AFRICA CENTER OF EXCELLENCE FOR WATER MANAGEMENT
ADDIS ABABA UNIVRSITY
SCHOOL OF GRADUATE STUDIES
COLLEGE OF NATURAL AND COMPUTATIONAL SCIENCES

CARBON STORAGE AND FLUXES FROM A TROPICAL FRESHWATER WETLAND IN UGANDA: IMPLICATIONS FOR CLIMATE CHANGE MITIGATION

BY

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A PhD dissertation submitted to Africa Center of Excellence for Water Management, the School of Graduate Studies of Addis Ababa University in partial fulfilment of the requirements for The Degree of Doctor of Philosophy in Water Management (Aquatic Ecosystem Management)

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Africa Center of Excellence for Water Management

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DECLARATION

I, David Were (GSR/9813/10), hereby declare that this research Dissertation titled *"**Carbon Storage and Fluxes from a Tropical Freshwater Wetland in Uganda: Implications for Climate Change Mitigation**"* has been developed by me and has not been submitted to any other institution for award of any academic qualification. The content of the dissertation has not been plagiarized and where works of other researchers have been used, they have been appropriately cited.

PhD Candidate's Name	**Signature**	**Date**
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A PHD DISSERTATION SUBMITTED
TO
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APPROVED BY BOARD OF EXAMINERS

This is to certify that we have read this PhD research report and that in our opinion; it is fully adequate, in scope and quality, as a PhD dissertation for The Degree of Doctor of Philosophy in Water Management (Aquatic Ecosystem Management).

Advisor
Name
___________________________Signature__________________Date__________________

Co-Advisor
Name
___________________________Signature__________________Date__________________

Examiner
Name
___________________________Signature__________________Date__________________

Examiner
Name
___________________________Signature__________________Date__________________

Chairperson
Name
___________________________Signature__________________Date__________________

DEDICATION

This research work is dedicated to my late parents Ojiambo Joseph and Nafula Jenifer, my wife, daughters and my PhD supervisors

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This PhD would not have been successful without the support of my supervisors Prof. Dr. Frank Kansiime and Assoc. Prof. Dr. Tadesse Fetahi. The innovative idea of writing "dummy" papers prior to data collection was very instrumental in the timely completion of this PhD research. Similarly, I am greatly indebted to Prof. Thomas Hein, who offered additional supervision for this PhD research. May the Almighty God reward you abundantly.

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My sincere thanks go to my fellow PhD students, and MSc residents in the hostel. Your encouragement and company kept me moving even during the most stressing moments. God bless you.

Lastly, I thank my wife, Caroline Akinyi and our beloved children; Lisa, Anne and Natasha for their love, support and prayers, despite the little time given to them during this period.

Proverbs 16:3: ***"Commit to the Lord whatever you do, and He will establish your plans"***

Nelson Mandela: ***"It always seems impossible until it's done"***

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LIST OF ABREVIATIONS

A	Basal area
ANOVA	Analysis of variance
C	Carbon
°C	Degrees Celsius
C:N	Carbon to nitrogen ratio
CH_4	Methane
cm	Centimetres
CO_2	Carbon dioxide
Db	Bulky density
DW	Dry weight
g cm^{-3}	Grams per cubic centimetre
g C kg^{-1}	Grams of carbon per kilogram
g C m^{-2} h^{-1}	Grams of carbon per square metre per hour
GHGs	Greenhouse gases
IPCC	Intergovernmental Panel on Climate Change
L	Litres
LOI	Loss on ignition
MAAIF	Ministry of Agriculture, Animal Industry and Fisheries
mg	Milligrams
mS m^{-1}	Millisiemens per meter
n	Number of samples
NEMA	National Environment Management Authority
P	Pressure
Q	Mass
R	Ideal gas constant
SE	Standard error
SOC	Soil organic carbon
SOM	Soil organic matter
T	Temperature
t C km^{-2}	Tonnes of carbon per square kilometre
UNMA	Uganda National Meteorological Authority
UN-REDD+	United Nation-Reducing Emissions from Deforestation and Forest Degradation
V	Volume
WMO	World Meteorological Organization

ABSTRACT

Natural wetlands have been shown to be among the most important ecosystems in climate change mitigation, through carbon (C) sequestration. However, natural wetlands also act as C sources, emitting part of the sequestered C back into the atmosphere, in form of carbon dioxide (CO_2) and methane (CH_4). Storage and emission of C are of interest in tropical wetland studies because the high and relatively stable temperatures year-round enhance both primary productivity and organic matter decomposition. However, most of the studies on C sequestration and emission have mainly focussed on temperate and boreal wetlands. Further, many natural tropical freshwater wetlands are increasingly being converted into rice paddies, with limited knowledge on its impact on wetland C balance. This study investigated soil organic carbon (SOC) storage and emission of CO_2 and CH_4 from a tropical freshwater wetland in Uganda, under natural and rice paddy conditions. The natural section is dominated by *Cyperus papyrus* (Papyrus), *Typha latifolia* (Typha) and *Phragmites mauritianus* (Phragmites) vegetation communities. Soil samples for determination of SOC were obtained up to 50 cm depth, using a Russian peat borer, while CO_2 and CH_4 gas samples were obtained using static flux chambers. Within the natural wetland section, SOC content (123.7±2.6 [mean±SE] g C kg^{-1} dry soil) in Papyrus was significantly higher ($p < 0.05$) than those obtained in Typha and Phragmites. On the other hand, there was no significant variation ($p > 0.05$) in SOC contents of Typha and Phragmites. Comparing SOC contents of the natural and rice paddy wetland sections, all the three vegetation communities of the natural section had SOC contents (Papyrus = 123.7±2.6, Typha = 85.3±1.1 and Phragmites = 78.2±3.4 g C kg^{-1} dry soil) significantly higher ($p < 0.05$) than that recorded in the rice paddy section (39.7±0.7 g C kg^{-1} dry soil). Considering fluxes of gases from the wetland, variation among the vegetation communities of the natural section was only noticed in Phragmites during the dry season. During this season, Phragmites showed significantly higher flux ($p < 0.05$) of CO_2 (871.8±56.7 mg C m^{-2} h^{-1}) and lower ($p < 0.05$) flux of CH_4 (8.7±0.5 mg C m^{-2} h^{-1}) than those measured in both Papyrus and Typha. No significant variation in gas fluxes ($p > 0.05$) occurred among the vegetation communities during the wet season, for both CO_2 and CH_4. Further, comparing the natural and rice paddy wetland sections, variabilities in gas flux rates were observed. CO_2 fluxes (mg C m^{-2} h^{-1}) from the rice paddy section during the dry and wet seasons were 1045.4±46.6 and 804.4±50.2 respectively, both significantly higher ($p < 0.05$) than those obtained in all the three vegetation communities of the natural section. However, CH_4 fluxes from the rice paddy section during the dry and wet seasons were 2.1±0.4 and 5.1±0.5 mg C m^{-2} h^{-1} respectively, both significantly lower ($p < 0.05$) than those observed in all the three vegetation communities of the natural section. Nevertheless, considering total C flux (summation of CO_2 and CH_4 fluxes), it was observed that the rice paddy wetland section emitted significantly higher ($p < 0.05$) C than the natural section. Plant biomass density, and soil physico-chemical characteristics: bulk density, salinity, pH and temperature significantly correlated ($p < 0.05$) with SOC, while water level had a significant correlation ($p < 0.05$) with CO_2 and CH_4 fluxes in both sections of the wetland. The observation of significantly higher SOC content and significantly lower total C flux from the natural wetland section compared to the rice paddy section suggests that conserving a natural tropical freshwater wetland is a better climate mitigation option than converting into a rice paddy wetland.

CHAPTER ONE

1. Introduction

1.1 Background

Over the past century, there has been a drastic increase in the concentration of greenhouse gases (GHGs) in the atmosphere, which has contributed to global warming and subsequent climate change. The fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC) identifies carbon dioxide (CO_2) and methane (CH_4) as the major GHGs contributing to global warming (IPCC, 2014). According to the most recent report by the World Meteorological Organization (WMO), CO_2 and CH_4 respectively contribute about 66% and 17% of the radiative forcing by long-lived GHGs (WMO, 2019). This report further shows a 147% and 259% increase in atmospheric concentrations of CO_2 and CH_4 respectively, in 2018 relative to their pre-industrial concentrations in 1750. Besides, whereas CO_2 accounts for the highest level of radiative forcing, CH_4's global warming potential on a 100-year scale is 34 times that of CO_2 (IPCC, 2013; Mitsch and Mander, 2018). Without effective mitigation measures, global climate change is anticipated to cause detrimental effects on natural and human systems (IPCC, 2007).

To counter climate change, there are increasing international calls for scientific studies on the potential of natural ecosystems to sequester carbon (C) (Mitra *et al.*, 2005; Villa & Bernal, 2018). Carbon sequestration, in this context, refers to the capture of atmospheric CO_2 and its long-term storage, with minimal chances of being released back to the atmosphere. In natural ecosystems, C is sequestered when primary productivity exceeds loses mainly due to organic matter decomposition.

Natural wetlands have been shown to be among the most important ecosystems in climate change mitigation through C sequestration. Wetlands are estimated to contain 350-535 Gt C (Mitra *et al.*, 2005) or about 20-30% (Zeng *et al.*, 2014; Lane *et al.*, 2016; Nahlik & Fennessy, 2016) of the world's C in organic soils, despite covering only 5-8% of the earth's surface (Mitsch *et al.,* 2013). The hypoxic conditions in wetlands slow down organic matter decomposition processes. This makes wetlands to accumulate large amounts of C, even up to 40% soil C in some cases, a figure that is substantially greater than the 0.5–2% C commonly found in agricultural soils (Nahlik & Fennessy, 2016).

Wetlands are therefore widely seen as promising C sinks given their wider spatial distribution.

On the other hand, depending on the management practices, natural wetlands may also act as C sources, emitting part of the sequestered C back into the atmosphere, in form of CO_2 and CH_4 (Belger *et al.*, 2011; Butterbach-Bahl *et al.*, 2016; Mitsch & Mander, 2018; Gutenberg *et al.,* 2019; Ishikura *et al.,* 2019). For example, wetlands are estimated to account for up to 25% of the total natural and anthropogenic sources of CH_4 (Oertel *et al.,* 2016). Nevertheless, considering the magnitudes of C assimilation and emissions, although wetlands could be net C sinks on a global perspective (Mitsch *et al.,* 2013; Mitsch, 2016), the accuracy of estimation of global wetland C balance may be limited because particular wetlands may be net C sources at local scales (Kayranli *et al.*, 2010; Sjögersten *et al.*, 2014; Villa & Bernal, 2018). Thus, clear knowledge of global wetland C balance, and the role of wetlands in climate change mitigation requires a comprehensive understanding of C storage and emission in all wetlands spread across the globe. The aim of this study was, therefore, to assess C storage and fluxes from a tropical freshwater wetland in Uganda under natural (dominated by *Cyperus papyrus*, *Typha latifolia* and *Phragmites mauritianus*) and rice paddy conditions.

1.2 Problem Statement

Carbon storage and emission from wetlands are controlled by a number of biotic and abiotic factors, which have been relatively well studied (Mitra *et al.*, 2005; Bernal & Mitsch, 2008; Kayranli *et al.*, 2010; Sjögersten *et al.*, 2014; Villa & Bernal, 2018; Ishikura *et al.,* 2019; Were *et al.,* 2019). However, these factors can vary across wetland types and geographical locations. For example, unlike wetlands in boreal and temperate regions where cold temperatures limit primary production and decomposition (Sjögersten *et al.,* 2014), high and relatively stable temperatures year-round in tropical regions enhance both productivity and organic matter decomposition rates in tropical wetlands. Further, as compared to boreal and temperate wetlands where organic matter input originates from fewer plant species, tropical wetlands show a wide diversity of plant species, which contribute organic matter with variable degrees of recalcitrance (Bernal & Mitsch, 2008; Sjögersten *et al.,* 2014). More still, Chimner & Ewel (2005) reported faster plant root turnover rates (70% per yr^{-1}) in tropical wetlands compared to 55% and 44% per yr^{-1} in temperate and boreal wetlands, respectively. Such differences have a potential to create variabilities in the magnitude of C storage and emission between tropical and temperate/boreal wetlands.

Tropical wetlands occupy a considerably large spatial extent, about 30% of the total global wetland area (Marín-Muñiz *et al.,* 2015). Tropical wetlands are therefore important ecosystems which cannot be ignored in the computation of the global C pool and cycling. However, most of the studies on C sequestration and emission have mainly focussed on temperate and boreal wetlands (Mitra *et al.,* 2005; Kayranli *et al.*, 2010; Sjögersten *et al.,* 2014; Nahlik & Fennessy, 2016). As a result, there is limited understanding of C stocks and emissions from tropical wetlands, and the controlling factors.

Further, many natural tropical freshwater wetlands are increasingly being converted into other land uses, mainly rice paddies. However, it is still not clearly known how conversion of natural freshwater wetlands into rice paddy wetlands may impact their C balance. Indeed, recent review studies (Sjögersten *et al.,* 2014; Villa & Bernal, 2018; Were *et al.,* 2019) on C storage and cycling in wetlands have recommended more work on tropical wetlands in order to have a candid understanding of how they differ from the well-studied northern wetlands.

1.3 Objectives

1.3.1 General Objective

To assess the influence of wetlands, and their conversion into rice paddies on C stock and flux.

1.3.2 Specific Objectives

I. To assess the variation of soil organic carbon (SOC) stock in a natural tropical freshwater wetland under different vegetation communities in Uganda

II. To assess the impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on soil organic carbon (SOC) stock in Uganda

III. To assess the variation of carbon dioxide (CO_2) and methane (CH_4) fluxes from a natural tropical freshwater wetland under different vegetation communities in Uganda

IV. To assess the impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on carbon dioxide (CO_2) and methane (CH_4) fluxes in Uganda

1.4 Research Questions

Objective 1

I. Does SOC stock in a natural tropical freshwater wetland vary under different dominant vegetation communities (*Cyperus papyrus*, *Typha sp* and *Phragmites sp*)?
II. Under *Cyperus papyrus* vegetation community, does SOC stock vary between floating and emergent growth forms?
III. How do soil physico-chemical and plant characteristics affect SOC stock in a natural tropical freshwater wetland?

Objectives 2

I. How does conversion of a natural tropical freshwater into a rice paddy wetland affect SOC stock?
II. Does conversion of a natural tropical freshwater into a rice paddy wetland affect soil physico-chemical characteristics that influence SOC storage?

Objective 3

I. Do CO_2 and CH_4 fluxes from a natural tropical freshwater wetland vary under different dominant vegetation communities (*Cyperus papyrus, Typha sp* and *Phragmites sp*)?
II. Do CO_2 and CH_4 fluxes from a natural tropical freshwater wetland vary with season (dry vs wet)?
III. How do environmental parameters affect CO_2 and CH_4 fluxes from a natural tropical freshwater wetland?

Objectives 4

I. How does conversion of a natural tropical freshwater wetland into a rice paddy wetland affect fluxes of CO_2 and CH_4?
II. Does conversion of a natural tropical freshwater into a rice paddy wetland affect soil physico-chemical characteristics that influence CO_2 and CH_4 fluxes?

1.5 Justification

Natural freshwater wetlands are essential components of the landscape, providing a variety of ecosystem services. They recharge underground aquifers and protect open water bodies such as lakes from pollution by filtering inflowing waters from streams, rivers and other surface point and nonpoint discharges. They also act as major sources of water in many rural areas of developing countries. However, globally and Uganda in particular, there is an increasing loss of natural freshwater wetlands due to conversion to other land uses like agriculture, especially rice cultivation. With the increasing advocacy and pressure on national governments to mitigate climate change, scientific studies on the role of wetlands in global climate change are necessary to inform decision makers concerning wetland conservation and/or restoration of degraded ones, in view of climate change mitigation and other wetland ecosystem services.

Additionally*, Cyprus papyrus, Typha latifolia* and *Phragmites sp*. being common wetland plant species in Uganda, and the East African region in general, quantifying the soil organic carbon (SOC) stocks in the wetland sections under these vegetation types will provide a foundation to appraise national wetland carbon stock and CO_2 and CH_4 emissions for Uganda, and for other countries which have similar wetland types. This is important for global C accounting and planning, and inclusion of these wetlands in C-offset programs, that may be similar to the United Nation's "Reducing Emissions from Deforestation and Forest Degradation (UN-REDD+)" programme.

1.6 Overview of the Dissertation Structure

This dissertation is based on four (i to iv) published papers. The four papers were founded from a comprehensive literature review process, which was undertaken at the early stages of this PhD study and produced a review paper. The review paper (which is not included in this dissertation) can be cited as: Were, D., Kansiime, F., Fetahi, T., Cooper, A., & Jjuuko, C. (2019). Carbon Sequestration by Wetlands: A Critical Review of Enhancement Measures for Climate Change Mitigation. *Earth Systems and Environment*, *3*, 327–340. https://doi.org/10.1007/s41748-019-00094-0 (Publisher: Springer Nature).

The investigations of these four papers are guided by the specific objectives outlined in section 1.3. Structure wise, each of the four papers comprises an abstract, introduction, methodology, results, discussion, conclusions and references. The papers can be cited as follows:

(i) Were, D., Kansiime, F., Fetahi, T., & Hein, T. (2020). Soil organic carbon storage in a tropical freshwater wetland: the influence of vegetation type. *African Journal of Aquatic Science,* 1-12. https://doi.org/10.2989/16085914.2020.1804821 (Publisher: Tailor and Francis)

(ii) Were, D., Kansiime, F., Fetahi, T., & Hein, T. (2020). A natural tropical freshwater wetland is a better climate change mitigation option through soil organic carbon storage compared to a rice paddy wetland. *SN Applied Sciences*, *2*, 1-13. https://doi.org/10.1007/s42452-020-2746-8 (Publisher: Springer Nature)

(iii) Were, D., Kansiime, F., Fetahi, T., & Hein, T. (2021). Carbon dioxide and Methane Fluxes from Various Vegetation Communities of a Natural Tropical Freshwater Wetland in Different Seasons. *Environmental Processes*. https://doi.org/10.1007/s40710-021-00497-0 (Publisher: Springer Nature).

(iv) Were, D., Kansiime, F., Fetahi, T., & Hein, T. (2021). Carbon dioxide and Methane Fluxes from a Tropical Freshwater Wetland under Natural and Rice Paddy Conditions: Implications for Climate Change Mitigation. *Wetlands*. https://doi.org/10.1007/s13157-021-01451-4 (Publisher: Springer Nature).

Generally, the dissertation comprises of six chapters. Chapter one provides an introduction to the study. It brings out the context of the study and presents the overall picture of climate change, and the influence of wetlands on climate change through carbon storage and fluxes. It also provides a justification as to why knowledge of C stocks and emissions from tropical wetlands is important in understanding global wetland carbon balance and cycling.

Chapter two (Paper i) investigates the influence of vegetation community on SOC stock in a natural tropical freshwater wetland. The chapter compares SOC stocks in the wetland under *Cyperus payrus, Typha latifolia* and *Phragmites mauritianus* vegetation communities. Further, freshwater wetlands in Uganda, and the tropical region in general, are rapidly being converted into rice paddy fields. As a result, Chapter three (Paper ii) examines the effect of converting a natural tropical freshwater into a rice paddy wetland on SOC, by comparing SOC stocks under natural and rice paddy wetland conditions.

Chapter four (Paper iii) assesses CO_2 and CH_4 fluxes from the natural tropical freshwater wetland under different dominant vegetation communities (as stated in Chapter two). In Chapter five (Paper iv), the effect of converting a natural tropical freshwater into a rice paddy wetland on C flux is investigated, by comparing of CO_2 and CH_4 fluxes under natural and rice paddy wetland conditions. The last chapter (Chapter six) presents the conclusions and recommendations of the study.

1.7 Scope of the Study

This study was limited to Naigombwa wetland ecosystem, located in Iganga District, South-eastern Uganda (Figure 1.1). The wetland can be divided into two sections, based on land use; natural and rice paddy. The natural section can further be sub-divided into three different parts, in view of dominant wetland vegetation communities that form a permanent cover throughout the year: *Cyperus papyrus* (Papyrus), *Typha latifolia* (Typha) and *Phragmites mauritianus* (Phragmites). However, it is important to note that though these vegetation communities are dominant, they do not make pure stands in their places of occurrence because there is occurrence of some small patches of other vegetation communities. The converted section (rice paddy wetland) occurs upstream of the natural section, where natural vegetation was replaced with rice cultivation.

This wetland was selected because unlike other wetlands, it exhibits all the 3 common wetland plant species in Uganda, and rice paddy fields on spatial extents large enough to allow comparative studies. Further, there exists baseline data on morphology and water level dynamics for this wetland (Kayendeke, 2018; Kayendeke *et al.,* 2018). Carbon assessment was limited to soil organic carbon (SOC), and CO_2 and CH_4 fluxes from wetland soil.

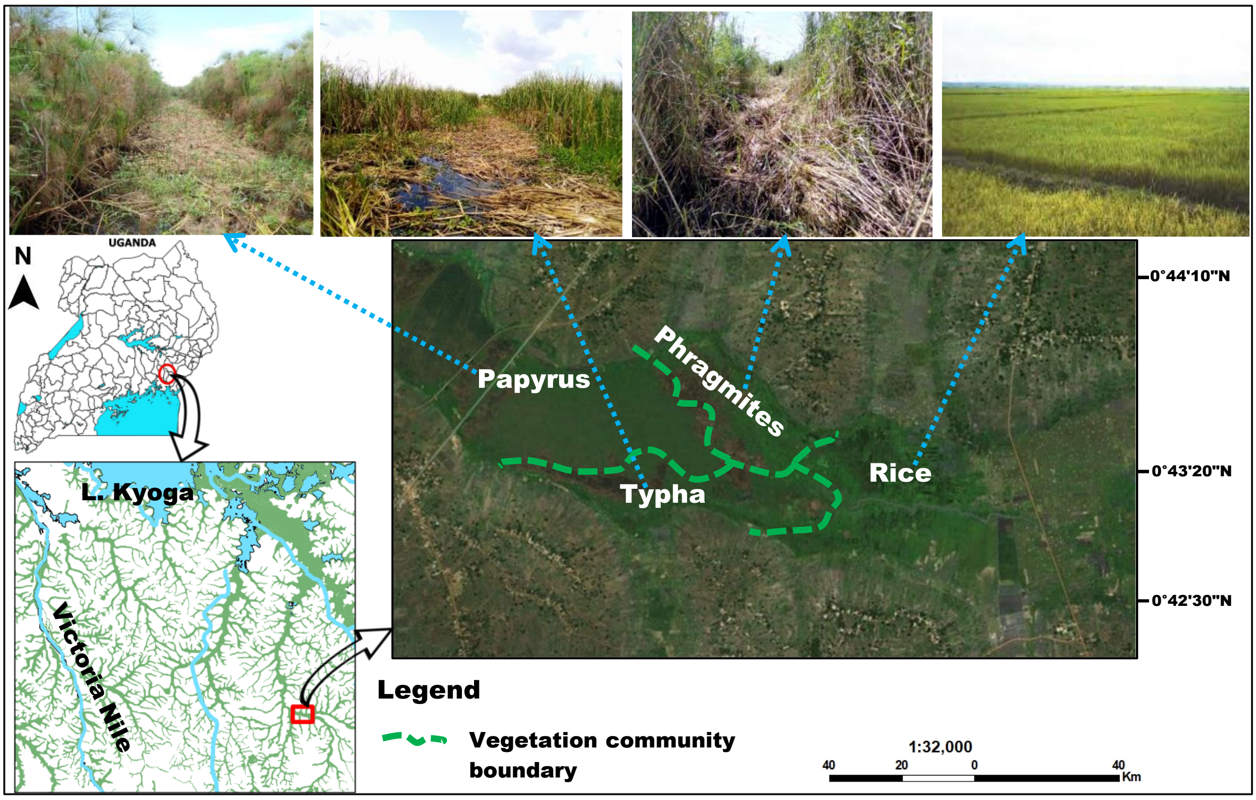

Figure 1.1 Location of the study area on the map of Uganda

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CHAPTER TWO

2 Soil Organic Carbon in a Tropical Freshwater Wetland Under Different Vegetation Communities

This Chapter is based on:

Were, D., Kansiime, F., Fetahi, T., & Hein, T. (2020). Soil organic carbon storage in a tropical freshwater wetland: the influence of vegetation type. *African Journal of Aquatic Science,* 1-12. https://doi.org/10.2989/16085914.2020.1804821

Abstract

Wetlands are among the most important ecosystems in the response strategy to global climate change. Their high primary productivity, together with hypoxic conditions enable them to accumulate large quantities of soil organic carbon (SOC). However, within tropical freshwater wetlands with diverse vegetation communities, SOC storage may vary among vegetation communities due to differences in plant characteristics. In this study, the impact of different vegetation communities on soil organic carbon (SOC) in a tropical freshwater wetland in Uganda was investigated. SOC content, density and storage potential were determined under 3 different dominant vegetation communities: *Cyperus papyrus* (Papyrus), *Typha latifolia* (Typha) and *Phragmites mauritianus* (Phragmites). SOC content (123.7±2.6 [mean±SE] g C kg^{-1} dry soil) in Papyrus was significantly higher ($p < 0.05$) than in Typha and Phragmites, while SOC density (kg C m^{-2}) insignificantly varied ($p > 0.05$) among the 3 vegetation communities (Papyrus = 7.2±0.1, Typha = 6.7±0.1 and Phragmites = 6.2±0.1). Similarly, for the entire sampled soil depth (0-50 cm), SOC storage potential was significantly higher ($p < 0.05$) in Papyrus (36118.08±552.52 t C km^{-2}), and was in the order of decreasing magnitude: Papyrus > Typha > Phragmites. It was found that plant biomass density, and soil physico-chemical characteristics: bulk density, salinity, pH and temperature significantly correlated ($p < 0.05$) with SOC. Where climate change mitigation is considered as a wetland ecosystem service, restoration priorities for degraded/lost tropical freshwater wetlands need to consider Papyrus plants. Further, comparing SOC storage by ecosystems, it was estimated that Uganda's wetlands contain three times more SOC than is contained in the country's forests.

2.1 Introduction

Sequestration of current atmospheric carbon (C) is crucial to counter climate change. The IPCC (2007) argues that soil C sequestration presents an inexpensive yet effective option for mitigating climate change. Soils, on a global scale, contain the largest share of the terrestrial C pool, nearly twice and thrice higher than what is contained in the atmosphere and vegetation, respectively (Sun *et al.,* 2013). Wetland ecosystems are among the most important sinks of atmospheric C. For example, wetlands are estimated to contain 20-30% of the earth's soil organic carbon (SOC) pool, despite covering only 5-8% of the earth's surface (Lane *et al.,* 2016).

Natural tropical wetlands attract a great interest in climate change mitigation efforts because the high and relatively stable temperatures year-round enhance primary productivity and SOC storage (Bernal & Mitsch, 2013a; Nahlik & Fennessy, 2016; Villa & Bernal, 2018). Further, tropical wetlands occupy a considerably large spatial extent, about 30% of the total wetland area (Marín-Muñiz *et al.,* 2015). Tropical wetlands are therefore important ecosystems which cannot be overlooked in the computation of the global SOC pool.

Several field studies have demonstrated the influence of vegetation community on SOC in wetlands. Differences in vegetation communities within the same wetland are likely to affect SOC sequestration due to differences in plant characteristics such as primary productivity (Jones *et al.,* 2018) and recalcitrance of organic matter (Hernandez & Mitsch, 2007; Sjögersten *et al.,* 2014). For instance, a study on various Mexican wetlands by Marín-Muñiz *et al.* (2014) showed that though wetland geomorphology had minimal impacts on SOC stocks in wetlands, changes in vegetation community caused significant variabilities in SOC among wetlands. In the same sense, Hernandez & Mitsch (2007) noted significant variations in soil organic matter among three wetland vegetation communities in a temperate wetland.

In the recent past, recognition of wetlands as important ecosystems in C sequestration has attracted research on SOC stocks in wetland soils. Such studies, nonetheless, have mainly focussed on either temperate or boreal wetlands (Mitra *et al.,* 2005; Kayranli *et al.,* 2010; Marín-Muñiz *et al.,* 2015; Were *et al.,* 2019). As a result, SOC storage in tropical wetland soils has been accorded minimal attention, hindering a proper understanding of their contribution to the global SOC pool. Thus, to assess the contribution of wetlands in mitigating climate change, it is necessary to have good knowledge on SOC storage in different wetlands spread across different geographical and climatic conditions. Indeed, recent review studies (Sjögersten *et al.,* 2014; Villa & Bernal, 2018; Were *et al.,* 2019) on C sequestration have recommended more work on tropical wetlands. In this study, SOC storage in a natural tropical freshwater wetland under different vegetation communities was investigated. Such knowledge is necessary to allow inclusion of tropical freshwater wetlands in global climate change models, and for decision making concerning prioritization of wetland conservation or restoration in view of climate change mitigation as an ecosystem service.

2.2 Materials and Methods

2.2.1 Study Area

The study was conducted on Naigombwa wetland, located in Iganga District, Southeastern Uganda (Figure 1.1). The natural section of the wetland can be divided into 3 different parts, based on dominant wetland vegetation communities that form a permanent cover throughout the year: *Cyperus papyrus* (commonly known as Papyrus), *Typha latifolia* (commonly known as Typha) and *Phragmites mauritianus* (commonly known as Phragmites).

Papyrus vegetation community dominate the downstream areas of the wetland, while Typha and Phragmites vegetation communities dominate the upstream areas. Papyrus vegetation community exhibits 2 growth forms, growing either as emergent (rooted in the sediment) close to the wetland edges or as floating (rooted in the mat above the water column) towards the wetland mid-sections where the water level is high (Figure 2.1). The mat is composed of loosely intertwined roots and rhizomes, allowing penetration of dead plant biomass to the peat sediment layer (Azza *et al.,* 2000). On the other hand, both Typha and Phragmites vegetation grow only emergent, and tend to be outcompeted by Papyrus vegetation in areas with high water levels (Kansiime *et al.,* 2007).

The water level in Naigombwa wetland varies during different seasons of the year (Kayendeke *et al.,* 2018). Wetland edges tend to experience intermittent flooding and drying cycles during wet and dry seasons, respectively. However, wetland areas away from the edge are mainly flooded throughout the year, though the water level depth fluctuates between wet and dry seasons. Throughout the sampling period, water was above the soil surface. Mean recorded water levels were: 12.4±2.3 (mean±SE) cm in the emergent growth form and 57.6±5.0 cm in the floating growth form of the Papyrus vegetation community, 11.3±2.6 cm and 5.3±1.5 cm in the Typha and Phragmites vegetation communities, respectively. Water level in the floating growth form was taken as the depth of the free water column (Figure 2.1).

Existing historical data (1961-1990) of weather stations in the Lake Kyoga basin show average annual temperature of 21°C and annual rainfall of 1300 mm, occurring on a bimodal pattern, from March to May and September to November (Kayendeke *et al.,* 2018). In recent years however, unpredictable rainfall patterns in terms of period of onset and secession, frequency and intensity are being experienced (Kayendeke, 2018).

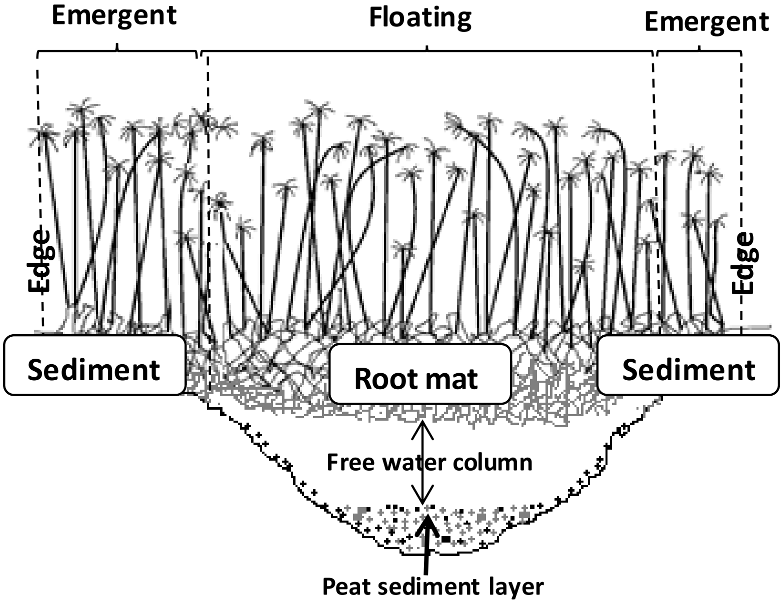

Figure 2.1 Schematic overview of a transverse cross-section through a Papyrus vegetation community in the wetland. Generated from this study

2.2.2 Collection and Analysis of Soil Samples

Soil sampling was done from February to April 2019 in the 3 vegetation communities described in section 2.2.1 above. In each vegetation community, three 1 m^2 sampling plots were randomly selected along transects. The lengths of the transects varied depending on the spatial coverage of the vegetation community, but ranged from 50 m to 100 m. In each sampling plot, 4 cores (50 cm deep by 5.0 cm wide) were taken using a Russian peat borer (Marín-Muñiz *et al.,* 2014; Figure 2.2). The thin, sharp-walled edges of this borer provide for coring with minimum compaction, distortion and disturbance. Each core was sectioned with a blade at 10 cm increments (up to 50 cm). One of the 4 cores at each sampling plot was used for bulk density analysis. The core depth was restricted to 50 cm following preliminary coring trials that established this depth as the possible maximum. Beyond 50 cm it was not possible to drive the peat borer further due to presence of compacted clay. For the case of the Papyrus vegetation community which exhibits differences in growth forms (floating Vs emergent; Figure 2.1), soil sampling was done both in the sediment of the emergent growth form and the peat sediment layer of the floating growth form.

Composite samples were obtained by mixing 3 samples of the same depth in each sampling plot. Differences in SOC contents in the same sampling plot that might occur due variations in decomposition were accounted for by spacing cores in a triangular pattern, 40 cm between each other as in Bernal & Mitsch (2008, 2012). With triplicates, 45 composite samples were obtained for each depth increment in each vegetation community. Composite samples were placed in labelled ziploc polyethylene bags and transported to the Soil Science Laboratory, College of Agricultural and Environmental Sciences, Makerere University, Kampala, Uganda for analysis.

Prior to analysis, composite soil samples were re-mixed to increase homogeneity, and visible plant residues were removed. The samples were air dried at room temperature for 21 days, ground and sieved through a 2 mm nylon sieve. Dry soil samples were used to determine soil organic matter (SOM) content and soil physico-chemical characteristics (pH, salinity and nitrogen [N]). To determine SOM, 2 g of each soil sample (in triplicate) was placed in pre-weighed crucibles and pre-treated with 10 M HCl until zero bubbling was achieved to prevent possibilities of carbonate interference (Hernandez & Mitsch, 2007; Marín-Muñiz *et al.,* 2014). The samples were then dried in an oven (Carbolite CWF 13/5) at 105 °C until constant weight before being ignited at 450 °C for 4 hours (Bernal & Mitsch, 2008; Marín-Muñiz *et al.,* 2014). Soil organic matter percentage (SOM%) of each sample was calculated following weight loss on ignition (LOI), from where SOC percentage (SOC%) was obtained as a portion of SOM%, using Van Bemmelen's index of 0.58 (Marín-Muñiz *et al.,* 2014).

SOC content (g C kg^{-1} dry soil) and SOC density (kg C m^{-2}) for each soil layer, and SOC storage potential (t C km^{-2}) along the entire sampled soil depth (0-50 cm) were respectively determined as depicted in equations *(2.1)* (Bernal & Mitsch, 2008), *(2.2)*

(Huo *et al.,* 2013; Marín-Muñiz *et al.,* 2014) and *(2.3)* (Huang *et al.,* 2013; Were *et al.,* 2020):

$$SOCi\ content = 10 * SOCi\% \tag{2.1}$$

$$SOCi\ density = SOCi\% *\ Dbi *\ hi \tag{2.2}$$

$$SOC\ storage\ potential = \sum_{i=1}^{n} SOCi\ \% *\ Dbi * hi \tag{2.3}$$

where: SOC*i%* is the SOC% of layer *i*, *Dbi* is the bulk density at layer *i* (g cm^{-3}) and *hi* is the depth of soil layer *i* (cm).

Soil pH and salinity were determined using a multi-parameter meter (CyberScan PC 300), after equilibration of soil with deionized water (soil: water, 1:5; Huang *et al.,* 2013; Wang *et al.,* 2018). Soil N content was determined using the Kjeldahl digestion procedure (Huang *et al.,* 2013; Wang *et al.,* 2018). Bulk density (Db) was determined by drying a known volume of sample (determined from the dimensions of the core) at 105 °C until a constant weight, cooled to room temperature in a desiccator, and weighed again. Bulk density was then expressed as dry weight of soil per unit volume (Huang *et al.,* 2013). As all sites were fully submerged, there was no need for soil moisture content measurements.

Figure 2.2 Taking soil samples in the wetland

2.2.3 *In-situ* Measurements, and Collection and Analysis of Plant Samples

Soil temperature was measured in the field using a digital soil thermometer. Plants (Papyrus, Typha and Phragmites) were destructively harvested in 0.3 m^2 triplicate plots along each transect for determination of biomass density (above and below ground), N and organic C contents. For above ground biomass, all plants in each sampling plot were harvested by cutting at the base and weighed to establish the total fresh weight. Plant parts below the soil surface (below ground biomass) were carefully removed to prevent root breakage, washed to remove all the soil and other attached material and weighed to establish the total fresh weight. A portion of fresh biomass (for both above and below ground biomass) was then sub-sampled and taken for laboratory analysis of plant biomass (as dry weight). For N content, portions of plant parts (roots, stems and leaves) were obtained and mixed to make representative samples. In total, 45 composite plant samples were obtained from each vegetation community.

Plant biomass (dry) was obtained from dry to wet weight ratio, after drying plant samples at 105 °C to a constant weight. Plant biomass density was expressed as the dry weight of plants per unit area. To determine plant N content, plant samples were oven dried at 65 °C until constant weight and ground (Chen *et al.,* 2017), after which N content was determined using the Kjeldahl digestion procedure (Huang *et al.,* 2013; Wang *et al.,* 2018). Plant organic C content was determined from the weight loss on ignition (LOI) procedure, as described for determination of SOC above.

2.2.4 Data Analysis

Statistical analysis was carried out in Microsoft Excel (2016) and R programming software (version 3.2.2). Data was first tested for normal distribution and homogeneity of variance, and it was found to satisfy these conditions. As a result, parametric statistics one-way ANOVA and Tukey HSD post-hoc test were used to determine the vertical and spatial variation of SOC content and density, and storage potential among vegetation communities, at a significance level of 95% ($p < 0.05$) (Hernandez & Mitsch, 2007; Marín-Muñiz *et al.,* 2014). The relationships between soil physico-chemical and plant characteristics with SOC were determined using Spearman rank correlation, at $p < 0.05$ significance.

2.3 Results

2.3.1 Soil Physico-chemical and Plant Characteristics

Most soil physico-chemical parameters varied with soil depth and among vegetation communities (Table 2.1). Within the Papyrus vegetation community, differences were observed between the floating and emergent growth forms. Soil temperature, salinity and N content generally decreased with increasing soil depth. Soil pH and bulk density, on the hand, displayed a general increase with increasing soil depth.

Soil temperatures of the top (0-10 cm) and bottom (40-50 cm) soil layers varied greatest in the Typha vegetation community. Temperature difference between 0-10 cm and 40-50 cm soil layers in this vegetation community was 0.6 °C. Temperatures of 0-10 cm and 40-50 cm soil layers in the Papyrus vegetation community varied by 0.4 °C both in the emergent and floating growth forms respectively, higher than the 0.3 °C variation observed in the Phragmites vegetation community.

Soil pH values in all the 3 vegetation communities were generally acidic, with the lowest pH range observed in the Papyrus vegetation community. In this vegetation community, pH increased from the top to the bottom soil layer by 1.40 units and 0.70 units in the floating and emergent growth forms respectively, as compared to 0.84 units and 0.82 units in the Typha and Phragmites vegetation communities, respectively.

Soil salinity showed a great variation with depth, and among vegetation communities. For example, in the Papyrus vegetation community, salinity decreased (from top to bottom soil layer) by close to 87% in the floating growth form, and by 77% in the emergent growth form. In the Phragmites vegetation community salinity decreased by about 73%, while the Typha vegetation community showed the lowest salinity decrease of about 53%. On average, both floating and emergent growth forms of the Papyrus vegetation community had salinity values higher than those recorded in the Typha and Phragmites vegetation communities.

Bulk density and N content showed slight variations with depth, and among vegetation communities. The difference between the highest and lowest average bulk density among the vegetation communities was 0.16 g cm^{-3}, while N differed by only 0.15%. Soil C:N ratio did not show any clear trend with depth in all the 3 vegetation communities, though highest average values were recorded in the Papyrus vegetation community.

Table 2.1 Soil physico-chemical characteristics at different depths in the different wetland vegetation communities. Values are mean±SE (n = 45)

Parameter	Vegetation community		Soil depth (cm)					
			0-10	10-20	20-30	30-40	40-50	Average
Temperature (°C)	Papyrus	Floating	26.5±0.0	26.4±0.1	26.3±0.1	26.3±0.1	26.1±0.0	26.3±0.1
		Emergent	26.6±0.0	26.6±0.0	26.5±0.0	26.4±0.1	26.2±0.1	26.5±0.0
	Typha		26.9±0.1	26.7±0.1	26.5±0.1	26.4±0.2	26.4±0.2	26.6±0.1
	Phragmites		26.6±0.1	26.4±0.1	26.4±0.1	26.4±0.1	26.3±0.0	26.4±0.1
pH	Papyrus	Floating	5.14±0.01	5.92±0.01	6.00±0.01	6.31±0.05	6.54±0.02	5.98±0.01
		Emergent	5.44±0.01	5.56±0.01	5.87±0.03	5.92±0.01	6.14±0.01	5.79±0.01
	Typha		6.23±0.01	6.26±0.02	6.67±0.02	7.00±0.01	7.07±0.06	6.64±0.02
	Phragmites		6.06±0.01	6.34±0.01	6.50±0.04	6.80±0.01	6.88±0.01	6.52±0.01
Salinity (mS m^{-1})	Papyrus	Floating	580.89±6.96	146.73±1.93	78.89±1.72	50.22±8.99	78.42±5.16	187.03±4.96
		Emergent	232.83±7.93	192.63±2.13	96.35±0.66	61.37±1.59	54.61±0.66	127.55±2.59
	Typha		129.22±2.40	122.64±0.95	120.66±2.37	88.81±7.25	61.74±0.44	104.61±2.68
	Phragmites		118.59±2.48	64.09±0.33	46.30±1.08	34.25±0.28	33.17±0.15	59.27±0.86
Bulk density (g cm^{-3})	Papyrus	Floating	0.61±0.01	0.62±0.04	0.73±0.03	0.74±0.02	0.74±0.05	0.69±0.03
		Emergent	0.32±0.02	0.54±0.01	0.56±0.03	0.83±0.02	0.88±0.01	0.63±0.02
	Typha		0.67±0.01	0.68±0.01	0.82±0.01	0.84±0.01	0.92±0.01	0.79±0.01
	Phragmites		0.38±0.01	0.58±0.06	0.92±0.04	1.00±0.01	1.10±0.12	0.76±0.05
N (%)	Papyrus	Floating	0.92±0.03	0.25±0.01	0.24±0.02	0.12±0.01	0.21±0.01	0.37±0.01
		Emergent	0.74±0.02	0.63±0.01	0.37±0.01	0.37±0.01	0.21±0.01	0.47±0.01
	Typha		0.43±0.01	0.34±0.01	0.32±0.01	0.26±0.01	0.26±0.03	0.32±0.01
	Phragmites		0.50±0.01	0.47±0.01	0.32±0.01	0.20±0.01	0.20±0.01	0.34±0.01
C:N	Papyrus	Floating	23.5:1±4.1:1	47.2:1±5.9:1	35.7:1±2.2:1	37.5:1±3.1:1	36.0:1±4.2:1	36.0:1±5.4:1
		Emergent	36.4:1±4.9:1	21.7:1±5.4:1	34.3:1±6.6:1	19.4:1±6.5:1	28.5:1±5.0:1	28.1:1±4.1:1
	Typha		29.3:1±5.5:1	28.8:1±4.6:1	24.0:1±2.7:1	28.8:1±4.1:1	24.0:1±2.4:1	27.0:1±5.1:1
	Phragmites		41.2:1±3.7:1	22.7:1±4.2:1	20.3:1±2.6:1	28.1:1±5.3:1	24.6:1±4.1:1	27.4:1±3.2:1

Plant characteristics also varied among vegetation communities (Table 2.2). Plant biomass density (both above and below ground) was highest in the Papyrus vegetation community, and respectively followed by Typha and Phragmites vegetation communities. Plant C and N contents were also highest in the Papyrus vegetation community, followed by Phragmites vegetation community and least in the Typha vegetation community. Plant C:N ratio followed the order Typha > Papyrus > Phragmites.

Table 2.2 Plant characteristics in the different wetland vegetation communities. Values are Mean±SE (n=45)

Vegetation community		Plant characteristics				
		Biomass density (kg DW m^{-2})		C (%)	N (%)	C:N
		Above ground	Below ground			
Papyrus	Floating	9.02±0.84	11.80±0.09	28.56±1.20	0.52±0.03	55.4:1±8.1:1
	Emergent	8.43±0.85	9.74±0.92	29.75±1.17	0.83±0.01	36.0:1±12.6:1
	Average	8.72±0.84	10.77±0.51	29.16±0.80	0.67±0.07	43.5:1±9.8:1
Typha		7.55±1.13	7.36±0.17	23.86±1.65	0.48±0.01	49.9:1±10.4:1
Phragmites		5.51±0.42	6.81±0.13	25.10±0.13	0.62±0.03	40.5:1±9.2:1

DW = Dry weight at 105 °C, C = Carbon, N = Nitrogen

2.3.2 Soil Organic Carbon in the Different Vegetation Communities

Both soil organic carbon (SOC) content and density showed considerable variabilities in vertical and spatial distribution. Generally, a decreasing trend for both SOC content and density with increase in soil depth was noted in all the 3 vegetation communities (Figure 2.3). Changes in SOC contents and densities were observed in all soil layers, in order of decreasing magnitude: 0-10 cm > 10-20 cm > 20-30 cm > 30-40 cm > 40-50 cm. However, in all the 3 vegetation communities, only the top (0-10 cm) soil layer had significantly higher ($p < 0.05$) SOC content and density, while other soil depths showed no significant variations ($p > 0.05$). For example, SOC content (243.0±9.6 [mean±SE] g C kg^{-1} dry soil) in the Papyrus vegetation community at soil layer 0-10 cm exceeded those of soil layers 10-20 cm, 20-30 cm, 30-40 cm and 40-50 cm by over 47%, 56%, 69% and 72% respectively, compared to about 24%, 40%, 41%, and 51%, and 49%, 69%, 72% and 76% in the Typha and Phragmites vegetation communities, respectively. SOC densities of Papyrus (10.86±1.12 kg C m^{-2}), Typha (8.53±0.09 kg C m^{-2}) and Phragmites (7.81±0.04 kg C m^{-2}) vegetation communities at soil layer 0-10 cm were more than those at the bottom (40-50 cm) soil layer by over 50%, 32% and 30%, respectively.

On a spatial perspective, SOC content (123.7±2.6 g C kg^{-1} dry soil) of the Papyrus vegetation community was higher than those of Typha and Phragmites vegetation communities by significant amounts ($p < 0.05$), while SOC densities of the 3 vegetation communities did not vary significantly ($p > 0.05$; Figure 2.3). Likewise, for the entire sampled soil depth (0-50 cm), the Papyrus vegetation community's SOC storage potential of 36118.08±552.52 t C km^{-2} was significantly greater ($p < 0.05$) than those of Typha and Phragmites vegetation communities, and followed the order: Papyrus vegetation community > Typha vegetation community > Phragmites vegetation community (Figure 2.4). Nevertheless, differences in SOC storage potentials of Typha and Phragmites vegetation communities were negligible ($p > 0.05$).

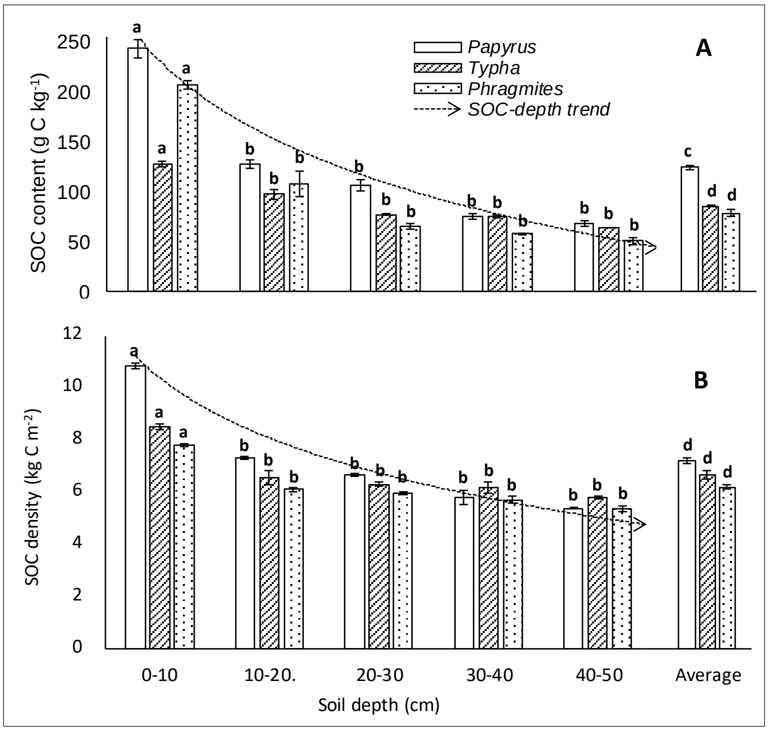

Figure 2.3 **Variation of SOC content (A) and SOC density (B) with soil depth in different wetland vegetation communities. Error bars are standard errors (SE) of the mean. Different letters on bars show significant differences (at different soil depth categories) within the same vegetation community, except for 'Average' bars where different letters show significant differences among vegetation communities (Tukey HSD, n=45, $p < 0.05$)**

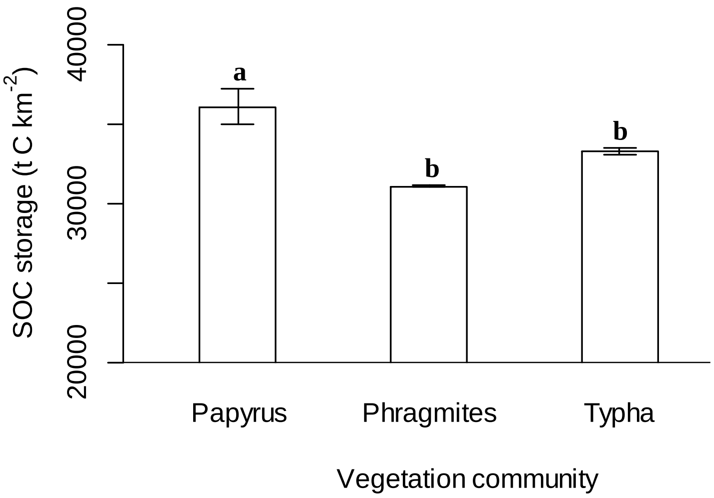

Figure 2.4 **SOC storage potential for the top 50 cm soil layer in different wetland vegetation communities. Error bars are standard errors (SE) of the mean. Bars with different letters are significantly different (Tukey HSD, n = 27, $p < 0.05$)**

Whereas results of SOC content, density and storage potential of the Papyrus vegetation community (Figure 2.3 and Figure 2.4 respectively) were based on average values from floating and emergent growth forms, some differences were noticed between these two growth forms. For instance, although average SOC contents in both growth forms were insignificant ($p > 0.05$), soil layer 0-10 cm of the emergent growth form presented significantly higher ($p < 0.05$) SOC content (269.3±16.0 g C kg^{-1} dry soil) than that of the floating one (216.7±3.2 g C kg^{-1}, Figure 2.5). On the other hand, SOC density (13.13±0.20 kg C m^{-2}) in the floating growth form at the same soil layer was significantly greater ($p < 0.05$) than that in the emergent growth form by about 16%. The high SOC density of this soil layer in the floating growth form (despite having a SOC content lower than in the emergent growth form) could be a reflection of the influence of bulk density. The bulk density at this soil layer in the floating growth form was close to 2-fold higher than in the emergent growth form (see Table 2.1). On average, however, differences in SOC densities of floating and emergent growth forms were of negligible significance ($p > 0.05$).

SOC storage potential (38063.49±567.91 t C km^{-2}) of the entire sampled depth (0-50 cm) in the floating growth form was significantly higher ($p < 0.05$) than that recorded in the emergent growth form (Figure 2.6), which could also be a reflection of the high bulk density in the floating growth form.

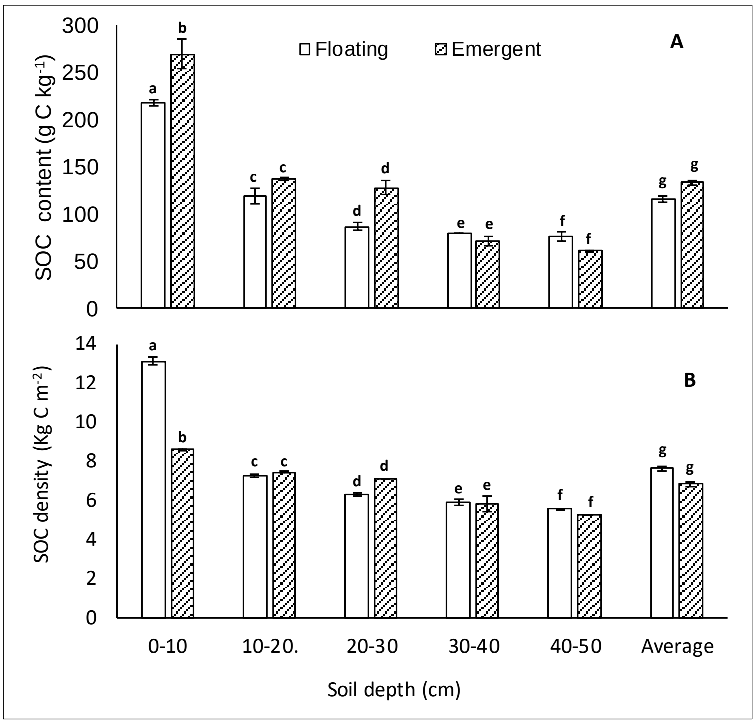

Figure 2.5 Variation of SOC content (A) and density (B) with soil depth in the floating and emergent growth forms of the Papyrus wetland vegetation community. Error bars are standard errors (SE) of the mean. Grouped bars (at each soil depth category) with different letters are significantly different (Tukey HSD, n=45, $p < 0.05$)

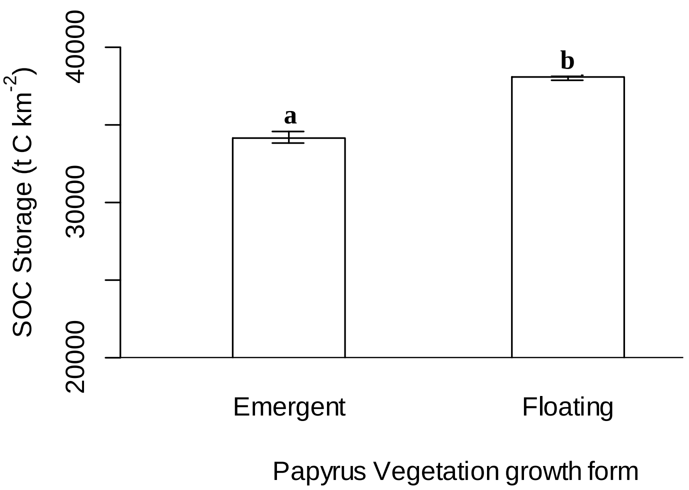

Figure 2.6 SOC storage potential for the top 50 cm soil layer in floating and emergent growth forms of Papyrus vegetation community. Error bars are standard errors (SE) of the mean. Different letters on bars show a significant difference (ANOVA, n = 27, p < 0.05)

2.3.3 Influence of Soil Physico-chemical and Plant Characteristics on SOC

The relationships between soil physico-chemical and plant characteristics and SOC varied, both in terms of magnitude and direction, as reflected by the Spearman rank correlation coefficients (Table 2.3). With respect to the significance of correlations, plant biomass density, and soil bulk density, salinity, pH and temperature presented significant correlations ($p < 0.05$) with SOC. On the other hand, soil C:N ratio insignificantly correlated ($p > 0.05$) with SOC. In view of direction of the correlations, plant biomass density, soil salinity, temperature and C:N ratio were positively correlated with SOC, unlike pH and bulk density which exhibited negative correlations with SOC.

Table 2.3 Spearman rank correlations between SOC and soil salinity, pH, temperature, bulk density, C:N ratio, and plant biomass density (n=45)

	SOC	pH	Salinity	Temperature	Bd	C:N ratio	Plant BMD
SOC	1.00						
pH	-0.79*	1.00					
Salinity	0.83*	-0.74*	1.00				
Temperature	0.68*	-0.27	0.41	1.00			
Bd	-0.89*	0.79*	-0.64*	-0.46	1.00		
C:N ratio	0.46	0.55	-0.18	0.13	0.47	1.00	
Plant BMD	0.98*	-0.43	0.48	-0.73*	-0.34	-0.05	1.00

* Significant at p < 0.05, *Bd = bulk density, BMD = biomass density, C = Carbon, N = Nitrogen*

2.4 Discussion

2.4.1 Soil Organic Carbon in Different Wetland Vegetation Communities

It was observed that SOC content and density decreased with increase in soil depth in all the 3 vegetation communities (Figure 2.3). SOC density being a product of SOC content and bulk density (which generally increased with soil depth; see Table 2.1), its decreasing trend with increase in soil depth is an indication that the increase of bulk density with increase in soil depth was not important to reverse the SOC density-soil depth trend. This implies that SOC density-soil depth trend was mainly dictated by SOC content rather than bulk density. Other studies (Bernal & Mitsch, 2008, 2013b; Huang *et al.,* 2013; Marín-Muñiz *et al.,* 2014; Chen *et al.,* 2017; Wang *et al.,* 2018) have also reported similar trends of SOC content and density with soil depth in tropical wetland soils. This observation could be attributed to continuous input of freshly dead plant biomass on the top soil layers (Huang *et al.,* 2013; Were *et al.,* 2019). Cases of harvesting standing plant biomass in the wetland were rarely observed, and of negligible significance. This implies that biomass from senescent plants is continuously added to the top soil over the years, hence increasing the SOM and the subsequent SOC compared to deep soil layers. However, this trend appears opposite to that in temperate and boreal wetland soils, where SOC content and density have been reported to increase with increase in soil depth (Bernal & Mitsch, 2008, 2012; Huo *et al.,* 2013; Nahlik & Fennessy, 2016). For example, Bernal & Mitsch (2008, 2012) recorded an increase in SOC content and density with increasing soil depth in 2 temperate wetlands dominated by *Typha* spp. and *Phragmites australis* vegetation communities. These contrasting trends in tropical vs temperate/boreal wetlands have been explained in terms of temperature regimes. In tropical regions, the high temperatures throughout the year induce both high plant productivity and decomposition of dead plant biomass (Bernal & Mitsch, 2008; Kayranli *et al.,* 2010). Therefore, whereas there is high biomass input in tropical wetlands, high decomposition rates in the soil profile, reduce SOC accumulation in deep soil layers. This makes large quantities of SOC to accumulate in top layers where plant biomass input outweighs losses due to decomposition (Bernal & Mitsch, 2008). On the other hand, cold temperatures in the temperate/boreal regions suppress not only plant productivity but also decomposition of dead plant biomass (Dick & Gregorich, 2004). As a result, most of the dead plant biomass, contributed from the limited plant productivity tend to accumulate in the soil profile overtime. However, during summer, when temperatures are warmer, rapid decomposition rates in the top soil layers reduces SOC as compared to cooler lower soil layers along the depth profile.

Among wetland vegetation communities, SOC content and storage potential in Papyrus were significantly higher than those in Typha and Phragmites communities. The explanation of this result can be made in relation to differences in primary productivities of these vegetation communities (Wang *et al.,* 2018). Plant biomass is the main source of SOM and the subsequent SOC (Were *et al.,* 2019). Therefore, assuming similar decomposition rates of plant biomass, highly productive plants are likely to generate more SOC compared to less productive plants. Papyrus plants have been reported to be highly productive. In Africa, for example, Jones *et al.* (2018) have found net primary productivity of Papyrus wetlands ranging between 2.51-3.09 C kg m^{-2} yr^{-1}, and suggested that Papyrus wetlands represent one of the highest productivity rates recorded in any natural ecosystem. This productivity is more than 3-fold the average productivity (0.790 kg C m^{-2} yr^{-1}) documented for boreal wetlands (Peregon *et al.,* 2008). Definitely, an observation of high plant biomass density in this study (Table 2.2) in the Papyrus vegetation community supports the reports of high productivity of Papyrus plants. The high productivity of Papyrus plants seems to be favoured by their ability to rapidly take up nutrients, as it has been shown from studies (Kyambadde *et al.,* 2004; Kansiime *et al.,* 2007; Van Dam *et al.,* 2014).

Additionally, Huang *et al.* (2013) noted an increase in SOC with increase in duration of soil inundation. The location of Papyrus vegetation community downstream of both Typha and Phragmites vegetation communities in this study's wetland could have enabled sustenance of a high water table for a longer period in the Papyrus vegetation community due to a lower water flow gradient than in the Typha and Phragmites vegetation communities, which are located upstream. Certainly, the water level recorded in Papyrus vegetation community was higher than what was recorded in both the Typha and Phragmites vegetation communities. However, Hernandez & Mitsch (2007) and Sjögersten *et al.* (2014) in their studies attributed variations in SOC in wetlands with different vegetation communities to differences in the level of structural carbohydrates such as lignin in plant biomass. Plant biomass rich in lignin is recalcitrant, making it resistant to decomposition (Bernal & Mitsch, 2008; Villa & Bernal 2017). Nevertheless, though the lignin contents of the respective plant biomass were not investigated in this study, it is thought that differences in lignin contents in plant biomass could not have accounted for this study's findings. This thought is definitely supported by studies that have found comparable lignin contents of Papyrus (12–34%; Elnaggar *et al.,* 2015), Typha (24%; Colbers *et al.,* 2017), and Phragmites (22–23%; Köbbing *et al.,* 2013) plant biomasses.

Within the Papyrus vegetation community, SOC content and density did not vary significantly between emergent and floating growth forms, while SOC storage potential was significantly higher in the floating growth form. However, it would be expected that the floating part has significantly higher SOC content. In view of the water table depth, the floating growth form tends to be flooded for most periods of the year (Kayendeke, 2018). This does not only favour continuous high productivity of plants over the year but also ensures that most of the SOM input from plant biomass undergoes limited decomposition (Villa & Bernal, 2018). The lush and denser appearance of vegetation in the floating growth form as observed in the field gave an indication of high plant productivity, and is further supported by the high biomass density compared to the emergent growth form (Table 2.2). On the other hand, the emergent growth form is subjected to intermittent flooding and drying patterns during the course of the year. During dry periods, plant productivity in this growth form is limited, while SOM is exposed to high decomposition rates, hence restricting SOC accumulation in soil (Bernal & Mitsch, 2008). Therefore, the lack of significant differences in SOC contents of both growth forms could be attributed to sediment transport in the floating growth form (Villa & Bernal, 2018). Because the root mat of this growth form floats on the water column, the peat sediment layer is exposed to erosion due to water movement, hence freshly dead biomass is washed off to downstream areas. This implies that the SOC content of the floating growth form of the papyrus wetland is only indicative of part of the carbon that was not transported and stored downstream. Therefore, since SOC storage potential is a function of SOC content and density, the observed significantly high SOC storage potential of the floating growth form could be possibly explained by bulk density (Upton *et al.,* 2018), which was on average higher in this growth form.

Findings of this study are comparable to results of other studies on tropical freshwater wetlands. Bernal & Mitsch (2008) investigated SOC contents and densities in Costa Rican wetlands with different dominant vegetation communities, including *Typha* spp. For the sampled top 54 cm soil layer, mean SOC content of wetlands ranged from 32.8±2.2 - 81.5±8.5 g C kg^{-1} dry soil, while mean SOC density ranged from 0.90±0.26 - 1.78±0.13 kg C

m^{-2}. Even though the soil depth sampled (54 cm) was higher than that in this study (50 cm), findings of Mitsch (2008) were in order of magnitude less than in this study (SOC content; 78.2±3.4 - 123.7±2.6 g C kg^{-1} dry soil and density; 6.20±0.06 - 7.22±0.11 kg C m^{-2}). Similarly, the maximum possible SOC storage potential (0-54 cm) for the Costa Rican wetlands was 15986.3±130.0 t C km^{-2}, less than the lowest SOC storage potential in this study (Phragmites vegetation community; 31016.69±316.08 t C km^{-2}) by close to 2-fold. Further, in Botswana, Bernal & Mitsch (2013b) obtained average SOC content and density in different freshwater marsh wetlands ranging from 16.7±3.4 - 33.3±7.3 g C kg^{-1} dry soil and 0.8±0.1 - 1.5± 0.07 kg C m^{-2} respectively, with a maximum SOC storage potential of 1500±70 t C km^{-2}. This study's findings being higher than those of other tropical freshwater wetlands could be explained by the location of Uganda along the equator, which favors high productivity of ecosystems (Saunders *et al.,* 2007). Globally, a literature review by Köchy *et al.* (2015) has shown that for the top 1 m soil depth, tropical freshwater marsh wetlands have the highest average SOC density of 38 kg C m^{-2}, compared to 35.4 kg C m^{-2} in fens, bogs and mires, 33.8 kg C m^{-2} in swamp forests, 21.9 kg C m^{-2} in mangrove wetlands and 7.5 kg C m^{-2} in brackish/saline wetlands.

Findings of SOC contents in this study were also compared to those reported from cold climates. In Ohio, USA, Bernal & Mitsch (2012) reported average SOC contents (for the top 35 cm) of 2 temperate freshwater wetlands, one dominated by *Typha* spp. and the other by *Phragmites australis*. Mean SOC contents were 156.7±7.5 and 22.3±1.1 g C kg^{-1} dry soil in Typha and Phragmites dominated wetlands, respectively. If the top 30 cm soil depth in this study is considered, average SOC content (100.3±2.8 g C kg^{-1} dry soil) in Typha vegetation community in this study's wetland was less than that of the temperate Typha wetland. On the other hand, average SOC content (126.5±6.7 g C kg^{-1} dry soil) in Phragmites vegetation community of this study's wetland was higher than that of the temperate Phragmites wetland. Despite the higher SOC content of the temperate Typha wetland compared to Typha and Phragmites vegetation communities in this study's tropical wetland, it was less than the SOC content of the Papyrus vegetation community (158.9±6.7 g C kg^{-1} dry soil). Findings of this study concur with Mitsch *et al.* (2013) who in their literature review, demonstrated a C sequestration rate of Ugandan Papyrus wetlands of 480 g C m^{-2} yr^{-1}, higher than any other tropical, temperate or boreal wetland ecosystem.

Further, a comparison of SOC in Uganda's wetlands and forests was made. Wetlands in Uganda cover a total area of 26,315 km^2, representing about 11% of country's land area (Government of Uganda, 2016). On the other hand, forests occupy 18,297.79 km^2, which is about 9% of the country's land area (Ministry of Water and Environment, 2016). Papyrus, Typha and Phragmites being the common vegetation types in Uganda's wetlands, if a consideration is made that all wetlands are covered by these three vegetation types implies that Uganda's wetlands contain over 883.01*10^6 t of SOC (taking an average SOC storage potential of 33555.40±495.56 t C km^{-2} for the top 50 cm soil layer as per this study results). On the other hand, Akodi *et al.* (2016) recorded a SOC storage potential of 15,000.00 t C km^{-2} for the top 60 cm soil layer in a strictly nature protected area of Mabira forest. Taking this SOC storage potential as a representative of Uganda's forests, then Uganda's forests contain 274.47*10^6 t of SOC, three times less than that contained in wetlands. In this case, the higher amount of SOC contained in wetlands as compared to forests is not only because wetlands have a large spatial extent but also because of their high SOC storage potential (which is more than double that of forests).

The IPCC (2014) emphasizes that achieving global climate change mitigation targets requires adoption of strategies that maximize C sequestration. Therefore, considering this study's findings in the interest of climate change mitigation, a Papyrus dominated wetland is a better option compared to those dominated by Typha and Phragmites vegetation communities. However, the role of wetlands in climate change mitigation is not only limited to C sequestration, but also includes other ecosystem services that help in adaptation to climate change impacts (IPCC, 2007; Were *et al.,* 2019). This suggests that prioritization of wetland conservation or restoration for climate change mitigation, based on vegetation community should not only consider its C storage potential but also needs to evaluate other ecosystem services provided by the wetland under that vegetation community.

2.4.2 Influence of Soil Physico-chemical and Plant Characteristics on SOC

Soil bulk density, salinity, pH and temperature, and plant biomass density had significant correlations with SOC, while the correlation of soil C:N ratio with SOC was negligible. These findings are in agreement with other studies. Upton *et al.* (2018) also reported a significant negative correlation between SOC and bulk density, and explained that bulk density affects water infiltration, rooting depth, microbial activity and nutrient availability. These in turn, affect plant productivity and the consequent SOC turnover. Salinity has been shown to affect SOC by regulating soil microbial respiration. Chambers *et al.* (2011) observed that exposure of freshwater wetland soil to 3.5 g kg^{-1} saline water increased SOC mineralization rate by 17%. However, Weston *et al.* (2011) suggested that the influence of salinity on SOC is more important for tidal coastal freshwater wetlands that are usually subject to sea level rise. The high level of salinity in Papyrus compared to Typha and Phragmites could be associated with the channelized flow in floating section of Papyrus, which promotes transport and deposition of catchment mobilized salts (Bugan *et al.,* 2015). In terms of pH, the activities of soil microbial communities involved in SOC turnover are optimum within a particular pH range (Batty & Younger, 2007). Villa & Bernal (2017) showed that temperature impacts microbial metabolism and population dynamics, directly affecting SOC. Davidson & Janssens (2006) further pointed out the influence of soil temperature on SOC by observing a doubling of SOM decomposition rates for every 10 °C temperature increase. In this study, because the soil sampling plan did not cover a full annual cycle, variations in soil temperatures due to seasonal (dry and wet) changes were not captured. However, Sjögersten *et al.* (2014) have shown that seasonal variations may have a limited influence on SOC sequestration in tropical wetlands as compared to temperate ones. Chen *et al.* (2017) recognized a strong control of plant biomass density on SOC stocks in both natural and restored wetlands, an observation also backed by Wang *et al.* (2018). The insignificant correlation between soil C:N ratio and SOC in wetland soil has been observed by Wang *et al.* (2018). This finding appreciates an earlier understanding by Christensen *et al.* (1999) that the influence of C:N ratio on SOC may be negligible in wetland soils with high SOC content. However, Villa & Bernal (2018) reported a significant control of C:N ratio on SOC by indicating an inverse relationship between C:N ratio and SOM decomposition rates.

2.5 Conclusions

Soil organic carbon (SOC) content (g C kg^{-1} dry soil) and density (kg C m^{-2}) in Papyrus, Typha and Phragmites vegetation communities of a tropical freshwater wetland was noticed to decrease with increasing soil depth. Wetland vegetation community influences SOC content, and storage potential but not SOC density. Papyrus vegetation community has SOC content and storage potential significantly higher than those of Typha and Phragmites vegetation communities, while the SOC densities of the 3 vegetation communities are not significantly different. Further, SOC contents, densities and storage potentials of Typha and Phragmites communities are not significantly different. Within the Papyrus vegetation community, differences in SOC contents and densities occur between floating and emergent growth forms, but are only significant at soil layer 0-10 cm. The emergent growth form has higher SOC content than the floating growth form, while the SOC density of the floating growth form is higher than that of the emergent growth form at this soil layer. Additionally, the SOC storage potential of the floating growth form is significantly greater than of the emergent growth form.

From this study, it is argued that where climate change mitigation is considered as a wetland ecosystem service, restoration actions for degraded/lost tropical freshwater wetlands need to give priority to Papyrus plants. Further, comparing SOC storage by ecosystems, it is estimated that Uganda's wetlands contain three times more SOC than is contained in the country's forests.

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CHAPTER THREE

3 Impact of Conversion of a Natural Tropical Freshwater Wetland into a Rice Paddy Wetland on Soil Organic Carbon Storage

This Chapter is based on:

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Abstract

The high productivity, together with hypoxic conditions in sediments enable wetlands to accumulate large amounts of soil organic carbon (SOC). However, natural tropical freshwater wetlands are increasingly being converted into other land uses, mainly rice cultivation. In this study, the impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on SOC was investigated, by comparing SOC content, density and storage potential in the natural section (dominated by *Cyperus papyrus* [Papyrus], *Typha latifolia* [Typha] and *Phragmites mauritianus* [Phragmites] vegetation communities) and in the converted section (under rice cultivation). The SOC contents (g kg^{-1}) and densities (kg m^{-2}) of the three vegetation communities (Papyrus; 123.7±2.6 [mean±SE] and 7.22±0.11, Typha; 85.3±1.1 and 6.71±0.12, and Phragmites; 78.2±3.4 and 6.20±0.06 respectively) of the natural section of the wetland were significantly higher ($p < 0.05$) than those (39.7±0.7 and 3.90±0.06 respectively) of the converted section. Similarly, for the entire sampled soil depth (0-50 cm), SOC storage potentials (t km^{-2}) of Papyrus (36118.08±552.52), Typha (33531.44±618.07) and Phragmites (31016.69±316.08) significantly exceeded ($p < 0.05$) that of the converted section by nearly 46%, 42% and 38%, respectively. Soil physico-chemical characteristics: bulk density, salinity, pH and temperature showed comparably significant correlations ($p < 0.05$) with SOC in both the natural and converted sections of the wetland. With these results, exploration of alternative options for increasing rice production outside wetlands is paramount if natural tropical freshwater wetlands are to remain important ecosystems carbon sequestration and climate change mitigation.

3.1 Introduction

Due to global warming and the subsequent climate change, it is increasingly becoming vital to the scientific community to understand and quantify carbon (C) pools and fluxes in terrestrial ecosystems such as wetlands (Mitsch *et al.,* 2013; Köchy *et al.,* 2015; Were *et al.,* 2019). On the other hand, minimizing C emission to the atmosphere, and increasing the capture and long-term storage of atmospheric carbon dioxide has been considered a winning strategy for climate change mitigation (Mitsch *et al.,* 2013; Were *et al.,* 2019).

Soil organic carbon (SOC) storage presents an inexpensive yet effective option for mitigating climate change (IPCC, 2007). Globally, soils store the largest terrestrial C pool, about thrice and twice higher than that sequestered in vegetation and the atmosphere, respectively (Sun *et al.,* 2013). Thus, a small change in SOC pool may have a significant impact on climate change. The high productivity of natural wetlands, together with the hypoxic conditions enable them to accumulate large amounts of organic C in their soils (Lane *et al.,* 2016; Nahlik & Fennessy, 2016; Villa & Bernal, 2018; Were *et al.,* 2019). For example, wetlands are estimated to contain 20-30% of the earth's soil C pool, despite covering only 5-8% of the earth's surface (Lane *et al.,* 2016). More importantly, the high and relatively invariable temperatures in tropical regions induce high production rates of wetlands that increases organic matter input in soil. Natural tropical wetlands are therefore widely recognized as promising C sinks, given that they cover approximately 30% of the world's wetlands area (Marín-Muñiz *et al.,* 2015).

However, the most recent global wetland inventories (Davidson, 2014; Davidson & Finlayson, 2018; Ramsar Convention on Wetlands, 2018) highlight an increasing rate of conversion of natural tropical freshwater wetlands into other wetland types, mainly rice paddy wetlands. In Uganda for instance, NEMA (2018) has estimated current annual wetland loss at 846 km^2 (about 2% of total wetland cover), and rice cultivation is identified as one of the leading causes of wetland conversion in the country (MAAIF, 2009). Such a trend raises concerns about the future role of natural tropical freshwater wetlands in global C balance, cycling and climate change mitigation.

Carbon sequestration in wetland soil is a function of both primary productivity and organic matter decomposition. Land use change is recognized as an important factor that influences SOC quantity and quality in wetland soil (Huo *et al.,* 2018), because it alters vegetation and water table characteristics (Lane *et al.,* 2016). The top soil layer in wetlands soil is generally composed of the living root zone, and is most geomorphically unstable (Lane *et al.,* 2016). This implies that SOC stock of the top soil in wetlands is more susceptible to land use change compared deep layer SOC. With specific reference to agricultural land use change, SOC stocks of natural ecosystems are known to decrease following conversion into plantation or cropland (Yan *et al.,* 2011; Oertel *et al.,* 2016; Huo *et al.,* 2018). However, SOC stocks of rice paddy wetlands have been shown to be highly variable depending on management practices (Conrad, 2002; Shang-Qi *et al.,* 2013; Zhang *et al.,* 2016; Jiang *et al.,* 2019; Hasanah *et al.,* 2019). Application of nitrogen fertilizer, manure, conservation tillage, and crop residues significantly increased SOC sequestration of a rice paddy wetland from 107 to 121 kg ha^{-1} yr^{-1}, 159 to 326 kg ha^{-1} yr^{-1}, 78 to 128 kg ha^{-1} yr^{-1}, and 489 to 1005 kg ha^{-1} yr^{-1}, respectively (Zhang *et al.,* 2016). Hasanah *et al.* (2019) showed that modification of water depth altered C sequestration in a rice paddy wetland, whereas maintaining the water table depth at -5 cm below the soil surface significantly increased C sequestration. A 4-years experiment by Shang-Qi *et al.* (2013) reported that rice paddy fields under no tillage had SOC content of 129.32 Mg ha^{-1}, significantly higher than those of fields under conventional plow tillage (121.12 Mg ha^{-1}) and rotary tillage (125.09 Mg ha^{-1}). Variation of C sequestration in rice paddy soils based on changes in rice plant variety was reported by Conrad (2002).

Most of the existing literature on rice paddy wetlands in Africa and Uganda in particular has given much attention to rice yields rather than C storage (Bado & Ndiaye, 2010; Oonyu, 2011; Boateng *et al.,* 2017; Mboyerwa, 2018). This limits an understanding of SOC stocks of rice paddy wetlands in this region. Therefore, to improve the accuracy of global SOC accounting and climate change models, it is a prerequisite to have a good understanding of SOC stocks in different ecosystems spread across the globe right from local scales. Further, in the face of climate change, comparative studies of SOC stocks in natural and rice paddy wetlands are a prerequisite for informed decision-making concerning wetland management in view of climate change mitigation as an ecosystem service. This is true because a number of studies indicate lack of consensus on the influence of rice cultivation on wetland SOC stocks (Yan *et al.,* 2011; Minasny *et al.,* 2012; Wang *et al.,* 2015; Zhang *et al.,* 2016). In this study, the impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on SOC was investigated, by comparing SOC content, density and storage potential in the natural section (under three naturally occurring dominant vegetation communities) and in the converted section, where natural vegetation was replaced by rice cultivation.

3.2 Materials and Methods

3.2.1 Study Area

The study was conducted on Naigombwa wetland, located in Iganga District, Southeastern Uganda (Figure 1.1). Based on land use; the wetland can be divided into two sections, natural and converted. The natural section can further be sub-divided into three different parts, in view of dominant wetland vegetation communities that form a permanent cover throughout the year: *Cyperus papyrus*, *Typha latifolia* and *Phragmites mauritianus*. For simplicity in the proceeding text, *Cyperus papyrus*, *Typha latifolia* and *Phragmites mauritianus* are referred to as “Papyrus”, “Typha”, and “Phragmites”, respectively.

The converted section occurs upstream of the natural section, where natural vegetation was replaced with rice cultivation. In the context of this study, the term “converted section”, is therefore exclusively used to refer to the wetland area under rice cultivation, a section also commonly known as rice paddy wetland. The rice is grown under flood irrigation, using natural gravity flow of surface water from the catchment. Rice is planted either through broadcasting of rice grains, or through transplanting of rice seedlings from nursery beds into the fields. There is no specified planting density of rice plants, while planting seasons are limited to two in a year.

Basing on the information provided by rice farmers, the ages of sampled rice fields were in the range of 1-5 years. The farmers clarified that they had not previously witnessed human activities in the wetland areas where they were cultivating rice. This implies that the given ages of the rice fields represented the period since conversion of the wetland area from its natural state.

The water level in Naigombwa wetland varies between the natural and rice paddy sections. Edges of the natural section of the wetland tend to experience intermittent flooding and drying cycles during the wet and dry seasons, respectively. However, areas away from the edges are mainly flooded throughout the year, though the water level depth fluctuates between the wet and dry seasons. In the converted section, intermittent flooding and drying regimes are also experienced during wet and dry seasons, respectively. However, unlike the natural section of the wetland, both the level and duration of flooding during the wet season in this section are manually regulated depending on the need, and both are generally lower than in the natural section. Throughout the sampling period, water was above the soil surface in both sections of the wetland. Mean recorded water levels were: 34.6±7.9 (mean±SE) cm, 11.3±2.6 cm and 5.3±1.5 cm in the Papyrus*,* Typha and Phragmites vegetation communities of the natural section respectively, and 2.3±0.5 cm in the converted section.

3.2.2 Collection and Analysis of Soil Samples

Soil sampling was done in the three vegetation communities of the natural section and in the converted section (rice fields) of the wetland. Three 1 m^2 sampling plots were randomly selected along transects established in each vegetation community of the natural section, and in the converted section. The lengths of the transects varied depending on the spatial extent of the vegetation community and rice field, but ranged from 50 m to 100 m. In each sampling plot, four cores (50 cm deep by 5.0 cm wide) were taken using a Russian peat borer (Marín-Muñiz *et al.,* 2014; Figure 3.1). The thin, sharp-walled edges of this borer provide for coring with minimum compaction, distortion and disturbance. Each core was sectioned with a blade at 10 cm increments. One of the four cores at each sampling plot was used for bulk density measurement.

Composite samples were obtained by mixing three samples of the same depth in each sampling plot. Differences in SOC pools in the same sampling plot that might occur due to variations in decomposition were accounted for by spacing cores in a triangular pattern, 40 cm between each other as described by Bernal & Mitsch (2008, 2012). With triplicates, 45 composite samples were obtained for each depth increment in each vegetation community. Composite samples were placed in labelled ziploc polyethylene bags and transported to the Soil Science Laboratory, College of Agricultural and Environmental Sciences, Makerere University, Kampala, Uganda for analysis.

Prior to analysis, composite soil samples were re-mixed to increase homogeneity, and visible plant residues were manually removed. The samples were air dried at room temperature for 21 days, ground and sieved through a 2 mm nylon sieve. Dry soil samples were used for determination of soil organic matter (SOM) content and soil physico-chemical characteristics (pH, salinity and nitrogen [N]). To determine SOM, 2 g of each soil sample (in triplicate) was placed in pre-weighed crucibles and pre-treated with 10 M HCl until zero bubbling was achieved to prevent possibilities of carbonate interference (Marín-Muñiz *et al.,* 2014; Hernandez & Mitsch, 2007). The samples were then dried in an oven (CARBOLITE CWF 13/5) at 105 °C until constant weight before being ignited at 450 °C for 4 hours (Bernal & Mitsch, 2008; Marín-Muñiz *et al.,* 2014). Soil organic matter percentage (SOM%) of each sample was calculated following weight loss on ignition (LOI), from where SOC percentage (SOC%) was obtained as a portion of SOM%, using Van Bemmelen's index (0.58) (Marín-Muñiz *et al.,* 2014):

SOC content ($g\ kg^{-1}$) and SOC density ($kg\ m^{-2}$) for each soil layer, and SOC storage potential ($Mg\ ha^{-1}$) along the entire sampled 50 cm soil depth were respectively, determined as depicted in equations *(3.1)* (Bernal & Mitsch, 2008), *(3.2)* (Marín-Muñiz *et al.,* 2014) and *(3.3)* (Huang *et al.,* 2013):

$$SOC\ content = 10 * SOCi\% \qquad (3.1)$$

$$SOC\ density = SOCi\% * \ Dbi * \ hi \qquad (3.2)$$

$$SOC\ storage\ potential = \sum_{i=1}^{n} SOCi\ \% * \ Dbi * hi \qquad (3.3)$$

where: SOC*i%* is the SOC% of layer *i*, *Dbi* is the bulk density at layer *i* ($g\ cm^{-3}$) and *hi* is the depth of soil layer *i* (cm).

Soil pH and salinity were determined using a multi-parameter meter (CyberScan PC 300), after equilibration of soil with deionized water (soil: water, 1:5) (Huang *et al.,* 2013; Wang *et al.,* 2018). Soil N content was determined using Kjeldahl digestion procedure (Huang *et al.,* 2013; Wang *et al.,* 2018). Bulk density (Db) was determined by drying a known volume of soil sample (determined from the dimensions of the core) at 105 °C until it reached a constant weight, cooled to room temperature in a desiccator, and weighed again. Bulk density was then expressed as dry weight of soil per unit volume (Huang *et al.,* 2013). Because all sites were fully submerged, there was no need for measurement of soil moisture content.

Figure 3.1 Taking soil samples in the natural and rice paddy sections of the wetland

3.2.3 *In-situ* Measurements, and Collection and Analysis of Plant Samples

Soil temperature was measured *in-situ* using a digital soil thermometer. Plants (Papyrus, Typha, Phragmites, and rice) were destructively harvested in 0.3 m^2 triplicated plots along each transect for determination of biomass density (above and below ground), N and organic C contents. For above ground biomass, all plants in each sampling plot were harvested by cutting at the base and weighed to establish the total fresh weight. Plant parts below the soil surface (below ground biomass) were carefully removed to prevent root breakage, washed to remove all the soil and other attached material and weighed to establish the total fresh weight. Except samples of rice plants, which were all carried (because of their low biomass density), portions of Papyrus, Typha and Phragmites plant samples were carried to the laboratory for analysis of plant biomass. For N content, portions of plant parts (roots, stems and leaves) were mixed to make representative samples. In total, 45 composite plant samples were obtained from each vegetation community in the natural section, and in the converted section (rice fields) wetland.

Plant dry biomass was obtained from dry to wet weight ratio, after drying plant samples at 105 °C to a constant weight. Plant biomass density was expressed as the dry weight of plants per unit area. To determine plant N content, plant samples were oven dried at 65 °C until constant weight and ground (Chen *et al.,* 2017), after which N content was determined using Kjeldahl digestion procedure (Huang *et al.,* 2013; Wang *et al.,* 2018). Plant organic C content was determined from the weight loss on ignition (LOI) procedure, as described for determination of SOC.

3.2.4 Data Analysis

Statistical analysis was carried out partly in Microsoft Excel (2016) and R programming software (version 3.2.2). Data were first tested for normal distribution and homogeneity of variance, and were found to satisfy these conditions. As a result, parametric statistics one-way ANOVA and Tukey HSD post-hoc test were used to determine the vertical and spatial variation of SOC content and density, and storage potential between natural and converted sections of the wetland, at a significance level of 95% ($p < 0.05$) (Hernandez & Mitsch, 2007; Marín-Muñiz *et al.,* 2014). The relationships between soil physico-chemical and plant characteristics and SOC were determined using Spearman rank correlation, at a significance level of 95% ($p < 0.05$).

3.3 Results

3.3.1 Soil Physico-chemical and Plant Characteristics

Most soil physico-chemical parameters varied with soil depth in both sections of the wetland. Temperature, salinity and N content generally decreased with increasing soil depth. On the other hand, pH and bulk density generally increased with increasing soil depth (Table 3.1).

Soil temperature was highest in the converted section, which also showed the greatest drop in soil temperature from the top (0-10 cm) to the bottom (40-50 cm) soil layer of 0.7 °C, compared to 0.5 °C, 0.4 °C and 0.3 °C in Typha, Papyrus and Phragmites vegetation communities respectively, of the natural section of the wetland.

The pH values in all the three vegetation communities of the natural section of the wetland were generally acidic, contrasting from those in the converted section that were in the alkaline region. On average, pH in the converted section was 2.21, 1.57 and 1.45 units higher than in the papyrus, Phragmites and Typha vegetation communities, respectively.

Salinity showed a great variation with soil depth, and between natural and converted sections of the wetland, it was on average highest in the natural section. For example, salinities of the top (0-10 cm) soil layer in the Papyrus, Phragmites and Typha vegetation communities were over 83%, 72% and 52% higher than those at the bottom (40-50 cm) layer respectively, compared to only 27% in the converted section of the wetland.

Bulk density was highest in the converted section of the wetland, though variations between the two wetland sections were small. Average bulk density of the converted section of the wetland exceeded the natural section by 0.33, 0.19 and 0.23 g cm^{-3} (in view of Papyrus, Typha and Phragmites vegetation communities, respectively). Nitrogen (N) content also showed minimal variations with soil depth and between natural and converted sections of the wetland. Average values of N content in the Papyrus, Typha and Phragmites vegetation communities were above that in the converted section by only 0.22%, 0.12% and 0.14%, respectively. Soil C:N ratio did not show any clear trend with soil depth, but was higher in the natural section of the wetland.

Table 3.1 Soil physico-chemical characteristics at different depths in the different sections of the wetland. Values are mean±SE (n=45)

Parameter	Wetland section		Soil depth (cm)					
			0-10	10-20	20-30	30-40	40-50	Mean (0-50)
Temperature (°C)	Natural	Papyrus	26.6±0.0	26.5±0.1	26.4±0.1	26.3±0.1	26.2±0.0	26.4±0.1^{a}
		Typha	26.9±0.1	26.7±0.1	26.5±0.2	26.4±0.2	26.4±0.2	26.6±0.1^{a}
		Phragmites	26.6±0.1	26.4±0.1	26.4±0.1	26.4±0.1	26.3±0.0	26.4±0.1^{a}
	Converted (rice fields)		27.8±0.1	27.7±0.1	27.6±0.1	27.5±0.1	27.1±0.1	27.5±0.1^{a}
pH	Natural	Papyrus	5.29±0.01	5.74±0.01	5.94±0.02	6.12±0.03	6.34±0.01	5.88±0.02^{a}
		Typha	6.23±0.01	6.26±0.02	6.67±0.02	7.00±0.01	7.07±0.06	6.64±0.02^{a}
		Phragmites	6.06±0.01	6.34±0.01	6.50±0.04	6.80±0.01	6.88±0.01	6.52±0.01^{a}
	Converted (rice fields)		7.47±0.03	7.34±0.02	8.24±0.04	8.60±0.10	8.81±0.02	8.09±0.04^{b}
Salinity (mS m^{-1})	Natural	Papyrus	406.86±7.45	169.68±2.03	87.62±1.19	55.79±5.29	66.51±2.91	157.29±3.77^{a}
		Typha	129.22±2.40	122.64±0.95	120.66±2.37	88.81±7.25	61.74±0.44	104.61±2.68^{a}
		Phragmites	118.59±2.48	64.09±0.33	46.30±1.08	34.25±0.28	33.17±0.15	59.27±0.86^{b}
	Converted (rice fields)		56.25±0.25	49.45±1.59	48.71±0.70	43.38±0.17	41.00±2.05	47.76±0.95^{b}
Bulk density (g cm^{-3})	Natural	Papyrus	0.46±0.01	0.58±0.02	0.65±0.03	0.79±0.02	0.81±0.03	0.66±0.02^{a}
		Typha	0.67±0.01	0.68±0.01	0.82±0.01	0.84±0.01	0.92±0.01	0.79±0.01^{a}
		Phragmites	0.38±0.01	0.58±0.06	0.92±0.04	1.00±0.01	1.10±0.12	0.76±0.05^{a}
	Converted (rice fields)		0.75±0.09	0.83±0.06	1.03±0.05	1.15±0.04	1.16±0.02	0.98±0.05^{a}
N (%)	Natural	Papyrus	0.83±0.03	0.44±0.01	0.31±0.01	0.29±0.01	0.21±0.01	0.42±0.01^{a}
		Typha	0.43±0.01	0.34±0.01	0.32±0.01	0.26±0.01	0.26±0.03	0.32±0.01^{a}
		Phragmites	0.50±0.01	0.47±0.01	0.32±0.01	0.20±0.01	0.20±0.01	0.34±0.01^{a}
	Converted (rice fields)		0.29±0.01	0.26±0.02	0.15±0.01	0.13±0.01	0.13±0.01	0.20±0.01^{a}
C:N	Natural	Papyrus	29.9:1±4.9:1	34.4:1±5.4:1	35.0:1±6.6:1	28.5:1±6.5:1	32.3:1±5.0:1	32.0:1±4.1:1^{a}
		Typha	29.3:1±5.5:1	28.8:1±4.6:1	24.0:1±2.7:1	28.8:1±4.1:1	24.0:1±2.4:1	27.0:1±5.1:1^{a}
		Phragmites	41.2:1±3.7:1	22.7:1±4.2:1	20.3:1±2.6:1	28.1:1±5.3:1	24.6:1±4.1:1	27.4:1±3.2:1^{a}
	Converted (rice fields)		21.3:1±4.8:1	20.8:1±3.3:1	26.7:1±3.2:1	21.0:1±2.0:1	20.1:1±7.4:1	22.0:1±3.5:1^{a}

Plant characteristics also varied amongst the wetland sections (Table 3.2). Plant biomass density was highest in the natural section of the wetland. Above ground and below ground biomass densities of the Papyrus vegetation community were above 12 and 17 folds respectively, higher than in the converted section, followed by the Typha section, whose both biomass densities were respectively over 10 and 9 folds greater than in the converted section. Above and below ground biomass densities in the Phragmites section were also considerably higher than in the converted section, with respective differences of over 7 and 8 folds. Both plant C and N contents were highest in the converted section of the wetland, differing from the lowest observed values in the natural section (Typha vegetation community) by 8.4% and 0.8% in that order. However, C:N ratio followed the order: natural section (Typha vegetation community > Papyrus vegetation community > Phragmites vegetation community) > converted section.

Table 3.2 Plant characteristics in the different wetland sections. Values are Mean±SE (n=45)

Wetland section		Plant characteristics				
		Biomass density (kg m^{-2})		C (%)	N (%)	C:N
		Above ground	Below ground			
Natural	Papyrus	8.72±0.84^{a}	10.77±0.51^{a}	29.16±0.80^{a}	0.67±0.07^{a}	43.5:1±9.8:1^{a}
	Typha	7.55±1.13^{ab}	7.36±0.17^{b}	23.86±1.65^{b}	0.48±0.01^{a}	49.9:1±10.4:1^{a}
	Phragmites	5.51±0.42^{b}	6.81±0.13^{b}	25.10±0.13^{b}	0.62±0.03^{a}	40.5:1±9.2:1^{a}
Converted (rice fields)		0.72±0.06^{c}	0.79±0.03^{c}	32.24±0.67^{a}	1.24±0.08^{b}	25.9:1±18.11^{a}

Superscript letters indicate statistical difference at $p < 0.05$, C = Carbon, N = Nitrogen

3.3.2 Soil Organic Carbon in the Natural and Converted Sections of the Wetland

Both SOC content and density presented notable variations in vertical and spatial distribution. They both generally decreased with increase in soil depth in both sections of the wetland (Figures 3.2 and 3.3, respectively). Changes in SOC contents and densities were observed in all soil layers, in order of decreasing magnitude: 0-10 cm > 10-20 cm > 20-30 cm > 30-40 cm > 40-50 cm. However, the decrease was most pronounced in the natural section than the converted section of the wetland. For instance, SOC content decreased from the top (0-10 cm) to the bottom (40-50 cm) soil layer by over 66% in the natural section compared to about 57% in the converted section. Similarly, SOC densities of these two soil layers differed by over 25% in the natural section compared to only about 15% in the converted section. However, in both sections of the wetland, the top 20 cm accounted for more than half of the total SOC content, while the top 30 cm had more than 64% of the total SOC density.

All the three vegetation communities (Papyrus, Typha and Phragmites) of the natural section of the wetland had both SOC contents and densities significantly higher ($p < 0.05$) than in the converted section at all soil layers. However, the magnitude of variation was most pronounced at the top (0-10 cm) soil layer, and decreased with increase in soil depth. On average, SOC contents and densities of the all the three vegetation communities of the natural section of the wetland were higher than those recorded in the converted section with significant amounts ($p < 0.05$). For example, average SOC contents of Papyrus (123.7±2.6 g kg^{-1}), Typha (85.3±1.1 g kg^{-1}) and Phragmites (78.2±3.4 g kg^{-1}) vegetation communities exceeded that of the converted section (39.7±0.7 g kg^{-1}) by over 3-fold, 2-fold and close to 2-fold, respectively. Similarly, average SOC density in Papyrus (7.22±0.11 kg m^{-2}), Typha (6.71±0.12 kg m^{-2}) and Phragmites (6.20±0.06 kg m^{-2}) were about 46%, 42% and 38% higher than that (3.90±0.06 kg m^{-2}) of the converted section.

In consideration of SOC storage potential for the entire sampled soil depth (0-50 cm), all the three vegetation communities of the natural section of the wetland had SOC stocks higher than the converted section, with significant magnitudes ($p < 0.05$, Figure 3.4). The SOC storage potentials of Papyrus (36 118.08±552.52 t km^{-2}), Typha (33 531.44±618.07 t km^{-2}) and Phragmites (31 016.69±316.08 t km^{-2}) vegetation communities were nearly 46%, 42% and 38% respectively, greater than that (19 509.97±281.61 t km^{-2}) of the converted section.

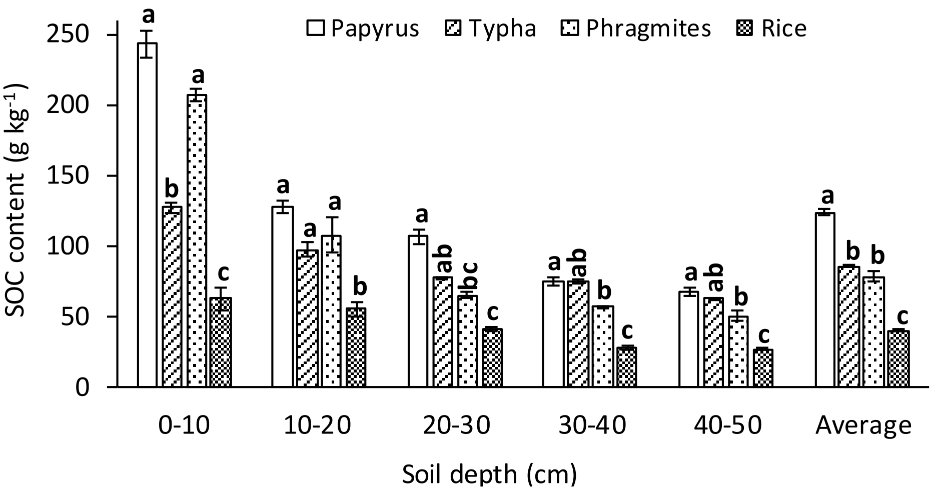

Figure 3.2 Comparison of SOC contents at different depths in the natural (Papyrus, Typha and Phragmites) and converted (rice) sections of the wetland. Error bars are standard errors (SE) of the mean. Grouped bars (for each soil depth category) with different letters are significantly different (Tukey HSD, n=45, $p < 0.05$)

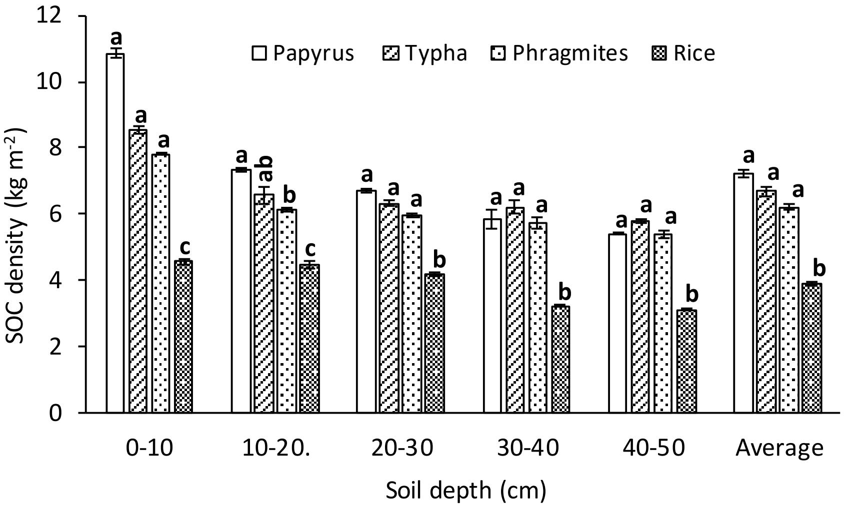

Figure 3.3 Comparison of SOC densities at different depths in the natural (Papyrus, Typha and Phragmites) and converted (rice) sections of the wetland. Error bars are standard errors (SE) of the mean. Grouped bars (for each soil depth category) with different letters are significantly different (Tukey HSD, n=45, $p < 0.05$)

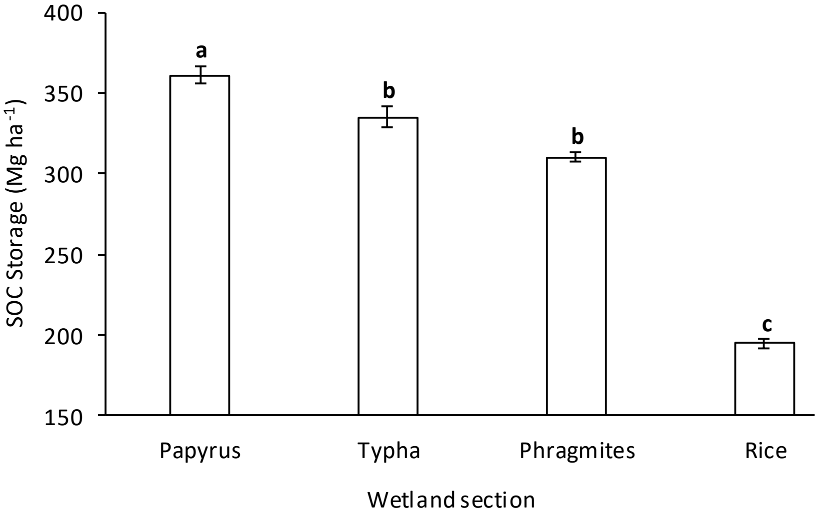

Figure 3.4 SOC storage potential of the natural (Papyrus, Typha and Phragmites) and converted (rice) sections of the wetland. Error bars are standard errors (SE) of the mean. Bars with different letters are significantly different (Tukey HSD, n = 27, $p < 0.05$)

3.3.3 Relationship Between Soil Physico-chemical and Plant Characteristics and SOC

The relationship between soil physico-chemical and plant characteristics and SOC were comparable (both in terms of magnitude and direction) in both sections of the wetland, as reflected by the Spearman rank correlation coefficients (Table 3.3). With respect to the significance of correlations, plant biomass density, and soil physico-chemical characteristics: bulk density, salinity, pH and temperature presented significant correlations ($p < 0.05$) with SOC in that order of decreasing magnitude in both sections of the wetland. On the other hand, soil C:N ratio insignificantly correlated ($p > 0.05$) with

SOC. In view of direction of the correlations, plant biomass density, soil salinity, and temperature and C:N ratio were positively correlated with SOC, unlike pH and bulk density that showed negative correlations with SOC.

Table 3.3 Spearman rank correlations between SOC and soil salinity, pH, temperature, bulk density, C:N ratio, and plant biomass density in natural and (converted) sections of the wetland (n =45)

	SOC	pH	Sal	Temp	Db	C:N	Plant BmD
SOC	1.00(1.00)						
pH	-0.79*(-0.81*)	1.00(1.00)					
Sal	0.83*(0.85*)	-0.74*(-0.86*)	1.00(1.00)				
Temp	0.68*(0.70*)	-0.27(-0.34)	0.41(0.71*)	1.00(1.00)			
Db	-0.89*(-0.88*)	0.79*(0.75*)	-0.64*(-0.68*)	-0.46(-0.32)	1.00(1.00)		
C:N	0.46(0.48)	0.55(0.51)	-0.18(-0.24)	0.13(0.20)	0.47(0.42)	1.00(1.00)	
Plant BmD	0.98*(0.95*)	-0.43(-0.40)	0.48(0.47)	-0.73*(-0.69*)	-0.34(-0.46)	-0.05(-0.22)	1.00(1.00)

* Significant at $p < 0.05$, Sal =salinity, Temp = temperature, Db = bulk density, BmD = biomass density, C = Carbon, N = Nitrogen

3.4 Discussion

3.4.1 Soil Organic Carbon in the Natural and Converted Sections of the Wetland

In the present study, SOC content and density were decreasing with soil depth in both the natural and converted sections of the wetland (Figures 3.2 and 3.3, respectively). Other studies have also reported similar trends in natural tropical freshwater wetland soils (Bernal & Mitsch, 2008, 2013; Huang *et al.,* 2013; Marín-Muñiz *et al.,* 2014; Chen *et al.,* 2017; Wang *et al.,* 2018) and in rice paddy wetland soils (Sun *et al.,* 2013; Huo *et al.,* 2018). This occurrence is associated with the continuous input of freshly dead plant biomass on the top soil layers (Huang *et al.,* 2013; Were *et al.,* 2019). Cases of harvesting standing plant biomass in the natural section of the wetland were rarely observed, and of minor significance. Even in the converted section, rice plants were being left in the fields after harvesting. This implies (for both the natural and converted sections) that plant biomass is continuously added to the top soil, hence increasing the SOM and the subsequent SOC compared to deep soil layers. However, the converted section of the wetland had a less pronounced variation of SOC content and density between top and bottom soil layers compared to the natural one. This could be attributed to tillage-induced soil mixing along the soil profile (Shang-Qi *et al.,* 2013).

In view of magnitude of variation of SOC content, density and storage potential, all the three vegetation communities of the natural section of the wetland had values significantly greater than what was recorded in the converted section. The explanation for this observation can be made in terms of differences of three aspects: 1) primary productivity (Jones *et al.,* 2018; Wang *et al.,* 2018), 2) organic matter recalcitrance (Hernandez & Mitsch, 2007; Sjögersten *et al.,* 2014), and 3) flooding regimes (Bernal & Mitsch, 2008; Villa & Bernal, 2018) between the natural and converted sections of the wetland. Plant biomass is the main source of SOM and the subsequent SOC in wetlands (Huo *et al.,* 2018; Were *et al.,* 2019). Therefore, a high primary productivity is likely to translate into high SOC. Natural tropical freshwater wetlands have already been described as having some of the highest rates of primary productivity of any ecosystem (Morison *et al.,* 2000; Mitsch *et al.,* 2013; Jones *et al.,* 2018).

Unlike the converted section of the wetland (rice fields) where plant biomass productivity is mainly limited only to the growing seasons, productivity of plants in the natural section of the wetland is continuous year-round, ensuring uninterrupted input of SOM into the soil. Further, the specific macrophytes in the natural section of the wetland under this study have been reported to be among the most productive wetland plants. In Africa for example, Jones *et al.* (2018) have found net primary productivity of Papyrus wetlands ranging between 2.51-3.09 kg m^{-2} yr^{-1}, and suggested that they represent one of the highest productivity rates recorded in any natural ecosystem. Net primary productivities of Papyrus and Typha vegetation communities in littoral wetlands of Lake Ziway, Ethiopia were 2.39 kg m^{-2} yr^{-1} and 2.20 kg m^{-2} yr^{-1} respectively, higher than any other wetland macrophytes in the area (Tamire & Mengistou, 2014). The net primary productivity of Phragmites in tropical wetlands has also been reported, ranging from 0.88-2.2 kg m^{-2} yr^{-1} (Lee, 1990; Hamdan *et al.,* 2010). Though data on net primary productivity of rice plants is not readily available due to great variations in soil and cropping management practices (Shah & Wu, 2019), an estimate by Aselmann & Crutzen (1989) showed that it's over six times less than that of macrophytes in natural wetlands. Biomass densities obtained in this study in all the three vegetation communities of the natural section of the wetland were in an order of magnitude greater than in the rice fields, supporting the high productivity of natural wetlands. Further, to enhance SOC accumulation in rice paddy soils, studies (Minasny *et al.,* 2012; Sun *et al.,* 2013; Arunrat *et al.,* 2017; Mboyerwa, 2018) have suggested continuous cropping, with a view of increasing plant biomass production and the consequent organic matter input into the soil.

Organic matter recalcitrance is one of the most critical aspects of SOC in wetland soil. Studies by Hernandez & Mitsch (2007) and Sjögersten *et al.* (2014) attributed inequalities in SOC in wetlands under different plant communities to differences in the degree of recalcitrance of organic matter from plant biomass. Plant biomass rich in lignin is recalcitrant, making the resultant organic matter resistant to decomposition (Bernal & Mitsch, 2008). Nevertheless, though lignin contents of the respective plant biomass were not investigated in this study, it is thought that organic matter from rice plant biomass is less recalcitrant (more labile), making it prone to rapid decomposition. Indeed, this argument is supported by Conrad (2002), who established a lower lignin content (5-15%) of rice plant biomass, compared to 24% for Typha (Colbers *et al.,* 2017), 22–23% for Phragmites (Köbbing *et al.,* 2013) and 12–34% for Papyrus (Elnaggar *et al.,* 2015). Additionally, Sun *et al.* (2013) observed that the biggest fraction of SOC pool in rice paddy soils exists as labile organic C.

In consideration of flooding regimes, the role of water table height in regulation of SOC has been widely documented as significant (Lane *et al.,* 2016; Nahlik & Fennessy, 2016; Villa & Bernal, 2018; Were *et al.,* 2019). These studies show that organic matter decomposition increases with a decrease in water table height. This is an indication that SOC declines with a corresponding decline in water table height. In the natural section of this wetland, the soil is mainly permanently flooded throughout the year (Kayendeke *et al*., 2018), though flooding and drying cycles are experienced close to the wetland edges. In the converted section (rice fields), however, flooding occurs only during the wet season, where the flooding level and duration are regulated, and lower than in the natural section. The presence of drainage channels in this section of the wetland enhances water table drawdown, facilitating rapid drying up of rice fields during the dry season and hence promoting SOM decomposition and a consequent reduction in SOC storage.

Findings of SOC in the different sections of the wetland in this study are comparable to results of other studies. The content and density of SOC in a natural wetland were significantly higher than in a rice paddy wetland, 15 years after conversion to rice cultivation (Huo *et al.,* 2018). At different soil depths, SOC contents in the rice paddy wetland were 75-83% lower than those in the natural wetland. Total SOC density (15.98 kg m^{-2}) in the natural wetland was over 20% higher than that (12.74 kg m^{-2}) recorded in the rice paddy. A similar study by Mao *et al.* (2015) reported results both in agreement and contrast to this study. In terms of spatial variation of SOC between natural and rice paddy wetlands, the authors obtained SOC densities of natural wetlands at the top 60 cm and 100 cm soil layers as 23.50 kg m^{-2} and 29.59 kg m^{-2} respectively, about 34% and 33% higher than those of rice paddy wetlands. These values translated into SOC storage potentials of 23500 t km^{-2} and 29 590 t km^{-2} at the respective soil depths, compared to 15 530 and 19 790 t km^{-2} respectively, in the rice paddy wetlands. However, considering vertical distribution of SOC stocks, this study's results contradict those of Mao *et al.* (2015) who pointed out that SOC densities in both natural and rice paddy wetlands increased with depth. Nonetheless, the study was carried out in a temperate environment, where SOC stocks have already been reported to increase with increase in soil depth (Bernal & Mitsch, 2008, 2012; Huang *et al.,* 2013; Nahlik & Fennessy, 2016). On a global perspective, Köchy *et al.* (2015) reported average SOC density in freshwater marsh wetlands (same as this study's wetland) as 38 kg m^{-2}, more than 3-fold that (12.1 kg m^{-2}) for rice paddy wetlands for the top 1 m soil depth.

Besides, it has been previously reported that the impact of agricultural land use change on soil C stock can only be significant after a longer period (possibly on a decadal timescale) due to the inherently long-term stability of soil C (Trumbore, 1997; Minasny *et al.,* 2012; Wang *et al.,* 2015; Huo *et al.,* 2018). For example, Oertel *et al.* (2016) showed that 30–35% of the soil C stored in the top 7 cm was lost in the first 30 years after turning a forest into agricultural land, while no changes were observed below plough depth. However, this study showed significant changes in SOC stocks even at a short period, as the sampled rice fields only ranged 1-5 years old. The stability and duration of C in soil following agricultural land use change could therefore be variable depending on the characteristics of the original and new ecosystems (Were *et al.,* 2019).

With the already high concentration of GHGs CO_2 and CH_4 in the atmosphere, achieving rapid climate change mitigation requires maximizing C storage (IPCC, 2014). The natural wetland section had nearly 46%, 42% and 38% (in view of Papyrus, Typha and Phragmites vegetation communities respectively) higher SOC storage potential than the converted section. Therefore, assuming similar conditions in other natural wetlands of Uganda, conversion of the country's natural wetlands into rice paddy wetlands will approximately reduce the former's SOC storage potential by a range of 38-46%. This outcome implies a significant compromise on the ability of the country's natural wetlands to mitigate climate change. This argument especially resonates with the understanding that emission of GHGs in rice paddy wetlands is higher than is natural wetlands (Sun *et al.,* 2013; Hasanah *et al.,* 2019). In the same sense consequently, whereas high demand for rice (as food) may be the major driver for conversion of tropical freshwater wetlands, other options of increasing rice production need to be explored. Some studies have reported a potential of increasing rice production using upland rice cropping systems (Oonyu, 2011; Xu *et al.,* 2012; Corpuz *et al.,* 2015; Hagos *et al.,* 2018).

3.4.2 Relationship Between Soil Physico-chemical and Plant Characteristics and SOC

It was observed that soil physico-chemical and plant characteristics had comparable relationships with SOC in both sections of the wetland. Soil bulk density, salinity, pH and temperature, and plant biomass density had significant impacts on SOC. Soil C:N ratio on the other hand, showed an insignificant control on SOC. These results are not an exception as other studies have obtained related findings (Chambers *et al.,* 2012; Villa & Bernal, 2018; Wang *et al.,* 2018).

A significant negative correlation between SOC and bulk density was reported by Upton *et al.* (2019). Exposure of freshwater wetland soil to 3.5 g kg^{-1} saline (as sodium chloride) water increased SOC mineralization rate by 17% (Chambers *et al.,* 2012). Temperature influences microbial metabolism and population dynamics, directly affecting SOM decomposition and SOC storage (Villa & Bernal, 2018). This was further emphasised by (Davidson & Janssens, 2006) who observed a doubling of SOM decomposition rates for every 10 °C temperature increase. In terms of pH, the activities of soil microbial communities involved in SOC turnover are at their optimum within a particular pH range. A study by Batty & Younger (2007) established that decomposition rates of plant biomass were negatively affected outside a pH range of 3.0-6.5. For rice paddy wetlands, Liu *et al.* (2011) found SOC in rice fields with lower soil pH (4.66-5.10) greater than in fields with high soil pH (5.16-5.66), and attributed it to reduced microbial activity in the low soil pH rice fields. Strong positive correlations between plant biomass density and SOC stocks in natural wetlands (Chen *et al.,* 2017; Wang *et al.,* 2018) and rice paddy wetlands (Sun *et al.,* 2013) have been acknowledged.

An insignificant correlation between soil C:N ratio and SOC was observed by Wang *et al.* (2018) in natural wetlands under different vegetation communities. However, in rice paddy wetlands, other studies have established a significant correlation between C:N ratio and SOC (Liu *et al.,* 2011; Zhang *et al.,* 2016; Upton *et al.,* 2019). Nonetheless, Jiang *et al.* (2019) have recently indicated that the correlation between C:N ratio and SOC stocks is mostly expected to be significant in rice paddy wetlands where nitrogen fertilization is practiced. The explanation given is that soil nitrogen enhancement lowers the C:N ratio, stimulating microbial activity and corresponding SOM decomposition. This observation could help explain this study's results, as fertilization of rice fields in this study was not being practiced. Farmers depend on the natural fertility of soil, which minimises manipulation of soil C:N ratio.

3.5 Conclusions

Both SOC content and density decrease with increasing soil depth under natural and converted (rice paddy) tropical wetland conditions. However, the decrease is more pronounced in the natural section than the converted section. In view of SOC storage potential for the sampled 0-50 cm soil depth, a tropical freshwater wetland under natural conditions stores significantly higher SOC than under converted (rice paddy) conditions. Assuming similar conditions in other natural wetlands of Uganda, conversion of the country's natural wetlands into rice paddy wetlands will reduce the former's SOC storage potential of the top 50 cm soil layer by a range of 38-46%.

Basing on this study's findings, if the current trend of conversion of natural tropical freshwater wetlands into rice paddy wetlands is to continue, their role in climate change mitigation will be significantly reduced. As a result, if natural tropical freshwater wetlands are to remain relevant in climate change mitigation, alternative options for increasing rice production outside wetlands need to be explored.

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CHAPTER FOUR

4 Carbon dioxide and Methane Fluxes from a Tropical Freshwater Wetland under Different Dominant Vegetation Communities

This Chapter is based on:

Were, D., Kansiime, F., Fetahi, T., & Hein, T. (2021). Carbon dioxide and Methane Fluxes from Various Vegetation Communities of a Natural Tropical Freshwater Wetland in Different Seasons. *Environmental Processes.* https://doi.org/10.1007/s40710-021-00497-0 (Publisher: Springer Nature).

Abstract

Natural wetlands are vital in climate change mitigation through carbon sequestration. Nevertheless, these ecosystems also emit greenhouse gases (GHGs) such as carbon dioxide (CO_2) and methane (CH_4) into the atmosphere. Emission of CO_2 and CH_4 is of interest in tropical wetland studies because the high and relatively stable temperatures year-round induce both high productivity and decomposition rates. Nonetheless, there is scarcity of data on emission of GHGs from tropical wetlands. Fluxes of CO_2 and CH_4 were investigated in a natural tropical freshwater wetland in Uganda under different dominant vegetation communities (*Cyperus papyrus* [Papyrus], *Typha latifolia* [Typha] and *Phragmites mauritianus* [Phragmites]) during the dry and wet seasons. Fluxes (mg C m^{-2} h^{-1}) of both CO_2 and CH_4 from Papyrus (732.9±48.7 [mean±SE] 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, CO_2 and CH_4 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 CO_2 and CH_4 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 CO_2 and CH_4 fluxes from the wetland, suggesting its importance in any efforts to regulate CO_2 and CH_4 fluxes from the wetland. This study estimated total annual CO_2 and CH_4 emissions from Uganda's wetland soils in the ranges of 159.5×10^6-180.2×10^6 T C and 278.9×10^4-359.7×10^4 T C, respectively.

4.1 Introduction

Global warming and the subsequent climate change have been attributed to greenhouse gases (GHGs), 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 (CO_2) and methane (CH_4) as the most important GHGs, respectively contributing about 66% and 17% of the radiative forcing by long-lived GHGs. This report further estimated atmospheric concentration of CO_2 in 2018 at 407.8 ppm, a 147% increase from pre-industrial level in 1750. Similarly, within the same period, atmospheric CH_4 concentration increased by 259% to 1869 ppb. While CO_2 accounts for the highest level of radiative forcing, CH_4's global warming potential on a 100-year scale is 34 times that of CO_2 (IPCC, 2013; Mitsch & Mander, 2018). With this in mind, setting successful climate mitigation strategies requires a clear understanding of sources and controls of both gases.

Natural wetlands provide favourable environments for carbon (C) sequestration, through capture and long-term storage of atmospheric C, 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 C in their soils (Lane *et al.,* 2016; Nahlik & Fennessy, 2016; Villa & Bernal, 2018). With a coverage of only 5–8% of the earth's land surface (Nahlik & Fennessy, 2016), wetlands' C content is estimated to be as high as a third of the world's C stored in organic soils (Were *et al.,* 2019). In contrast, natural wetlands also emit C, in form of CO_2 and CH_4 into the atmosphere (Belger *et al.,* 2011; Butterbach-Bahl *et al.,* 2016; Mitsch & Mander, 2018; Gutenberg *et al.,* 2019; Ishikura *et al.,* 2019). For instance, it's estimated that wetlands could account for up to 25% of the total natural and anthropogenic sources of CH_4 (Oertel *et al.,* 2016). Thus, understanding the net contribution of wetlands to climate change mitigation entails knowledge of not only their C sequestration potential but also their C emission rate. Besides, emission of GHGs has been shown to vary across wetland types (Belger *et al.,* 2011; Sjögersten *et al.,* 2014; Turetsky *et al.,* 2014; Butterbach-Bahl *et al.,* 2016; Oertel *et al.,* 2016), suggesting the need for studies across all wetland types for proper accounting of total emission from global wetlands.

Factors controlling CO_2 and CH_4 emissions from wetlands have been relatively well studied and documented (Belger *et al.,* 2011; Olsson *et al.,* 2015; Oertel *et al.,* 2016; Duval

& Radu, 2018; Veber *et al.,* 2018; Villa & Bernal, 2018; Were *et al.,* 2019). One of the important characteristics of wetlands and which has also been reported to affect CO_2 and CH_4 flux from these ecosystems is vegetation. Wetland plants may exert variable effects on CO_2 and CH_4 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 & 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, CO_2 and CH_4 fluxes can vary spatially among vegetation communities. For example, in a Swiss wetland, Bhullar *et al.* (2014) recorded a six-fold difference in CH_4 emission among plant species. Maucieri *et al.* (2019) reported over 2-times higher emission of CO_2 from wetlands under *A. donax, M. giganteus* and *P. australis* than under *C. zizanioides* and unvegetated wetlands. In the same study, CH_4 flux from the vegetated wetlands significantly exceeded that in the unvegetated wetland. Understanding CO_2 and CH_4 fluxes from the different vegetation communities is therefore inevitable in the accurate estimation of whole wetland scale emissions for wetlands with different vegetation communities.

Knowledge of current fluxes of CO_2 and CH_4 in wetlands is necessary since temperature increases associated with climate change could elevate future fluxes of these GHGs (Nahlik & Mitsch, 2011; Sjögersten *et al.,* 2014). However, 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 CO_2 and CH_4 emission from temperate and boreal wetlands (Sha *et al.,* 2011; Sjögersten *et al.,* 2014; Marín-Muñiz *et al.,* 2015). As a result, CO_2 and CH_4 fluxes from tropical wetlands are less understood in comparison to their temperate and boreal counterparts. 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 CO_2 and CH_4 fluxes from tropical wetlands. Indeed, Villa & Bernal (2018) and Were *et al.* (2019) in their recent review studies on C 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, an evaluation of CO_2 and CH_4 emission from a natural tropical freshwater wetland under three naturally occurring dominant vegetation communities was done, on a temporal basis, considering both the dry and wet seasons. Understanding of CO_2 and CH_4 emissions and their controlling factors in tropical wetlands is a prerequisite to enable the inclusion of tropical wetlands into global climate change models.

4.2 Materials and Methods

4.2.1 Study Area

This study was carried on Naigombwa wetland ecosystem, located in Iganga District, South-eastern Uganda (Figure 1.1). Based on dominant vegetation communities that form a permanent cover throughout the year, this wetland can be sub-divided into three different parts: *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) Vs floating (rooted in the mat above the water column, towards the wetland mid-sections where the water level is high) (Figure 2.1). 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 high water level areas (Kansiime *et al.,* 2007).

4.2.2 Gas Sampling and Analysis

Gas sampling from each of the vegetation communities described in section 4.2.1 was done using static flux chambers (Nicoloso *et al.,* 2013; Butterbach-Bahl *et al.,* 2016; Figure 4.1). For the Papyrus vegetation community which displays two growth forms (Figure 2.1), 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 coloured 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 cm^2.

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 minutes (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 (CO_2 and CH_4) fluxes were calculated using equation *(4.1)* (Nicoloso *et al.,* 2013).

$$f = \frac{\Delta Q}{\Delta t}\frac{PV}{RT}\frac{1}{A} \tag{4.1}$$

where: f is the CO_2 or CH_4 flux (mg m^{-2} h^{-1}), Q is the mass of the gas (mg) inside chamber at a given sampling time (t), 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 atm L mol^{-1} 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).

Figure 4.1 Taking gas samples in the wetland

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

Soil samples of the top (0-10 cm) soil layer (Nahlik & Mitsch, 2011; Järveoja *et al.,* 2016) 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 analysis was done, 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 hours (Bernal & 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 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).

4.2.4 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, Kruskal-Wallis H test was 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, box plots were used (Nahlik & Mitsch, 2011; Sha *et al.,* 2011). 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.

4.3 Results

4.3.1 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 4.1). Mean soil temperature (°C), pH, salinity (mS m^{-1}) and SOC (%) across the three vegetation communities ranged from 26.6-26.9, 6.00-6.23, 118.6-132.8 and 11.7-16.3 respectively, in the dry season, compared to 26.3-26.8, 5.98-6.24, 91.3-128.7 and 10.0-15.0 respectively, in the wet season.

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. In comparison of vegetation communities, water levels during the dry season in the Papyrus and Typha vegetation communities were not significantly different ($p > 0.05$), but were both significantly higher ($p < 0.05$) than that 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 (SE) °C, and insignificantly varied ($p > 0.05$) from that (21.3±0.2 °C) recorded in the wet season.

Table 4.1 Soil physico-chemical characteristics and water levels in the different vegetation communities of the wetland. Values are mean±SE (n = 36)

Parameter	Vegetation community					
	Papyrus		Typha		Phragmites	
	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season
Temperature (°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±4.4**	7.1±3.2	29.1±4.2**	1.9±0.8[a]	21.0±4.1**

[a] Significant seasonal variation among vegetation communities

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

4.3.2 Carbon dioxide and Methane Fluxes

Carbon dioxide (CO_2) fluxes from the wetland showed variations among the vegetation communities, following the order of Phragmites > Typha > Papyrus, and it accounted for over 97% of the total C flux from each vegetation community of the wetland (Table 4.2). Mean CO_2 fluxes (mg C m^{-2} h^{-1}) during the dry season were respectively, 871.8±56.7 from Phragmites, 759.7±51.4 from Typha, and 732.9±48.7 from Papyrus. Mean CO_2 flux from Phragmites during the dry season was significantly higher ($p < 0.05$) than those observed in Typha and Papyrus, both of which did not vary significantly ($p > 0.05$; Figure 4.2(a)). During the wet season, CO_2 fluxes among the vegetation communities followed the same trend as the dry season, with values of 691.9±55.8, 682.0±53.3 and 651.2±49.0 mg C m^{-2} h^{-1} from Phragmites, Typha and Papyrus, respectively. Nonetheless, the magnitudes of variation in mean CO_2 fluxes among the vegetation communities during this season were insignificant ($p > 0.05$; Figure 4.2(b)).

Like CO_2, CH_4 fluxes also showed variabilities among vegetation communities, and were in the order of decreasing magnitude: Papyrus > Typha > Phragmites. During the dry season, mean CH_4 fluxes were 14.1±0.8, 13.5±1.2 and 8.7±0.5 mg C m^{-2} h^{-1} in the Papyrus, Typha and Phragmites vegetation communities, respectively. Variations in mean CH_4 fluxes during the dry season in Papyrus and Typha were, however, insignificant ($p > 0.05$), but were both significantly higher ($p < 0.05$) than that recorded in Phragmites (Figure 4.2(c)). During the wet season, mean CH_4 fluxes (mg C m^{-2} h^{-1}) were 17.1±1.7, 16.3±1.2 and 15.6±1.1 in Papyrus, Typha and Phragmites, respectively. Again, just as it was the case with CO_2, variations in mean CH_4 fluxes among the three vegetation communities during the wet season were of negligible significance ($p > 0.05$).

In comparison of seasons, whereas CO_2 fluxes during the dry season in all the three vegetation communities were generally higher than during the wet season, the variation was insignificant ($p > 0.05$), except only for Phragmites ($p < 0.05$). Similarly, whereas seasonal CH_4 flux values observed during the wet season in all 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 CO_2 and CH_4 even within the same sampling season. For instance, point CO_2 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 fromS 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 CH_4 emissions (mg C m^{-2} h^{-1}) ranged from 7.3-21.0, 7.2-19.6 and 6.4-10.8 in 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.

Table 4.2 **Carbon dioxide (CO_2) and CH_4 fluxes from different vegetation communities of the wetland as a percentage of the total carbon flux. Values are mean±SE (n = 36). Total C flux is the sum of average CO_2 and CH_4 fluxes**

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	Average	Dry season	Wet season	Average			
Papyrus	732.9±48.7	651.2±49.0	692.1±48.8	14.1±0.8	17.1±1.7	15.6±1.3	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	14.9±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	12.1±0.8	794.0±57.0	98.5	1.5

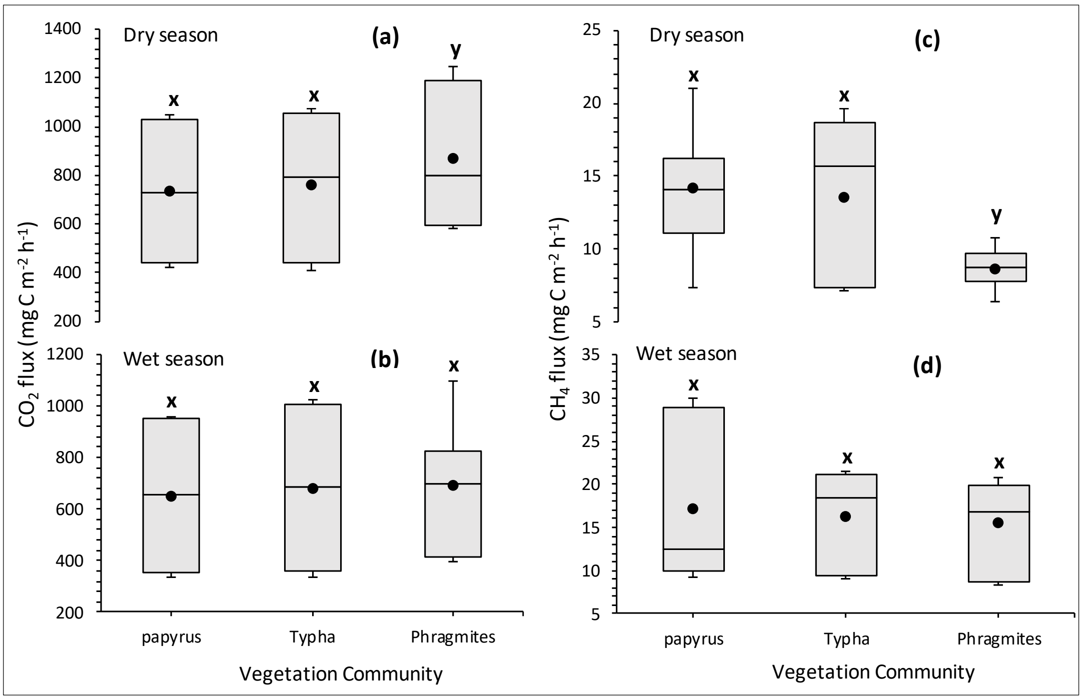

Figure 4.2 **Comparison of CO_2 and CH_4 fluxes from the Papyrus, Typha and Phragmites vegetation communities during the dry ((a) and (c) respectively) and wet ((b) and (d) respectively) seasons. Box lines indicate upper and lower quartiles. Horizontal lines within boxes show medians, while black dots 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 ($p > 0.05$)**

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

The Spearman rank correlations (Table 4.3) 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 ($p > 0.05$). On the other hand, water level was found to have significant correlations ($p < 0.05$) with both CO_2 and CH_4 fluxes. A significant negative correlation ($p < 0.05$) was obtained between water level and CO_2 flux, while CH_4 flux showed a significant positive correlation ($p < 0.05$) with water level. These relationships between water level and CO_2 and CH_4 fluxes are further clearly depicted in

Figure 4.3. Also, the correlation between CO_2 and CH_4 fluxes was significantly negative ($p < 0.05$), implying that at any given time organic matter degradation and C emission processes favoured one gas over the other, as reflected in Figure 4.4.

Table 4.3 Spearman rank correlations between soil physico-chemical characteristics, water level, air temperature and CO_2 and CH_4 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

* Significant correlation ($p < 0.05$), Soil temp = Soil temperature, Air temp = Air temperature

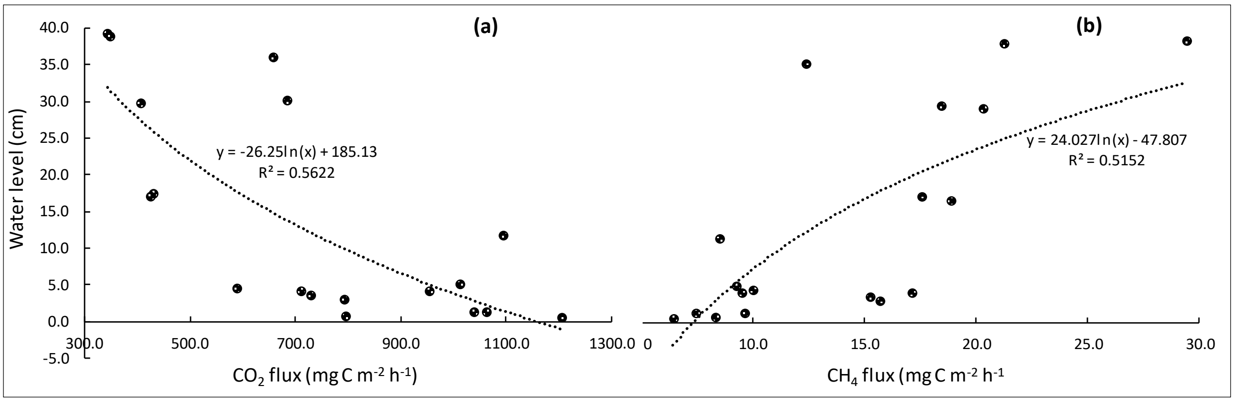

Figure 4.3 Relationship between water level and CO_2 ((a)) and CH_4 ((b)) fluxes from the wetland

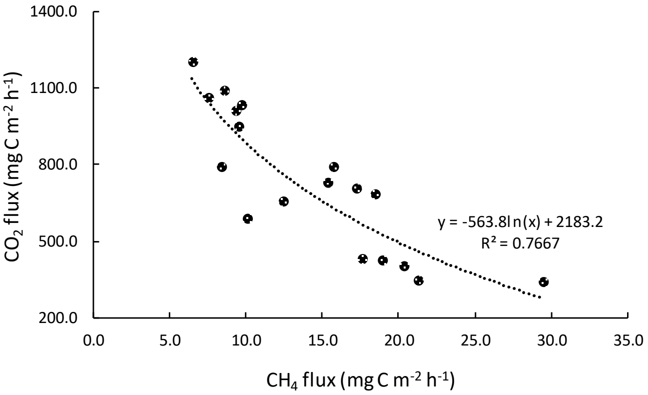

Figure 4.4 Relationship between CO_2 and CH_4 fluxes from the wetland

4.4 Discussion

4.4.1 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 GHGs in wetland soils. Both the amount and quality of organic matter deposited into wetland soils are dependent on the type of plants (Hernandez & Mitsch, 2007; Sjögersten *et al.,* 2014; Maucieri *et al.,* 2017). Ding *et al.* (2005) noted that CH_4 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 C availability and input rate into soil. Duval & Radu (2018) observed different flux rates of both CO_2 and CH_4 in peat samples collected from three fen areas with each representing distinct vegetation types: 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) reported that presence of *Pontederia cordata* and *Phragmites australis* in a wetland enhanced CO_2 emission, while the influences of both *Typha orientalis* and *Lythrum salicaria* on CO_2 emissions were negligible. Maucieri *et al.* (2019) also found variable rates of CO_2 fluxes from Mediterranean wetlands with different vegetation communities, which they attached to differences in organic matter input into soils. With this knowledge, it was expected in this study to observe significant differences of both CO_2 and CH_4 fluxes among the three vegetation communities. However, during the dry season, no significant variations of both CO_2 and CH_4 fluxes among the three vegetation communities were noticed, except only for Phragmites (Figure 4.2(a) and (c)). Similarly, during the wet season, variations of both CO_2 and CH_4 flux rates among all the three vegetation communities were insignificant (Figure 4.2(b) and (d)). The lack of a significant difference in organic C content among the vegetation communities (Table 4.1) could be used to explain these findings. While studying Mexican wetlands, Marín-Muñiz *et al.* (2015) did not find significant variation of both CO_2 and CH_4 fluxes among vegetation communities with similar organic C contents. Gagnon *et al.* (2007) understood that fluxes of GHGs 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, the observation of significant differences in CO_2 and CH_4 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 4.1).

4.4.2 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 4.1). Soil anaerobicity was enhanced under conditions of continuous flooding because soil pore spaces were filled (Marín-Muñiz *et al.,* 2015). CO_2 emission from wetland soil is minimized under anaerobic conditions that impede aerobic organic matter decomposition, while methanogenesis and the ensuing CH_4 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 CH_4 emissions but lowered CO_2 emissions from several freshwater wetlands, including that dominated by Typha plants. Lawrence *et al.* (2017) observed variations in CH_4 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 CO_2 emissions by 120% and reduced CH_4 emissions by 75% (Yang *et al.,* 2013). Olsson *et al.* (2015) found significant variations in CH_4 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 CO_2 and CH_4 in a Chinese wetland. Ishikura *et al.* (2019) noticed that lowering groundwater level in a Malaysian wetland increased daily mean flux of CO_2. Bernal & 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 CH_4 fluxes from a wetland has reported that increasing soil moisture content by 1 unit increased CH_4 flux by 457 $\mu g\ m^{-2}\ h^{-1}$. These observations are further supported by Maucieri *et al.* (2017), who in a literature review found significantly higher emission rates of CO_2 under low water table, and significantly higher emission rates of CH_4 under high water table. In the present study, nevertheless, flux rates of both CO_2 and CH_4 in Papyrus and Typha differed insignificantly between the dry and wet seasons, despite water levels differing significantly between the two seasons. This could be because the soils had already reached maximum saturation during the dry season such that any increase in water level during the wet season couldn't further affect gas fluxes (Moore & Knowles, 1989; Mander *et al.,* 2011; Nahlik & 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 (Nahlik & Mitsch, 2011; Olsson *et al.,* 2015; Oertel *et al.,* 2016; Duval & Radu, 2018; Veber *et al.,* 2018), pH (Oertel *et al.,* 2016; Veber *et al.,* 2018; Wanyama *et al.,* 2019), C:N ratio (Batson *et al.,* 2015; Wanyama *et al.,* 2019) and bulk density (Wanyama *et al.,* 2019). However, in line with this study's findings, a number of other studies have also not found significant correlations between soil physico-chemical characteristics and gas fluxes. Wanyama *et al.* (2019) observed weak correlations between soil temperature and CO_2 and CH_4 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 & Bernal (2018) also supported this understanding as they explained that low O_2 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. A study by Wang *et al.* (2018) noted no significant correlation between C:N ratio and SOC, suggesting its insignificant influence on CO_2 and CH_4 fluxes. Batson *et al.* (2015) reported insignificant correlations between soil bulk density and fluxes of both CO_2 and CH_4. Bhullar *et al.* (2014) found no correlation between soil pH and CH_4 emission. Richards & Craft (2015) observed no correlations between GHGs fluxes and all measured soil properties in both natural and restored wetlands. They explained that disagreements over correlations between soil parameters and gas fluxes as reported by different studies could arise because CH_4 and CO_2 emission is an interplay between several factors and processes, and the dominant one may vary according to existing conditions. The lack of correlations between soil properties and CO_2 and CH_4 fluxes in this study could be because they were not the major limiting factors.

4.4.3 Comparison of Carbon dioxide and Methane Fluxes with Literature Data

This study obtained average (combining both dry season and wet season fluxes) CO_2 fluxes among the three vegetation communities in the range of 692.1-781.8 mg C m^{-2} h^{-1}, while CH_4 emissions ranged from 12.1-15.6 mg C m^{-2} h^{-1} (Table 4.2). In comparison with other studies, it was noticed that CO_2 flux rates recorded in this study were lower than those obtained in other tropical wetlands, though higher than those reported from boreal and temperate wetlands (Table 4.4). Conversely, this study's CH_4 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 CO_2 flux rates compared to those from other tropical wetlands could be attributed to the fact that this present study wetland was under continuous flooding, which suppressed aerobic organic matter decomposition (Liu *et al.,* 2015). Differences in flux rates of CO_2 and CH_4 between this study's tropical wetland and those of temperate and boreal wetlands could be explained by temperature differences (Sha *et al.,* 2011; Oertel *et al.,* 2016; Gomez *et al.,* 2017). High temperatures in tropical regions are associated with high organic matter decomposition rates in wetland soils, which enhance gas emissions (Villa & Bernal, 2018; Were *et al.,* 2019).

Nonetheless, both CO_2 and CH_4 flux rates recorded in this study are within ranges reported for wetland types with more or less similar conditions to this study's wetland. Sjögersten *et al.* (2014) have reported CO_2 emission from related tropical wetlands ranging from 317.0-905.0 g C m^{-2} yr^{-1}, while Nahlik & Mitsch (2011) have reported CH_4 emission ranging from as low as 6.0 g C m^{-2} yr^{-1} to 788.0 g C m^{-2} yr^{-1}.

Table 4.4 Carbon dioxide (CO_2) and methane (CH_4) emissions from wetland soil from different studies. For the ease of comparisons, emission values have been organic ted 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)

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)

na = not available

4.4.4 Carbon dioxide and Methane Emission from Uganda's Wetlands

Wetlands comprise a considerably big share 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 km^2) of the country's land area. Whereas there exists a wide body of literature on Uganda's wetlands, C flux from wetlands is a relatively newer concept with a limited number of studies. Currently, no single study has estimated the totality of GHGs emitted from Uganda's wetlands. Therefore, this study's findings were used to give a rough estimate of CO_2 and CH_4 emissions from Uganda's wetlands so as to provide a basis for future studies on gas emissions from the country's wetlands. To make this possible, simple assumptions were made that all the country's wetlands present more or less similar conditions to this present study wetland or if variations exist, they are minimal to exert significant variations on gas fluxes. This study obtained CO_2 and CH_4 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 km^2 of the country's land area under wetlands, total CO_2 and CH_4 emissions from Uganda's wetlands are roughly estimated to be in the range of 159.5×10^6-180.2×10^6 T C yr^{-1} and 278.9×10^4-359.7×10^4 T C yr^{-1}, respectively. However, it is also acknowledged 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 these flux estimates. Additionally, the lack of other studies to compare this study's gas flux estimates for Uganda's wetlands limits a precise understanding of the robustness of the estimates.

Further, it is important to note that this study only considered CO_2 and CH_4 from wetland soil. Nevertheless, CO_2 emission involving plants (plant respiration) (Sjögersten *et al.,* 2014; Mitsch & Mander, 2018; Maucieri *et al.,* 2019; Sun *et al.,* 2019; Xi *et al.,* 2019) and CH_4 emission mediated by plants (Bhullar *et al.,* 2014; Turetsky *et al.,* 2014; Bhattacharyya *et al.,* 2019; Jeffrey *et al.,* 2019) have also been shown to be important processes of CO_2 and CH_4 emission from wetlands. However, there is a possibility to offset C emitted by C fixed through photosynthesis (Mitsch & Mander, 2018; Maucieri *et al.,* 2019). Nevertheless, a clearer understanding of C balance of Uganda's wetlands requires full knowledge of total C emission and assimilation from all the country's wetlands.

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}.

4.5 Conclusions

Carbon dioxide (CO_2) and CH_4 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 CO_2 per unit area than both Papyrus and Typha vegetation communities. However, in terms of CH_4, Phragmites had the lowest impact on climate during this season as it emitted less CH_4 per unit area than Papyrus and Typha. During the wet season, nonetheless, no variation in flux (for both CO_2 and CH_4) was noticed among the three vegetation communities. In view of seasonal variabilities among wetland vegetation communities, significant differences in CO_2 and CH_4 fluxes between the dry and wet seasons were observed only in the Phragmites vegetation community as well. Dry season CO_2 flux from Phragmites exceeded its wet season counterpart, while dry season CH_4 flux from this vegetation community was less than that observed during the wet season.

Water level was the main driver of CO_2 and CH_4 fluxes from the wetland. High water levels were associated with lower CO_2 fluxes but higher CH_4 fluxes. The reverse was true for lower water levels. This suggests the importance of understanding water level dynamics for regulation of CO_2 and CH_4 fluxes from tropical wetlands.

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CHAPTER FIVE

5 Impact of Conversion of a Natural Tropical Freshwater Wetland into a Rice Paddy Wetland on Carbon Dioxide (CO_2) And Methane (CH_4) Fluxes in Uganda

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Abstract

Natural tropical freshwater wetlands are increasingly being converted into agricultural land uses, mainly rice cultivation. Currently, nonetheless, there is limited knowledge on the impact of conversion of natural tropical freshwater wetlands into rice paddy wetlands on climate change mitigation, through carbon emission. In this study, fluxes of carbon dioxide (CO_2) and methane (CH_4) were investigated in a tropical freshwater wetland in Uganda under natural conditions (with different vegetation communities dominated by *Cyperus papyrus*, *Typha latifolia* and *Phragmites mauritianus*) and under rice paddy conditions, during the dry and wet seasons. CO_2 fluxes (mg C m^{-2} h^{-1}) from the rice paddy section during the dry and wet seasons were 1045.4±46.6 (mean±SE) and 804.4±50.2 respectively, both significantly higher ($p < 0.05$) than those obtained in all the three vegetation communities of the natural section. However, CH_4 fluxes (mg C m^{-2} h^{-1}) from the rice paddy section during the dry and wet seasons were 2.1±0.4 and 5.1±0.5 respectively, both significantly lower ($p < 0.05$) than those observed in all the three vegetation communities of the natural section. Considering total carbon emission, it was observed that whereas conversion of natural tropical freshwater wetlands into rice paddies may limit CH_4 emission, it compromises climate change mitigation efforts by increasing total carbon emission, that could make rice paddy wetlands net carbon sources. Water level was the major driver of CO_2 and CH_4 fluxes from the wetland. Further, this study estimated that rice paddy wetlands currently emit only 0.72% and 0.14% of the total annual CO_2 and CH_4 respectively, emitted from Uganda's wetland soils due to their low spatial coverage. However, it is predicted that future emission of both gases from Uganda's wetlands will originate mainly from rice paddy wetlands due to their rapid expansion rate.

5.1 Introduction

Natural wetlands are vital ecosystems in climate change mitigation because they offer favourable conditions for carbon (C) sequestration, through capture and long-term storage of atmospheric CO_2. Apart from being highly productive, the hypoxic conditions permit natural wetlands to accumulate large amounts of organic C in their soils (Nahlik & Fennessy, 2016). For instance, despite covering as small as 5–8% of the earth's land surface (Nahlik & Fennessy, 2016), estimated amount of C stored in wetland soils is as high one third of the world's C in organic soils (Were *et al.,* 2019). On the other hand, natural wetlands also emit both CO_2 and CH_4 into the atmosphere, which has a potential to compromise their net contribution to climate change mitigation (Laanbroek, 2010; Butterbach-Bahl *et al.,* 2016; Ishikura *et al.,* 2019; Mitsch & Mander, 2018; Were *et al.,* 2019).

Carbon emission studies are of interest especially for tropical wetlands because the high and relatively stable temperatures year-round in tropical regions favour high productivity of these wetlands and also enhance organic matter decomposition. Further, with a spatial extent estimated at 30% of the world's wetlands area (Marín-Muñiz *et al.,* 2015), tropical wetlands present a considerably high influence on global C balance and cycling.

Rates of gas fluxes from natural wetland environments are dependent on a number of factors, as has been widely explored by several studies. Vegetation characteristics (Kao-Kniffin *et al.,* 2010; Laanbroek, 2010; Marín-Muñiz *et al.,* 2015; Olsson *et al.,* 2015), water table depth (Yang *et al.,* 2013; Batson *et al.,* 2015; Olsson *et al.,* 2015; Mitsch *et al.,* 2018; Ishikura *et al.,* 2019; Were *et al.,* 2019), soil-physico-chemical characteristics (Sha *et al.,* 2011; Inglett *et al.,* 2012; Olsson *et al.,* 2015), and climatic factors (Mitsch *et al.,* 2013; Villa & Bernal, 2018; Were *et al.,* 2019) have been identified as some of the important factors. Gas fluxes are, thus, expected to vary across different wetlands spread in different parts of the globe. Henceforth, quantifying greenhouse gases (GHGs) fluxes from global wetlands with more accuracy requires a clear understanding of fluxes from the different wetland types right from local scales. On the other hand, unlike temperate and boreal wetlands, the biogeochemistry of tropical wetlands is less understood (Mitsch *et al.,* 2010). This should be well studied to prevent disagreements on the controls and magnitude of CO_2 and CH_4 fluxes from tropical wetlands.

The most recent global wetland inventories (Davidson, 2014; Davidson & Finlayson, 2018; Ramsar Convention on Wetlands, 2018) highlight an increasing rate of conversion of natural wetlands into other wetland types, mainly rice paddy wetlands. Globally, Davidson (2014) highlighted an increase of wetland area under rice cultivation by 41.5% between 1961 and 2012, while Davidson & Finlayson (2018) recently reported an annual increase in global wetland area under rice cultivation of 0.6%. With paddy rice cultivation being mostly undertaken in the tropics, such a trend raises concerns on the future role of natural tropical freshwater wetlands in global C balance and cycling.

Since the recent past, when climate change became an issue of global interest, most studies have prioritised understanding CO_2 and CH_4 emission from temperate and boreal wetland soils (Sha *et al.,* 2011; Sjögersten *et al.,* 2014; Marín-Muñiz *et al.,* 2015). Few studies have been conducted on tropical wetlands, which has limited their inclusion into global climate change models. Ishikurura *et al*. (2019) observed that CO_2 and CH_4 fluxes in a tropical wetland were driven by ground water level movement. A study by Marín-Muñiz *et al*. (2015) on Mexican tropical freshwater wetlands did not find significant variation in GHGs emission between wetland types (marshes vs swamps), but rather showed that emissions were influenced by season. However, because emission of GHGs from wetlands is an interplay between various factors (Richards & Craft, 2015), more studies on the various tropical wetlands are necessary to increase our certainty of the magnitude of GHGs emitted from these ecosystems. Indeed, recent reviews (Villa & Bernal, 2018; Were *et al.,* 2019) on C sequestration in wetlands have recommended more work on tropical wetlands. Besides, a review by Boateng *et al.* (2017) has highlighted the reliance of estimation of GHGs emissions from wetlands on emission factors calibrated using temperate conditions, which do not necessarily suit tropical conditions. In this study, the first of its kind in a tropical freshwater wetland, a comparative investigation of CO_2 and CH_4 emission under natural and altered (rice paddy) wetland conditions, during both dry and wet seasons was made. This is study is further important because it is a prerequisite for formulation of informed decisions concerning prioritization of conservation and/or restoration of wetlands in view of climate change mitigation as a wetland ecosystem service.

5.2 Materials and Methods

5.2.1 Study Area

The studied wetland ecosystem (Naigombwa) is located in Iganga District, Southeastern Uganda (Figure 1.1). Based on land use, the wetland can be divided into two sections; natural and rice paddy. Additionally, the natural wetland section can sub-divided into three different parts, based on dominant vegetation communities: *Cyperus papyrus* (Papyrus), *Typha latifolia* (Typha) and *Phragmites mauritianus* (Phragmites).

The converted section occurs upstream of the natural section, where natural vegetation was replaced with rice cultivation. The rice is grown under flood irrigation, using natural gravity flow of surface water from the catchment. Rice is planted either through broadcasting of rice grains, or through transplanting of rice seedlings from nursery beds into the fields. There is no specified planting density of rice plants, while planting seasons are limited to two in a year.

The water level in Naigombwa wetland varies between the natural and rice paddy sections. Edges of the natural section of the wetland tend to experience intermittent flooding and drying cycles during the wet and dry seasons, respectively. However, areas away from the edges are mainly flooded throughout the year, though the water level depth fluctuates between wet and dry seasons. In the converted section, intermittent flooding and drying regimes are also experienced during wet and dry seasons, respectively. However, unlike the natural section of the wetland, both the level and duration of flooding during the wet season in this section are manually regulated depending on the need, and both are generally lower than in the natural section. However, throughout the sampling period the water level in both sections of the wetland was above the soil surface, representing conditions of continuous flooding.

5.2.2 Gas Sampling and Analysis

Static gas chambers (Nicoloso *et al.,* 2013; Butterbach-Bahl *et al.,* 2016) were used to sample CO_2 and CH_4 emission from soil in both sections of the wetland (Figure 5.1). Each chamber was fitted with a probe thermometer for monitoring internal air temperature, a vent tube to prevent drastic changes of inside air pressure during chamber deployment, and an air sampling port with a septum, which was used for obtaining gas samples and also for manually homogenizing internal air using a syringe and needle (Collier *et al.,* 2014; Minamikawa *et al.,* 2015). To minimize heating up of the chamber during sampling due to solar radiation, white chambers were used whose external surfaces were covered with an aluminium reflective tape. The chamber lids were inverted over chamber bases that were sunk into the soil to a minimum of 10 cm (Butterbach-Bahl *et al.,* 2016) and the whole system provided a gas tight enclosure, preventing exchange of inside and outside air. Chamber bases were installed at least 7 days prior to sampling (Butterbach-Bahl *et al.,* 2016). The chamber headspace (excluding the water column above the soil surface) had an average height of 25 cm, volume of 10 L and basal area of 490.63 cm^2.

Sampling was done in randomly selected quadrats along transects, and in each quadrat, 3 chambers were deployed and sampled consecutively (Collier *et al.,* 2014). Physical soil disturbance and artificial ebullition of the gases at sampling points was prevented by installing wooden walking platforms.

Gas sampling was spread across the dry (February, March and April 2019) and the wet (August, September and October 2019) seasons. Samples were collected at times 0, 10, 20, and 30 minutes (inside the chamber), while ambient air samples were collected outside the chamber prior to start of each sampling event for quality control (Butterbach-Bahl *et al.,* 2016). The air accumulated in chambers was collected using 60 ml polypropylene syringes, fitted with a luer lock and a needle. Of the 60 ml gas sample in the syringe, 40 ml was used for evacuation of the 10 ml gas vial while the remaining 20 ml was stored in the gas vial (under high pressure) for analysis. To prevent contamination of samples prior to analysis, the vial tops were covered with a parafilm. Due to logistical challenges and the labour intensity associated with gas sampling using static flux chambers, sampling frequency was limited to twice a month, on a fortnightly basis. This brought the total number of gas samples for each season and wetland vegetation community to 72. Analysis of gas samples was done at the International Livestock Research Institute, Nairobi, Kenya by gas chromatography (SRI 8610C gas chromatograph, USA), following the procedure described by Collier *et al.* (2014) and Minamikawa *et al.* (2015).

Carbon dioxide (CO_2) and CH_4 fluxes were calculated and compared among the wetland vegetation communities/sections using equation *(5.1)* (Nicoloso *et al.,* 2013).

$$f = \frac{\Delta Q}{\Delta t}\frac{PV}{RT}\frac{1}{A} \tag{5.1}$$

where: f is the CO_2 or CH_4 flux (mg m^{-2} h^{-1}), Q is the mass of the gas (mg) inside the chamber at a given sampling time (t), 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 atm L mol^{-1} 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).

Figure 5.1 Taking gas samples in the natural (Left) and rice paddy (Right) sections of the wetland

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

For each gas sampling event, soil samples for the top (0-10 cm) soil layer (Inglett *et al.,* 2012) were collected in triplicate using a Russian peat borer for determination of soil physico-chemical characteristics (salinity, pH and organic carbon [SOC]). Soil temperature was taken *in-situ* using a digital soil thermometer. Since the soil was fully flooded throughout the sampling period, there was no need for measuring soil moisture content.

Samples were composited by mixing three samples in each sampling plot. The composite samples were transported to the Soil Science Laboratory, College of Agricultural and Environmental Sciences, Makerere University, Kampala, Uganda for analysis. Before analysis, samples were re-mixed to increase homogeneity. The 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), 2 g of dry soil samples were place in pre-weighed crucibles and pre-treated with 10 M HCl until zero bubbling to prevent possibilities of carbonate interference (Marín-muñiz *et al.,* 2014). The samples were then dried in an oven (CARBOLITE CWF 13/5) at 105 °C until constant weight, after which they were ignited at 450 °C for 4 hours (Bernal & Mitsch, 2008; Marín-muñiz *et al.,* 2014). The percentage of soil organic matter (SOM%) of each sample was calculated following weight loss on ignition (LOI), after which SOC percentage (SOC%) was calculated as a portion of SOM%, using Van Bemmelen's index of 0.58 (Marín-muñiz *et al.,* 2014).

pH and salinity of the soil were obtained using a multi-meter (CyberScan PC 300), after equilibration of soil with deionized water (soil: water, 1:5; Ishikura *et al.,* 2019). Water level in the wetland was obtained using a cm-marked wooden stick, as the distance from the soil surface to the surface of the overlying water. Ambient air temperature data at the wetland site during the sampling period were obtained from Uganda National Meteorological Authority (UNMA).

5.2.4 Data Analysis

Microsoft Excel (2016) and R programming software (version 3.2.2) were used for statistical analysis. Data were first checked for normal distribution using Shapiro-Wilk test, and though soil physico-chemical characteristics and water level data showed normal distribution, gas flux data failed to meet the criteria for normal distribution. As a result, ANOVA together with Tukey HSD post-hoc test were used to test the significance of mean soil physico-chemical characteristics and water level between the wetland sections and between seasons. On the other hand, Kruskal-Wallis H test was used to test the significance of mean CO_2 and CH_4 fluxes between the wetland sections and between seasons, at $p < 0.05$ (Nahlik & Mitsch, 2011; Sha *et al.*, 2011). The relationship between soil physico-chemical characteristics, water level, and ambient air temperature and CO_2 and CH_4 fluxes were determined using Spearman rank correlation, at $p < 0.05$ significance. Values are presented as mean ± standard error (SE).

5.3 Results

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

Soil temperature (°C) was generally higher in the rice paddy wetland section compared to natural section (Table 5.1). However, the variations between the two wetland sections during both the wet and dry seasons were found insignificant ($p > 0.05$). Seasonal variabilities in soil temperature were minimal, with soil temperature in the rice paddy wetland section slightly decreasing from 27.0±0.1 during the dry season to 26.9±0.1

during the wet season, compared to 26.6±0.0 to 26.3±0.0, 26.9±0.1 to 26.8±0.1 and 26.6±0.1 to 26.5±0.1 in the Papyrus, Typha and Phragmites vegetation communities respectively, of the natural section of the wetland. pH in both sections of the wetland was mainly acidic (ranging from 5.33-6.98), and despite the rice paddy section having higher values during both seasons, mean pH in this wetland section did not vary significantly ($p > 0.05$) from those of the three vegetation communities of the natural section. Similarly, though the dry season pH values were higher than their wet season counterparts for both sections of the wetland, the variations were negligible ($p > 0.05$). Salinity values in all the three vegetation communities of the natural section of the wetland were higher compared to the rice paddy wetland section, though the differences were of insignificant magnitude ($p > 0.05$). Likewise, salinity during the dry and wet seasons did not differ significantly ($p > 0.05$) in both sections of the wetland. Unlike other soil physico-chemical characteristics, SOC showed significant variabilities ($p < 0.05$) between the two wetland sections, though seasonal variabilities were negligible ($p > 0.05$; Table 5.1).

Although the wetland was continuously flooded throughout the sampling period, water levels showed significant variations ($p < 0.05$) between the two wetland sections and between seasons. In comparison of wetland sections, water levels in all the three vegetation communities of the natural section of the wetland were significantly higher ($p < 0.05$; Table 5.1) than in the rice paddy section during both the dry and wet seasons. In view of seasonal variabilities, as it was expected, water levels in the wet season were significantly higher ($p < 0.05$) than those recorded in the dry season for both sections of the wetland.

Because the wetland site in this study occurs within the same climatic zone, variation of climatic conditions among the wetland sections were assumed negligible. Therefore, ambient air temperature data, which was collected at the whole-wetland scale, was applied uniformly to the two wetland sections. Mean air temperature during the dry season was 23.4±0.1 (SE) °C, and insignificantly varied ($p > 0.05$) from mean temperature (21.3±0.2 °C) recorded during the wet season.

Table 5.1 Soil physico-chemical characteristics and water levels in the natural and rice paddy wetland sections. Values are mean±SE (n = 36)

Parameter	Wetland section	Season	
Temperature (°C)	Natural	Dry	Wet
	Papyrus	26.6±0.0	26.3±0.0
	Typha	26.9±0.1	26.8±0.1
	Phragmites	26.6±0.1	26.5±0.1
	Rice paddy	27.0±0.1	26.9±0.1
pH	Natural		
	Papyrus	6.00±0.01	5.98±0.01
	Typha	6.23±0.01	6.24±0.02
	Phragmites	6.06±0.01	6.20±0.01
	Rice paddy	6.87±0.03	6.54±0.02
Salinity (mS m^{-1})	Natural		
	Papyrus	132.8±4.9	128.7±3.8
	Typha	129.2±2.4	125.9±1.7
	Phragmites	118.6±2.5	91.3±1.4
	Rice paddy	102.9±5.8*	91.1±2.2*
SOC (%)	Natural		
	Papyrus	16.3±0.0	15.0±0.1
	Typha	13.3±0.2	12.9±0.1
	Phragmites	11.7±0.1	10.0±0.1
	Rice paddy	6.46±0.03*	5.99±0.06*
Water level (cm)	Natural		
	Papyrus	7.5±3.2	31.5±4.4[a]
	Typha	7.1±3.2	29.1±4.2[a]
	Phragmites	1.9±0.8	21.0±4.1[a]
	Rice paddy	0.4±0.1*	10.9±1.3*[a]

* Significant variation ($p < 0.05$) within the same season

[a] Significant variation ($p < 0.05$) between seasons

5.3.2 Carbon dioxide and Methane Fluxes

Both CO_2 and CH_4 fluxes showed spatial and temporal variabilities, though CO_2 was the major component of the gaseous flux, accounting for over 97% of the total C flux from both sections of the wetland (Table 5.2). Spatially and temporally, CO_2 fluxes followed the orders of rice paddy section > natural section, and dry season > wet season, respectively. Mean CO_2 fluxes recorded in the rice paddy section during both the dry and wet seasons were significantly higher ($p < 0.05$) than fluxes obtained in all the three vegetation communities of the natural section of the wetland (Figure 5.2). CO_2 flux (mg C m^{-2} h^{-1}) from the rice paddy section during the dry season was 1045.4±46.6, exceeding those in Phragmites, Typha and Papyrus vegetation communities by 16.6%, 27.3%, and 29.9%, respectively. During the wet season however, the magnitude of variation between the two wetland sections was lower as compared to the dry season. CO_2 flux (mg C m^{-2} h^{-1}) from the rice paddy section during the wet season was 804.4±50.2, higher than in the natural section by 14.0%, 15.2%, and 19.1% with respect to Phragmites, Typha and Papyrus vegetation communities. On a seasonal basis, whereas dry season CO_2 flux was significantly higher than wet season flux from the rice paddy section, variation of seasonal fluxes among the vegetation communities of the natural section was negligible ($p > 0.05$), except only in Phragmites ($p < 0.05$).

Methane (CH_4) fluxes presented a different trend as compared to CO_2 fluxes. Unlike CO_2 fluxes, spatial and temporal variabilities of CH_4 fluxes were of the orders natural section > rice paddy section, and wet season > dry season, respectively. During both the dry and wet seasons, mean CH_4 fluxes from the rice paddy wetland section were significantly lower ($p < 0.05$) than those in all the three vegetation communities of the natural section of the wetland (Figure 5.3). During the dry and wet seasons, CH_4 fluxes (mg C m^{-2} h^{-1}) were 14.1±0.8, 13.5±1.2, and 8.7±0.5 from Papyrus, Typha and Phragmites vegetation communities, respectively. These fluxes were in order magnitude over 85%, 84% and 75% respectively, higher than in the rice paddy section. The degree of variation, nevertheless, reduced during the wet season. During this season fluxes (mg C m^{-2} h^{-1}) from Papyrus, Typha and Phragmites were 17.1±1.7, 16.3±1.2, and 15.6±1.1 respectively, higher than in rice paddy section by about 70%, 69% and 67%, respectively. In comparison of seasons, like CO_2, though wet and dry season CH_4 fluxes from the rice paddy section differed significantly ($p < 0.05$), the difference was insignificant ($p > 0.05$) in the natural section, except only in the Phragmites vegetation community ($p < 0.05$).

Further, occurrence of great variations in gas fluxes from both sections of the wetland, even within the same sampling season was observed. For instance, point CO_2 emissions ranged from 422.1-1044.5 mg C m^{-2} h^{-1} in Papyrus, 411.5-1073.8 mg C m^{-2} h^{-1} in Typha and 583.8-1196.2 mg C m^{-2} h^{-1} in Phragmites, and 826.4-1390.6 mg C m^{-2} h^{-1} in the rice paddy section during the dry season, compared to 333.5-958.3 mg C m^{-2} h^{-1}, 337.9-1015.9 mg C m^{-2} h^{-1}, 395.5-1092.5 mg C m^{-2} h^{-1} and 531.3-1104.2 mg C m^{-2} h^{-1} respectively, during the wet season (Figure 5.2). Point CH_4 emissions (mg C m^{-2} h^{-1}) ranged from 7.3-21.0, 7.2-19.6 and 6.4-10.8, and 0.1-4.9 in Papyrus, Typha and Phragmites, and the rice paddy section respectively, during the dry season in comparison with 9.2-30.0, 9.1-21.4 and 8.3-20.9, and 2.7-7.5 respectively, during the wet season (Figure 5.3).

Table 5.2 Carbon dioxide (CO_2) and CH_4 fluxes from the natural and rice paddy wetland sections as a percentage of the total C flux. Except percentage values, all values are mean±SE (n = 72). Total C flux is the sum of average CO_2 and CH_4 fluxes

Wetland section	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	Average	Dry season	Wet season	Average			
Natural									
Papyrus	732.9±48.7	651.2±49.0	692.1±48.8	14.1±0.8	17.1±1.7	15.6±1.3	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	14.9±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	12.1±0.8	794.0±57.0	98.5	1.5
Average	788.1±52.2	675.0±52.7	731.6±52.5	12.1±0.8	16.3±1.3	14.2±1.1	745.8±53.6	98.1	1.9
Rice paddy	1045.4±46.6	804.4±50.2	924.9±48.4	2.1±0.4	5.1 ±0.5	3.6±0.4	928.4±48.8	99.6	0.4

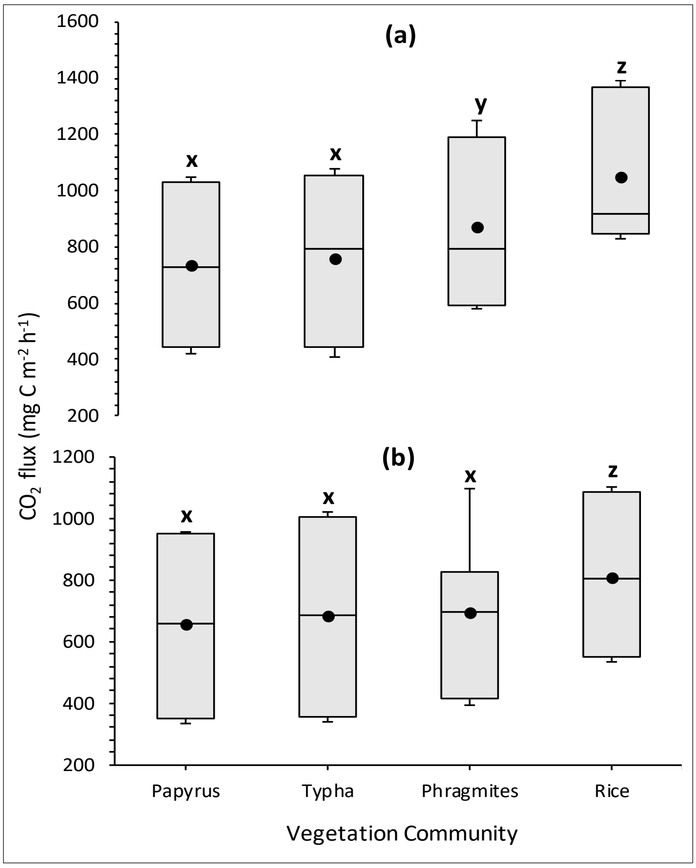

Figure 5.2 Comparison of CO_2 fluxes from the natural (Papyrus, Typha and Phragmites) and rice paddy (Rice) sections of the wetland during the dry ((a)) and wet ((b)) seasons. Box lines indicate upper and lower quartiles. Horizontal lines within boxes show medians, while black dots show means. Whiskers extend 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 ($p > 0.05$)

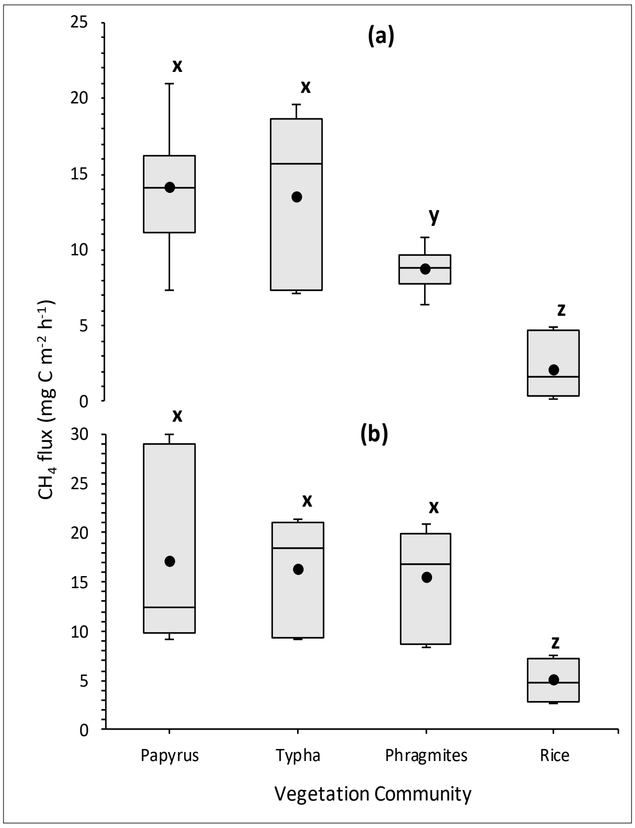

Figure 5.3 Comparison CH$_4$ fluxes from the natural (Papyrus, Typha and Phragmites) and rice paddy (Rice) sections of the wetland during the dry ((a)) and wet ((b)) seasons. Box lines indicate upper and lower quartiles. Horizontal lines within boxes show medians, while black dots show means. Whiskers extend 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 ($p > 0.05$)

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

The influences of soil physico-chemical characteristics, water level and air temperature on CO_2 and CH_4 were comparable in both sections of the wetland, as depicted by the Spearman rank correlation coefficients (Table 5.3). In both sections of the wetlands, the Spearman rank correlation coefficients indicated that none of the soil physico-chemical parameters had a significant correlation ($p > 0.05$) with gaseous fluxes. The same observation was made for air temperature ($p > 0.05$). These observations are not surprising since both soil physico-chemical characteristics (see Table 5.1) and air temperature did present any significant variations ($p > 0.05$) either among vegetation communities or between seasons.

Water level was found to have a significant correlation ($p < 0.05$) with gaseous fluxes. Significant ($p < 0.05$) positive and negative correlations were obtained between water level and CO_2 and CH_4 fluxes respectively, in both sections of the wetland. These relationships between water level and CO_2 and CH_4 fluxes are further highlighted in Figure 5.4. Similarly, CO_2 and CH_4 fluxes showed a significant negative correlation with each other, an indication of a negative feedback of one gas on the other (Table 5.3 and Figure 5.5).

Table 5.3 Spearman rank correlations between soil physico-chemical characteristics, water level, air temperature and CO_2 and CH_4 fluxes from the natural and (rice paddy) sections of the wetland (n = 36)

	CO_2	CH_4	Soil temp	SOC	Soil pH	Soil salinity	Water level	Air temp
CO_2	1.00(1.00)							
CH_4	-0.99*(-0.92*)	1.00(1.00)						
Soil temp	0.30(0.30)	0.23(0.31)	1.00(1.00)					
SOC	0.24(0.33)	0.25(0.34)	-0.05(-0.22)	1.00(1.00)				
Soil pH	-0.07(-0.08)	0.12(0.14)	-0.39(-0.31)	-0.06(-0.14)	1.00(100)			
Soil salinity	0.04(0.34)	-0.01(0.05)	0.28(0.21)	0.26(0.18)	-0.36(-0.30)	1.00(1.00)		
Water level	-0.87*(0.80*)	0.86*(0.74*)	-0.39(-0.54*)	0.04(0.03)	0.08(0.23)	-0.08(-0.17)	1.00(1.00)	
Air temp	0.29(0.30)	0.26(0.37)	0.45*(0.46*)	0.27(0.14)	-0.20(0.08)	0.31(0.36)	-0.34(0.43*)	1.00(1.00)

* Significant correlation ($p < 0.05$), temp = temperature

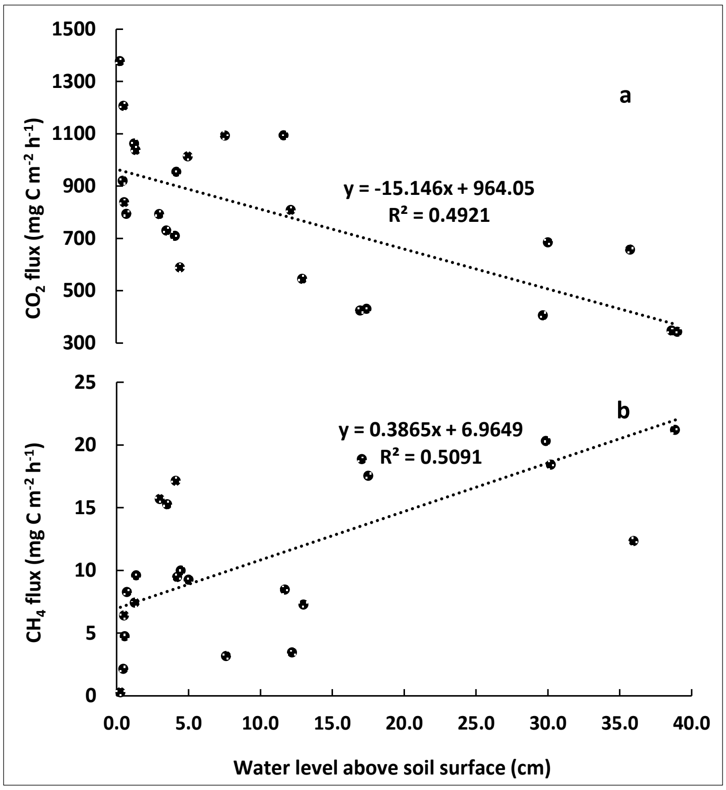

Figure 5.4 Relationship between water level and CO_2 (a) and CH_4 (b) fluxes from the wetland

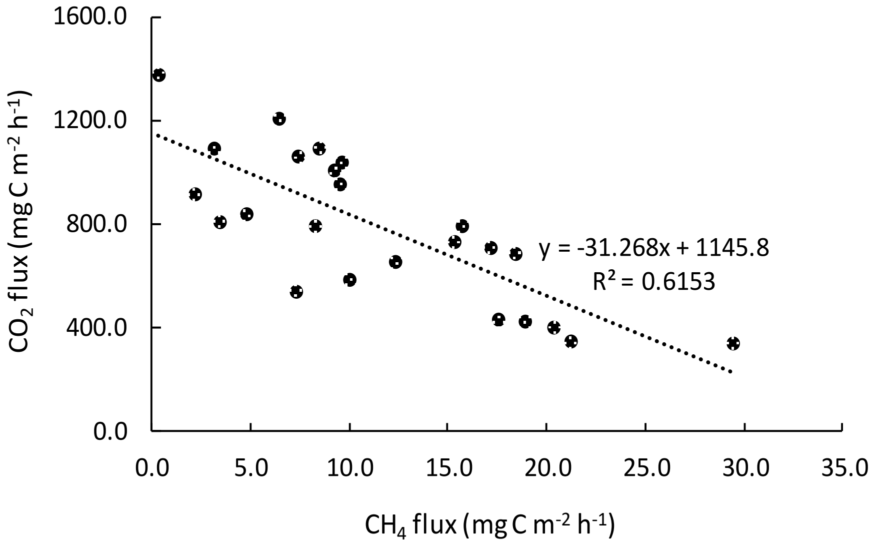

Figure 5.5 Relationship between CO_2 and CH_4 fluxes from the wetland

5.4 Discussion

5.4.1 Spatial and Temporal Variabilities of Carbon dioxide and Methane Fluxes

In the present study, as presented in section 5.3.2, CO_2 and CH_4 fluxes varied significantly among wetland sections based on land use. CO_2 fluxes from all the three vegetation communities of the natural section of the wetland were significantly lower than what was recorded in the rice paddy wetland section (Figure 5.2). In contrast, CH_4 fluxes from all the three vegetation communities of the natural section of the wetland were significantly higher than what was observed in the rice paddy section (Figure 5.3). On a temporal perspective, whereas dry season CO_2 flux was significantly higher than wet season flux from the rice paddy wetland section, variation of seasonal fluxes from the natural section was negligible, except only in the Phragmites vegetation community. Likewise, though wet and dry season CH_4 fluxes from the rice paddy wetland section differed significantly, the difference was insignificant among the vegetation communities of the natural section, except only in Phragmites.

Low and high fluxes of CO_2 and CH_4 respectively, from the natural section of the wetland compared to the rice paddy section could be attributed to factors such as water table depth (Moore & Knowles, 1989; Liu *et al.,* 2015; Mitsch *et al.,* 2018; Ishikura *et al.,* 2019; Were *et al.,* 2019), organic matter recalcitrance (Sjögersten *et al.,* 2014) and carbon substrate availability (Inglett *et al.,* 2012). A high water table depth is associated with an increase in soil anaerobicity, and therefore, hinders CO_2 emission by suppressing aerobic organic matter decomposition while at the same time enhancing methanogenesis and the ensuing CH_4 emission. All the three vegetation communities of the natural section of the wetland had water levels higher than in the rice paddy wetland section (see Table 5.1). In terms of organic matter recalcitrance, lignin-rich plant biomass is relatively recalcitrant, making the resultant organic matter less degradable (Bernal & Mitsch, 2008). The lignin contents of the respective plant biomass in this study were not examined, but it is thought that organic matter from rice plants is less recalcitrant, making it susceptible to faster decomposition. This view is supported by the work of Conrad (2002), who reported lignin content of 5-15% in rice plant biomass, in comparison to Typha (24%; Colbers *et al.,* 2017), Phragmites (22–23%; Köbbing *et al.,* 2013) and Papyrus (12–34%; Elnaggar *et al.,* 2015). Sun *et al.* (2013) further highlighted that the biggest fraction of SOC pool in rice paddy soils is labile. Therefore, whereas lower CH_4 flux was observed from the rice paddy wetland section, it could have been oxidized to CO_2 due to the lower water table compared to the natural section (Laanbroek, 2010; Batson *et al.,* 2015). Additionally, with specific reference to CH_4 flux, Inglett *et al.* (2012) showed that methanogenic activity in tropical wetlands is sensitive to carbon substrate availability. Therefore, apart from water level and organic matter recalcitrance, this knowledge could partly help explain the observation of significantly higher CH_4 fluxes from all the three vegetation communities of the natural section of the wetland, given that they all had significantly higher soil carbon contents compared to the rice paddy section of the wetland (Table 5.1).

Similarly, existence of significant seasonal variations (dry vs wet) for both CO_2 and CH_4 fluxes from the rice paddy wetland but not in the natural wetland section (except for the Phragmites vegetation community) could be linked to water level. During the dry season, water level in the rice paddy wetland section was significantly lower than during the wet season. The same observation was made in the Phragmites vegetation community of the natural section of the wetland. However, whereas dry season water levels in both Papyrus and Typha vegetation communities of the natural wetland section were significantly lower than wet seasons counterparts, the magnitude of variation was smaller. Therefore, in both vegetation communities, the soils could have been maximally saturated during the dry season so that any increase in water level during the wet season could not further influence gaseous fluxes (Moore & Knowles, 1989; Mander *et al.,* 2011; Nahlik & Mitsch 2011; Yang *et al.,* 2013). Indeed, seasonal variations in fluxes of GHGs have been shown to be more pronounced in wetlands which experience marked drying and wetting circles (Bernal & Mitsch, 2013; Batson *et al.,* 2015), or in temperate wetlands where winter and summer season conditions present great variabilities (Sha *et al.,* 2011; Gomez *et al.,* 2017). Sjögersten *et al.* (2014) have also observed that unless associated with significant water level changes, other seasonal variations such as temperature are unlikely to have a major influence on CO_2 and CH_4 fluxes from tropical wetlands.

With the already high concentration of GHGs CO_2 and CH_4 in the atmosphere, achieving rapid climate change mitigation requires minimizing emission of GHGs to the atmosphere (IPCC, 2014). From this study, we saw higher CO_2 and low CH_4 emission from the rice paddy wetland section compared to the natural section. However, if we view total C emission (combining both CO_2 and CH_4) from each section of the wetland, the rice paddy section emitted more C (928.4±48.8 mg C m^{-2} h^{-1}) than all the three vegetation communities of the natural section (Table 2). Therefore, whereas conversion of a natural wetland into a rice paddy wetland may limit CH_4 emission, it compromises climate change mitigation by increasing total C emission to the atmosphere. Natural wetlands have been shown to contribute up to 40% of the total global CH_4 emitted into the atmosphere (Inglett *et al.,* 2012; Batson *et al.,* 2015), compared to 6-29% emitted by rice paddy wetlands (Singh *et al.,* 2017; Bhattacharyya *et al.,* 2019). However, studies (Inglett *et al.,* 2012; Knox *et al.,* 2015; Were *et al.,* 2019) have indicated that despite the high CH_4 emission, natural wetlands are net C sinks because their CO_2 sequestration rate exceeds CH_4 emission rate. On the other hand, converting a natural wetland into a rice paddy wetland, enhances release of CO_2 as drainage and tillage promote rapid decomposition of the long-held organic C, making rice paddy wetlands net C emitters (Inglett *et al.,* 2012; Knox *et al.,* 2015; Were *et al.,* 2020). Consequently, a natural wetland presents a better climate change mitigation option compared to a rice paddy wetland.

5.4.2 Comparison Carbon dioxide and Methane Fluxes with Literature Data

Average (both dry and wet season) CO_2 and CH_4 fluxes obtained in this study were 731.6 mg C m^{-2} h^{-1} and 14.2 mg C m^{-2} h^{-1} respectively, in the natural section of the wetland, lower and higher respectively, than in the rice paddy section (CO_2 flux = 924.9 mg C m^{-2} h^{-1} and CH_4 flux = 3.6 mg C m^{-2} h^{-1}). Further, in both sections of the wetland, CO_2 accounted for more than 97% of the total C flux (Table 5.2). This study's results are comparable to other studies, as discussed in the subsequent paragraphs.

Knox *et al.* (2015) studied the effects of agricultural land-use change on CO_2 and CH_4 fluxes from the Sacramento-San Joaquin Delta wetland, California, USA and obtained similar results. They reported annual CO_2 flux of 1108 g C m^{-2} from the reference wetland, lower than 1203 g C m^{-2} recorded in the section converted to a rice paddy wetland. On the other hand, they obtained CH_4 flux from the unaltered wetland as 38.7 g C m^{-2}, over seven times higher than what was recorded in the rice paddy wetland (5.3 g C m^{-2}). Conversion of a previously drained tropical forested wetland into a lowland flooded rice paddy decreased CO_2 flux from 266 to 30 mg C m^{-2} h^{-1}, while CH_4 flux increased from 0.1 to 4.2 mg C m^{-2} h^{-1} (Furukawa *et al.,* 2015). Couwenberg *et al.* (2010) found soil CH_4 emissions from south-east Asian rice paddy wetlands ranging from 3.5–14 mg C m^{-2} h^{-1}, compared to 0.5-12.6 mg C m^{-2} h^{-1} in the natural wetlands. A study by Hadi *et al.* (2001) on Indonesian wetlands showed that CO_2 and CH_4 emissions in the rice paddy (276 and 195 µg C m^{-2} h^{-1} respectively) were higher than in the natural forested wetland (140 and 146 µg C m^{-2} h^{-1}, respectively). Olsson *et al.* (2015) also compared GHGs emissions in wetlands in china. Methane emission from the rice paddy wetland was 0.75 mg C m^{-2} h^{-1}, significantly higher than in the natural wetland (0.15 mg C m^{-2} h^{-1}). Similarly, CO_2 flux from the rice paddy wetland (532 mg C m^{-2} h^{-1}) was higher than in the natural wetland (484 mg C m^{-2} h^{-1}). Chen *et al.* (2013) studied CH_4 fluxes from several Chinese wetlands and found an average flux rate of 11.35 ± 12.41 (SD) mg C m^{-2} h^{-1} from rice paddy wetlands, above that (9.71 ± 5.53 mg C m^{-2} h^{-1}) in natural wetlands. They attributed the high CH_4 flux from rice paddy wetlands (compared to natural wetlands) to increased use of domestic sewage water for irrigation of rice paddies, and proliferation of *Azolla* sp. in surface water of rice paddies due to water pollution.

It is important to note that this study only considered gaseous fluxes from wetland soils in this study. However, other studies have included plants and have shown that the role of plants in CO_2 and CH_4 fluxes from both natural and rice paddy wetlands is of considerable significance. A network of intercellular spaces (aerenchyma) in the leaf blade, sheath, culm and roots of wetland and rice plants makes a good passage for gas exchange between the soil and the atmosphere (Kao-Kniffin *et al.,* 2010; Laanbroek 2010; Bhattacharyya *et al.,* 2019). However, the aernchyma seems to be more developed in rice plants compared to other wetland macrophytes. For instance, Bhattacharyya *et al.* (2019) have shown that generally, as high as 90% of CH_4 produced in rice soil is emitted through aerenchyma in rice plants, compared to 30-85% in various wetland macrophytes (Kao-Kniffin *et al.,* 2010). Plants also contribute to CO_2 emission through respiration, which can vary depending on plant characteristics (Knox *et al.,* 2015; Olsson *et al.,* 2015). Olsson *et al.* (2015) found CO_2 emission due to plant respiration in a natural wetland higher than that in a rice paddy wetland, and associated the results to differences in above ground biomass between the two wetlands.

5.4.3 The Future of Carbon dioxide and Methane Fluxes from Uganda's Wetlands in the Face of Rice Cultivation

Wetlands comprise a considerably big part of Uganda's land surface. 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, showed that wetlands cover about 11% (equivalent to 26,315 km^2) of the country's land area. The Atlas however, highlights a rapid decrease in the country's wetland area. NEMA (2018) has estimated annual wetland loss at 846 km^2 (about 2% of total wetland cover), and projects total wetland loss by 2040 if effective measures are not put in place to curb the loss. These reports identify rice cultivation as one of the key causes of conversion and loss of natural wetlands. For example, a study by the MAAIF (2009) on rice production in Uganda estimated total wetland area under rice production at 150 km^2. This leaves 26,165 km^2 (out of the total 26, 315 km^2) as total natural wetland area (assuming no losses from other land uses). The MAAIF (2009) also reported an increase in rice paddy acreage of at a rate of 10 $km^2\ yr^{-1}$, which implies a similar rate of loss of natural wetland area to rice paddy fields. These statistics were used to roughly upraise and project this study's findings. However, to make this possible, simple assumptions are made that all the country's wetlands present more or less similar conditions to this study's wetland, and that the current trend in wetland use will persist in future. Basing on these statistics, current total CO_2 and CH_4 emissions from Uganda's rice paddy soils are estimated at $121.5*10^4$ t C yr^{-1} and $4.7*10^3$ t C yr^{-1} respectively, compared to $167.7*10^6$ t C yr^{-1} and $325.5*10^4$ t C yr^{-1} respectively, in natural wetland soils. These results indicate that rice paddy soils currently emit only 0.72% and 0.14% of the total CO_2 and CH_4 respectively, emitted from the country's wetland soils. Therefore, whereas per unit area CO_2 emission in rice paddy soils is significantly higher than in the natural wetland soil, total CO_2 emission in Uganda's natural wetland soils is higher because of their large spatial extent compared to rice paddy wetlands. However, a 10 km^2 annual increase in rice paddy acreage will possibly increase total annual CO_2 and CH_4 emissions from the country's rice paddy soils increase annually by 6.67% and 6.71% respectively, compared to an annual reduction of 0.04% for each of CO_2 and CH_4 from the natural wetland soils. With this knowledge, therefore, future emissions of CO_2 and CH_4 from Uganda's wetland soils are predicted that they will mainly originate from rice paddy wetlands. As a result, unless the current conversion trend of natural wetlands into rice paddy wetlands is reversed, future climate change mitigation strategies need to consider addressing CO_2 and CH_4 emission from rice paddy wetlands.

5.5 Conclusions

Conversion of a natural wetland into a rice paddy influences gaseous fluxes. Fluxes of CO_2 from the rice paddy wetland section are significantly higher than from the natural section, both in the dry and wet seasons. On the hand, CH_4 fluxes from the rice paddy section are significantly lower than in the natural wetland section. However, in terms of total C emission, though conversion of natural tropical freshwater wetlands into rice paddies may limit CH_4 emission, it compromises climate change mitigation efforts by increasing C emission, that could make rice paddy wetlands net carbon sources.

Water level is the main driver of CO_2 and CH_4 fluxes in a tropical freshwater wetland under natural and rice paddy conditions. High water levels are associated with lower CO_2 fluxes but higher CH_4 fluxes. The reverse is true for lower water levels, and therefore, any effort to regulate either CO_2 or CH_4 emissions from either natural or rice paddy wetlands needs to give attention to water level dynamics.

On a national scale, Uganda's rice paddy soils currently emit only 0.72% and 0.14% of the total CO_2 and CH_4 respectively, emitted from the country's wetland soils. This finding is attributed to a low spatial extent of rice paddy wetlands rather than per unit area emission. However, future emissions of both gases from Uganda's wetland soils are predicted that they will mainly originate from rice paddy wetlands due to their rapid expansion rates. As a result, unless the current conversion trend of natural wetlands into rice paddy wetlands is reversed, future climate change mitigation strategies need to consider addressing CO_2 and CH_4 emission from rice paddy wetlands.

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CHAPTER SIX

6 Study Conclusions and Recommendations

6.1 General Conclusions

The following are the main conclusions from this research, which are in line with the set objectives:

Specific Objective i: Soil organic carbon (SOC) stock in a natural tropical freshwater wetland under different vegetation communities

- Wetland vegetation community influences SOC content, but not SOC density. Papyrus vegetation community had SOC content significantly higher than those of Typha and Phragmites vegetation communities. The SOC contents of Typha and Phragmites communities did not differ significantly. Therefore, in view of vegetation community, where climate change mitigation is considered as a wetland ecosystem service, restoration actions for degraded/lost tropical freshwater wetlands need to give priority to Papyrus plants.
- Within the Papyrus vegetation community, growth form (emergent vs floating) does not affect SOC content and density, except only at 0-10 cm soil layer. At this soil layer, the emergent growth form had higher SOC content than the floating growth form, while the SOC density of the floating growth form was higher than that of the emergent growth form at this soil layer.

Specific objective ii: Impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on soil organic carbon (SOC) stock

- Converting a natural tropical freshwater wetland into a rice paddy wetland compromises its SOC storage ability. The natural section of the wetland had 46%, 42% and 38% higher SOC storage potentials (with respect to Papyrus, Typha and Phragmites vegetation communities) than that of the rice paddy section.
- Basing on this study's findings, if the current trend of conversion of natural tropical freshwater wetlands into rice paddy wetlands is to continue, their role in climate change mitigation will be significantly reduced. As a result, if natural tropical freshwater wetlands are to remain relevant in climate change mitigation, alternative options for increasing rice production outside wetlands need to be explored.

Specific objective iii: Carbon dioxide (CO_2) and methane (CH_4) fluxes in a natural tropical freshwater wetland under different vegetation communities

- Vegetation community influences CO_2 and CH_4 fluxes from soils of a natural tropical freshwater wetland, but only during the dry season. During the dry season, Phragmites dominated areas of the wetland emitted significantly more CO_2 and less CH_4 compared to wetland areas dominated by Papyrus and Typha vegetation communities.
- Seasonal variabilities do not influence CO_2 fluxes in the vegetation communities of a natural tropical freshwater wetland under continuous flooding, except only in Phragmites. CO_2 and CH_4 fluxes in Phragmites vegetation significantly varied between wet and dry seasons.
- Water level is the main driver of CO_2 and CH_4 fluxes in the wetland. This suggests the importance of understanding water level dynamics for regulation of CO_2 and CH_4 fluxes in tropical wetlands.

Specific objective iv: Impact of conversion of a natural tropical freshwater wetland into a rice paddy wetland on carbon dioxide (CO_2) and methane (CH_4) fluxes

- Conversion of a natural wetland into a rice paddy influences gaseous fluxes. Fluxes of CO_2 fluxes from the rice paddy wetland section were significantly higher than in the natural section, both in the dry and wet seasons. On the other hand, CH_4 fluxes from the rice paddy wetland section were significantly lower than in the natural wetland section. However, in terms of total C emission, though conversion of natural tropical freshwater wetlands into rice paddies may limit CH_4 emission, it compromises climate change mitigation efforts by increasing total C emission, that could make rice paddy wetlands net carbon sources.
- Water level is the main driver of CO_2 and CH_4 fluxes from a tropical freshwater wetland under both natural and rice paddy conditions.
- Uganda's rice paddy wetlands currently emit a small fraction of the total CO_2 and CH_4 emitted from the country's wetland soils due their small spatial extent. However, future emissions of both gases from Uganda's wetland soils are predicted that they will mainly originate from rice paddy wetlands due to their

rapid expansion rates. As a result, unless the current conversion trend of natural wetlands into rice paddy wetlands is reversed, future climate change mitigation strategies need to consider addressing CO_2 and CH_4 emission from rice paddy wetlands.

6.2 Recommendations

This study has demonstrated several findings regarding C storage and fluxes from a tropical freshwater wetland under natural and rice paddy conditions. However, a number of unanswered questions have been generated from this study and are the basis the following recommendations:

- This study was carried out under conditions of continuous flooding. Further studies need to investigate the impact of drying and wetting cycles on gas fluxes from tropical freshwater wetlands.
- Gas sampling in this study only considered emission from soil. Gas emissions from plants were not included. Future studies need to consider measurement of the totality of gas emission from the whole wetland (including both soil and plants i.e., ecosystem respiration). The use of eddy covariance, which can measure wetland ecosystem respiration need to be considered in future studies.
- In the Papyrus vegetation community, gas sampling was not possible in floating growth form because of shaking of the root mat while moving on it. This resulted into artificial gas ebullition. Future studies need to devise a walking planform that minimizes gas ebullition to enable sampling in this growth form. This could involve designing a walking platform that is anchored in the peat sediment layer.
- This study roughly estimated total SOC storage and gas emission from all Ugandan natural and rice paddy wetlands. However, due to differences in wetland conditions at local scales, more studies need to be done on all natural and rice paddy wetland systems in Uganda to have more accurate estimates of the total SOC storage and C fluxes from the country’s wetlands.