel	DOC	$f = -14.4133 + 1.4173e^{0.6047x}$	0.9965	<0.0001
Floodplain	DOC	$f = -18.4358 + 5.2416e^{0.3094x}$	0.8627	0.0001
Lagoon	DOC	$f = -9.6492 + 0.8366e^{0.5515x}$	0.9741	<0.0001

Table 4 Curve fit parameters between water temperature (°C; X-variable) and EC ($\mu\text{S cm}^{-1}$), turbidity (NTU), DO (mg L^{-1}) and pH in the Okavango Delta (see Fig. 6)

Site/Habitat	Y-variable	Equation	Rsqr	<i>p</i> value
Guma				
Channel	EC	$f = 40.4446 + 1.2160 \times 10^{-8} e^{0.8216x}$	0.8796	<0.0001
Floodplain	EC	$f = 42.3736 + 9.1039 \times 10^{-12} e^{1.0808x}$	0.9515	<0.0001
Lagoon	EC	$f = 38.6755 + 0.04461e^{0.2337x}$	0.6734	<0.0001
Nxaraga				
Channel	EC	$f = 107.0775 - 0.6827x$	0.6859	0.0003
Floodplain	EC	$f = 79.9840 + 1.6310x$	0.53203	0.0020
Lagoon	EC	$f = 134.5743 - 1.5218x$	0.4918	0.0008
Xakanaxa				
Channel	EC	$f = 120.0179 - 1.4786x$	0.5542	0.0006
Floodplain	EC	$f = 121.4320 - 1.4037x$	0.3337	0.0191
Lagoon	EC	$f = 120.2978 - 0.9994x$	0.3841	0.0080
Guma				
Channel	Turbidity	$f = 0.6000 + 7.5498 \times 10^{-10} e^{0.8211x}$	0.8378	<0.0001
Floodplain	Turbidity	$f = 0.5726 + 4.1813 \times 10^{-8} e^{0.6620x}$	0.8247	<0.0001
Lagoon	Turbidity	$f = 0.7201 + 7.2645 \times 10^{-7} e^{0.5291x}$	0.7390	<0.0001
Nxaraga				
Channel	Turbidity	$f = 0.6669 + 4.1691 \times 10^{-8} e^{0.5982x}$	0.8070	<0.0001
Floodplain	Turbidity	$f = 0.7703 + 4.0876 \times 10^{-7} e^{0.5745x}$	0.5832	0.0052
Lagoon	Turbidity	$f = 0.3262 + 0.4143e^{0.0402x}$	0.2650	0.0731
Xakanaxa				
Channel	Turbidity	$f = 0.9052 + 0.0002e^{0.3261x}$	0.4979	0.0040
Floodplain	Turbidity	$f = 1.0983 - 0.0153x$	0.1524	0.0888
Lagoon	Turbidity	$f = 0.5256 + 0.0358e^{0.1007x}$	0.1709	0.1851
Guma				
Channel	DO	$f = 5.5055 - 0.1876x$	0.8957	<0.0001
Floodplain	DO	$f = 9.7490 - 0.3398x$	0.9833	<0.0001
Lagoon	DO	$f = 11.5904 - 0.3575x$	0.9636	<0.0001
Nxaraga				
Channel	DO	$f = 4.0040 - 0.0918x$	0.5724	0.0028
Floodplain	DO	$f = 3.7838 - 0.0516x$	0.2219	0.1222
Lagoon	DO	$f = 20.1683 - 0.7562x$	0.9174	<0.0001
Nxaraga				
Channel	pH	$f = 5.9765 + 0.0123x$	0.0567	0.3262
Floodplain	pH	$f = 8.1364 - 0.0719x$	0.5737	0.0004
Lagoon	pH	$f = 6.3600 + 0.0004x$	0.0001	0.9638

Table 4 continued

Site/Habitat	Y-variable	Equation	Rsqr	p value
Xakanaxa				
Channel	pH	$f = 6.4970 - 0.0025x$	0.0105	0.6675
Floodplain	pH	$f = 6.8995 - 0.0159x$	0.4038	0.0109
Lagoon	pH	$f = 6.8165 - 0.0090x$	0.4339	0.0364

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