Carbon Dynamics of Subtropical Wetland Communities in South Florida

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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2014

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Abstract

Emission and uptake of greenhouse gases and the production and transport of dissolved organic matter in different wetland plant communities are key wetland functions determining two important ecosystem services, climate regulation and nutrient cycling. The objective of this dissertation was to study the variation of methane emissions, carbon sequestration and exports of dissolved organic carbon in wetland plant communities of a subtropical climate in south Florida.

The plant communities selected for the study of methane emissions and carbon sequestration were located in a natural wetland landscape and corresponded to a gradient of inundation duration. Going from the wettest to the driest conditions, the communities were designated as: deep slough, bald cypress, wet prairie, pond cypress and hydric pine flatwood. In the first methane emissions study, non-steady-state rigid chambers were deployed at each community sequentially at three different times of the day during a 24-month period. Methane fluxes from the different communities did not show a discernible daily pattern, in contrast to a marked increase in seasonal emissions during inundation. All communities acted at times as temporary sinks for methane, but overall were net sources. Median and mean ± standard error fluxes in g CH$_4$-C.m$^{-2}$.d$^{-1}$ were higher in the deep slough (11 and 56.2 ± 22.1), followed by the wet prairie (9.01 and 53.3 ± 26.6), bald cypress (3.31 and 5.54 ± 2.51) and pond cypress (1.49, 4.55 ± 3.35) communities. The
pine flatwood community acted as a net sink during the study period (0.0 and -1.22 ± 0.81). Seasonality in methane emissions was positively correlated with the water levels, but not with soil temperature. However, longer inundation periods did not necessarily result in higher methane emissions.

The study of carbon sequestration was conducted in parallel to the methane study. For this second study, three separate soil cores were extracted at each of the same plant communities and analyzed for total carbon content to determine the carbon pools and tested for $^{137}$Cs and $^{210}$Pb activity through the profile to estimate the accretion rates. The mean carbon concentration from the surface to the depth of maximum $^{137}$Cs activity between communities was similar in the deep slough, bald and pond cypress (446, 405 and 369 g-C Kg$^{-1}$, respectively). However, carbon sequestration rates (g-C.m$^{-2}$.yr$^{-1}$) were highest in the deep slough (104 + 14), followed by the pond cypress (60 + 9), bald cypress (30 + 2), wet prairie (24 + 1) and pine flatwood (15 + 1) communities, without an apparent relationship with the duration of the inundation period. Using the latest accepted global warming potentials of methane, it was concluded that the negative effects of contemporary methane emissions from these communities is offset by their long-term carbon sequestration.

The study of dissolved organic carbon export was conducted at a mesocosm scale using outflow water from the Storm Treatment Area 1W (STA-1W). The STA’s are a series of large treatment wetlands designed to intercept runoff from agriculture and to improve water quality of the water flowing downstream. The plant communities planted in the mesocosms were those conspicuous to the marsh environments of the Everglades
and are of interest in the design of future wetlands to intercept runoff from agricultural zones in the region and remove nutrients from it. The species dominating the different treatments in the mesocosms were: *Typha domingensis*, *Cladium jamaicense*, *Nymphaea* sp., *Nymphaea* sp./*Eleocharis* sp., *Najas* sp./*Chara* sp. and *Najas* sp. *Nymphaea* sp./*Eleocharis* sp. and *Najas* sp./*Chara* sp. treatments functioned as temporary sinks for DOC, but, otherwise, all treatments were net sources of dissolved organic carbon, suggesting the importance of autochthonous material from within the mesocosms in the export of carbon. A two-source carbon isotope mixing model was used to estimate the contribution from inflow water and biomass into the outflow’s dissolved organic carbon in each treatment. Dissolved organic carbon from biomass was relatively higher in treatments with emergent and floating vegetation (20 - 32 %) than in treatments containing submerged aquatic vegetation (<5 %). This suggests a faster turnover of the organic matter in treatments dominated by submerged aquatic vegetation and presumably a comparative lower contribution of dissolved organic nutrients exported to the outflow water.
Acknowledgments

This dissertation would not have been possible without the kind support of my advisor Professor William J. Mitsch and dissertation committee members Professors Gil Bohrer, Jim Bauer and Jay Martin. I warmly thank all for the time and knowledge they shared with me during classes, office hours or casually during their spare time.

There were also many people involved in the completion of this dissertation. First, I want to acknowledge the tutoring offered by former graduate students at the Olentangy Wetland Research Park: Blanca Bernal, Kay Stefanik, Sara Nedrich and Evan Waletzko. They introduced me to this country, the university and were always my role models as a graduate student.

Many staff, students and volunteers made the field and lab work possible: Li Zhang, Lynn McCready, Blanca Bernal, Brent Macolley, Darryl Marois, Hilary Thompson, Andrea Pereira, Daniel Marchio, Margareth Mohr, Olivia Staman, Rachel Maltese, Emily Webster, Bingbing Jiang, Olga Connors, Trevor Falk and Sarah Tseng. My wife, Diana Lombana, deserves a special mention here, as my second hand in the field. She never minded the mosquitoes or the mud, and even being pregnant with Pascual, she was there to support me (or was it her perfect excuse to bird watch?). I appreciate the additional help during the writing and results analysis offered by Blanca Bernal, Darryl Marois and Alvaro Cabezas. They were always up for a good scientific
discussion, to check my spelling, and to help me organize my thoughts or to simply enjoy a mathematical challenge.

I want to acknowledge my co-authors in the paper derived from Chapter 4: Keunyea Song from Trent University and ShiLi Miao from the South Florida Water Management District, who made logistics possible and offered their scientific support in all stages of that specific project. The faculty and staff of the Environmental Science Graduate Program at The Ohio State University offered me the institutional support that allowed me to focus on my courses and research during these four years. Thanks Maurea Al-Khouri, Sarah Straley, Richard Moore and Gil Bohrer; let the ESGP graduates be many more!

The staff and close friends of the Corkscrew Swamp Sanctuary, Mike Duever, Ed Carlson, Shawn Clem, Mike Knight and Jason Lauritsen granted the permission to work and offered key insights for the selection of the sites used for the studies presented in Chapters 2 and 3. Thanks for letting me enjoy one of the most beautiful swamps on Earth.

My work in southwest Florida would not have been possible without the kindly support of faculty, staff, students and volunteers of the Everglades Wetland Research Park at the Florida Gulf Coast University. This institution embraced me as visiting student and offered the ease to conduct many lab analyses and field work required in this research without the hindrances involved in the periodic travel back and forth from Ohio.

My stipends for the time being came from The Colombian Government through the ‘Francisco Jose de Caldas” scholarships. These funds were efficiently managed by LASPAU. Thanks for all the people involved in this task. Support for this dissertation
work also came from the National Science Foundation (CBET-1033451 and CBET-0829026), the South Florida Water Management District (contracts 4600001988 and 4500070343 to The Ohio State University and Florida Gulf Coast University, respectively), the Environmental Science Graduate Program and the Olentangy River Wetland Research Park at The Ohio State University, and the Everglades Wetland Research Park at Florida Gulf Coast University.
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Fields of Study

Major Field: Environmental Science
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Chapter 1: Introduction

1.1 Background

Wetlands offer a wide range of ecosystem services to humankind (Table 1.1). Two of these services, climate regulation and nutrient cycling, are intimately connected with the cycling of carbon through the different components of the ecosystem (i.e. water, plants and soils). In regard to climate regulation, the carbon cycle features the potential of wetland ecosystems to function as a temporary source and a sink of carbon dioxide (CO$_2$) and methane (CH$_4$), two of the main greenhouse gases (Figure. 1.1).

In general, wetlands are thought to be net sinks of atmospheric CO$_2$ (Roulet, 2000; Roehm, 2005; Cole et al., 2007). This inorganic CO$_2$ is incorporated into the system as organic compounds by autotrophs (i.e. plants and algae) during photosynthesis. After senescence, the organic matter synthesized by autotrophs undergoes a series of physical, photochemical and biochemical decomposition processes that leads to the production and subsequent potential emission of CO$_2$ back to the atmosphere (McLatchey and Reddy, 1998; Scully et al., 2003; Davidson and Janssens, 2006; Aiken et al., 2011; Todd-Brown et al., 2012). However, net primary production often offsets decomposition (Brinson et al., 1981). This results in the net accumulation of partially degraded plant material or peat that is accreted or buried in wetland anaerobic sediments/soils.
The process of carbon sequestration in wetlands accounts for an estimated 455-700 Pg of C worldwide (Mitsch and Gosselink, 2007) or about one third of the ~1550 Pg C stored in earth’s soils as organic carbon (Lal, 2008). Considering that wetlands occupy only between 5 to 8% of the terrestrial land surface (Mitsch and Gosselink, 2007), these global estimates rank them as the terrestrial ecosystems with the highest carbon density. This has led scientists from different disciplines to question the role that wetlands may be playing on global climate regulation (Kayranli et al., 2010; Mitsch et al., 2013).

To properly address the role that wetlands play in climate regulation, emissions of CH$_4$ must also be taken into account in wetland carbon budgets (Mitra et al., 2005). CH$_4$ is produced by the anaerobic decomposition of the same organic matter “sequestered” in wetlands (Fig. 1.1). This CH$_4$ can eventually be oxidized aerobically or anaerobically, or leave the wetland environment via diffusion, ebullition or through the vascular systems of plants (Megonigal et al., 2004; Chanton, 2005). Emissions of CH$_4$ from wetlands account for about 25% (i.e. 190 ± 90 Tg CH$_4$ yr$^{-1}$) of global CH$_4$ emissions, constituting the single largest natural source (Walter et al. 2001; Melton et al., 2012). According to Forster et al. (2007), once in the atmosphere, CH$_4$ has an adverse effect on the radiation budget of earth with a warming potential 25 times greater than the potential of the same mass of CO$_2$ over 100 years. This warming potential can be as 33 times greater when indirect interactions with atmospheric aerosols are included (Shindell et al., 2009).

Estimates of C fluxes in wetlands are far from definitive. For example, Bridgham et al. (2006) estimated that global wetland C sequestration and CH$_4$ emissions may be within the 100% and 50%, respectively, of the values reported in the literature. In both
cases, estimates were based on rough extrapolations from average values, within which tropical and subtropical wetlands are often underrepresented. An increasing number of studies of C sequestration and CH$_4$ emissions in the tropics in recent years (e.g. Chimner and Ewel, 2005; Jauhiainen et al., 2005; Lähteenoja et al., 2009; Couwenberg et al., 2010; Nahlik and Mitsch, 2011; Bernal and Mitsch, 2013), together with new developments in the modeling of global CH$_4$ emissions (e.g. Bergamaschi et al., 2007; Bloom et al., 2010; Bridgham et al., 2013; Stocker et al., 2013), will lead to better estimates of these fluxes at global scales. Nonetheless, while this information is important to ensure international political attention to wetlands in the climate debate (e.g. Roulet, 2000; Dunn and Freeman, 2011); a more downscaled understanding of C fluxes is still needed to properly manage wetland ecosystems in a changing climate (Erwin, 2009; Abril et al., 2014). Thus, achieving a better understanding of the spatial and temporal variability of the rates of C sequestration and CH$_4$ emissions within wetlands should be a priority (Dilling et al., 2003; Bragazza et al., 2013; Bridgham et al., 2013).

Nutrient cycling and its direct connection with water quality improvement is an ecosystem service that has been recognized in wetlands for a long time (Reddy et al., 1999; Fisher and Acreman, 2004; Mitsch and Day Jr., 2006). Dissolved organic carbon (DOC) produced in wetlands fuels microbial growth and hence, influences biochemical processes involved in the cycling of other nutrients like nitrogen, phosphorus and sulfur (Amon and Benner, 1996; Hullar et al., 1997; Aiken et al., 2011). This DOC is part of the organic matter that enters the wetland environment as dissolved organic matter (DOM). DOM can be produced from upstream allochthonous sources or from autochthonous
sources within the wetland environment. DOM is produced autochthonously by the initial leaching and fragmentation of senesced plant and algae material (Davis et al., 2006; Osborne et al., 2007). Then, DOM can be further produced by microbial degradation of residual organic matter in the surface water and soils (Wetzel, 1992; Young et al., 2005). DOM is also an important mode of transport for other dissolved nutrients to adjacent downstream aquatic ecosystems (Harrison et al., 2005; Mayorga et al., 2005). For example, more than 90% of carbon and nitrogen and 25% of phosphorus in the Everglades is transported as dissolved organic compounds bonded in DOM (Qualls and Richardson, 2003). Thus, the design and implementation of management alternatives that can mitigate the potential negative impacts of wetland DOM to downstream aquatic ecosystems is important. This particularly pertains to constructed wetlands in lands formerly used in agriculture to water storage and nutrient removal purposes (Aiken et al., 2011).

Plant communities play a key role in the emission and uptake of greenhouse gases in wetland ecosystems. Plant community structure regulates the quality and quantity of the organic matter entering the wetland environment. The quantity and quality of the organic matter is crucial in determining the rates at which it is decomposed. For example, in order to have C sequestration, it is essential to have slower decomposition rates in comparison to primary productivity rates. High C:N and lignin:N ratios in organic matter are usually associated with slow decomposition rates (e.g. Chimner and Ewel, 2005). In turn, production of CH$_4$ in anaerobic wetland soils depends on a complex step-wise decomposition of the organic matter (Chasar et al., 2000; Chanton et al., 2008). First,
organic polymers from plants and soil organic matter serve as an important source of C for soil microbes. Then, recent plant photosynthates, in the form of root exudates in the rhizosphere, fuel methanogenesis and enhance the decomposition of recalcitrant forms of soil organic matter through priming effects (Whiting and Chanton, 1993; Megonigal et al., 1999; Updegraff et al., 2001; Guenet et al., 2010; Dorodnikov et al., 2011; Basiliko et al., 2012). Intra-species physical differences can also influence CH₄ emissions through the relative predominance of the different transport pathways or by differences in rhizospheric oxidation of CH₄ (Chanton, 2005; Ström et al., 2005).

Plant communities also play a key role in the production, cycling and consequent export of DOM. For example, plant tissue nutrient concentrations (e.g. N and P) and structural components (e.g. cellulose and lignin) can significantly influence the chemical characteristics of the resulting DOM (Osborne et al., 2007). Then, depending on these chemical characteristics, DOM can take more or less time to be decomposed and thus, be reutilized within the system or be exported to downstream systems. Plants can also influence DOM cycling indirectly by modifying the environment. For example, carbon turnover rates are usually higher in wetlands dominated by submerged aquatic vegetation due to increased production of oxygen in the surface water (e.g. Hagerthy et al., 2010).

1.2 Goal and Objectives

The goal of this dissertation was to examine how the emissions/uptake of greenhouse C gases and DOC exports varied between different wetland plant communities. Specifically, the objectives were:
i. To determine the variability of CH$_4$ emissions from five wetland plant communities representing a gradient in hydroperiods

ii. To determine the variability of C sequestration in these same five wetland plant communities

iii. To determine the contribution of different wetland plant species to the DOC exported from a mesocosm experiment in the Florida Everglades

The plant communities selected for these studies are conspicuous to wetlands in south Florida (Figure 1.2). For the first and second objectives, we selected plant communities that are characteristic of a natural wetland landscape, while for the third we used some of the most common plant species found in the Everglades. This work is presented in the three chapters following this introductory chapter, each corresponding to one objective. These chapters have their own introduction, methods, results, discussions and conclusions sections. In the final chapter, the general conclusions of the dissertation are presented.

1.3 References


### 1.4 Tables and figures

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<tr>
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<tr>
<td>Food</td>
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<td>Fiber and fuel</td>
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<td>Biogeochemical</td>
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<td><strong>Regulating</strong></td>
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<td>Spiritual and inspirational</td>
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Table 1.1 Ecosystem services provided by or derived from wetlands, highlighting the services addressed in this dissertation (Millenium Ecosystem Assessment, 2005).
Figure 1.1 Carbon cycle in wetlands featuring pathways for C sequestration (green), CH$_4$ emissions (red) and DOC production and transport (blue). Adapted from Mitsch and Gosselink, (2007).
Figure 1.2 General location of the study sites: Corkscrew Swamp and the Mesocosm study. EAA = Everglades agricultural area, STA = storm treatment area, WCA = water conservation area.
Chapter 2: Methane emissions from five wetland plant communities with different hydroperiods in the Big Cypress Swamp region of Florida Everglades

2.1 Abstract

The majority of the methane (CH₄) emitted from wetlands comes from tropical and subtropical zones. On a global scale, the variability of these emissions had been attributed to water table variations; however, at landscape scales this variability is poorly understood. We measured CH₄ fluxes from five characteristic wetland plant communities of southwest Florida representing a gradient in inundation periods. From wettest to driest conditions, communities were designated as: deep slough, bald cypress, wet prairie, pond cypress and hydric pine flatwood. Non-steady-state rigid chambers were deployed at each community sequentially at three different times of the day during a 24-month period. CH₄ fluxes from the different communities did not show a discernible daily pattern, in contrast to a marked increase in emissions during inundation. All wetland habitats acted as temporary sinks of CH₄, but overall were net CH₄ sources. Median and mean ± standard error fluxes in CH₄-C m⁻² d⁻¹ were higher in deep slough (11 and 56.2 ± 22.1), followed by the wet prairie (9.01 and 53.3 ± 26.6), bald cypress (3.31 and 5.54 ± 2.51) and pond cypress (1.49, 4.55 ± 3.35). The pine flatwood community acted as a net sink during the study period (0.0 and -1.22 ± 0.81). Seasonality in CH₄ emissions was positively correlated with water levels, but not with soil temperature. However, longer inundation periods did not necessarily result in higher CH₄ emissions. These findings add to our
current knowledge of $\text{CH}_4$ fluxes from subtropical wetland ecosystems and have implications for modeling at ecosystem scales in heterogeneous wetland landscapes.

2.2 Introduction

Around 25% (i.e. 190 ± 39 Tg CH$_4$ yr$^{-1}$) of global methane (CH$_4$) emissions to the atmosphere come from wetlands, the largest single natural source (Melton et al., 2012), with the majority of this CH$_4$ (i.e. 52 - 58%) produced in tropical wetlands (Bloom et al., 2010). CH$_4$ is produced in wetlands when organic matter undergoes anaerobic decomposition in the anaerobic conditions characteristic of these ecosystems. Once in the atmosphere, CH$_4$ has an adverse effect on the radiation budget of earth with a warming potential 25 times greater than the potential of the same mass of carbon dioxide over 100 years (Forster et al., 2007), although recent studies suggest this effect may be 33 times greater when indirect interactions with atmospheric aerosols are included (Shindell et al., 2009). However, models based on the carbon equivalents basis of current estimates suggest that the effect of CH$_4$ emissions from wetlands is usually outweighed by the long-term carbon sequestration potential of these ecosystems (Whiting and Chanton, 2001; Mitsch et al., 2013).

Understanding CH$_4$ fluxes from wetlands and the factors controlling them is important to better assess possible feedbacks to climate (Cao et al., 1996; Cao et al., 1998; Shindell et al., 2004; Bridgham et al., 2013). Annual patterns of CH$_4$ emission vary with latitude, more specifically they vary with the latitude-seasonal variability in water table and soil temperature, that are the two main factors controlling CH$_4$ production and
consumption (Segers, 1998; Whalen, 2005). For example, at high latitude, arctic and boreal wetlands’ CH$_4$ emissions are highly influenced by seasonal changes in temperature. At lower latitudes, emissions from temperate wetlands are somewhat less dependent on temperature given its more restricted seasonal variation, while in the tropics, CH$_4$ emissions are more correlated with the seasonal amplitude and the position of the water table relative to the soil surface (Devol et al., 1990; Cao et al., 1998; Walter et al., 2001; Bloom et al., 2010). Notwithstanding the increasing understanding of large-scale controls on global CH$_4$ emissions, most of the knowledge of CH$_4$ emission dynamics in warm tropical and subtropical climates is still based on data derived from models made at spatial resolutions (e.g. 111 km x 111 km) that exceed the variability of plant communities and topography observed in natural landscapes (Bridgham et al., 2013). This variability has been shown to be particularly important in wetlands of high latitudes (Joabsson et al., 1999; Hirota et al., 2004; Dorodnikov et al., 2011).

In this study CH$_4$ fluxes were measured across a wetland landscape in subtropical southwest Florida comprising five different wetland communities that represented a gradient in hydroperiods (i.e. the seasonal pattern of the water level). These fluxes were evaluated relative to the water levels and soil temperatures measured in each of the communities. Our initial hypotheses were that: 1) the height of the water table will be a better explanatory variable than the soil temperature for the CH$_4$ fluxes in each plant community type, and 2) that plant communities with longer inundation periods will have higher CH$_4$ emissions than those having shorter inundation periods.
2.3 Methods

Study Site

This study was conducted in The National Audubon’s Society Corkscrew Swamp Sanctuary in southwest Florida (26°N 23°W, 81°N 35°W) (Figure 2.1). This nature preserve embedded into the Corkscrew Regional Ecosystem Watershed, is a collection of relatively undisturbed freshwater wetlands characteristic of southwest Florida. Climate in this portion of Florida is characterized by warm and wet summers, and mild winters with occasional light frost and spring droughts. In its 5,260 ha, Corkscrew Swamp contains the most important stand of large *Taxodium distichum* (bald cypress) in Florida and is also renowned to be home for large nesting colonies of wood stork (*Mycteria americana*) as well as other emblematic species such as the Florida Panther, a subspecies of the mountain lion (*Puma concolor*), the american alligator (*Alligator mississippiensis*), the Florida black bear (*Ursus americanus floridanus*) and the rare ghost orchid (*Dendrophylax lindenii*).

Geomorphologically, Corkscrew Swamp is a riverine cypress strand on a relatively small and flat watershed. Low erosive force of the river allows the development of vegetation and accumulation of peat in what would normally be the main stream channel, leading to a diffuse system of shallow irregular channels (Duever et al., 1984). The most significant factor in the distribution of the different plant communities is the hydroperiod with more than 250 days with water above the soil surface in deep sloughs, depending on the amount and distribution of yearly rainfall (Duever et al., 1984). However, maximum wet season water levels and, to a lesser extent, minimum dry season
water levels can also be important determining plant community zonation (Duever et al., 1984).

For this study five distinct wetland plant communities were selected across a gradient of hydroperiods in the Corkscrew Swamp landscape (Figure 2.2). The plant communities investigated were designated as: 1) deep slough, mostly bare soil with sparse emergent macrophytes like *Peltandra virginica*, *Thalia geniculata* and *Pontederia cordata*, a subcanopy dominated by *Annona glabra*, *Fraxinus caroliniana*, and *Cephalanthus occidentalis* and an open canopy of tall *Taxodium distichum*. 2) Bald cypress, also bare soil with a sparse understory dominated by *Osmunda regalis* in small mounds created by dead trees and roots and *Crinum americanum* in small depressions; both under a closed canopy of tall *Taxodium distichum* and a subcanopy similar to that of deep slough. 3) Wet prairie, co-dominated by *Cladium jamaicense*, *Pontederia cordata* and *Ludwigia* sp., *Alisma subcordatum* Raf. with no bare soil, and 4) pond cypress, a dense stand and closed canopy of *Taxodium distichum* var. *nutants* relatively smaller than the trees in the bald cypress community, with *Ludwigia* sp. and *Sagittaria graminea* primarily covering the forest floor. An adjacent hydric pine flatwoods (*Pinus elliottii*, *Serenoa repens* and *Aristida stricta*) community that was never inundated during the study period was also included.

*Methane Sampling*

Three non-steady-state transparent chambers were installed in the floor of each plant community investigated. An extra set of three chambers was installed in a mound at
the bald cypress community to investigate if there were discernible differences due to microtopography within this community. The chambers were made with 53 L plastic storage containers, following the design used by Sha et al. (2011). Each chamber consisted of a 10 cm tall buried frame made with a bottom removed container and a removable top made of a full inverted container. The removable tops were fitted with a 2 mm Tygon vent tube (1.6 mm i.d.) for pressure relief, a non-mercury, 1 °C increments thermometer for temperature recording and grey butyl rubber ports for sampling.

During sampling, the removable tops were sealed around the buried frames with vinyl foam weather seal bond with duct tape, petroleum jelly and held in place with binder clips. The total volume in the chambers under dry conditions was 73 L. When water levels in the chambers were lower than 10 cm in height, the new volume was calculated subtracting the volume occupied by water according to the geometry of the buried frames. When water levels exceeded 10 cm in height, modified floating 56 L plastic storage containers with foam around the bottoms for buoyancy were deployed on top of the buried frames. In each site, frames were installed in a triangular arrangement with less than 5 meters apart between any given pair of frames. Small wooden platforms to stand on were installed in front of each chamber to prevent soil disturbance in samplings during waterlogged conditions.

Sequential samplings, 11 in total, were conducted during 24 months from June 2011 to May 2013 and included 2 annual hydroperiods, each with one inundation cycle. Each inundation cycle was composed of 4 hydrological phases: 1) raising groundwater
levels without standing water, 2) raising standing water, 3) dropping standing water and 4) dropping groundwater levels without standing water.

The first 4 samplings out of the 11, were conducted 3 months apart with a replication of each site in separate days. Water levels at each of these samplings corresponded to one hydrological phase in the inundation cycle. For the remaining 7 samplings, frequency increased to approximately every 1.5 months, but without day replications. Water levels during these later samplings also corresponded for the same four hydrological phases, but included intermediate samplings between phases.

Samplings consisted of chamber deployment and sample collection at three times of the day: morning (i.e., 7-10 am), noon (i.e., 11 am-2 pm) and afternoon (i.e., 3-6 pm). Sample collection in the chambers was performed over 25 min at 5 min interval with a 30 mL syringe. The samples were injected into pre-evacuated 10 mL glass vials sealed with gray butyl septa and transported to the lab for analyses.

**Environmental Variables**

Hourly water levels and soil temperature at 2 cm depth in the five plant communities were recorded using HOBO U20 water level and water temp pro v2 data loggers, respectively. Additionally, precipitation data in the research sites was recorded at one centric location with a Davis Vantage Pro2 plus weather station. When present, data gaps in water levels were filled using correlations with the closest community data or with nearby Corkscrew Swamp Sanctuary monitoring records. Similarly, daily precipitation gaps were filled with the Sanctuary records.
Analytical Methods

CH$_4$ concentrations were determined by flame ionization detection on a gas chromatograph (Shimadzu GC-2014 Kyoto, Japan) equipped with a 64 position AOC-5000 headspace autosampler. A 1.8 m Porapack Q column detector with Helium as carried gas was used for sample preparation. One check standard with known concentration of CH$_4$ was run every 20 field samples for quality control.

CH$_4$ volume/volume concentrations ($C_v$, µL CH$_4$.L$^{-1}$) were converted into mass/volume concentration ($C_m$, mg CH$_4$.C.m$^{-3}$) using the ideal gas law, as follows (Holland et al., 1999):

\[
C_m = \frac{C_v \times M \times P}{R \times T} \quad \text{(Eq. 2.1)}
\]

where $M$ is the molar mass of carbon in methane ($M = 12.01$ µg CH$_4$-C µmole CH$_4^{\cdot}$); $P$ is barometric pressure assumed as 1 atm; $R$ is the universal gas constant ($R = 0.0820575$ L atm $^\circ$K$^{-1}$ mole$^{-1}$) and $T$ is the air temperature within the chamber at the time of sampling ($^\circ$K).

Resulting $C_v$’s values were plotted versus sampling time for each chamber run and a linear regression was performed to determine the rate of emission as the slope in the regression line ($C_{rate}$, mg CH$_4$.C.m$^{-2}$.min$^{-1}$). Then, this rate was used to calculate hourly CH$_4$ flux ($f_h$, mg CH$_4$-C m$^{-2}$.h$^{-1}$) as:

\[
f_h = \left( V \times \frac{C_{rate}}{A} \right) \times 60 \text{ min} \quad \text{(Eq. 2.2)}
\]

where, $V$ is the internal volume of the chamber (m$^3$) and $A$ is the surface area covered by the chamber (m$^2$).
Then, $f_h$'s were averaged per day and multiplied by 24 to estimate daily fluxes ($f_d$, mg CH$_4$-C m$^{-2}$ d$^{-1}$):

$$f_d = f_h \times 24$$  \hspace{1cm} (Eq. 2.3)

**Data analysis**

One-way ANOVA was used to test difference in soil temperature between communities. Linear regressions of $C_v$'s versus sampling times were performed at a significance level of $\alpha = 0.1$. Emission rates estimated from regression lines that were not statistically significant were assumed to represent zero net emissions and their fluxes (also zero) were averaged in the sampling estimates. Outliers in the regression lines were determined as those sudden increases in concentration that resulted in instant emissions accounting for more than 10 times the maximum emissions reported by Harriss et al. (1988) (i.e. 353 CH$_4$-C m$^{-2}$ d$^{-1}$). We only identify such outliers in two occasions in the deep slough (i.e. December 2011 and March 2012). Morning, noon and afternoon replicated $f_h$ in each community during the four samplings comprising the first hydroperiod, were used to assess the daily variability in CH$_4$ fluxes, while $f_d$ from all sites covering the complete sampling period were used to evaluate seasonal variability.

A non-parametric Wilcoxon signed ranks test was performed to test the difference between fluxes in the bald cypress depression and mound. Kruskal-Wallis tests were performed to test for differences in $f_h$ between sampling times of the day and for differences in $f_d$ between communities during the study period. Follow-up test for pairwise comparisons were conducted using Mann-Whitney U. Spearman's rank-order
correlation were conducted between the average $f_h$ at different times of the day in each sampling with its corresponding water level and soil temperature. All difference tests and correlations were conducted at a significance level of $\alpha = 0.05$.

2.4 Results

*Precipitation, water levels and soil temperature*

Monthly precipitation in Corkscrew Swamp as well as water levels and soil temperature of the different wetland communities during the study period are shown in Figure 2.3. Monthly precipitation distribution shows a distinct rainy season between June and October characteristic of southwest Florida (Figure 2.3a). Total rainfall amounts were similar in the two seasons recorded, 582 and 579 mm, for 2011 and 2012, respectively. However, the monthly distribution during these seasons was different between years, with higher rainfall in October 2011 towards the end of the season and higher rainfall in August 2012 close to the middle of the season.

Water levels in the sites also showed a distinct seasonal hydroperiod variable across the communities studied (Figure 2.3b). Inundation started half way through the rainy seasons (i.e late August or early September in 2011 and 2012) in all the communities and prolonged up to 7 months in some cases. In general, longer inundated conditions and maximum water levels were observed in the first hydroperiod (Table 2.1). By community, the deep slough had the longest inundation and the maximum water levels, followed by the bald cypress and wet prairie while the pond cypress had the
shorter and lowest. The hydric pine flatwood was never inundated during the study period.

Soil temperatures were the lowest during winter time and the highest in late spring during the dry months that preceded rainy seasons. When the sites were dry, temperatures were considerably more variable than when sites had standing water and daily variation in temperature was buffered (Figure 2.3c,d,e,f,g). Mean ± standard error (SE) temperatures in °C were 21.6 ± 0.7, 22.2 ± 0.7, 22.5 ± 0.7, 22.7 ± 0.7 and 24.4 ± 0.9 in deep slough, bald cypress, wet prairie, pond cypress and pine flatwood, respectively. Similarly temperatures ranged from 11.1 to 39.4 °C, 10.1 to 38.6 °C, 7.3 to 46.4 °C, 8.5 to 50.1 °C and 3.9 to 63.3 °C, respectively. Regardless of seasonal variation within sites, mean monthly soil temperatures were not significantly different between sites ($F_{4,115} = 2.04, p = 0.09$).

**Methane fluxes**

Hourly CH$_4$ fluxes during the first inundation cycle were more variable in the deep slough and the wet prairie, ranging from -0.047 to 46.9 and from -2.17 to 17.0 mg CH$_4$-C m$^{-2}$ h$^{-1}$, respectively. In turn, this variation was considerably lower in the bald cypress, pond cypress and pine flatwood (Table 2.2). There was no significant difference in hourly fluxes between depression and mound at the bald cypress community ($Z = -0.56, p = 0.96$).

CH$_4$ fluxes measured at different times of the day (e.g. morning, noon and afternoon) during the first inundation cycle were not significantly different in the wet
prairie, pond cypress and pine flatwood. Differences were observed for deep slough during the sampling in June 2011 ($\chi^2_{2,18} = 10.8, p = 0.004$) and the sampling in March 2012 ($\chi^2_{2,18} = 6.27, p = 0.044$). At the former, fluxes were higher during the afternoon while at the later were higher during noon time. Differences were also observed in hourly fluxes in the bald cypress during December 2011 ($\chi^2_{2,18} = 7.37, p = 0.025$). In this case, morning fluxes were only significantly higher than those measured during noon.

Variability in CH$_4$ fluxes per sampling in the different communities is shown in Figure 2.4 and summarized in Table 2.3. All communities acted as temporary CH$_4$ sinks, particularly during dry conditions (negative values in lower range for the study period, column 5 in Table 2.3). Mean CH$_4$ ± SE, temporary uptake (i.e. oxidation) in CH$_4$-C m$^{-2}$ d$^{-1}$ was 2.05 (n = 1) in deep slough; 1.59 ± 0.51 (n = 3) in bald cypress; 3.28 ± 0.96 (n = 3) in wet prairie; 3.28 ± 0.52 (n = 3) in pond cypress and 3.90 ± 1.41 (n = 4) in pine flatwood. However, when all samplings are considered, only the hydric pine flatwood acted as a net sink.

Daily CH$_4$ fluxes per sampling from deep slough were significantly higher during the first inundation cycle (i.e 139.9 and 134.9 ± 28) than during the second (3.77 and 9.81 ± 6.24) ($U_{10} = 0, Z = -2.65, p = 0.008$). Conversely, for the rest of the communities, the fluxes did not differ between the two cycles evaluated, but the ranges were much greater (Figure 2.4). By community, overall median fluxes for the two hydroperiods combined were significantly different ($\chi^2_{4,55} = 12.28, p = 0.015$). Pairwise comparisons among communities indicated that fluxes from the deep slough were similar to fluxes from bald cypress and wet prairie, and were significantly different from fluxes from pond cypress
and pine flatwood ($U_{22} = 24, Z = -2.40, p = 0.016$ and $U_{22} = 13.5, Z = -3.12, p = 0.002$, respectively). In addition, fluxes from bald cypress were significantly different from those in pine flatwood ($U_{22} = 25, Z = -2.74, p = 0.019$) (Figure 2.5).

**Relationship between CH$_4$ fluxes, hydrology and soil temperature**

CH$_4$ emissions from each wetland community were in general the lowest during dry seasons and the highest when water was above the soil surface. This trend was more noticeable for deep slough and the wet prairie. Spearman’s correlations were positive and significant for all communities, except for pond cypress (Table 2.4, Figure 2.6). In addition, fluxes when water was above the soil surface in bald cypress, wet prairie and pond cypress exhibited a Shelford-type nonlinear relationship with days after inundation (DAI) (Figure 2.7). This relationship suggest that there is an optimum for CH$_4$ emissions half way through the inundation period and that emissions are relative lower at the onset and towards the end of it.

In contrast to hydrology, CH$_4$ fluxes failed to correlate with soil temperature. Spearman’s correlations coefficients were relatively lower than those with the water levels and correlations were not significant for each community, including pine flatwood (Table 2.4).
2.5 Discussion

\textit{CH}_4 \textit{fluxes in Corkscrew Swamp}

Mean CH$_4$ fluxes from Corkscrew wetland communities are at the low range of fluxes reported in other subtropical and tropical regions of the world. For instance, Nahlik & Mitsch (2011) in a summary of 12 independent studies, accounting for CH$_4$ fluxes from 27 wetland types, found flux rates to be between 3.6 and 2875 CH$_4$-C m$^-2$ d$^-1$. Mean CH$_4$ fluxes from the deep slough, bald cypress and wet prairie in this study (Table 2.3) were within ranges reported previously for the Corkscrew Swamp: 10.9 – 367 CH$_4$-C m$^-2$ d$^-1$ by Harriss and Sebacher (1981) and 10.7 – 353 CH$_4$-C m$^-2$ d$^-1$ by Harriss et al. (1988). In addition, mean fluxes ± SE from deep slough and wet prairie were similar to those reported by Harriss et al. (1988), 78.7 ± 22.7 and 81.3 ± 9.3 CH$_4$-C m$^-2$ d$^-1$, respectively; but with lower median values (i.e. 11 and 9.01 vs 33 and 55 CH$_4$-C m$^-2$ d$^-1$, respectively). In turn, mean flux from pond cypress was below the range reported in previous studies.

Despite the fact that wetland communities represented net emissions of CH$_4$ to the atmosphere over the study period, we found that these communities also acted as temporary sinks, oxidizing CH$_4$ under dry conditions (Table 2.3). The rates of uptake in this study in CH$_4$-C m$^-2$ d$^-1$ agreed well with those reported in other subtropical forested swamps (Happell and Chanton, 1993; Pulliam, 1993). In most cases, CH$_4$ uptake from wetland communities in this study was one order of magnitude below the emissions of CH$_4$. However, for pond cypress, the community with the shorter hydroperiod, uptake and emissions were in the same order of magnitude and not statistically different from
those at the hydric pine flatwood (i.e. net CH$_4$ sink during the study period), suggesting the relative importance that uptake may have in the annual balance of CH$_4$ fluxes in some of the wetland communities in this study.

*Diurnal variability in CH$_4$ fluxes*

Hourly variation in CH$_4$ fluxes at different times of the day was not important for the communities evaluated in this study (Table 2.2). Fluxes were different only in the deep slough and bald cypress on one occasion during different samplings and without any consistent trend. High temperatures in the bare, moist soil of the open-canopied deep slough community may explain the relative increased fluxes observed at these particular samplings (Inglett et al., 2012). However, this explanation is not sufficient to account for higher afternoon fluxes from bald cypress under a relatively closed canopy and with standing water buffering daily changes in soil temperature.

Diurnal variations in CH$_4$ emissions from wetlands have been more frequently associated to macrophyte gas transport than to any other factor (Whiting and Chanton, 1996). Still, none of the chambers installed in the bald cypress contained macrophytes. Thus, other factors affecting CH$_4$ diffusion such as increased winds right before the time of sampling, or simply the natural spatial and temporal variability of CH$_4$ fluxes maybe more plausible explanations for the difference observed in afternoon fluxes in the bald cypress during the December 2011 sampling (Sebacher et al., 1983; Hargreaves and Fowler, 1998).
**CH₄ fluxes and temperature**

CH₄ fluxes in this study did not correlate well with soil temperature. Methanogenic bacteria, the microorganisms responsible for CH₄ production, are mesophilic with an optimal range for growth between 30 to 40 °C (Zinder, 1993). Field studies conducted in boreal wetlands have found a strong positive relationship between soil temperature and CH₄ fluxes (Bartlett and Harriss, 1993; Hargreaves and Fowler, 1998; Christensen et al., 2003). Seasonal temperature variation at such latitudes is well pronounced, with long freezing winters and short mild summers. During the warmest months of the year after soil thawing, temperature conditions for CH₄ production are at or near optimal, resulting in a pronounced increased CH₄ flux. In tropical and subtropical zones in turn, seasonal variations in temperature are far less pronounced and temperatures is maintained at a near optimal or at optimal methanogens growth range during more prolonged periods, resulting in low correlations between CH₄ fluxes and variations in soil temperature (Happell and Chanton, 1993; Jauhiainen et al., 2005; Bloom et al., 2010). Moreover, the response of CH₄ microbial oxidation to variations in temperature is relatively small, with reported values of $Q_{10}$ in the order of 1.4, in comparison to values for CH₄ production ranging from 0.6 to 35 (Smith et al., 2003; Whalen, 2005).

**CH₄ fluxes and hydrology**

In contrast to temperature, variations in the water table relative to the soil surface are often correlated to variations in CH₄ fluxes from subtropical and tropical wetlands (Bloom et al., 2010; Couwenberg et al., 2010). In fact, water levels have a strong
influence in both, CH$_4$ production and CH$_4$ oxidation. Methanogenic bacteria are obligate anaerobes, while methanotrophic bacteria is facultative, being able to resist short periods in the presence oxygen. Water level fluctuations in wetland ecosystems determines the aeration status of the soil and hence the predominance of CH$_4$ production over oxidation or vice versa.

In this study, CH$_4$ fluxes in most of the wetland communities showed a unimodal distribution during each inundation cycle analyzed, with a distinct increase in CH$_4$ emissions during inundated periods contrasted with a very low emission or uptake during dry periods. Not surprisingly, correlation between CH$_4$ fluxes and water levels was positive and statistically significant for most wetland communities evaluated, validating our initial hypothesis. Notwithstanding the positive correlation, the relationship was not straightforward. In the first place, most fluxes from the different communities were more variable during the second inundation cycle, which had the shorter inundated period and had the lower water levels. Secondly, fluxes from the deep slough were distinctively lower during this second cycle compared to the fluxes during the first inundation cycle. Lastly, longer inundation periods did not necessarily result in more CH$_4$ emissions. Average fluxes for the study period were indeed the highest and lowest in the communities that had the longest and shortest inundation periods, deep slough and pond cypress, respectively. However, wet prairie, having the third longest inundation period, had the second largest emissions.

Aeration status can be the main effect of hydrology in CH$_4$ emissions from wetlands, but hydrology can also affect other factors that determine CH$_4$ emissions, for
instance the transport of CH$_4$ from the anaerobic soils to the atmosphere. When water is above the soil surface transport can occur through 3 different pathways: ebullition, diffusion and through the vascular system of emergent macrophytes. CH$_4$ ebullition is episodic, but can be detected with static chambers as those used in this study, by discontinuous increases in CH$_4$ concentration during each chamber run (Happell and Chanton, 1993). In our data we found such discontinuous increases only for two chamber runs in the deep slough, therefore we regard diffusion and emergent macrophytes as the dominant pathways for CH$_4$ release during the time of our samplings.

When transported by emergent macrophytes, CH$_4$ in the soils is vented to the atmosphere through the plant lacunal tissue due to differences in pressure that leads to gas transport to the different organs of the plant (Whiting and Chanton, 1996). Macrophyte populations are limited by shading and water depth, thus in swamp forest and shaded floors, diffusive transport has been determined as the dominant pathway for CH$_4$ release. However, when macrophytes are present, CH$_4$ emissions have been found to be up to 10 times greater relative to non-vegetated areas (Whiting et al., 1991; Happell and Chanton, 1993; Joabsson et al., 1999; Chanton, 2005); although Altor and Mitsch (2006) found no difference in emissions between sites with and without emergent macrophytes.

In the wet prairie and pond cypress communities investigated here, higher and more prolonged water levels during the first inundation submersed the floor vegetation for more time, hence curtailing direct transport to the atmosphere (Hirota et al., 2004). In turn, lower water levels during the second inundation allowed the same vegetation to be
exposed to the atmosphere for more time, possibly leading to an increase in CH$_4$ flux in comparison to that observed during the first hydroperiod. Similarly, the presence of macrophytes on the wet prairie in contrast to the bare soil in the bald cypress and the consequent differences in CH$_4$ transport, may explain why average fluxes for the study period from wet prairie were greater and more variable than fluxes from bald cypress, regardless of the shorter hydroperiod observed in the former.

That deep slough CH$_4$ fluxes were lower and less variable during the second inundation cycle was clearly not due to the influence of water levels on CH$_4$ macrophytes transport, since the chambers were installed on bare soil. A possible explanation for these differences in CH$_4$ fluxes between inundation cycles is presented by Happell and Chanton (1993) and Happell et al. (1995). This group of researchers attributed the differences between empirical and in-situ diffusive CH$_4$ emission rates (i.e. empirical being up to three times higher), to the presence of a hydrophobic surface film that formed in the water surface. A similar film was also observed in this study in the deep slough community and was more predominant during the second inundation. According to Happell et al. (1995), this layer appeared to have impeded significantly the transfer of CH$_4$ across the water-air interface of the forested swamp in their study. Unfortunately, research on this subject is still to be done and to date it is not clear if the inhibitory effect observed in these studies was due to physical effects, chemical effects, biological activity, or a combination of the three effects.

Timing and length of inundation periods can also be determinant in the concentration and chemical characteristics of dissolved nutrients (Chow et al., 2013).
These serve as electron acceptors in the microbial degradation of organic matter and more specifically, the dissolved organic carbon (DOC) serve as substrate for methanogenic bacteria (Clymo et al., 1995; Chasar et al., 2000; Glatzel et al., 2004). We found a Shelford-type relationship between CH$_4$ fluxes and the time that the sites remained inundated that suggests an optimum in CH$_4$ emissions towards the middle of the inundation period with relative lower fluxes towards the beginning and end of it. Lower CH$_4$ fluxes at the onset of inundation have been attributed to mobilization of sulphate during the preceding aerobic dry period (Freeman et al., 1992). In turn, relative higher CH$_4$ emissions half way through the inundation period (i.e November), could have been the result of an increase in DOC from cypress and some macrophytes fresh litter that usually peaks in late September and early October (Duever et al., 1984). For example, Chow et al. (2013) found highest DOC inputs to be from litter fall in a coastal forested wetland in South Carolina, with its actual concentrations through the wet and dry seasons regulated mainly by hydrology. More research in the underlying biochemical processes involved in CH$_4$ emissions from these communities and its variation through the different inundation phases at a field scale is still needed.

**Global and regional implications**

Recent climate change and changes in land use to meet the demands of a growing global population are inducing a shift in the ecological functions of wetlands and other ecosystems at a rate never seen before in human history (Scholes and Breemen, 1997; Vörösmarty et al., 2000). Perhaps, the most significant stressor induced in wetlands is the
change in their hydrological budgets and hydroperiods (Li et al., 2007; Mitsch et al., 2013). Changes in precipitation patterns and altered groundwater aquifers are likely to impact the hydrological cycles of most wetlands, with particular severity on wetlands fed by rain and groundwater recharge, such as the ones in this study (Erwin, 2009).

Despite the fact that around 60% of the CH$_4$ produced in wetlands comes from tropical and subtropical regions of the world (Bloom et al., 2010), there is still a lot of uncertainty on how changes in the hydrological patterns will affect those emissions. Studies at field scale in tropical and subtropical latitudes on the variability of CH$_4$ fluxes and the factors determining it are still scarce in comparison to other latitudes (Mitsch et al., 2010). Such studies are an important link to couple spatial and temporal scales of global models with the scales at which environmental management plans, including restoration and conservation; must be designed and implemented in a global changing context. Specifically, this study offer important considerations for the inclusion of more detailed characterizations of wetland plant community structure in conjunction to detailed water table dynamics in CH$_4$ emissions. These later, also considered as an important feature to be included in future modeling efforts to better understand CH$_4$ dynamics (Bridgham et al., 2013).

The context of wetlands in south Florida is not much different from the global context. The historic Everglades have been massively drained since the beginning of the 20$^{th}$ century (Chimney and Goforth, 2001). Current efforts to restore pre-draining conditions are embodied in the Comprehensive Everglades Restoration Plan (CERP). The ultimate goal of the CERP is to redirect unused freshwater for restoration purposes and to
enhance the distribution for human demands (Perry, 2004). Under this scenario, it is reasonable to expect that hydroperiods will be modified in different wetland ecosystems in the entire region, either as a restoration measure or for water diversion. In either case, the results from this research, developed in a relatively undisturbed wetland landscape of southwest Florida, could offer valuable baseline information for managers to assess the possible effects of hydrological or plant community structure changes on CH$_4$ fluxes.

2.6 Conclusions

In this study methane fluxes were measured in five different wetland plant communities along a gradient of hydroperiod in a wetland landscape in Southwest Florida. The measurements encompassed two consecutive inundation cycles with different flood durations. The spatial and temporal variation in CH$_4$ was tested for correlation with water levels and soil temperatures as the two main environmental drivers of CH$_4$ production and consumption in wetlands.

Our first hypothesis, that the variation of the water table will be a better explanatory variable to the variability in CH$_4$ emissions than soil temperature held true. Pooled water levels and CH$_4$ fluxes showed a positive and significant Spearman’s rank-order correlation, while correlations with temperature by community or pooled were weak and no significant.

However, our second hypothesis that communities inundated during longer periods have higher CH$_4$ emissions than those having shorter inundation periods, that is, CH$_4$ emissions from deep slough > bald cypress > wet prairie > pond cypress, was not
supported. Emissions from deep slough and pond cypress were indeed the highest and lowest, respectively. However, wet prairie, having the third longest inundation periods, had the second largest emissions after the bald cypress community. Moreover, shorter inundation periods with reduced water levels had an adverse effect on CH$_4$ emissions in the different plan communities. For the slough community fluxes were reduced and less variable, while for bald cypress, wet prairie and pond cypress the fluxes not statistically different but with a considerable greater variation range.

We primarily discussed the possible effects of hydrology on the different CH$_4$ transport pathways and in nutrient dynamics. Future studies on the spatial variability in CH$_4$ emissions at tropical and subtropical latitudes should include the effects of hydrology on coupled biogeochemical processes and other variables known to affect CH$_4$ production and consumption, like source and quantity of organic matter and microbial populations (Dorodnikov et al., 2011; Bridgham et al., 2013).

Findings in this study could be of significance in the global context, especially for the improvement of C models in tropical and subtropical zones. Similarly, findings could be of relevance for local managers in the assessment of effects induced by hydrology or plant community structure changes on the dynamics of CH$_4$ fluxes.

2.7 References


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2.8 Tables and figures

<table>
<thead>
<tr>
<th>Plant community</th>
<th>Hydroperiod 1</th>
<th></th>
<th>Hydroperiod 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flood duration (days)</td>
<td>Mean water level (cm)</td>
<td>Maximum water height (cm)</td>
</tr>
<tr>
<td>Deep Slough</td>
<td>264</td>
<td>56.5</td>
<td>92.1</td>
</tr>
<tr>
<td>Bald Cypress</td>
<td>181</td>
<td>30.4</td>
<td>59.1</td>
</tr>
<tr>
<td>Wet Prairie</td>
<td>138</td>
<td>16.9</td>
<td>38.3</td>
</tr>
<tr>
<td>Pond Cypress</td>
<td>125</td>
<td>15.7</td>
<td>36.9</td>
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</table>

Table 2.1 Flood duration, mean water level and maximum water height for the hydroperiods recorded during the study period.

<table>
<thead>
<tr>
<th>Plant community</th>
<th>Morning Range</th>
<th>Median</th>
<th>Mean ± SE</th>
<th>Noon Median</th>
<th>Mean ± SE</th>
<th>Afternoon Median</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep Slough</td>
<td>-0.047, 46.9</td>
<td>1.03</td>
<td>1.84 ± 0.44</td>
<td>4.02</td>
<td>10.6 ± 2.89</td>
<td>3.86</td>
<td>4.40 ± 0.93</td>
</tr>
<tr>
<td>Bald Cypress</td>
<td>-0.35, 1.53</td>
<td>0</td>
<td>0.20 ± 0.072</td>
<td>0</td>
<td>0.095 ± 0.070</td>
<td>0</td>
<td>0.095 ± 0.040</td>
</tr>
<tr>
<td>Wet Prairie</td>
<td>-2.17, 17.0</td>
<td>0</td>
<td>0.80 ± 0.28</td>
<td>0.093</td>
<td>1.47 ± 0.72</td>
<td>0.16</td>
<td>1.57 ± 0.55</td>
</tr>
<tr>
<td>Pond Cypress</td>
<td>-1.63, 5.92</td>
<td>0</td>
<td>0.15 ± 0.15</td>
<td>0</td>
<td>0.33 ± 0.26</td>
<td>0</td>
<td>0.68 ± 0.20</td>
</tr>
<tr>
<td>Pine Flatwood</td>
<td>-2.17, 3.65</td>
<td>0</td>
<td>0.23 ± 0.10</td>
<td>0</td>
<td>0.28 ± 0.23</td>
<td>1</td>
<td>1.11 ± 0.22</td>
</tr>
</tbody>
</table>

Table 2.2 Hourly range, median and mean ± standard error (SE) of CH₄ fluxes at different times of the day from the different wetland communities. The hourly fluxes correspond to four replicated samplings during the first hydrological cycle.
Table 2.3 Median and mean ± standard error (SE) of CH₄ fluxes by habitats during the 2 inundation cycles and summary for the study period.

<table>
<thead>
<tr>
<th>Plant community</th>
<th>Hydroperiod 1</th>
<th>Hydroperiod 2</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Mean ± SE</td>
<td>Range</td>
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<tr>
<td>Deep Slough</td>
<td>139.9</td>
<td>134.9 ± 28</td>
<td>3.77</td>
</tr>
<tr>
<td>Bald Cypress</td>
<td>2.48</td>
<td>3.14 ± 2.01</td>
<td>3.31</td>
</tr>
<tr>
<td>Wet Prairie</td>
<td>30.8</td>
<td>30.7 ± 14.9</td>
<td>0</td>
</tr>
<tr>
<td>Pond Cypress</td>
<td>2.31</td>
<td>5.25 ± 4.97</td>
<td>0</td>
</tr>
<tr>
<td>Pine Flatwood</td>
<td>0.12</td>
<td>0.27 ± 0.64</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 2.4 Spearman's rank-order correlation between CH₄ fluxes, water level and soil temperature at 2 cm depth. Data is presented as: correlation coefficient (n), p-value; * = correlations are significant at α = 0.05.

<table>
<thead>
<tr>
<th>Plant community</th>
<th>Water level</th>
<th>Soil Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep slough</td>
<td>0.58 (45), &lt;0.001*</td>
<td>0.10 (45), 0.50</td>
</tr>
<tr>
<td>Bald cypress</td>
<td>0.59 (45), &lt;0.001*</td>
<td>-0.18 (45), 0.24</td>
</tr>
<tr>
<td>Wet prairie</td>
<td>0.80 (44), &lt;0.001*</td>
<td>-0.03 (44), 0.85</td>
</tr>
<tr>
<td>Pond cypress</td>
<td>0.027 (44), 0.86</td>
<td>0.09 (44), 0.57</td>
</tr>
<tr>
<td>Pine flatwood</td>
<td>--</td>
<td>0.11 (42), 0.48</td>
</tr>
<tr>
<td>All communities</td>
<td>0.62 (178), &lt;0.001*</td>
<td>-0.11 (220), 0.095</td>
</tr>
</tbody>
</table>
Figure 2.1 Map showing the relative location of Corkscrew Swamp (darker gray area) in southwest Florida.

Figure 2.2. Schematic depicting the arrangement in the landscape of the five wetland communities selected in this study. The view is perpendicular to the direction of surface water flow. The dashed line represents the maximum water level.
Figure 2.3 Environmental conditions during the study period (i.e. from June 2011 to May 2013): (a) monthly precipitation. (b) water level variation in the different wetland plant communities down to 20 cm below surface. (c), (d), (e), (f) and (g) soil temperature at 2 cm depth in deep slough, bald cypress, wet prairie, pond cypress and pine flatwood respectively.
Figure 2.4 CH₄ flux in each of the five wetland communities. Circles and triangles represent median and mean values respectively. Whiskers extend to the 10th (low) and 90th (high) percentile. Shaded areas represent measured water levels. Pine flatwood community was never flooded during the study period (i.e. from June 2011 to May 2013).
Figure 2.5 Boxplot with CH₄ fluxes per community. Horizontal line and dashed line within the boxes represent the median and mean values respectively for the study period (i.e. from June 2011 to May 2013). Edges in the boxes represent the 25th and 75th percentiles. Whiskers extend to the 10th and 90th percentiles. Outliers are presented by hollow circles and correspond to values outside the 10th and 90th percentiles. Pair-wise differences in the median values were calculated with Mann-Whitney and are represented with capital letters.
Figure 2.6 Linear regressions between the rank of CH$_4$ flux vs the rank of water level for a) deep slough, b) bald cypress, c) wet prairie, d) pond cypress and e) all these communities combined.
Figure 2.7 Relationship between CH₄ emissions and days after inundation (DAI) for each wetland plant community (bottom) and the correspondent hydroperiods (top). Circles represent the means for samplings with standing water and the error bars the standard error.
3.1 Abstract

Wetlands offer many ecosystem services to humankind; including the long term storage or “sequestering” of carbon (C) in their soils. Here we present a study of the variability in the C sequestration rates in a pristine wetland landscape of subtropical southwest Florida. Accordingly, C sequestration was determined in four wetland plant communities and an adjacent hydric pine flatwood community representing a gradient of hydroperiods. Going from the wettest to the driest, the communities were designated as: deep slough, bald cypress, wet prairie, pond cypress and pine flatwood. Three separate soil cores extracted at each of these communities were analyzed for total C content to determine the C pools and tested for $^{137}$Cs and Pb$^{210}$ activity through the profile to estimate the accretion rates. The mean carbon concentration from the surface to the depth of maximum $^{137}$Cs activity between communities was similar in the deep slough, bald and pond cypress (446, 405 and 369 g-C Kg$^{-1}$, respectively). However, C sequestration rates (g-C m$^{-2}$ yr$^{-1}$) were the highest the deep slough (104 ± 14), followed by the pond cypress (60 ± 9), bald cypress (30 ± 2), wet prairie (24 ± 1) and pine flatwood (15 ± 1) without an apparent relationship with hydroperiods duration. These results suggests that impediment of decomposition by anaerobic conditions caused by prolonged wet cycles, may not account for all the variability in C sequestration rates observed in this subtropical setting.
Instead, variability could also be attributed to the litter chemical composition, the productivity of the plant community.

3.2 Introduction

Climate regulation through carbon (C) sequestration in wetlands soils may be one of the most important ecosystem services of wetlands in the long term. C is sequestered in wetlands when productivity offsets decomposition and the senesced plant material is accumulated in the wetland’s anaerobic sediment layers as a mat of partially decayed organic material, or peat. A fraction of this organic matter may also be incorporated into the mineral fraction of the soil as soil organic C. Globally, it is estimated that 455-700 Pg-C is sequestered in wetlands (Mitsch and Gosselink, 2007), or about one third of the 1550 Pg-C stored in the earth’s soils as organic carbon (Lal, 2008). Considering that wetlands occupy only 5-8% of the terrestrial land surface (Mitsch and Gosselink, 2007), these global estimates rank them as the terrestrial ecosystems with the highest C density (Kayranli et al., 2010), leading scientists from different disciplines to question the role that wetland ecosystems may be playing on the Earth’s radiative forcing (Whiting and Chanton, 2001; Frolking et al., 2006; Page et al., 2011; Mitsch et al., 2013).

However, estimates on C fluxes in wetlands are far from definitive (Roulet, 2000). For instance, early estimates of C sequestration rates for North America (52.7 Tg-C yr⁻¹) and the world (137 Tg-C yr⁻¹) had an uncertainty of more than 100% according to Bridgham et al. (2006). More recent, Mitsch et al. (2013) revised this number. After
include tropical wetlands, they estimated that worldwide sequestration may be around 830 Tg-C yr\(^{-1}\).

Much of our current knowledge of the wetland’s C sink or source strengths comes from the traditionally more studied northern boreal peatlands. In general, wetlands in boreal and subarctic biomes experience low temperatures that reduce organic matter decomposition and also limit productivity. In the case of wetlands in warm subtropical and tropical climates, this temperature constraint seems to be more complex and less understood. On one hand, wetlands are generally more productive towards the tropics. On the other hand, higher temperatures in these climates could lead to a more rapid rate of decomposition of that productivity (Mitsch et al., 2010).

But beyond the controlling effect that macroclimate may have on productivity and decomposition, C sequestration seems also to differ according to the wetland type or hydrogeomorphic setting and the plant communities therein. For example, in a study of temperate wetlands of different hydrogeomorphic settings, Bernal and Mitsch (2012) found depressional and isolated wetlands to sequester up to two times more C than riverine flow-though wetlands (317 versus 140 g-C m\(^{-2}\) yr\(^{-1}\), respectively). Conversely, the same authors in a subsequent study in the tropics, found C sequestration rates in tropical slow flow through wetlands to be as much as 3 to 4 times higher than in tropical depressional and seasonal riverine wetlands (Bernal and Mitsch, 2013). They attributed the differences observed in C sequestration in these studies to site-specific features, like extent of inundation or to the recalcitrant nature of the organic matter entering their systems.
The estimation of C sequestration in wetlands across different landscapes and its variation is of critical importance for constructing more accurate C budgets that ultimately will improve or understanding of their potential as greenhouse gases (GHG) sinks or sources in future climate scenarios. Here, we present a study of C sequestration rates along different wetland plant communities that are characteristic of southwest Florida. These wetland plant communities are embodied in a single hydrogeomorphic setting, but represent a gradient of duration of inundation period. We further discuss possible causes for the variability observed between these communities and infer about their radiative forcing impact as possible net GHG sinks.

3.3 Methods

Study Site

This study was conducted in Corkscrew Swamp Sanctuary in southwest Florida (26°N 23°W, 81°N 35°W). This nature preserve embedded into the Corkscrew Regional Ecosystem Watershed, is a collection of relatively undisturbed freshwater wetlands characteristic of southwest Florida. Climate in this portion of Florida is characterized by very warm and wet summers, mild winters with occasional light frost and spring droughts. A complete ecological description of Corkscrew Swamp is presented by Duever et al. (1984). Briefly, Corkscrew Swamp is a riverine cypress strand on a relatively small and flat watershed. Low erosive force of the river allows the development of vegetation and accumulation of peat in what would normally be the main stream channel, leading to a diffuse system of shallow irregular channels. Mineral substrates
profiles, consisting mainly of sands overlying limestone, decline along a line perpendicular to the general flow direction, from the surrounding pinelands to the deepest channels in the strand. However, ground surface remains relatively flat because of organic soils have level to the overall topography gradient. The most significant factor in the distribution of the plant communities is the duration of the inundation period that can last for more than 250 days in deep sloughs, depending on the amount and distribution of yearly rainfall. However, maximum wet season water levels and, to a lesser extent, minimum dry season water levels can also be important in determining plant community zonation.

For this study, four distinct wetland plant communities were selected across a gradient of inundation period in the Corkscrew Swamp landscape. The plant communities investigated were designated as: 1) deep slough, mostly bare soil with sparse emergent macrophytes like *Peltandra virginica*, *Thalia geniculata* and *Pontederia cordata*; a subcanopy dominated by *Annona glabra*, *Fraxinus caroliniana*, and *Cephalanthus occidentalis* and an open canopy of tall *Taxodium distichum*. 2) Bald cypress, also bare soil with a sparse understory dominated by *Osmunda regalis* in small mounds created by dead trees and roots and *Crinum americanum* in small depressions; both under a closed canopy and subcanopy similar in composition to that of deep slough. 3) Wet prairie, co-dominated by *Cladium jamaicense*, *Pontederia cordata*, *Ludwigia* sp., *Alisma subcordatum* Raf. with no bare soil, and 4) pond cypress, a dense stand of *Taxodium distichum var. nutants* relatively smaller than the trees in the bald cypress community but with a relatively closed canopy, with *Ludwigia* sp. and *Sagittaria graminea* primarily
covering the forest floor. A hydric pine flatwood (*Pinus elliottii, Serenoa repens* and *Aristida stricta*) community that was never flooded during the study period was also included. Inundations during 2011 and 2012 had duration in days of 264 and 198; 181 and 149; 138 and 117 and; 125 and 67 for deep slough, bald cypress, wet prairie and pond cypress respectively.

*Sample collection and preparation*

Three 6.5-cm diameter cores were collected in each plant community between June 2011 and March 2012 (15 cores in total). When sites had standing water, surface water in the corer was siphoned out before processing the soil core. Processing in the field consisted of carefully dissecting the core in 2-cm depth increments, then packaging and sealing them in separate plastic bags. During this dissection we cleaned the working area after each increment packaging to avoid any possible soil mixing. The dissection of the top surface layers was considerably challenging in the deep slough and bald cypress communities. Several cores from these two communities had to be discarded during field processing due to mixing with other depth increments.

Once in the lab, samples corresponding to each triplicated depth increment were dried at 55 °C for 48 hr. After drying, samples were weighed to calculate the soil bulk density. Then, all samples were ground to a 2-mm particle size, homogenized and stored in sealed bags until analysis. Cores depths varied between and within sites. Only depth increments that had the three replicates were used in the analyses and calculations.
Analyzed cores depths (cm) were 32, 48, 32, 26 and 14 for deep slough, bald cypress, wet prairie, pond cypress and pine flatwood, respectively.

**Accretion rates**

Accretion rates were determined non-destructively by measuring $^{137}$Cs and $^{210}$Pb activity through the 2-cm soil increments (Craft and Richardson, 1993; Bernal and Mitsch, 2013). Accordingly, composite subsamples (~10 g) corresponding to each depth increment at each plant community were run in a high efficiency Germanium Detector (GL 2820R, Canberra). $^{137}$Cs is a man-made radionuclide worldwide distributed primarily as the consequence of atmospheric deposition after nuclear weapon testing (Smith et al., 2000). Depositional patterns of this isotope exhibit a distinct peak in the activity that corresponds to year 1964, one year after the Test Ban Treaty (Ritchie and McHenry, 1990). Thus, by knowing the layer with the peak in the activity, the soil accretion rates ($AR$) can be estimated assuming a constant accumulation rate, as:

$$AR = \frac{d_{\text{peak}}}{t}$$  \hspace{1cm} (Eq. 3.1)

Where $AR$ is in mm.yr$^{-1}$, $d_{\text{peak}}$ is the depth of the layer with the peak in $^{137}$Cs activity (mm) and $t$ is the time from 1964 to the year of sampling (yr).

The rates estimated with $^{137}$Cs were validated with the naturally occurring radioisotope $^{210}$Pb using the constant initial concentration (CIC) model (Oldfield and Appleby, 1984):

$$Ad = A_0 e^{-\lambda t}$$  \hspace{1cm} (Eq. 3.2)

Where $Ad$ is the $^{210}$Pb activity at depth $d$ (pCi g$^{-1}$), $A_0$ is the $^{210}$Pb activity at the surface (pCi g$^{-1}$), $\lambda$ is the decay constant of $^{210}$Pb (0.0311 yr$^{-1}$), $d$ is the depth in cm and $t$ is the time from 1964 to the year of sampling (yr).
is time (yr). The average of the constant $^{210}$Pb activity in the soil profile was assumed to represent the supported $^{210}$Pb activity. The method to establish accretion rates using $^{210}$Pb is based on the underlying principle that unsupported $^{210}$Pb from the decay of $^{222}$Rn in the atmosphere is deposited at a constant rate in the wetland bottom. Following, accumulation with complementary radioactive decay is assumed to create a vertical distribution with a characteristic decrease in its activity as a function of depth, from which a chronology can be inferred (MacKenzie et al. 2011). This model also assumes a constant sedimentation rate and unless there is evidence in the soil profile of the opposite, it can provide an independent estimation for the accretion rates estimated with $^{137}$Cs (e.g. Bernal and Mitsch, 2012; Bernal and Mitsch, 2013).

**Soil analyses and C sequestration rates**

Duplicate samples corresponding to each core 2-cm depth increment (i.e 3 duplicates per depth per community) were analyzed for total C (TC, %) and inorganic C (IC, %) in a Total Carbon Analyzer for soil samples (TOC-V series, SSM-5000A; Shimadzu Corporation, Kyoto, Japan). TC was determined by total combustion at 900 °C, while IC was determined by digestion with 10 mol L$^{-1}$ H$_3$PO$_4$ at 200 °C. The organic carbon (OC) fraction per depth was later calculated as the difference between TC and IC. The soil bulk density at each depth increment was calculated as the difference between TC and IC. The soil bulk density at each depth increment was calculated as the difference between TC and IC. Soil C concentration ($C_{\text{conc, layer}}$) of each depth increment per site was calculated using the following equation (Bernal and Mitsch, 2012):

$$C_{\text{conc, layer}} (\text{g-C.kg}^{-1}) = 10 \times TC_{\text{layer}} (%)$$  

(Eq. 3.3)
Where, TC<sub>layer</sub> is the average percentage of total carbon in the layer.

Finally, the C sequestration rate (C seq, g-C m<sup>-2</sup> yr<sup>-1</sup>) was calculated for each community as:

\[
C \text{ seq} = AR \times \rho_b \times C \text{ conc} \tag{Eq. 3.4}
\]

Where \(\rho_b\) (g cm<sup>-3</sup>) and \(C\text{ conc}\) (g-C kg<sup>-1</sup>) are the average bulk density and carbon concentration of the soil from the surface to the depth of maximum \(^{137}\text{Cs}\) activity, respectively.

**Statistical analysis**

Statistical analyses were conducted in IBM SPSS Statistics 21 (IBM corp.). Shapiro-Wilk test was used to test the normality of the carbon concentration from the surface to the depth of maximum \(^{137}\text{Cs}\) activity of the pooled three cores of each community. Then one-way ANOVA test was used to compare these carbon concentrations between plant communities. Games-Howell post hoc test was used to determine differences between each community. Wilcoxon signed rank test was used to compare the accretion rates estimated with \(^{137}\text{Cs}\) to those estimated using \(^{210}\text{Pb}\). All statistical analyses were conducted at a 0.05 significance level.

### 3.4 Results

**Soil profiles**

The variation of soil bulk density and TC concentrations with depth for each plant community is shown in Figure 3.1 (a and b respectively). The cores extracted at the bald
Cypress community had a thick root zone between 20 and 28 cm depth that was not included in the bulk density and carbon calculations. Bulk density remained low (i.e. < 1 g cm\(^{-3}\)) through most of the depths sampled in deep slough and bald cypress, averaging 0.30 and 0.10 g cm\(^{-3}\) respectively. In turn, bulk density showed a significant increase with depth in the wet prairie, pond cypress and pine flatwood communities as the peat layer was gradually replaced by sand. Accordingly, bulk density (g cm\(^{-3}\)) in these communities went from 0.39, 0.17 and 0.63 at the top surface 2-cm depth increment, to values over 1 at the 8, 10 and 4 cm depth increments, respectively.

Most of the C measured in the different communities were as OC (i.e. >99%). Only the wet prairie showed some increase in IC from 24 cm in depth, going up to 49% inorganic C at 30 cm depth. Regardless, TC concentration in these depth increments of wet prairie was low (~10 g-C kg\(^{-1}\) or 1%). Soil TC concentrations decreased with depth in all communities. In deep slough and bald cypress this decrease was less pronounced, going from 435.8 and 415.6 g-C Kg\(^{-1}\) at the soil surface to 76.5 and 35 g-C Kg\(^{-1}\) at the deepest depth increment, respectively. On the contrary, C concentrations decreased sharply from the soil surface in the wet prairie, pond cypress and pine flatwood communities and remained low throughout the sandy layer. Values (g-C Kg\(^{-1}\)) in these three communities went from 145.3, 391.8 and 60 at the soil surface to 10.8, 3.81 and 0, respectively. The mean carbon concentration from the surface to the depth of maximum 137Cs activity between communities was significantly different (F(4,31) = 117, \(p < 0.01\)), but similar between deep slough ( 446 g-C Kg\(^{-1}\)), bald cypress (405 g-C Kg\(^{-1}\)) and pond cypress ( 369 g-C Kg\(^{-1}\)) \(p = 0.18, p = 0.64 \text{ and } p = 1.0\), respectively. 

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Soil accretion and carbon sequestration rates

All communities registered $^{137}$Cs and $^{210}$Pb activity at different soil depths (Figure 3.2). $^{137}$Cs peaks in wet prairie, pond cypress and pine flatwood were the most discernible, while peaks in deep slough and bald cypress were in comparison not as noticeable. $^{137}$Cs activity in the soil from these latter communities was relatively higher in the top depth increments, presumably as the result of $^{137}$Cs mobility in these high organic layers (Schell et al., 1989; Olid et al., 2008). Nonetheless, peaks were identified at 8 cm in deep slough and bald cypress, at 2 cm in wet prairie and pine flatwood and at 4 cm in pond cypress. Accordingly, accretion rates were estimated as 1.7 mm yr$^{-1}$ in deep slough, 1.7 mm yr$^{-1}$ in bald cypress, 0.4 mm yr$^{-1}$ in wet prairie, 0.9 mm yr$^{-1}$ in pond cypress and 0.4 mm yr$^{-1}$ in the pine flatwood. These rates were similar of those estimated with the $^{210}$Pb CIC model ($Z = -1.47, p = 0.14$): 1.9 mm yr$^{-1}$ in deep slough, 1.7 mm yr$^{-1}$ in bald cypress, 0.8 mm yr$^{-1}$ in wet prairie, 1.3 mm yr$^{-1}$ in pond cypress and 0.4 mm yr$^{-1}$ in the pine flatwood.

Carbon sequestration rates (mean ± SD) ranged from 104 ± 14 g-C m$^{-2}$ yr$^{-1}$ in deep slough to 15 ± 1 g-C m$^{-2}$ yr$^{-1}$ in pine flatwood, representing a seven-fold decrease in the rate from the wettest to the driest community. However, this decrease across the landscape did not follow the gradual decrease in the duration of the inundation periods (Figure 3.3). Bald cypress, having the second largest inundation after deep slough, had a carbon sequestration rate close to that of wet prairie, which had the smallest rate of the wetland communities (30 ± 2 and 24 ± 1 g-C.m$^{-2}$ yr$^{-1}$, respectively). In turn, pond
cypress, the wetland community that had the shortest inundation, had the second highest rate (60 ± 9 g-C.m⁻² yr⁻¹).

3.5 Discussion

Variability of carbon sequestration between wetland plant communities

Carbon sequestration in wetlands is a function of primary productivity and decomposition. However, it has been suggested that decomposition rather than productivity is the main process involved in the accumulation of peat, and hence, carbon sequestration in wetlands of warm and wet climates (Chimner and Ewel, 2005; Bernal and Mitsch, 2013). The rationale is given by the occurrence of prolonged yearly cycles with standing water above the soil surface or waterlogged soils that may well enhance carbon accumulation by the impediment of aerobic decomposition and by the attenuation of air temperature. Accordingly, it is not surprising that the deep slough community, with the longest inundation, also had the highest carbon sequestration rate.

However, carbon sequestration in Corkscrew wetland communities did not decrease progressively with the decrease in the duration of inundation period. For example, the pond cypress with the shortest inundation had the second largest sequestration rate, doubling the rate estimated for the bald cypress, the community with the second longest inundation. Therefore, if decomposition, or better, the slowing of it, is the main process determining carbon sequestration in Corkscrew communities; then it must be due to a combination of factors and not just to the occurrence and length of
anaerobic conditions or the attenuation of temperature by the standing water as previously suggested.

A similar conclusion was reached in a study comparing litter fall decomposition between the bald and pond cypress communities at Corkscrew. In that study, Duever et al. (1984) found that low temperatures are not cold enough to be a retarding influence; litter losses during winter did not differ significantly from spring and summer losses. Additionally, they did not find a consistent correlation between litter losses and water depth. Likewise, Deghi et al. (1980) found no differences between decomposition rates of cypress communities inundated all year and control communities with shallow inundation and at least three months of dry conditions. In turn, Battle and Golladay (2001) found more accumulation of litter from cypress-gum wetlands of southwest Georgia at sites with an intermediate flooding regime (e.g. 5 flooded, 6 months litter exposed) than in sites intermittently or permanently flooded. According to the authors, litter breakdown was stimulated in the intermediate flooding regime by occasional aerobic conditions brought about by drawdown and then subsequent inundations of intermittently flooded sites. This pulsing hydrological behavior has been found to create a peak in microbial activity following reflooding (Ryder and Horwitz, 1995; Lockaby et al., 1996).

In another study, Day (1982) attributed differences in the decay rates to the chemical characteristics of the litter, rather than to the environmental conditions resulting from flooding. Specifically, increases in decay rates were the result of relatively higher nutrient content (nitrogen and phosphorus), lignin and tannic acid content, and C:N ratios. These litter composition differences could help explain why, in our study, carbon
sequestration rates where the lowest in the wet prairie when compared with adjacent
wetland plant communities. In the first place, standing aboveground biomass from
cypress trees, the dominant taxa in the deep slough, bald cypress and pond cypress
communities, has higher percent lignin content than *Cladium jamaicense*, one of the co-
dominant species in the wet prairie (i.e. 17 vs. 9.8, respectively). Additionally, cypress
also have relatively higher C:N ratios than *C. jamaicense* (i.e. 51 vs. 24, respectively)
(Osborne et al., 2007). Secondly, decomposition rates, and therefore carbon turnover, are
up to one order of magnitude higher in other co-dominant plant species of the wet prairie
when compared with that of cypress trees (Deghi et al., 1980; Battle and Golladay, 2001;
Chimney and Pietro, 2006).

Yet, the different chemical composition of litter and its effects on litter
decomposition alone may not explain differences in C sequestration rates between bald
and pond cypress, since the two have a relatively similar litter composition. Litter from
these two communities is dominated by cypress leaves and to some extent during some
parts of the year, by leaves of different understory hardwood species (Duever et al.,
1984). Instead, differences in productivity between these two plant communities seem to
offer a better explanation for the sequestration rates measured at each of these sites. Pond
cypress had a comparatively higher net productivity than bald cypress (i.e. 1,542 g m$^{-2}$ yr$^{-1}$
vs. 896 g m$^{-2}$ yr$^{-1}$) and higher litter-fall (i.e. 589 vs. 334 g m$^{-2}$ yr$^{-1}$) (Duever et al., 1984).
In addition, despite having similar carbon concentrations from the surface to the depth of
maximum $^{137}$Cs activity, bulk density in the bald cypress was consistently lower through
the soil profile than that of pond cypress. This made the carbon sequestration rate higher in the pond cypress even though accretion rates were higher in bald cypress.

Excluding the deep slough community that experienced prolonged cycles of standing water and consequently more likely prevailing anaerobic soil conditions; the communities investigated experienced a dynamic environment of alternating prolonged dry and wet cycles. Despite differences in productivity and litter production and to some extent litter composition, it is not clear yet the fate of the organic matter once it reaches the soil surface. Future research efforts should focus on the synergic of environment (McLatchey and Reddy, 1998; Chimner and Ewel, 2005), timing and quality of litter fall (Pettit et al., 2011; Chow et al., 2013), and microbial and fungal communities activity (Pettit et al., 2011; Todd-Brown et al., 2012) in the decomposition of soil organic matter in these different wetland communities.

*Carbon sequestration in southwest Florida wetland ecosystems*

To better assess the role that wetland ecosystems of southwest Florida may be playing in the sequestering of carbon at a wider scale, we compared the rates measured in this study to that reported in previous studies from tropical and subtropical zones of America and Africa (Table 3.1). To avoid confusion introduced by the use of different methodologies in the estimation of the accretion rates, we only selected studies which used radiometric dating, either with $^{137}\text{Cs}$ or with $^{210}\text{Pb}$. We then arranged wetlands by geomorphic setting (Brinson, 1993). According to these studies, C sequestration in tropical and subtropical zones ranges between 18 and 232 g-C m$^{-2}$ yr$^{-1}$. Also, rates (mean
± SE) tend to be higher in riverine, low gradient alluvial (100 ± 25 g-C m⁻² yr⁻¹), than in depressional (62 ± 18 g-C m⁻² yr⁻¹) or riverine, low gradient non alluvial wetlands (56 ± 12 g-C m⁻² yr⁻¹). The rate for the latter geomorphic setting, excluding the data in this study, is 57 ± 17 g-C m⁻² yr⁻¹.

C sequestration in the communities we studied ranged from 24 to 104 g-C m⁻² yr⁻¹ lying in the lower middle portion of the rates observed along the tropical/subtropical latitudinal range. According to Bernal and Mitsch (2013), these relatively lower rates can be explained by the ratio of mean annual precipitation x 10⁻² (mm yr⁻¹) to mean annual air temperature (°C), a proxy for water availability. In a study of 12 freshwater wetland communities in contrasting wet and dry tropical climates, Bernal and Mitsch (2013) found a Shelford-type nonlinear relationship between C sequestration rates and this ratio. According to these authors, this trend suggests that there is a middle point in precipitation and temperature at which C sequestration in wetlands from lower latitudes is enhanced. Based on their findings, this point is around a precipitation/temperature ratio (10⁻² x mm yr⁻¹ °C⁻¹) of 1.2 and with minimum sequestration rates at ratios near 0.2 and 1.8. The precipitation/temperature ratio for Corkscrew (35 years average) is 0.16, meaning that wetlands in southwest Florida may not be at the optimal climatic location for sequestering carbon when compared with other tropical and subtropical freshwater wetlands. Nonetheless, its role for carbon sequestration at a landscape scale should not be undervalued. Our results indicate that wetland plant communities can sequester up to 7 times more C than its adjacent upland ecosystems (i.e. hydric pine flatowood).
Carbon sequestration vs. methane emissions in southwest Florida wetlands

Despite the apparent benefit that wetland ecosystems have on the reduction of Earth’s radiative forcing through carbon sequestration, possible feedbacks to the atmosphere of carbon in the form of methane (CH₄) introduce a rational concern (Gedney et al., 2004; Bridgham et al., 2006; Kayranli et al., 2010; Bastviken et al., 2011). CH₄ is a GHG produced in wetlands by organic matter decomposition under anaerobic conditions (Whalen, 2005). Once in the atmosphere, CH₄ has an adverse effect on the radiation budget of earth because of its global warming potential (GWP) that is 25 times greater than the potential of the same mass of carbon dioxide (CO₂) over 100 years (Forster et al., 2007). Calculations based on carbon equivalents (i.e. taking into account for the GWP of CH₄) of the global wetland area and its organic carbon stock suggested that these ecosystems should be regarded as a relatively small net source of GHG (Mitra et al., 2005). More recently, Mitsch et al. (2013) using a dynamic model of carbon fluxes from 21 wetlands in different climates estimated that wetlands in the world may be currently acting as net carbon sinks of about 830 Tg yr⁻¹, with an average of 118 g-C m⁻² yr⁻¹ of net carbon retention.

In order to assess the role that wetland plant communities in Southwest Florida may be playing in the climate change scenario, we used a simple approach similar to that presented by Whiting and Chanton (2001), relating the rate of instant emissions as CH₄ in carbon equivalents with the rate of CO₂ uptake. Briefly, we first establish a GHG compensation boundary by tracing an empirical best fit line of CH₄/CO₂ emissions/uptake ratio (x-axis) using the current GWP of CH₄ (y-axis) in the three time
horizons contemplated in (Forster et al., 2007) (i.e. 72 for 20 yr, 25 for 100 yr and 7.6 for 500 yr). Then, we calculate the CH₄/CO₂ for Corkscrew wetland plant communities with the annual CH₄ emissions rates measured in Chapter 2 and assumed the C sequestration rates in this study as the net atmospheric CO₂ assimilated by the system (Mitsch et al., 2013). Finally, we plotted the CH₄/CO₂ ratios versus the GWP of CH₄ for 20, 100 and 500 years. Accordingly, given a specific GWP, a system may be acting as a net GHG source if a system has a CH₄/CO₂ ratio that falls in the area above and right to this boundary. Conversely, it may be acting as a GHG sink if the ratio falls into the area below and left to this boundary (Figure 3.4).

Our assessment indicated that all wetland communities investigated here may act as net GHG source over a short time horizon (i.e. 20 years). However, this source character changes to sink in the bald and pond cypress communities when the time horizon expands to a 100 years, the time horizon adopted by the Kyoto protocol (Reilly et al., 1999). But when considered in the long term (i.e. 500 years), all communities may act as net sinks of GHG. In fact, we presume that this latter time horizon may be describing in a more realistic way the emissions/uptake status of Corkscrew wetland plant communities. This particular cypress strand is known to be relatively undisturbed and the plant communities there, have developed in response to long-term climatic, hydrologic, edaphic and fire influences (Duever et al., 1984). Thus, any possible positive radiative strength caused by sustained CH₄ emissions during the first stages of peat formation of these communities back in the past, might have been offset by now by their long-term C sequestration (Frolking et al., 2006; Frolking and Roulet, 2007).
3.6 Conclusions

In this study C sequestration in the soil of four different major wetland communities of southwest Florida was investigated. Sequestration rates were the highest in the community with longer inundation, but did not follow a discernible pattern with the duration of inundations for the rest of communities considered across the landscape. Overall, the slowed decomposition caused by prolonged anaerobic cycles brought about by high water levels and poor drainage observed in other tropical wetlands, could only partially explain the rates of C accumulation found in this subtropical setting. Rather, the rates observed in the communities that alternate prolonged wet and dry cycles may also be determined to some extent by the litter chemical composition and the community productivity.

3.7 References


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Earth’s radiative budget: Sustained methane emission versus sustained carbon


3.8 Tables and figures

<table>
<thead>
<tr>
<th>Geomorphic setting and Wetland type</th>
<th>Dominant plant sp.</th>
<th>Location</th>
<th>Latitude</th>
<th>C sequestration rate (g C m^{-2} yr^{-1})</th>
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*Mean + SE 62 + 18*

Continued

Table 3.1 Mean carbon sequestration rates from tropical and subtropical wetlands of America and Africa featuring their geomorphic setting, type dominant plant species and general location. The rates were calculated using $^{137}$Cs to estimate the accretion rates or $^{210}$Pb (*). Values in parentheses indicate reported ranges.
<table>
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<tr>
<th>Geomorphic setting and Wetland type</th>
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<th>Latitude</th>
<th>C sequestration rate (g C m(^{-2}) yr(^{-1}))</th>
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**Mean + SE** 100 + 25

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**Mean + SE** 56 ± 12
Figure 3.1 Soil profile at each wetland plant community showing: a) bulk density and b) carbon concentration.
Figure 3.2 $^{137}$Cs (left), $^{210}$Pb (center) and excess $^{210}$Pb (right) activity with soil depth in the wetland plant communities in this study. Dotted lines in the $^{137}$Cs profiles indicate the maximum activity. AR = accretion rate.
Figure 3.3 Carbon sequestration and inundation duration in wetland plant communities of southwest Florida. Bars represents mean carbon sequestration rates (n = 3) for: DS = deep slough, BC = bald cypress, WP = wet prairie, PC = pond cypress and PF = pine flatwood. Error bars denote the standard error of the mean. Circles represent the average 2011 and 2012 duration of inundation for each corresponding plant community.
Figure 3.4 Wetland plant communities in southwest Florida as sink or sources of GHG (i.e. \( \text{CH}_4 \) and \( \text{CO}_2 \)) evaluated for three different time horizons (after Whiting and Chanton, 2001). The curved line represents the GHG compensation boundary and is an empirical best fit of three global warming potential (GWP) contemplated in (Forster et al., 2007). Values below or left of the compensation boundary indicate a net sink of GHG, while values above and right of the boundary net source of GHG.
4.1 Abstract

Carbon stable isotopes were used to investigate the contribution of different wetland plant species commonly found in the Everglades to the dissolved organic carbon (DOC) in the water exported from a mesocosm experiment. The species conforming the different treatments in the mesocosms were: *Typha domingensis*, *Cladium jamaicense*, *Nymphaea* sp., *Nymphaea* sp./*Eleocharis* sp., *Najas* sp./*Chara* sp. and *Najas* sp. Results indicate that *Nymphaea* sp./*Eleocharis* sp. and *Najas* sp./*Chara* sp. treatments functioned as temporary sinks for DOC, but overall all treatments were sources of DOC. A two-source carbon isotope mixing model was used to estimate the contribution from inflow water and biomass into the outflow DOC in each treatment. DOC from biomass was relatively higher in treatments with emergent and floating vegetation (20 - 32 %) than in treatments containing submerged aquatic vegetation (<5 %). The relevance of these findings for restoration and management in the context of the Everglades region, specifically its implications for organic phosphorus exports, is discussed.

4.2 Introduction

Dissolved organic matter (DOM) export from wetlands may exert a significant control over productivity, biogeochemical cycles and attenuation of visible and UV
radiation over adjacent freshwater ecosystems (Pastor et al., 2003). Previous studies have shown that external DOM inputs can regulate the amount of dissolved organic carbon (DOC) available for microbial growth (Amon and Benner, 1996; Young et al., 2005; Davis et al., 2006). DOM is also important in the transport of nutrients. For example, more than 90% of carbon and nitrogen and 25% of phosphorus in the Everglades is transported as dissolved organic compounds bonded in the DOM (Qualls and Richardson, 2003). In addition, DOM export can influence the mobility and toxicity of metals bonded with refractory forms of DOM (Grybos et al., 2007), meanwhile impacting water quality in terms of color, taste, safety and aesthetics (Worrall et al., 2003). Therefore, estimating the effect of different management and restoration strategies on DOM export is required. This is of particular importance in wetlands with high carbon reactivity and transport such as the Florida Everglades, where DOM production and export is very high (Aiken et al., 2011).

The Florida Everglades were a vast natural system comprised of different wetland habitats that dominated the landscape of south Florida. Now the Everglades are heavily managed system encompassing a series of hydrological units connected by canals, weirs and pump stations (Chimney and Goforth, 2001). Downstream from the south shore of Lake Okeechobee, the Everglades receives runoff from the Everglades Agricultural Area (EAA) which increases nutrient loading and deteriorates water quality. As a mitigation measure, the South Florida Water Management District (SFWMD) constructed 16,000 ha of treatment wetlands, known as Stormwater Treatment Areas (STAs). The STAs were designed to intercept the EAA runoff and improve the water quality of water reaching the
Water Conservation Areas (WCAs) and ultimately the Everglades National Park by reducing nutrient (primarily phosphorus) concentrations. DOM concentrations and sources in the Everglades are variable in its flow from north to south. Near the EEA, DOM concentrations are higher and more likely the result of desorption from organic peat soils used for agriculture. This DOM is transported through canals and superficial flow while is subject to photo and bio-degradation. As it flows, it becomes diluted by rainwater inputs and eventually is gradually replaced by DOM originated mainly from the degradation and leaching of organic detritus from macrophytes and algae within the STAs and the less impacted downstream ecosystems (Wang et al., 2002; Qualls and Richardson, 2003; Stern et al., 2007; Qualls and Richardson, 2008; Yamashita et al., 2010; Aiken et al., 2011).

The composition of this DOM has been found to be influenced by the vegetation species present in the existing Everglades wetland ecosystems (Osborne et al., 2007). Considering that reciprocally, water quality improvement in the STAs depends to a great extent on this vegetation and that because hydrology and nutrient impacts to wetlands often results in changes to dominant vegetation patterns (e.g. Fink and Mitsch, 2007); there is a need to better understand the role of individual plant species as contributors to the DOM and possible modulators of DOM cycling in this environments (Davis et al., 2006; Osborne et al., 2007).

In an effort to better understand the role of wetland vegetation in DOM dynamics of the Everglades, we conducted a mesocosm experiment to determine the contribution of individual plant and algae species or of common assemblages of species found in the
Everglades to the DOC in the water exported from the mesocosms. Results from this study are expected to give useful insights for the design and management of wetlands in the Everglades region in regards to DOM and its associated organic phosphorus exports.

4.3 Methods

Study site

This study was part of a three year study (August 2010 – August 2013) conducted by joint efforts of the SFWMD and The Ohio State University, to test on a mesocosm scale different plant communities as treatment alternatives to improve the water quality of the waters flowing out of the STAs in south Florida (Figure 4.1). The mesocosms consisted of 18 fiberglass tanks (6 m L x 1 m W x 1 m D) that were filled with 30 cm of soil obtained from STA-1W. The water supply system to the mesocosms consists of a pump located in the southern canal of the STA-1W connected via pipelines to the tanks located at the inflow of each fiberglass tank. Flow rates in the system are controlled using electric and manual ball valves gauged to maintain a constant hydraulic retention time of 14 days. After its pass through the fiberglass tanks, water is conducted through an outlet pipeline to an outflow tank and from there is pumped back into the STA-1W (Figure 4.2). Mean inflow DOC concentrations measured during the study period were 28.3 ± 1.8 (Mitsch et al., 2010-2012). This average concentration was within the range previously reported by (Aiken et al., 2011) for the WCA-2A and WCA-2B and higher than those of the WCA-3A and the Everglades National Park.
The tanks were planted from April to July 2010 in soils from the nearby STA 1W in a randomized block design with one factor (type of vegetation stocked) at the following six levels (treatments): *Typha domingensis* (cattail), *Cladium jamaicense* (sawgrass), *Nymphaea* sp. (water lily), *Nymphaea* sp./*Eleocharis* sp. combination, *Najas guadalupensis/Chara* sp. (SAV - submerged aquatic vegetation), and a control without planting. Despite the efforts to control vegetation growth, this latter treatment underwent a natural colonization process. Up to the start date of the present study this treatment was dominated by *N. guadalupensis* and will be referred in the rest of the text as the self-design treatment. The initial TC:TN of the soils were: 16.1 for *Typha domingensis*, 14.4 for *Cladium jamaicense*, 15.3 for *Nymphaea* sp., 14.9 for *Nymphaea* sp./*Eleocharis* sp. combination, 15.5 for SAV and 15.4 for the control treatment.

*T. domingensis, N. guadalupensis.* and *Chara* sp., are currently found in the STA’s, while the rest species are commonly found in more pristine landscapes of the Everglades. Consequently, the different treatments represent possible DOM inputs to wetlands in the Everglades, and so could our results be further applied to the management of this area.

**Sampling and analytical methods**

Sampling for this study was conducted from March to September 2011. Our first sampling date took place 10 months after the initial operation of the tanks, which was assumed to be enough for those mesocosms to reach stable conditions.
Surface water sampling:

Superficial water samples were collected in order to estimate DOC production or consumption within the mesocosms and the proportion of DOC entering to them which was further exported. Water samples at the inflow were collected at the main pipe that delivers pumped water from the STA-1W canal and was common to all mesocosms; whereas outflow water sample were collected at the outflow chambers of each of the 18 mesocosms. Water sampling was conducted for both inflow and outflows on March 24, June 2 and September 2, 2011. These sampling dates corresponded to the end of the dry period, and the beginning and middle of the rain period, respectively. An important underlying assumption in this sampling scheme was that inflow and outflow samples could be directly compared, despite the hydraulic retention time of 14 days in the mesocosms.

After collection, water samples were refrigerated below 4°C and processed for analyses the same day. 30-mL water subsamples were run through a 0.45-micron syringe filter and sent for DOC and $^{13}$C-DOC analysis to the Stable Isotope Facility at UC-Davis. DOC and $^{13}$C were measured with an O.I. Analytical Model 1030 TOC Analyzer (O I Analytical, College Station, TX) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) utilizing a GD-100 Gas Trap Interface (Graden Instruments) according to methods described by (St-Jean, 2003).

Plant biomass and soil sampling:

Plant biomass samples were collected for further estimation of their contribution to DOM exports from the mesocosms. Samples were collected twice during the study
period (June 2 and September 2). Living leaf (i.e. aboveground) and root tissue (i.e. belowground) were collected within each mesocosm by clipping healthy mature specimens at inflow, outflow and mid-section locations in each mesocosms. After collection plant material was placed on ice and transported to a laboratory in Columbus, OH, for further preparation. Upon returning to the lab, plant tissue was washed with abundant water and a damp cloth to remove debris. Then the aerenchima and senesced portions in leaves and roots, when present, were carefully removed with a scalpel and finally milled to a powder after being dried at 55°C. Plant samples were analyzed at UC-Davis Stable Isotope Facility for total weight percent proportions of C and N, and for $^{13}\text{C}$ and $^{15}\text{N}$ isotope analysis using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Soil samples from each treatment were also collected in order to validate the assumption that plants are the main source of DOM produced within the mesocosms. Samples were analyzed for total weight percent proportions of C and N, and for $^{13}\text{C}$ and $^{15}\text{N}$ isotope ratios. Soil samples were collected twice during the study period (March 24 and September 2). In each treatment, two replicates were chosen randomly and one undisturbed soil core was collected in the mid-section of each of these replicates using a 4.5 cm diameter corer. Cores were sectioned into surface soils (0 to 2 cm) assumed to represent the detritus layer and deeper soil (2 to 10 cm). After collection, soils samples were placed on ice and transported to the lab together with the plant material, where they were dried at 55 °C and milled to powder. Following this, soil were fumed for 16 hours
with HCL 12M to remove inorganic carbon (Harris et al., 2001). Soil analyses were conducted following the same procedure as the plant material.

Stable isotope data from water, plant material and soils are reported relative to the Vienna PeeDee Belemnite (V-PDB) standard for C and Air for N, as \( \delta^{13}C \) or \( \delta^{15}N = \left[ \frac{R}{R_{\text{PDB Standard}}} - 1 \right] \times 1000 \) (‰); where \( R = \frac{^{13}C}{^{12}C} \) or \( \frac{^{15}N}{^{14}N} \) mass ratios in the sample. Analytical precision for water DOC and solid samples (e.g. plant material and soils) was ± 0.6‰ and < 0.2‰, respectively.

**Determining the contribution of vegetation to the DOM exported from the mesocosms**

The contribution of vegetation to the DOM exported from the mesocosms was determined using a two-source carbon isotope mixing model (Dawson et al., 2002; Stern et al., 2007; Lambert et al., 2011), with the isotopic signature \( \delta^{13}C \) from water at the inflow (i.e. \( \delta^{13}C\text{-DOC}_{\text{inflow}} \)) and that of new DOC produced within the mesocosms (i.e. \( \delta^{13}C_{\text{new}} \)), as end members:

\[
\delta^{13}C\text{-DOC}_{\text{outflow}} = (f) (\delta^{13}C_{\text{new}}) + (1-f) (\delta^{13}C\text{-DOC}_{\text{inflow}}) \quad \text{(Eq. 4.1)}
\]

Where \( \delta^{13}C\text{-DOC}_{\text{outflow}} \) is the isotopic signature at the outflow, \( f \) is the fraction of new DOC produced within the mesocosm relative to the residual DOC in the inflow water. The \( \delta^{13}C_{\text{new}} \) was assumed as the average \( \delta^{13}C \) of above and belowground biomass in each treatment.

To assess the effect that assuming equal proportions in the contribution to the resulting DOC from above and belowground biomass may have had on the final estimations for \( f \) in each treatment, a simple sensitivity analysis was ran using two
alternate weighted averages (i.e. 0.1 and 0.9) for above and belowground biomass isotopic signatures.

**Data analysis**

Throughout this chapter means are reported ± standard error. Values of δ\(^{13}\)C-DOC from the three sampling events were pooled for the inflow and each treatment to test for differences. Biomass isotope data were first also pooled by treatment to test differences between above and belowground biomass, and then by species to test differences across treatments. Soil isotopic data was pooled by depth (i.e. surface and deeper) to test for differences. The tests were conducted using non-parametric Mann-Whitney on IBM SPSS software inc. at a significance level of 5% and were reported as: U (degrees of freedom) = Mann-Whitney coefficient, Z value, P-value).

4.4 Results

**DOC concentrations and δ\(^{13}\)C-DOC signatures**

Summary statistics for DOC concentrations at the inflow and each treatment outflows are shown in Table 4.1 (top). Overall, mean DOC concentrations for the sampling period were 31.1 ± 9.2 at the inflow and 37.9 ± 0.8 mg-C L\(^{-1}\) for all treatment outflows pooled together (not shown in table). During this period the DOC concentrations ranged from 43.7 to 31.4 in *T. domingensis*; 46.0 to 30.6 in *C. jamaicensis*; 46.1 to 32.3 in *Nymphaea* sp; 43.2 to 29.6 in the *Nymphaea* sp./*Eleocharis* sp. combination; 40.7 to 28.7 in *N. guadalupensis/Chara* sp., and 42.7 to 30.7 in *N. guadalupensis*. In addition, all treatments
had relatively higher DOC values early on in the sampling period (end of March) and declined towards the end of the study (beginning of September); while inflow DOC was the lowest at the second sampling (early June). As a consequence, the difference between inflow and each of the treatments’ outflow DOCs (i.e. net DOC change) was notably different at this second sampling (Figure 4.3). In addition, negative net DOC change in the combined *N. guadalupensis/Chara* sp. treatment in the first and third sampling and the *Nymphaea* sp./*Eleocharis* sp. treatment in the third sampling indicated a temporary DOC sink nature in these two treatments (Figure 4.3).

$\delta^{13}$C-DOC signatures were relatively constant between samplings and treatments and did not reflect any possible variability due to the decreasing DOC concentrations observed at the outflows (Table 4.1, bottom). The difference between average inflow $\delta^{13}$C-DOC (-25.1‰) and each outflow $\delta^{13}$C-DOC, was small (< 1‰) and only statistically significant for the *T. domingensis* and the *Nymphaea* sp./*Eleocharis* sp. treatment ($U$(14) = 7, $Z$ = -2.36, $P$ = 0.018 and $U$(14) = 5, $Z$ = -2.60, $P$ = 0.009, respectively).

### Vegetation and soils $\delta^{13}$C and $\delta^{15}$N

A total of 188 samples were analyzed for $\delta^{13}$C and $\delta^{15}$N in plant biomass (above and belowground) and soil (0-2 cm and 2-10cm). A summary of the different isotopic signatures and C:N ratios per treatment is presented in Table 4.2. Aboveground biomass $\delta^{13}$C ranged from -28.4‰ in *T. domingensis* to -14.9‰ in *Chara* sp (self-desing). The values for *T. domingensis*, *C. jamaicense*, *Nymphaea* sp. and *Eleocharis* sp. were similar
to those observed in the Everglades Nutrient Removal Project (ENRP) and other natural and constructed wetlands in south Florida (Wang et al., 2002; Osborne et al., 2007).

Belowground biomass $\delta^{13}$C was not statistically different from aboveground biomass $\delta^{13}$C in most treatments. It was significantly lower only in SAV ($U(17) = 2, Z = -3.55, P < 0.001$) and self-desing ($U(17) = 5, Z = -3.56, P < 0.001$) treatments. In addition, biomass $\delta^{13}$C, both above and belowground for Nymphaea sp. and N. guadalupensis in the treatments where they were the only present species, was significantly lower in comparison to the treatments where they were mixed with Eleocharis sp. and Chara sp. ($U(17) = 0, Z = -3.73, P < 0.001$ and $U(17) = 0, Z = -3.37, P < 0.001$; respectively).

Similarly, $\delta^{15}$N isotopic values in above and belowground biomass were close in each treatment and were significantly different only for T. domingensis and Nymphaea sp. ($U(23) = 33.5, Z = -2.22, P = 0.026$ and $U(23) = 0, Z = -4.16, P < 0.001$).

In contrast to biomass, isotopic signatures for soil at both depths showed similar ranges of values. There was no significant difference in $\delta^{13}$C between the detritus layer (0-2 cm) and deeper soil (2-8 cm) for all the treatments combined, while the detritus layer and deeper soil difference was significant different for $\delta^{15}$N with a lower median value for deeper soil ($U(47) = 183, Z = -2.17, P = 0.03$) (Figure 4.4). Average soil $\delta^{13}$C and $\delta^{15}$N values were similar to previous values reported for the ENRP area by Wang et al. (2002) and the WCA-2A area by Inglett et al. (2007).

C:N mass ratios for aboveground biomass ranged from 13.1 in N. guadalupensis to 33.4 in T. domingensis. Species specific values for T. domingensis and C. jamaicense were similar to those reported for the WCA-2A by Inglett and Reddy (2006). The range
for belowground biomass C:N mass ratio was less restricted than the ratio for aboveground biomass, ranging from 14.2 in *N. guadalupensis* to 69 in *C. jamaicense*. Conversely, the range of C:N mass ratios for soils was quite narrow and did not show a distinct variation between depths (Table 4.2). The mean C:N ratio for surface and deeper soil was not significantly different (i.e. 15 ± 0.1 and 15.1 ± 0.04, respectively), and was similar to that reported for similar soils at the WCA-2A by Inglett and Reddy (2006).

**Contributions of different plant species to the DOC exported from the mesocosms**

Fractions estimated from the two-member isotope mixing model are presented in Table 4.3. The relative contribution from treatments with emergent plants ranged from 0.20 to 0.32 and was considerably higher than those treatments dominated by SAV (i.e. < 0.05). The sensitivity analysis that we ran to test the effect of assuming an equal contribution from above and belowground biomass, showed that the contributions from water and biomass to outflow’s DOC did not vary more than 5% and the difference between emergent and SAV remained consistent.

4.5 Discussion

**DOC change in the experimental mesocosms**

Inflow DOC concentrations during this study were considerably more variable than those measured in the treatment outflows. During the second sampling, beginning of the wet period, inflow DOC even decreased to about half of the average outflow. This decrease in the inflow DOC concentration was also observed by Mitsch et al. (2010-
2012) for the same mesocosms (Figure 4.5) and according to Lu et al. (2003) is likely the result of dilution of DOC with rainwater in the canal from which inflow is taken. As a consequence, net DOC on this sampling was higher in comparison to the other two sampling events for all treatments, even shifting the *Nymphaea* sp./*Eleocharis* sp. and SAV treatments DOC sink character observed for the other two samplings, into sources of DOC. This suggests that DOC was being produced within each treatment; otherwise it would be reasonable to expect a decrease in the outflow DOC corresponding with the reduction of inflow DOC concentration.

The production of DOC within the mesocosms is supported by evidence from adjacent sites in the ENRP presented by Wang et al. (2002) and Stern et al. (2007). Both groups of researchers concluded that inflow DOC degraded as it was transported downstream and was replaced by new DOC produced by vegetation within the systems investigated. Nonetheless, it was still not clear whether this addition of autochthonous DOC in the ENRP resulted in a corresponding increase in outflow DOC. For example, Stern et al. (2007) found the ENRP to be functioning as sink for DOC despite inputs of new DOC from within the system. In contrast, Wang et al. (2002) found higher DOC at the outflow in relation to that of the inflow, while Gu et al. (2006) using a 5 year data series did not find any difference between inflow and outflow DOC concentrations but evidenced a contrasting seasonal behavior of the ENRP from DOC sink during rain periods to source during dry periods.

The lack of difference observed on δ¹³C-DOC at the inflow and outflow for some of the treatments has two possible explanations. One is that the sources of DOC produced
within some treatments have a very similar $\delta^{13}$C values to that of the $\delta^{13}$C in the inflow as for example, in *C. jamaicense* and *Nymphaea* sp. treatments. The other possibility is that contributions of sources with different $\delta^{13}$C values of that of the inflow water were relatively negligible. This later was the case for SAV (*N. guadalupensis* /Chara sp.) and self-desing (*N. guadalupensis*) treatments in which above and belowground biomass $\delta^{13}$C were less depleted than their inflow and outflow $\delta^{13}$C-DOC values.

**Contribution of vegetation**

Overall, vegetation seems to represent a relatively lower source of DOC at the outflow from the different treatments (Table 4), although these contributions showed a clear differentiation between emergent plants and SAV. Such results coincide with those reported by Stern et al. (2007) in the STA-1W, although in their study, emergent plants like *T. domingensis* were considerable higher that those reported here, on the order of 40-80%. A possible explanation would be the differences on the amount of biomass produced by species. On average, biomass in the *T. domingensis* and *C. jamaicense* treatments showed the relatively highest values for April and June of 2011 (800 and 862 g m\(^{-2}\)), respectively; (Mitsch et al., 2010-2012), which would explain in part the high contributions from leached biomass to the DOC in these two treatments. However, other emergent and floating plant species’ biomass (*Nymphaea* sp./*Eleocharis* sp. and *Nymphaea* sp.) had the lowest biomass, 49 and 68 g m\(^{-2}\), respectively. This suggests that not only quantity, but also the quality of senesced biomass could explain the difference that we observed in the contribution to outflow DOC between treatments with emergent
and floating vegetation and treatments with SAV, which showed a mid-range biomass production averaging 461 g m\(^{-2}\). If biomass production were the only factor determining the concentrations of outflow DOC, it would have been reasonable to find SAV biomass contributions higher than those from *Nymphaea* sp./*Eleocharis* sp. and *Nymphaea* sp. However, this was not the case.

Chimney and Pietro (2006) summarized aboveground biomass decomposition of different plant species in the ENRP. Mean decomposition rates were one order of magnitude higher in submersed species (e.g., 0.026 d\(^{-1}\) for *Najas flexilis*) than in emergent species (0.0083 d\(^{-1}\) on average) with *T. domingensis* exhibiting the lowest rate (0.0012 d\(^{-1}\)). They attributed this difference in decomposition rates to the chemical composition of the organic matter undergoing decomposition (e.g., DeBusk and Reddy, 1998; Qualls and Richardson, 2003). The higher the C:P ratio of the resulting biomass, the lower the decomposition rate. Emergent plants like *T. domingensis*, *C. jamaicense* and *Eleocharis* sp. have higher C:P ratios than the species conforming the rest of the treatments (Chimney and Pietro, 2006; Osborne et al., 2007), thus the lower decomposition in the former. Alternatively, environmental factors may also help explain why exports of DOM from SAV were lower. For example, Hagerthy et al. (2010) noted higher carbon turnover rates from habitats dominated by SAV in which O\(_2\) production in the water column enabled aerobic respiration. Higher O\(_2\) production in the water column was also recorded in the SAV treatments in relation to those of emergent and floating plant treatments (Mitsch et al. 2010-2012).
An important assumption in the functioning of the mesocosms throughout this study was that the new DOC was produced mainly by the decomposition of vegetation, either in the water column or the top-detritus layer. Although some studies have highlighted the importance of deeper soils as sources of DOC in the Everglades by means of desorption (Qualls and Richardson, 2003; Qualls and Richardson, 2008), this addition seems to be predominant from soils in the areas directly impacted by agriculture (Wang et al., 2002). In addition, soils may still be acting as DOC sources by means of decomposition of the organic matter in the soil matrix (Kalbitz et al., 2000). However, isotopic evidence supporting addition by this pathway was weak.

Carbon isotopic values in soils are generally less depleted in $^{13}$C with depth (Melillo et al., 1989). According to Ehleringer et al. (2000), this feature could be the result of (1) a decrease in $^{13}$C of atmospheric CO$_2$ due to mixture with anthropogenic-originated more depleted CO$_2$ (Suess effect), (2) microbial fractionation, (3) preferential microbial decomposition of litter and soils organic matter, or (4) to carbon mixing. Of these, microbial fractionation and decomposition are directly involved in DOC production and transformation in wetland soils (Chasar et al., 2000; Kracht and Gleixner, 2000). Consequently, a soil profile showing less depleted $\delta^{13}$C values with depth may be indicating DOC production within the soil (Kracht and Gleixner, 2000). On the one hand, there was no statistical difference in average $\delta^{13}$C of treatments between the detritus layer and deeper soil. When considered by each independent treatment, this difference may still be within error range of analytical error. In addition, C:N mass ratios in the soil were close between depths and treatments suggesting similar decomposition degree (Janssen,
1996). On the other hand, values for $\delta^{15}\text{N}$ were different between depths. Higher $\delta^{15}\text{N}$ at surface soils may be an indication of loss of isotopically lighter N during decomposition (Natelhoffer and Fry, 1988; Martinelli et al., 1999). Thus, if DOC is being produced by humus decomposition in the mesocosms, its $^{13}\text{C}$ isotopic evidence may still not be noticeable after one year of operation, considering that isotopic changes in soil are often the result of longer time scale periods.

*Implications for restoration and management*

One of the main goals for ecosystem restoration in the Everglades region is the removal of excess nutrients, especially phosphorus, to improve water quality in areas downstream of the EAA. To achieve this goal, the use of STAs has been envisioned as an ecological alternative to more traditional technologies, at the expense of possible problems associated with its implementation such as the export of DOM (Aiken et al., 2011). According to our results, promoting the dominance of SAVs in wetland environments such as STAs could be a plausible alternative that can potentially reduce exports of dissolved organic nutrients (i.e DOC, DON, and DOP) derived from plant decomposition to downstream ecosystems in the Everglades region, at least during a startup period. This relative benefit of SAVs over emergent macrophytes adds to previous evidence that suggests that the former can also provide a comparatively or even higher alternative for P removal (Dierberg et al. 2002; Knight et al., 2003).
4.6 Conclusions

In this study we determined the contribution of individual plant species or of common assemblages of species found in the Everglades to the DOC in the water exported from a mesocosm experiment in an attempt to better understand the role that wetland vegetation plays in the dynamics of DOM in the Everglades.

The treatments containing *Nymphaea* sp./*Eleocharis* sp. and *Najas* sp./*Chara* sp. functioned as temporary sinks for DOC at the beginning and end of the study. However, when all the study was considered, all the treatments were net sources of DOC, indicating the incorporation of autochthonous material from the mesocosms. Inflow water was determined as the main source for DOC (68 – 97 %), while the contribution from biomass represented a relative minor proportion (3 – 32 %).

The biomass contribution to the exported DOC was considerably higher in treatments with emergent and floating attached vegetation (23- 32 %) than in treatments with SAV, including the self-design treatment (3 – 4%). This suggests a faster turnover of the organic matter in SAV communities and presumably a comparative lower contribution of dissolved organic nutrients exported in the outflow water.

4.7 References


<table>
<thead>
<tr>
<th>DOC (mg/L)</th>
<th>3/24/2011</th>
<th>6/2/2011</th>
<th>9/2/2011</th>
<th>Study average</th>
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</thead>
<tbody>
<tr>
<td>Inflow*</td>
<td>41.7</td>
<td>21.7</td>
<td>30</td>
<td>31.1 ± 9.2 (3)</td>
</tr>
<tr>
<td>Typha domingensis</td>
<td>43.7 ± 0.5</td>
<td>37.9 ± 0.9</td>
<td>31.4 ± 0.5</td>
<td>37.7 ± 5.4 (9)</td>
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<td>Cladium jamaicense</td>
<td>46 ± 1.2</td>
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<td>42.5 ± 0.13</td>
<td>32.3 ± 0.1</td>
<td>40.3 ± 6.3 (9)</td>
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<td>Nymphaea sp./ Eleocharis sp.</td>
<td>43.2 ± 0.8</td>
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<td>29.6 ± 0.5</td>
<td>37.6 ± 6.3 (9)</td>
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<td>40.7 ± 0.6</td>
<td>36.5 ± 0.9</td>
<td>28.7 ± 0.1</td>
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<tr>
<td>Najas guadalupensis (self-design)</td>
<td>42.7 ± 0.3</td>
<td>38.8 ± 0.4</td>
<td>30.7 ± 0.1</td>
<td>37.4 ± 5.3 (9)</td>
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\( \delta{}^{13}C\)-DOC (%)

<table>
<thead>
<tr>
<th>Inflow</th>
<th>-25.5</th>
<th>-24.8</th>
<th>-25.0</th>
<th>-25.1 ± 0.2 (6)</th>
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<td>-25.1</td>
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<td>Nymphaea sp./ Eleocharis sp.</td>
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<td>-26.2</td>
<td>-26.2</td>
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<td>-24.8</td>
<td>-24.8</td>
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<td>-24.8</td>
<td>-24.9</td>
<td>-24.9 ± 0.4 (9)</td>
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</table>

* Inflow DOC concentrations (mg L\(^{-1}\)) measured between 9 and 16 days before each sampling event in this study were 36.2, 25.8 and 27.8, respectively (Mitsch et al., 2010-2012).

Table 4.1 Mean ± standard error (SE) DOC and \( \delta{}^{13}C\)-DOC at the inflow and each treatment outflow during the sampling period. Numbers in brackets indicate sample size.
### 4.8 Tables and figures

<table>
<thead>
<tr>
<th>Plant species (Treatment)</th>
<th>Aboveground biomass</th>
<th>Belowground biomass</th>
<th>Soil (0-2 cm)</th>
<th>Soil (2-10 cm)</th>
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<td><strong>δ(^{13})C (‰)</strong></td>
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<td>-26.2</td>
</tr>
<tr>
<td>Mean ± SE</td>
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<td>-26.1 ± 0.1</td>
<td>-26.1 ± 0.04</td>
</tr>
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<td><strong>δ(^{15})N (‰)</strong></td>
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<td>5.8</td>
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<tr>
<td>Nymphaea sp./Eleocharis sp.</td>
<td>4.2 / 6.3</td>
<td>4.3 / 4.8</td>
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</tr>
<tr>
<td>Najas guadalupensis / Chara sp.</td>
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<tr>
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<td>4.7 ± 0.2</td>
<td>3.2 ± 0.1</td>
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<td><strong>C:N</strong></td>
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<td>15.0</td>
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<td>15.0</td>
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<td>Najas guadalupensis / Chara sp.</td>
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<td>14.8</td>
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<td>Najas guadalupensis (self-design)</td>
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<td>Mean ± SE</td>
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<td>39 ± 4.8</td>
<td>15 ± 0.1</td>
<td>15.1 ± 0.04</td>
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Table 4.2 Isotopic signatures (δ\(^{13}\)C, δ\(^{15}\)N) and C:N mass ratios for plant above and belowground biomass and surface and deeper soil samples in each treatment.
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<th>Treatment</th>
<th>Biomass</th>
<th>Inflow</th>
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<tr>
<td><em>Najas guadalupensis</em> (self-design)</td>
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<td>0.97</td>
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Table 4.3 Inflow and biomass contributions (%) to the outflow from each treatment. In the calculations, above and belowground biomass was assumed to contribute to the DOC in equal proportions. The contributions were calculated using a two-source carbon isotope mixing model with the average of above, and belowground biomass $\delta^{13}$C and inflow $\delta^{13}$C-DOC as the main sources.
Figure 4.1 Everglades region showing the major hydrological units (WCA: Water Conservation Areas, EAA: Everglades Agricultural Area and STA: Storm Treatment Area) and the relative location of the study site at the outflow of STA-1W.
Figure 4.2 Schematic of the mesocosm experiment.

Figure 4.3 Net DOC change (i.e. difference between inflow and outflow DOC concentrations) at each treatment during the three samplings events.
Figure 4.4 Cross plot of $\delta^{13}$C, $\delta^{15}$N for biomass and soils for each treatment in this study (1: Typha domingensis, 2: Cladium jamaicense, 3: Nymphaea sp., 4: Nymphaea sp./Eleocharis sp., 5: Najas guadalupensis/Chara sp. and 6: Najas guadalupensis).

Figure 4.5 DOC concentrations at the inflow and treatments outflows measured by Mitsch et al. (2010-2012) as part of a 3 year nutrient removal project using the same mesocosms. Dotted vertical lines indicates the dates of the samplings in this study.
Chapter 5: Conclusions

This dissertation addressed the dynamics of carbon pertaining to the emission and retention of greenhouse gases, and the production and transport of dissolved organic matter in different wetland plant communities in south Florida. The main conclusions for the different objectives are as follows:

- **CH$_4$ emissions varied between plant communities, and seasonally were positively correlated with water levels. However, longer inundation periods did not necessarily represent more CH$_4$ emissions.** Communities with the longest and shortest inundation periods had indeed the highest and lowest CH$_4$ emissions, respectively; but emissions from the other two communities did not seem to have depended on the extent of the inundation.

- **Shorter inundation periods with reduced water levels had a different effect on CH$_4$ emissions in the different plant communities.** In one community, fluxes were reduced and less variable, while for another three the fluxes were not statistically different but had a considerably greater range of variation.

- **CH$_4$ emissions did not show a significant correlation with soil temperature in the wetland plant communities investigated.** Spearman’s correlation coefficients were low and correlations were not significant.
• **Sequestration rates were the highest in the community with the longest inundation periods, but did not follow a discernible pattern across the inundation gradient.**

The effect that standing water had on the reduction of decomposition in other wetlands of warm climates did not seem to be the main factor in the rates of C sequestration found in the subtropical setting of this study.

• **C sequestration by wetland plant communities in this subtropical setting was moderate when compared with other tropical and subtropical studies.** However, these plant communities can sequester up to seven times more C than the adjacent upland environments.

• **If CH\(_4\) is accounted for, the wetland plant communities investigated seem to act as a net sink of C greenhouse gases.** CH\(_4\)/CO\(_2\) molecular weight ratios are lower than the long-term global warming potential of CH\(_4\).

• **Inflow water was the main source of the DOC exported from the mesocosms while biomass represented a relatively minor source.** The contribution of the inflow water to the DOC exported ranged from 68 to 97%.

• **Biomass contribution was higher in treatments with emergent and floating attached vegetation than in treatments with submerged aquatic vegetation.** For the latter, biomass contribution ranged from 23 to 32%, while for the former it ranged from 3 to 4%.

• **Promoting the dominance of submerged aquatic vegetation could be a feasible alternative to mitigate the negative impacts of DOM produced by created wetlands in the Everglades region.**
5.1 Recommendations for future studies

Based on the three studies presented in this dissertation, the following considerations and recommendations for future studies are presented:

- Future studies on the variation of CH$_4$ emissions from warm tropical and subtropical climates should go beyond the response effects to environmental conditions (i.e. water level and temperature). The studies must couple the effects of these environmental conditions and other variables known to affect CH$_4$ production and consumption in the soil-water-plant system, like source and quantity of organic matter and microbial population dynamics. This consideration should also apply to future C models.

- Similarly, studies on C sequestration should aim to better understand the role that the quality and quantity of organic matter in wetlands, and the dynamic environment of these ecosystems have on decomposition.

- Future studies to determine the source of DOM in wetlands should consider the measurement of $\delta^{15}$N in the inflow and outflow water DOM or include an additional stable isotope or the radioactive C isotope $^{14}$C, to further differentiate the contribution from soils to the resulting DOM.
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dissolved organic carbon: a stable isotope tracer approach tested by mass balance.

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Appendix A: General picture of sampling sites and methane fluxes per community

Figure A.1 Deep slough sampling site.

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<th>Site</th>
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<th>Dec-11</th>
<th>Mar-12</th>
<th>Jul-12</th>
<th>Sep-12</th>
<th>Oct-12</th>
<th>Dec-12</th>
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Table A.1 Methane fluxes for the different samplings in the deep slough (DS). M = morning, N = noon, A = afternoon.
Figure A.2 Bald cypress sampling site.

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Table A.2 Methane fluxes for the different samplings in the bald cypress (BC). M = morning, N = noon, A = afternoon.
Figure A.3 Wet prairie sampling site.

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Table A.3 Methane fluxes for the different samplings in the wet prairie (WP). M = morning, N = noon, A = afternoon.
Figure A.4 Pond cypress sampling site.

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Table A.4 Methane fluxes for the different samplings in the pond cypress (PC). M = morning, N = noon, A = afternoon.
Figure A.5 Pine flatwood sampling site.

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Table A.5 Methane fluxes for the different samplings in the pine flatwood (PF). M = morning, N = noon, A = afternoon.
Appendix B: Soil carbon and bulk density data for the plant communities

Table B.1 Deep slough. TC = Total carbon, OC = organic carbon.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Bulk Density (g/cm³)</th>
<th>Mean TC (%)</th>
<th>OC/TC ratio</th>
<th>C Pool (Kg-C/m²)</th>
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<td>C Pool (Kg-C/m²)</td>
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Table B.2 Bald cypress. TC = Total carbon, OC = organic carbon.
Table B.3 Wet prairie. TC = Total carbon, OC = organic carbon.

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<th>OC/TC ratio</th>
<th>C Pool (Kg-C/m$^2$)</th>
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Table B.4 Pond cypress. TC = Total carbon, OC = organic carbon.

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<th>OC/TC ratio</th>
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Table B.5 Pine flatwood. TC = Total carbon, OC = organic carbon.

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<th>OC/TC ratio</th>
<th>C Pool (Kg-C/m²)</th>
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