



Carbon Dioxide and Methane Fluxes from Various Vegetation Communities of a Natural Tropical Freshwater Wetland in Different Seasons

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Abstract

Emission of carbon dioxide (CO₂) and methane (CH₄) is of interest in tropical wetland studies because the high and relatively stable temperatures year-round enhance both primary productivity and organic matter decomposition. Nonetheless, there is scarcity of data on emission of these carbon-based greenhouse gases from tropical wetlands. We investigated CO₂ and CH₄ fluxes from a natural tropical freshwater wetland in Uganda under different dominant vegetation communities, i.e., *Cyperus papyrus* (Papyrus), *Typha latifolia* (Typha) and *Phragmites mauritianus* (Phragmites), during the dry and wet seasons. Gas samples were collected using static chambers and analyzed by gas chromatography. Fluxes (mg C m⁻² h⁻¹) of both CO₂ and CH₄ from Papyrus (732.9 ± 48.7 [mean ± standard error] and 14.1 ± 0.8, respectively) and from Typha (759.7 ± 51.4 and 13.5 ± 1.2, respectively) insignificantly varied ($p > 0.05$) during the dry season. However, CO₂ and CH₄ fluxes from both vegetation communities during this season were significantly lower and higher ($p < 0.05$), respectively, than in Phragmites (871.8 ± 56.7 and 8.7 ± 0.5). During the wet season, no significant variation ($p > 0.05$) occurred among the three vegetation communities for both CO₂ and CH₄ fluxes (Phragmites: 691.9 ± 55.8 and 15.6 ± 1.1, Typha: 682.0 ± 53.3 and 16.3 ± 1.2, and Papyrus: 651.2 ± 49.0 and 17.1 ± 1.7, respectively). Water level was the main driver of CO₂ and CH₄ fluxes from the wetland, suggesting its importance in any efforts to regulate fluxes of both gases in tropical wetlands. We estimated total annual CO₂ and CH₄ emissions from Uganda's wetland soils in the ranges of 159.5 × 10⁶–180.2 × 10⁶ t C (tonnes of carbon) and 278.9 × 10⁴–359.7 × 10⁴ t C, respectively.

Highlights

- Vegetation community does not influence CO₂ and CH₄ fluxes from a tropical freshwater wetland soil under continuous flooding
- High water level in a tropical freshwater wetland lowers CO₂ flux but increases CH₄ flux
- A wetland's role in climate change mitigation is a function of carbon sequestration and emission

Keywords Climate change · Greenhouse gases · Papyrus · Phragmites · Typha · Uganda's wetlands

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1 Introduction

Global warming and the subsequent climate change have been attributed to greenhouse gases, whose concentrations in the atmosphere have steadily increased over the past century. The most recent report by the World Meteorological Organization (WMO 2019) recognizes carbon dioxide (CO₂) and methane (CH₄) as the most important greenhouse gases, respectively contributing about 66% and 17% of the radiative forcing by long-lived greenhouse gases. This report further estimated atmospheric concentration of CO₂ in 2018 at 407.8 ppm, a 147% increase from pre-industrial level in 1750. Similarly, within the same period, atmospheric CH₄ concentration increased by 259% to 1869 ppb. While CO₂ accounts for the highest level of radiative forcing, the global warming potential of CH₄ on a 100-year scale is 34 times that of CO₂ (IPCC 2013; Mitsch and Mander 2018). With this in mind, we believe that setting successful climate mitigation strategies requires a clear understanding of sources and controls of both gases.

Natural wetlands provide favourable environments for carbon sequestration, through capture and long-term storage of atmospheric carbon, making them fundamental ecosystems in climate change mitigation efforts. Coupled with hypoxic conditions, the high primary productivity of these ecosystems permit them to accumulate large amounts of carbon in their soils (Lane et al. 2016; Nahlik and Fennessy 2016; Villa and Bernal 2018). With a coverage of only 5–8% of the earth's land surface (Nahlik and Fennessy 2016), wetlands' carbon content is estimated to be as high as one third of the world's carbon stored in organic soils (Were et al. 2019). In contrast, natural wetlands also emit carbon into the atmosphere, in the form of CO₂ and CH₄ (Belger et al. 2011; Butterbach-Bahl et al. 2016; Gutenberg et al. 2019; Ishikura et al. 2019; Mitsch and Mander 2018). For instance, it is estimated that wetlands account for up to 25% of the total natural and anthropogenic sources of CH₄ (Oertel et al. 2016). Thus, understanding the net contribution of wetlands to climate change mitigation entails knowledge of not only their carbon sequestration potential but also their carbon emission rate. Besides, emission of greenhouse gases has been shown to vary across wetland types (Belger et al. 2011; Butterbach-Bahl et al. 2016; Oertel et al. 2016; Sjögersten et al. 2014; Turetsky et al. 2014), suggesting the need for studies across all wetland types for proper accounting of total emission from global wetlands.

Factors controlling CO₂ and CH₄ emissions from wetlands have been relatively well studied and documented (Belger et al. 2011; Duval and Radu 2018; Oertel et al. 2016; Olsson et al. 2015; Veber et al. 2018; Villa and Bernal 2018; Were et al. 2019). One of the important characteristics of wetlands, which has also been reported to affect CO₂ and CH₄ flux from these ecosystems is vegetation. Wetland plants may exert variable effects on CO₂ and CH₄ fluxes from wetlands due to differences in factors such as anatomy, phenology, species composition, density (Maucieri et al. 2017) and age (Oertel et al. 2016). Organic matter originating from different plant species may present varying degrees of recalcitrance, with subsequent variations in the rates of decomposition (Hernandez and Mitsch 2007; Sjögersten et al. 2014). Likewise, the amount of organic matter input into wetland soil varies among plant species (Marín-Muñiz et al. 2015). The implication is that even within the same wetland, CO₂ and CH₄ fluxes from different vegetation communities can vary spatially. For example, in a Swiss wetland, Bhullar et al. (2014) recorded a six-fold difference in CH₄ emission among plant species. Maucieri et al. (2019) reported over 2-times higher emission of CO₂ from wetlands under *A. donax*, *M. giganteus* and *P. australis* than under *C. zizanioides* and unvegetated wetlands. In the same study, CH₄ flux from vegetated wetlands significantly exceeded that in the unvegetated wetland. Understanding

CO₂ and CH₄ fluxes from different vegetation communities is, therefore, inevitable in the accurate estimation of whole wetland emissions, for wetlands with different vegetation communities.

Knowledge of current fluxes of CO₂ and CH₄ in wetlands is also necessary since temperature increases associated with climate change could elevate future fluxes of these greenhouse gases (Nahlik and Mitsch 2011; Sjögersten et al. 2014). Despite tropical wetlands covering a large spatial extent (nearly 30% of the world's wetlands area; Marín-Muñiz et al. 2015), most studies have given attention to CO₂ and CH₄ emissions from temperate and boreal wetlands (Marín-Muñiz et al. 2015; Sha et al. 2011; Sjögersten et al. 2014). As a result, CO₂ and CH₄ emissions from tropical wetlands are less understood in comparison to their temperate and boreal counterparts. Moreover, CO₂ and CH₄ emissions are of interest for tropical wetland studies because the high and relatively stable temperatures year-round enhance both primary productivity and organic matter decomposition. Additionally, there is a limited understanding of tropical wetland biogeochemistry compared to boreal peatlands (Mitsch et al. 2010), which could result into disagreements over the controls and magnitude of CO₂ and CH₄ fluxes from tropical wetlands. Indeed, Villa and Bernal (2018) and Were et al. (2019) in their recent review studies on carbon sequestration have recommended more work on tropical wetlands in order to have a candid understanding of how they differ from the well-studied northern wetlands.

In this study, we evaluated CO₂ and CH₄ emissions from a natural tropical freshwater wetland under three naturally occurring dominant vegetation communities, on a temporal basis, considering both the dry and wet seasons. We sought to answer the following research questions: (i) do fluxes of CO₂ and CH₄ from a natural tropical freshwater wetland vary among various vegetation communities, and between seasons? and (ii) what are the major environmental factors that influence CO₂ and CH₄ fluxes from a natural tropical freshwater wetland? Understanding of CO₂ and CH₄ emissions and their controlling factors in tropical wetlands is a prerequisite to enable the inclusion of tropical wetlands into global climate change models.

2 Materials and Methods

2.1 Study Area

This study was conducted on Naigombwa wetland ecosystem, located in Iganga District, South-eastern Uganda (Fig. 1). Based on dominant vegetation communities that form a permanent cover throughout the year, this wetland can be sub-divided into three different sections: *Cyperus papyrus* (Papyrus), *Typha latifolia* (Typha) and *Phragmites mauritianus* (Phragmites).

Papyrus vegetation community mainly occur in the downstream areas of the wetland, unlike Phragmites and Typha vegetation communities which are mainly found in the upstream areas. Papyrus plants display two growth forms: emergent (rooted in the sediment, close to the wetland edges) and floating (rooted in the mat above the water column, towards the wetland mid-sections where the water level is high) (Fig. 2). The mat structure is made up of loosely entangled roots and rhizomes, alongside a thin layer of soil formed from dead plant matter (Azza et al. 2000). On the other hand, both Typha and Phragmites plants exhibit only an emergent form, limiting their competition with papyrus plants in

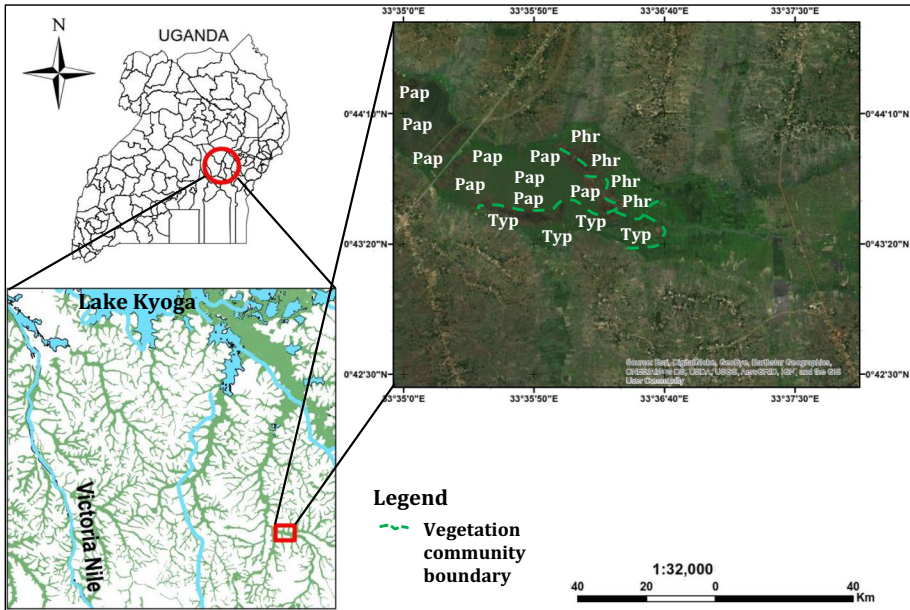
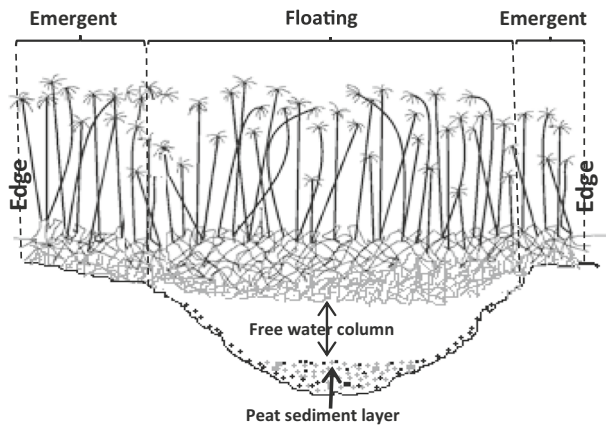


Fig. 1 Location of the study area on the map of Uganda. The specific sampled area was zoomed and geo-referenced from Google Earth. Pap = Papyrus, Typ = Typha, Phr = Phragmites

Fig. 2 Schematic overview of a transverse cross-section through a Papyrus wetland section. Generated from this study



high water level areas (Kansiime et al. 2007). All the three vegetation species are native to the wetland, and also dominate many other wetland ecosystems of Uganda.

Variation of water level in Naigombwa wetland is experienced during different seasons of the year (Kayendeke et al. 2018). Intermittent flooding and drying cycles occur at wetland edges during wet and dry seasons, respectively. On the contrary, areas away from the edge are mainly flooded year-round, but experience fluctuations in water level depth between wet and dry seasons. Nevertheless, for the whole sampling period during this study the wetland was continuously flooded. Surface water flow in the wetland is

natural, with minimal human alterations. The water flow is sustained by water inflow from the wider catchment, which is dependent on both precipitation, and input from streams.

2.2 Gas Sampling and Analysis

Gas sampling from each of the three vegetation communities described above was done using static gas chambers (Butterbach-Bahl et al. 2016; Nicoloso et al. 2013). For the Papyrus vegetation community which displays two growth forms (Fig. 2), gas sampling targeted both growth forms.

Chambers were fitted with a probe thermometer to monitor inside air temperature, a vent pipe for preventing radical changes of internal air pressure, and a sampling port with a septum, which also provided for manually homogenizing inside air using a syringe and needle (Collier et al. 2014; Minamikawa et al. 2015). White colour chambers, whose outside surfaces were covered using an aluminium reflective tape were selected to minimize heating up of the chambers during sampling due to radiation from the sun. To provide a gas tight enclosure that prevents exchange of inside and outside air, chamber lids were firmly inverted onto the chamber bases that were sunk into the soil to at least 10 cm (Butterbach-Bahl et al. 2016). Installation of chamber bases was done at least 7 days before sampling (Butterbach-Bahl et al. 2016). The chambers used had an average headspace with the following dimensions: height = 25 cm, volume = 10 L and basal area = 490.63 cm².

Gas sampling was carried out in quadrats that were randomly selected along transects. Three chambers were deployed and sampled consecutively in each quadrat (Collier et al. 2014). To prevent artificial ebullition of the gases and physical disturbance of soil at sampling points, wooden scaffolds were installed to act as walkways. In the floating growth form of the Papyrus vegetation community, however, due to the suspended nature of the mat over the water column, it was not possible to control artificial ebullition due to the shaking of the mat while moving on it. This was detected from the preliminary gas measurements that showed abnormally high gas concentrations. As a result, the floating growth form of Papyrus was excluded from the final sampling plan.

The gas sampling regime was spread across the months of February, March and April 2019 (dry season) and August, September and October 2019 (wet season). Samples were obtained at time intervals of 0, 10, 20, and 30 min (inside the chamber) (Butterbach-Bahl et al. 2016). Ambient air samples were collected outside the chamber prior to start of each sampling event for quality control. The air accumulated in chambers was obtained using a 60 mL polypropylene syringe, fitted with a luer lock and a needle. Of the 60 mL volume of the gas sample in the syringes, 40 mL was used for evacuation of the 10-mL gas vials and the remaining 20 mL was stored in the gas vials (under high pressure) for analysis. Contamination of samples prior to analysis was prevented by covering gas vial tops with a parafilm. In total, for each season and vegetation community, 72 samples were collected. Gas samples were analysed at the International Livestock Research Institute, Nairobi, Kenya using gas chromatography (SRI 8610C gas chromatograph, USA), and followed the procedure described by Collier et al. (2014) and Minamikawa et al. (2015). Before gas analysis, the gas chromatograph was first calibrated using standards of known concentrations (Minamikawa et al. 2015). Visual inspection of time series concentration plots was undertaken for quality control of gas concentrations (Collier et al. 2014). Gas (CO₂ and CH₄) fluxes were calculated using Eq. (1) (Nicoloso et al. 2013):

$$f = \frac{\Delta Q P V}{\Delta t R T A} \quad (1)$$

where: f is the CO_2 or CH_4 flux ($\text{mg m}^{-2} \text{h}^{-1}$), ΔQ is the change in mass of the gas (mg) inside chamber due to change in sampling time (Δt), P is the atmospheric pressure (atm) inside the chamber, which is assumed as 1 atm, V is the chamber volume (L), R is the constant for ideal gases ($0.08205 \text{ atm L mol}^{-1} \text{ K}^{-1}$), T is the temperature (K) within the chamber at a given sampling time, and A is the basal area of the chamber (m^2).

2.3 Soil Physico-chemical Characteristics, Water Level and Air Temperature

Soil samples of the top (0–10 cm) soil layer (Järveoja et al. 2016; Nahlik and Mitsch 2011) were collected in triplicate in each quadrat using a Russian peat borer for determination of selected physico-chemical characteristics (pH, salinity and organic carbon). Soil temperature measurement was done *in-situ* using a digital soil thermometer. Because the study was carried out under flooding conditions, there was no need to measure soil moisture content.

Samples were composited by mixing three samples in each sampling plot within a quadrat. Samples were sorted using polyethylene bags, placed in a cool box and transported to the Soil Science Laboratory, College of Agricultural and Environmental Sciences, Makerere University, Kampala, Uganda for analysis. Before the analysis, samples were re-mixed to homogenise them. Samples were ground and sieved through a 2 mm nylon sieve, after being air-dried at room temperature for 21 days. To obtain soil organic matter (SOM) content, 2 g of dry soil samples were placed in pre-weighed crucibles and then dried in an oven (CARBOLITE CWF 13/5) at 105°C to constant weight. The samples were then ignited at 450°C for 4 h (Bernal and Mitsch 2008). Soil organic matter percentage (SOM%) of each sample was calculated following weight loss on ignition (LOI), from where soil organic carbon percentage (SOC%) was obtained as a portion of SOM%, using Van Bemmelen's index of 0.58 (Marín-Muñiz et al. 2014).

Soil pH and salinity (obtained after conversion from electrical conductivity) were determined using a CyberScan PC 300 multi-parameter meter, after equilibration of soil with deionized water (ratio of soil: water = 1:5) (Wang et al. 2018). Water level was determined using a cm-marked wooden stick by measuring the distance from the soil surface to the surface of the overlying water layer. Data of ambient air temperature characteristics during the sampling period were obtained from the Uganda National Meteorological Authority (UNMA).

2.4 Data Analysis

Data analysis was carried out using Microsoft Excel (2016) and R programming software (version 3.2.2). Prior to analysis, data were first subjected to a normal distribution test using Shapiro–Wilk test. Although soil physico-chemical characteristics and water level data were normally distributed, gas flux data did not meet the criteria for normal distribution. Consequently, ANOVA alongside Tukey HSD post-hoc test were used to test the statistical significance of soil physico-chemical characteristics and water level among wetland vegetation communities and between seasons. In contrast, ANOVA together with Kruskal–Wallis H post-hoc test were used to test the significance of CO_2 and CH_4 fluxes among the wetland vegetation communities and between seasons ($p < 0.05$). Given the significance of median values in the description of non-normally

distributed gas flux data (Nahlik and Mitsch 2011; Sha et al. 2011), box plots were used. Spearman rank correlation, at $p < 0.05$ significance was used to determine the relationship between soil physico-chemical characteristics, water level and ambient air temperature, and CO_2 and CH_4 fluxes.

3 Results

3.1 Soil Physico-chemical Characteristics, Water Level and Air Temperature

Soil temperature, salinity and SOC did not vary significantly ($p > 0.05$) among the three vegetation communities across the two sampling seasons (Table 1). Although the wetland was continuously flooded throughout the sampling period, water levels were significantly higher ($p < 0.05$) during the wet season for all the three vegetation communities. Regarding the vegetation communities, water levels during the dry season in the Papyrus and Typha vegetation communities were not significantly different ($p > 0.05$), but they were both significantly higher ($p < 0.05$) than those recorded in the Phragmites vegetation community. However, in the wet season, water levels in the three vegetation communities did not differ significantly ($p > 0.05$).

Because all the three vegetation communities occur in the same wetland and in the same climatic zone, variation of climatic conditions among the vegetation communities were assumed negligible. Therefore, ambient air temperature data, which was collected at the whole wetland scale from UNMA were applied uniformly to all the three vegetation communities in the wetland. Mean air temperature during the dry season was 23.4 ± 0.1 (mean \pm standard error [SE]) $^\circ\text{C}$, and insignificantly varied ($p > 0.05$) from that (21.3 ± 0.2 $^\circ\text{C}$) recorded in the wet season.

Table 1 Soil physico-chemical characteristics and water levels in the different vegetation communities of the wetland

Parameter	Vegetation community					
	Papyrus		Typha		Phragmites	
	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season
Temperature ($^\circ\text{C}$)	26.6 ± 0.0	26.3 ± 0.0	26.9 ± 0.1	26.8 ± 0.1	26.6 ± 0.1	26.5 ± 0.1
pH	6.00 ± 0.01	5.98 ± 0.01	6.23 ± 0.01	6.24 ± 0.02	6.06 ± 0.01	6.20 ± 0.01
Salinity (mS m^{-1})	132.8 ± 4.9	128.7 ± 3.8	129.2 ± 2.4	125.9 ± 1.7	118.6 ± 2.5	91.3 ± 1.4
SOC (%)	16.3 ± 0.0	15.0 ± 0.1	13.3 ± 0.2	12.9 ± 0.1	11.7 ± 0.1	10.0 ± 0.1
Water level (cm)	7.5 ± 3.2	$31.5 \pm 4.4^{**}$	7.1 ± 3.2	$29.1 \pm 4.2^{**}$	1.9 ± 0.8^a	$21.0 \pm 4.1^{**}$

Values are mean \pm SE ($n = 36$)

^a Significant seasonal variation among vegetation communities

^{**} Significant seasonal variation ($p < 0.05$) within the same vegetation community

3.2 Carbon Dioxide and Methane Fluxes

Carbon dioxide (CO₂) fluxes from the wetland did not show variations among the vegetation communities, except in Phragmites. However, in all the three vegetation communities, it accounted for over 97% of the total carbon flux (Table 2). Mean CO₂ flux from Phragmites during the dry season was 871.8 ± 56.7 mg C m⁻² h⁻¹, significantly higher ($p < 0.05$) than those in Typha (759.7 ± 51.4 mg C m⁻² h⁻¹) and Papyrus (732.9 ± 48.7 mg C m⁻² h⁻¹) (Fig. 3a). During the wet season, mean CO₂ fluxes (mg C m⁻² h⁻¹) from the vegetation communities were 691.9 ± 55.8 , 682.0 ± 53.3 , and 651.2 ± 49.0 from Phragmites, Typha and Papyrus, respectively (Fig. 3b). Nonetheless, the magnitudes of variation among the vegetation communities during this season were insignificant ($p > 0.05$).

As for CO₂, also CH₄ fluxes did not show variabilities among vegetation communities, except only in Phragmites. During the dry season, mean CH₄ fluxes (mg C m⁻² h⁻¹) of 14.1 ± 0.8 and 13.5 ± 1.2 were measured in Papyrus and Typha, respectively, which did not vary significantly ($p > 0.05$), but both were significantly higher ($p < 0.05$) than in Phragmites (8.7 ± 0.5) (Fig. 3c). During the wet season, mean CH₄ fluxes were 17.1 ± 1.7 , 16.3 ± 1.2 , and 15.6 ± 1.1 mg C m⁻² h⁻¹ in Papyrus, Typha and Phragmites, respectively (Fig. 3d). Again, just as it was the case with CO₂, variations in mean CH₄ fluxes among the three vegetation communities during the wet season were of negligible significance ($p > 0.05$).

Regarding season effect, whereas CO₂ fluxes during the dry season in all the three vegetation communities were generally higher than during the wet season, the variations were insignificant ($p > 0.05$), except only for Phragmites ($p < 0.05$). Similarly, whereas seasonal CH₄ flux values observed during the wet season in the three vegetation communities were generally higher than those in the dry season, the variations were not statistically significant ($p > 0.05$), except for Phragmites ($p < 0.05$).

Great variations in fluxes occurred for both CO₂ and CH₄ even within the same sampling season. For instance, point CO₂ emissions (mg C m⁻² h⁻¹) ranged from 422.1–1044.5 from Papyrus, 411.5–1073.8 from Typha and 583.8–1196.2 from Phragmites during the dry season, compared to 333.5–958.3, 337.9–1015.9 and 395.5–1092.5, respectively, during the wet season. Similarly, point CH₄ emissions (mg C m⁻² h⁻¹) ranged from 7.3–21.0, 7.2–19.6 and 6.4–10.8 from Papyrus, Typha and Phragmites vegetation communities, respectively, during the dry season in comparison with 9.2–30.0, 9.1–21.4 and 8.3–20.9, respectively, during the wet season.

3.3 Influence of Soil Physico-chemical Characteristics, Water Level and Air Temperature on Carbon Dioxide and Methane Fluxes

The Spearman rank correlations (Table 3) indicated that none of the soil physico-chemical parameters had a significant correlation ($p > 0.05$) with gas fluxes. The same observation was true for air temperature ($p > 0.05$). These observations are not surprising since throughout the sampling period both soil physico-chemical characteristics (Table 1) and air temperature did not present significant variations ($p > 0.05$) either among vegetation communities or between seasons. On the other hand, water level was found to have significant correlations ($p < 0.05$) with both CO₂ and CH₄ fluxes. A significant negative correlation ($p < 0.05$) was obtained between water level and CO₂ flux, while CH₄ flux showed a significant positive correlation ($p < 0.05$) with water level.

Table 2 Carbon dioxide (CO₂) and CH₄ fluxes from different vegetation communities of the wetland as a percentage of the total carbon flux

Vegetation community	CO ₂ (mg C m ⁻² h ⁻¹)		CH ₄ (mg C m ⁻² h ⁻¹)		Total C flux (mg C m ⁻² h ⁻¹)	CO ₂ (% of Total C flux)	CH ₄ (% of Total C flux)	
	Dry season	Wet season	Dry season	Wet season				
	Average		Average					
Papyrus	732.9 ± 48.7	651.2 ± 49.0	692.1 ± 48.8	14.1 ± 0.8	17.1 ± 1.7	707.7 ± 50.1	97.8	2.2
Typha	759.7 ± 51.4	681.9 ± 53.3	720.8 ± 52.3	13.5 ± 1.2	16.3 ± 1.2	735.7 ± 53.6	98.0	2.0
Phragmites	871.8 ± 56.7	691.9 ± 55.7	781.8 ± 56.2	8.7 ± 0.5	15.6 ± 1.1	794.0 ± 57.0	98.5	1.5

Values are mean ± SE (*n* = 36). Total C flux is the sum of average CO₂ and CH₄ fluxes

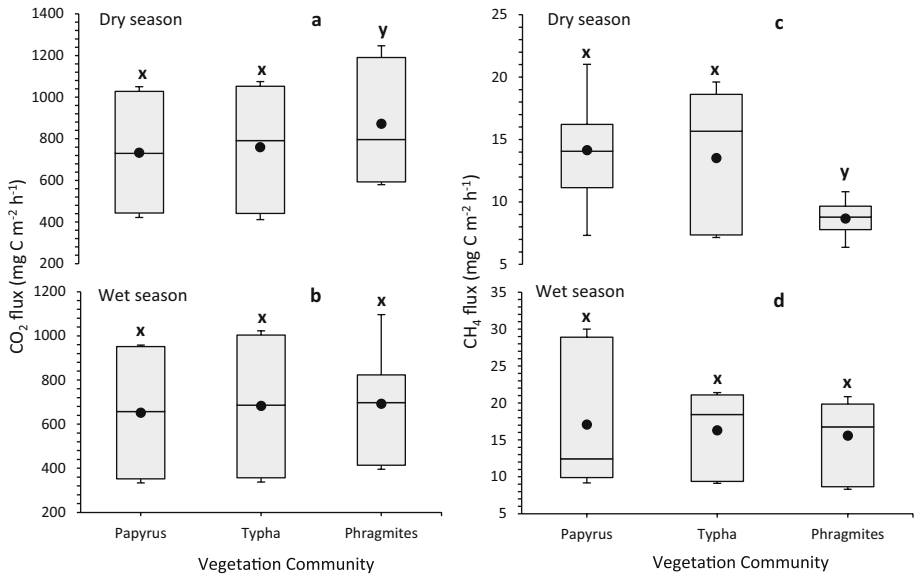


Fig. 3 Comparison of CO₂ and CH₄ fluxes from the Papyrus, Typha and Phragmites vegetation communities during the dry (**a** and **c**, respectively) and wet (**b** and **d**, respectively) seasons. Box lines indicate upper and lower quartiles. Horizontal lines within boxes show medians, while black dots show means. Whiskers extend up to the minimum and maximum values. Letters on box plots indicate significance, based on the mean and SE ($n=72$). Similar letters show no significant difference ($p > 0.05$)

Table 3 Spearman rank correlations between soil physico-chemical characteristics, water level, air temperature and CO₂ and CH₄ fluxes ($n=36$)

	CO ₂	CH ₄	Soil temp	SOC	Soil pH	Soil salinity	Water level	Air temp
CO ₂	1.00							
CH ₄	-0.99*	1.00						
Soil temp	0.30	0.23	1.00					
SOC	0.24	0.25	-0.05	1.00				
Soil pH	-0.07	0.12	-0.39	-0.06	1.00			
Soil salinity	0.04	-0.01	0.28	0.26	-0.36	1.00		
Water level	-0.87*	0.86*	-0.39	0.04	0.08	-0.08	1.00	
Air temp	0.29	0.26	0.45*	0.27	-0.20	0.31	-0.34	1.00

Soil temp Soil temperature, *Air temp* Air temperature

* Significant correlation ($p < 0.05$)

These relationships between water level and CO₂ and CH₄ fluxes are further clearly depicted in Fig. 4. Also, the correlation between CO₂ and CH₄ fluxes was significantly negative ($p < 0.05$), implying that at any given time organic matter degradation and carbon emission processes favoured one gas over the other, as reflected in Fig. 5.

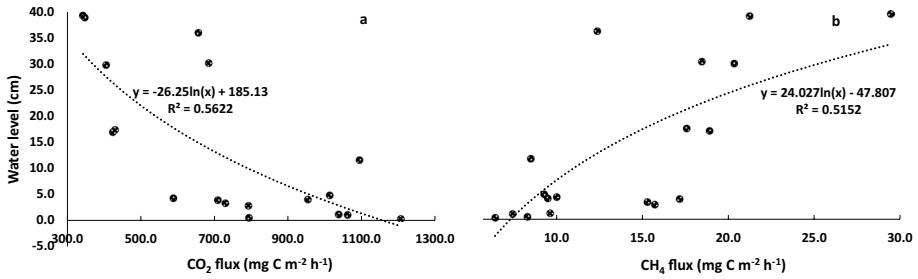
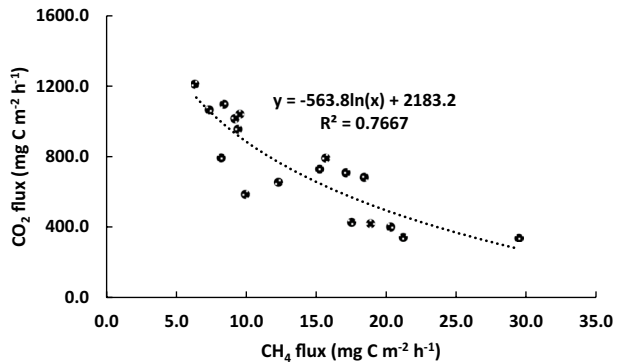


Fig. 4 Relationship between water level and CO₂ (a) and CH₄ (b) fluxes from the wetland

Fig. 5 Relationship between CO₂ and CH₄ fluxes from the wetland



4 Discussion

4.1 Effect of Vegetation Community on Carbon Dioxide and Methane Fluxes

Organic matter availability is recognized as one of the most important factors influencing fluxes of carbon-based greenhouse gases in wetland soils. Both the amount and quality of organic matter deposited onto wetland soils are dependent on the type of plants (Hernandez and Mitsch 2007; Maucieri et al. 2017; Sjögersten et al. 2014). Ding et al. (2005) noted that CH₄ emissions resulting from decomposition of plant organic matter are as high as 90%. Inglett et al. (2012) further linked variations in methanogenic activity in wetlands under differing vegetation types to differences in carbon availability and input rate into soil. Duval and Radu (2018) made an observation of dissimilar flux rates of both CO₂ and CH₄ in peat samples collected from three fen areas with each representing distinct vegetation communities: sedges, shrubs, and non-vascular communities (*Carex oligosperma*, *Chamaedaphne calyculata*, *Sphagnum capillifolium*, *Carex livida*, *Cornus stolonifera*, and *Chara* spp.). The authors observed a negative correlation between gas flux rates and the content of lignin and cellulose. Following a microcosm experiment, Sun et al. (2019) have recently reported that presence of *Pontederia cordata* and *Phragmites australis* in a wetland enhanced CO₂ emission, while the influences of both *Typha orientalis* and *Lythrum salicaria* on CO₂ emissions were negligible. Maucieri et al. (2019) have also found variable rates of CO₂ fluxes from Mediterranean wetlands with different vegetation communities, which they attached to differences in organic matter input into soils. With this

knowledge, our expectation was to observe significant differences of both CO₂ and CH₄ fluxes among the three vegetation communities we studied. However, during the dry season, no significant variations of both CO₂ and CH₄ fluxes among the three vegetation communities were noticed, except for Phragmites (Fig. 3a, c). Similarly, during the wet season, variations of both CO₂ and CH₄ flux rates among all the three vegetation communities were insignificant (Fig. 3b, d). The lack of a significant difference in organic carbon content among the vegetation communities (Table 1) could be used to explain our findings. While studying on Mexican wetlands, Marín-Muñiz et al. (2015) did not find significant variation of both CO₂ and CH₄ fluxes among vegetation communities with similar organic carbon contents. Gagnon et al. (2007) understood that fluxes of carbon-based greenhouse gases in wetland soils are impacted by organic matter input because it influences bacterial activity, with high organic matter content being associated with intensive bacterial activity. Further, Were et al. (2020) have reported comparable lignin contents of Papyrus, Typha and Phragmites, and suggested that they could not account for differences in SOC contents among the three plant species. Therefore, our observation of a significant difference in CO₂ and CH₄ fluxes only in Phragmites during the dry season could be attributed to other factors such as water level (Marín-Muñiz et al. 2015). During the dry season, water level in the Phragmites vegetation community was significantly lower than in both Papyrus and Typha vegetation communities (Table 1).

4.1.1 Effect of Water Level on Carbon Dioxide and Methane Fluxes

For the entire sampling period, the wetland was continuously flooded, though variations in water level occurred between the dry and wet seasons (Table 1). Soil anaerobicity was enhanced under conditions of continuous flooding because soil pore spaces were filled (Marín-Muñiz et al. 2015). CO₂ emission from wetland soil is minimized under anaerobic conditions that impede aerobic organic matter decomposition, while methanogenesis and the ensuing CH₄ emissions are promoted at the same time (Brooker et al. 2014). Irrespective of vegetation community, Marín-Muñiz et al. (2015) noted that high water levels during the wet (rain) season significantly enhanced CH₄ emissions but lowered CO₂ emissions from several freshwater wetlands, including that dominated by Typha plants. Lawrence et al. (2017) observed variations in CH₄ emissions under high (+10 cm) and low (−10 cm) water tables in wetland mesocosms with Typha plants. Reducing water level from high water table positions (2 to 14 cm) to lower water table positions (0 to −11 cm) increased CO₂ emissions by 120% and reduced CH₄ emissions by 75% (Yang et al. 2013). Olsson et al. (2015) found significant variations in CH₄ emission rates in two Phragmites wetlands, as water level moved from the soil surface to below the surface. Liu et al. (2015) reported that varying water levels significantly influenced flux rates of both CO₂ and CH₄ in a Chinese wetland. Ishikura et al. (2019) recently noticed that lowering groundwater level in a Malaysian wetland increased daily mean flux of CO₂. Bernal and Mitsch (2013) and Batson et al. (2015) also noted variations in gas fluxes from wetlands that experienced marked drying and wetting cycles. Similarly, in the USA, a study by Gutenberg et al. (2019) on the influence of water level on CH₄ fluxes from a wetland has reported that increasing soil moisture content by 1 unit increased CH₄ flux by 457 μg m^{−2} h^{−1}. These observations are further supported by Maucieri et al. (2017), who in a literature review found significantly higher emission rates of CO₂ under low water table, and significantly higher emission rates of CH₄ under high water table. In the present study, nevertheless, flux rates of both CO₂ and CH₄ in Papyrus and Typha differed insignificantly between the dry and wet seasons,

despite water levels differing significantly between the two seasons. Our view is that the soils might have already reached maximum saturation during the dry season such that any further increase in water level during the wet season could not affect gas fluxes (Mander et al. 2011; Moore and Knowles 1989; Nahlik and Mitsch 2011; Yang et al. 2013).

Apart from water level, gas fluxes have been shown to be affected by soil physico-chemical characteristics such as soil temperature (Duval and Radu 2018; Nahlik and Mitsch 2011; Oertel et al. 2016; Olsson et al. 2015; Veber et al. 2018), pH (Oertel et al. 2016; Wanyama et al. 2019; Veber et al. 2018), C:N ratio (Batson et al. 2015; Wanyama et al. 2019), and bulk density (Wanyama et al. 2019). However, in line with our findings, a number of other studies also have not found significant correlation between soil physico-chemical characteristics and gas fluxes. Wanyama et al. (2019) observed weak correlations between soil temperature and CO₂ and CH₄ fluxes. Sjögersten et al. (2014) showed that soil temperature was unlikely to be a major factor influencing decomposition and gas flux from tropical wetlands. Villa and Bernal (2018) also supported this, understanding that low O₂ availability under anaerobic conditions, due to water saturation in wetland soils, is more important in driving decomposition (and the resultant gas fluxes) than soil temperature. Wang et al. (2018) noted no significant correlation between C:N ratio and SOC, suggesting its insignificant influence on CO₂ and CH₄ fluxes. Batson et al. (2015) reported insignificant correlations between soil bulk density and fluxes of both CO₂ and CH₄. Bhullar et al. (2014) found no correlation between soil pH and CH₄ emission. Richards and Craft (2015) observed no correlations between greenhouse gas fluxes and all measured soil properties in both natural and restored wetlands. Richards and Craft (2015) explained that disagreements over correlations between soil parameters and gas fluxes, as reported by different studies, could arise because CH₄ and CO₂ emission is an interplay between several factors and processes, and the dominant one may vary according to existing conditions. Therefore, possibly the lack of correlations between soil properties and CO₂ and CH₄ fluxes in this study could be because they were not the major limiting factors.

4.2 Comparison of Carbon Dioxide and Methane Fluxes with Literature Data

By combining dry season and wet season fluxes, we obtained average CO₂ fluxes among the three vegetation communities in the range of 692.1–781.8 mg C m⁻² h⁻¹, while CH₄ emissions ranged from 12.1–15.6 mg C m⁻² h⁻¹ (Table 2). In comparison with other studies, we noticed that CO₂ flux rates recorded in our study were lower than those obtained in other tropical wetlands, though higher than those reported in boreal and temperate wetlands (Table 4). Conversely, our CH₄ flux rates were both higher and lower than some reported values for other tropical wetlands, but higher than reported rates for boreal and temperate wetlands. The low CO₂ flux rates compared to those from other tropical wetlands could be attributed to the fact that our study wetland was under continuous flooding, which suppressed aerobic organic matter decomposition (Liu et al. 2015). Differences in flux rates of CO₂ and CH₄ between our tropical wetland and those of temperate and boreal wetlands could be explained by temperature differences (Gomez et al. 2017; Oertel et al. 2016; Sha et al. 2011). High temperatures in tropical regions are associated with high organic matter decomposition rates in wetland soils, which enhance gas emissions (Villa and Bernal 2018; Were et al. 2019).

Nonetheless, both CO₂ and CH₄ flux rates recorded in our study are within ranges reported for wetland types with more or less similar conditions to our study wetland. Sjögersten et al. (2014) have reported CO₂ emission from related tropical wetlands ranging

Table 4 Carbon dioxide (CO₂) and methane (CH₄) emissions from wetland soil from different studies

Study location/Climate	CO ₂ (g C m ⁻² yr ⁻¹)	CH ₄ (g C m ⁻² yr ⁻¹)	Reference
Uganda/tropical	6062.8–6848.6	106.0–136.7	Current study
Malaysia/tropical	926.0	3.9	Ishikura et al. (2019)
Brazil/tropical	1022.4	27.5	Belger et al. (2011)
Zimbabwe/tropical	7850.7	258.4	Nyamadzawo et al. (2015)
Indonesia/tropical	7743.8	10.6	Sjögersten et al. (2014)
Malaysia/tropical	7928.8	na	Sjögersten et al. (2014)
Virginia, USA/temperate	543.12	20.2	Gutenberg et al. (2019)
New York, USA/temperate	222.7	na	Gomez et al. (2017)
Northeast China/temperate	3534.4	1.2	Liu et al. (2015)
Poland/temperate	na	20.0–29.0	Fortuniak et al. (2017)
Ohio, USA/temperate	57.8	44.7	Brooker et al. (2014)
Switzerland/temperate	na	0.002–0.01	Bhullar et al. (2014)
Virginia, USA/temperate	4301.5	–0.02	Batson et al. (2015)
Several/temperate	na	39.8	Turetsky et al. (2014)
Russia/boreal	na	21.9	Schneider et al. (2018)
Several/boreal	na	26.5	Turetsky et al. (2014)

For the ease of comparison, emission values have been computed to similar units. Values are given as single means or ranges of means (where means of several sampling sites are provided in the source document)

na: not available

from 317.0–905.0 g C m⁻² yr⁻¹, while Nahlik and Mitsch (2011) have reported CH₄ emission ranging from 6.0 g C m⁻² yr⁻¹ to 788.0 g C m⁻² yr⁻¹.

4.3 Carbon Dioxide and Methane Emission from Uganda's Wetlands

Wetlands cover a considerably big portion of Uganda's land surface. According to the most recent Uganda Wetland Atlas (<https://www.mwe.go.ug/library/uganda-wetlands-atlas>) published by the Ministry of Water and Environment in 2016, wetlands cover about 11% (representing 26,315 km²) of the country's land area. Whereas there exists a wide body of literature on Uganda's wetlands, carbon flux from wetlands is a relatively newer concept with a limited number of studies. Currently, no single study has estimated the totality of carbon-based greenhouse gases emitted from Uganda's wetlands. We, therefore, used our study findings to give an estimate of CO₂ and CH₄ emissions from Uganda's wetlands so as to provide a rough estimate for future studies on gas emissions from the country's wetlands. To make this possible, we made assumptions that all the country's wetlands present more or less similar conditions to our study wetland or if variations exist, they are minimal to exert significant variations on gas fluxes. Our study obtained CO₂ and CH₄ emissions ranging from 6062.8–6848.6 g C m⁻² yr⁻¹ and 106.0–136.7 g C m⁻² yr⁻¹, respectively. With 26,315 km² of the country's land area under wetlands, we estimated total CO₂ and CH₄ emissions from Uganda's wetlands to be in the range of 159.5 × 10⁶–180.2 × 10⁶ t C (tonnes of carbon) yr⁻¹ and 278.9 × 10⁴–359.7 × 10⁴ t C yr⁻¹, respectively. However, we also acknowledge that whereas Uganda's wetlands (and indeed other wetlands in general) are defined by common characteristics (water, hydric soils and hydrophytic plants), particular wetland conditions can

differ even at local scales (Belger et al. 2011), which may affect the accuracy of our rough estimates. Additionally, the lack of other studies to compare our gas flux estimates from Uganda's wetlands limits an understanding of the robustness of our estimates.

Further, it is important to note that our study only considered CO₂ and CH₄ from wetland soil. Nevertheless, CO₂ emission involving plants (plant respiration) (Maucieri et al. 2019; Mitsch and Mander 2018; Sjögersten et al. 2014; Sun et al. 2019; Xi et al. 2019) and plant-mediated CH₄ emission (Bhattacharyya et al. 2019; Bhullar et al. 2014; Jeffrey et al. 2019; Turetsky et al. 2014) have also been shown to be important processes of CO₂ and CH₄ emissions from wetlands. However, carbon emitted can be offset by carbon fixed through photosynthesis (Maucieri et al. 2019; Mitsch and Mander 2018). A clearer understanding of carbon balance of Uganda's wetlands, therefore, requires full knowledge of total carbon emission and assimilation. Globally, Mitsch et al. (2013) demonstrated that wetlands may be net C sinks of about 0.83 Pg C yr⁻¹, with an average net C retention of 118 g C m⁻² yr⁻¹.

5 Conclusions

Carbon dioxide (CO₂) and CH₄ fluxes did not vary significantly among vegetation communities during the wet and dry seasons, except only for Phragmites. During the dry season, Phragmites had the highest impact on climate as it emitted more CO₂ per unit area than both Papyrus and Typha vegetation communities. However, in terms of CH₄, Phragmites had the lowest impact on climate during this season as it emitted less CH₄ per unit area than Papyrus and Typha. During the wet season, nonetheless, no variation in flux (for both CO₂ and CH₄) was noticed among the three vegetation communities. In view of seasonal variabilities among wetland vegetation communities, significant differences in CO₂ and CH₄ fluxes between the dry and wet seasons were observed only in the Phragmites vegetation community as well. Dry season CO₂ flux from Phragmites exceeded its wet season counterpart, while dry season CH₄ flux from this vegetation community was less than that observed during the wet season. Water level was the main driver of CO₂ and CH₄ fluxes from the wetland. High water levels were associated with lower CO₂ fluxes but higher CH₄ fluxes. The reverse was true for lower water levels. This suggests the importance of understanding water level dynamics for regulation of CO₂ and CH₄ fluxes from tropical freshwater wetlands.

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Data Availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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