Tropical wetlands: seasonal hydrologic pulsing, carbon sequestration, and methane emissions

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Abstract This paper summarizes the importance of climate on tropical wetlands. Regional hydrology and carbon dynamics in many of these wetlands could shift with dramatic changes in these major carbon storages if the inter-tropical convergence zone (ITCZ) were to change in its annual patterns. The importance of seasonal pulsing hydrology on many tropical wetlands, which can be caused by watershed activities, orographic features, or monsoonal pulses from the ITCZ, is illustrated by both annual and 30-year patterns of hydrology in the Okavango Delta in southern Africa. Current studies on carbon biogeochemistry in Central America are attempting to determine the rates of carbon sequestration in tropical wetlands compared to temperate wetlands and the effects of hydrologic conditions on methane generation in these wetlands. Using the same field and lab techniques, we estimated that a humid tropical wetland in Costa Rica accumulated 255 g C m^{-2} $year^{-1}$ in the past 42 years, 80% more than a similar temperate wetland in Ohio that accumulated 142 g C m^{-2} $year^{-1}$ over the same period. Methane emissions averaged 1,080 mg-C m^{-2} day^{-1} in a seasonally pulsed wetland in western Costa Rica, a rate higher than methane emission rates measured over the same period from humid tropic wetlands in eastern Costa Rica (120–278 mg-C m^{-2} day^{-1}). Tropical wetlands are often tuned to seasonal pulses of water caused by the seasonal movement of the ITCZ and are the most likely to be have higher fire frequency and changed methane emissions and carbon oxidation if the ITCZ were to change even slightly.

Keywords Botswana · Carbon sequestration · Climate change · Costa Rica · Fire ecology · Inter-tropical convergence zone (ITCZ) · Methane emissions · Monsoonal wetlands · Okavango Delta · Pulsing hydrology · Tropical swamps

Foreword

In early May 2007, it seemed like the whole of subtropical Florida was in disarray. This is normally the end of the dry season in Florida, when wetlands often dry as polar fronts no longer reach that far south (25–30°N) and the convective storms and occasional hurricanes of the summer are not yet in season. The year 2007 was a particularly dry winter

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and spring that led to extreme drought condition and a number of wetland fires, particularly in areas around the Okefenokee Swamp on the northern Florida border and in the south Florida Everglades (Fig. 1a). *The smoke of these wetland fires was being carried hundreds of kilometers south along the Gulf of Mexico coastline by the cyclonic spin of a surprising subtropical storm Andrea in the Atlantic Ocean coastline of Florida* (Fig. 1b)—*a preview of the hurricane season that was not supposed to begin until June (and the first named tropical storm in May since 1981). That week, the sky in southwestern Florida was a murky grey* (see Fig. 1c), *caused by the smoke of these wetland fires, mostly hundreds of*

Fig. 1 Satellite imagery of the Florida peninsula during early May 2007 showing **a** fires in northern and southern Florida, and **b** seasonally early tropical storm Andrea off the eastern coast of Florida, firing up the fires even more and driving smoke from northern Florida to the south. **c** Hazy sun during in southwestern Florida on May 12, 2007 caused by wetland fires hundreds of kilometers away. (Imagery **a** and **b** from NOAA; **c** photo by WJ Mitsch)

kilometers to the north. And the tropical storm winds were making the wetland fires burn hotter and further. This sequence illustrates the complexity of tropical/subtropical climate on wetlands, with droughts, fires and tropical cyclonic storms affecting the environment and each other over great distances.

Perhaps on this week in May 2007, the whole of subtropical Florida's climate had gone mad.

Introduction

Per unit area, wetlands are among the most important yet vulnerable ecosystems on the planet. They are keenly tuned to the hydrology of their climate, their watersheds, and, in some cases, their coastlines. Wetlands are one of the largest natural sources of the greenhouse gas methane (Bergamaschi et al. 2007) yet at the same time, they have the best capacity of any ecosystem to sequester and retain carbon through permanent burial (Mitsch and Gosselink 2007). Carbon storage in wetlands has another implication. Of the total storage of organic carbon in the earth's soils, 20–30% or more may be stored in wetlands (Lal 2004, 2008) and is more vulnerable to loss back to the atmosphere as both carbon dioxide and methane if the climate warms or becomes drier.

When climate changes, wetlands are among the first ecosystems to experience the impact. If rainfall does not come on time, if droughts are prolonged by watershed changes, or if water tables drop, wetlands will dry out and sequestered carbon is sent back to the atmosphere by oxidation—either biological processes or sudden fires. Excessive precipitation can expand the areas of wetlands and possibly lead to excessive release of greenhouse gases such as methane and nitrous oxide. Dams and other water impediments to water pulses could lead to extreme anoxic conditions and even greater methane generation than that which occurs during normal river pulsing conditions (Altor and Mitsch 2006, 2008).

While some is known about the global extent and carbon dynamics of northern peatlands in the face of projected climatic changes (See e.g. Wieder and Vitt 2006, Strack 2008), relatively little is known about tropical wetlands—particularly their carbon biogeochemistry. Hydrology of large-scale tropical wetlands has been fairly well described from satellite observations (Hamilton et al. 2002; Prigent et al. 2007) as have overall methane patterns (e.g. Melack et al. 2004). Less is known, however, about the effects that climate shifts might have on tropical wetlands.

This paper first estimates the extent of wetlands in the tropics and then describes the importance of the inter-tropical convergence zone (ITCZ) in general and specifically on hydrologic conditions in southern Africa's Okavango Delta, a large wetland that is keenly tuned to a seasonal pulse of water coming from hundreds of kilometers away. We then summarize current studies on carbon biogeochemistry in Central America where we are attempting to determine both the importance of wetlands on carbon sequestration and methane emissions and the importance of hydrology, which can be affected at either a climate or watershed scale, on these fluxes of carbon.

The extent of tropical wetlands

The world's wetlands are generally thought to be from 7 to 10 million km^2 (Table 1), or about 5–8% of

Table 1 Estimates of extent of wetlands in the world by climatic zone (from Mitsch and Gosselink 2007)

Zone[a]	Wetland area ($\times 10^6$ km^2)						
	Maltby and Turner (1983)	Matthews and Fung (1987)	Aselmann and Crutzen (1989)	Gorham (1991)	Finlayson and Davidson (1999)	Ramsar Convention Secretariat (2004)	Lehner and Döll (2004)
Polar/boreal	2.8	2.7	2.4	3.5	–	–	–
Temperate	1.0	0.7	1.1	–	–	–	–
Subtropical/tropical	4.8	1.9	2.1	–	–	–	–
Rice paddies	–	1.5	1.3	–	–	1.3	–
Total wetland area	8.6	6.8	6.9	–	12.8	7.2	8.2–10.1

[a] Definitions of polar, boreal, temperate, and tropical vary among studies

the land surface of the Earth (Mitsch and Gosselink 2007). Lehner and Döll (2004) provide one of the most comprehensive and recent examinations of the global extent of wetlands. Their GIS-based Global Lakes and Wetlands Database (GLWD) system focused on three coordinated levels: (1) large lakes and reservoirs, (2) smaller water bodies, and (3) wetlands. With the first two categories excluded, they estimate 8.3–10.2 million km^2 of wetlands in the world. As with several of the other studies summarized in Table 1, they found the greatest proportion of wetlands in the northern boreal regions (peaking at 60°N latitude) and another peak of wetlands in the tropics (Fig. 2). As much as 30% of the world's wetlands are found in the tropics.

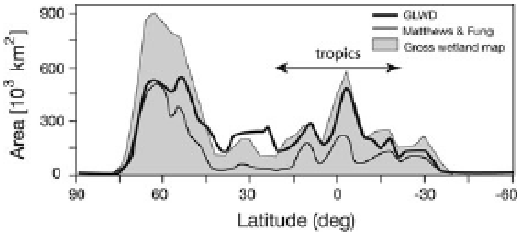

Fig. 2 Latitude distribution of wetlands based on data from Matthews and Fung (1987), global lakes and wetlands database (GLWD), and gross wetland map (redrawn from Lehner and Döll 2004)

The intertropical convergence zone (ITCZ)

Little has been speculated by IPCC (2007) or others about any effects that changing climate will have on the main heat engine of planet earth—the intertropical convergence zone (ITCZ). The ITCZ is the earth's "climatic" equator (Fig. 3). IPCC (2007) defines the ITCZ as:

> an equatorial zonal belt of low pressure near the equator where the northeast trade winds meet the southeast trade winds. As these winds converge, moist air is forced upward, resulting in a band of heavy precipitation. This band moves seasonally.

The ITCZ dominates the Earth's tropical and subtropical climate, is the energy origin of hurricanes and typhoons, and has significant seasonal movement from the northern to the southern hemispheres. Its importance for sustaining tropical ecosystems, including monsoonal tropical wetlands, is unmistakable. Close to the equator where the ITCZ persists all year, precipitation amounts of 3,000–4,000 mm/year are common—these regions are referred to as the humid tropics. Further away, where the ITCZ seasonally moves, precipitation is in the order of 500–1,500 mm/year and subsequent river runoff has a distinct flood pulse that is vital for wetlands that have seasonal patterns of wet and dry. In these tropical/subtropical regions the inter-annual variation in rainfall is large

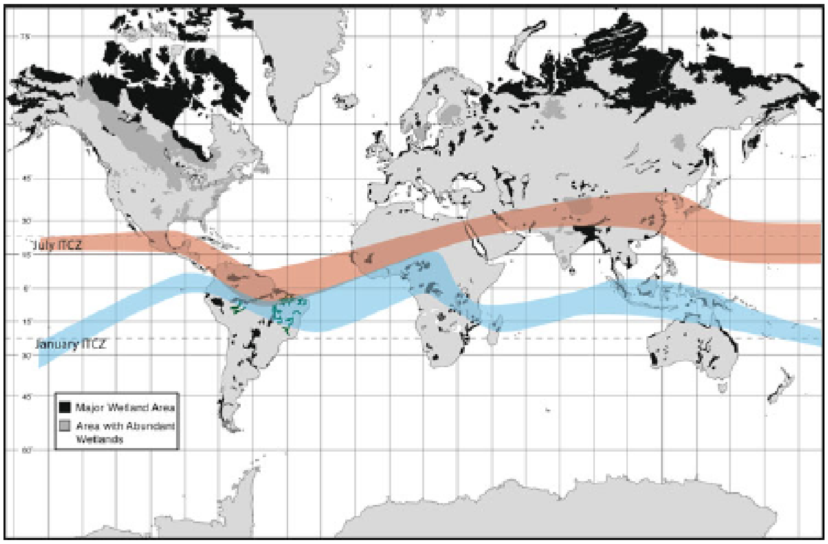

Fig. 3 Seasons of Inter-Tropical Convergence Zone (ITCZ) in January and July on map of major wetlands of the world (wetland map from Mitsch and Gosselink 2007)

with sometimes several consecutive very dry years that might dry up normally wet peaty areas and make them vulnerable to more (or less) methane emissions, droughts and oxidative loss of carbon with fires and microbial respiration.

The ITCZ is a cause of inter-annual variability of flow of many great tropical rivers. Tropical river flows, such as with the Ganges, Nile, Amazon, and Congo, have been shown, in turn, to be correlated with the more familiar El Nino-Southern Oscillation (ENSO) (Khan et al. 2006). Global climate model (GCM) projections as reported by IPCC (2007) suggest some of the tropics will have higher precipitation and streamflow as a result of climate change while other parts of the tropics, particularly the dry tropical regions, will have even less rainfall.

The ITCZ and seasonal pulsing in the Okavango

> Two annual endowments of water replenish the delta. The first comes as a quiet flood….The second flush of water comes as the flood recedes. Local rains fall in the austral summer….Over the course of a year, the Okavango expands and contracts to the syncopated rhythms of water. This wild, pulsing heart of the Kalahari is a constant that's constantly changing.
>
> Frans Lanting (1993), describing the Okavango Delta dual pulses of precipitation, followed by river flooding months later.

The importance of seasonal flooding that results from the seasonal oscillation of the ITCZ is no better illustrated than with the water budget and hydroperiod of the Okavango Delta in northern Botswana in southern Africa. The Okavango Delta is a 12,000 km^2 (total flooded area during average years) to 15,000 km^2 (total area inundated during extremely wet years) tropical freshwater wetland/upland complex in the semi-arid Kalahari Basin of northern Botswana, Africa. Water flows from Okavango River in Angola and is trapped between two faults (Gomare and Thamalakane Faults), forming the inland delta. Very little if any water leaves by surface or groundwater flow and the Delta is nowhere near a seacoast. Water takes about 4 months to flow 250 km from Mohembo (1,000 m above sea level) to Maun (940 m asl), a very slight gradient. Ecosystems in the Okavango include non-flooded uplands, seasonally flooded floodplains (which are mostly dominated by grasses and sedges rather than woody species) and stream channels and their permanently flooded floodplain dominated by hydrophytes (Ramberg et al. 2006a, b).

The overall water budget for the Okavango Delta, developed from 36 years of data is shown in Fig. 4. An average of 55 cm/year of water enters the Delta area from the Okavango River, an amount almost equal to the precipitation that occurs through the year of 49 cm/year. [If only the 12,000 km^2 flooded area of the Delta is counted, then the river input is 77 cm/year.] Almost all of the water that comes in by rainfall or river flooding is lost in evapotranspiration that occurs in both the floodplains and uplands of the Delta. Only about 1% of the water that enters the delta leaves the Delta at Maun.

The peak river flow at the inflow to the Delta (not shown here) occurs in March through May after the rainy season in the upstream Okavango watershed in Angola. The highest water level in the Okavango floodplain itself occurs much later—July through September (Fig. 5)—after which it drops precipitously as the river inflow drops and evapotranspiration increases as the summer season approaches. The rainfall season then restarts and the cycle upstream begins again. If this riverine hydrologic pulse into the Okavango Delta wetlands were to change, the wetlands and uplands in the Delta would change dramatically.

The flow of the Okavango River into the Delta, precipitation in the Delta, and the flow of the Thamalakane River in Maun are shown for the 37-year period 1970–71 to 2007–08 in Fig. 6. Because the river flow in Maun appears to have slowed to almost no flow from the early 1990s, it is tempting to suspect some human cause such as climate shifts or increased water use in

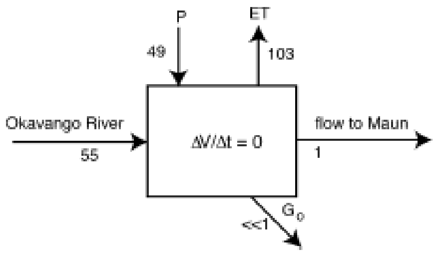

Fig. 4 Water budget, 1970–2006, for the Okavango Delta in northern Botswana. Units are cm/year; budget is for entire 15,000 km^2 Delta

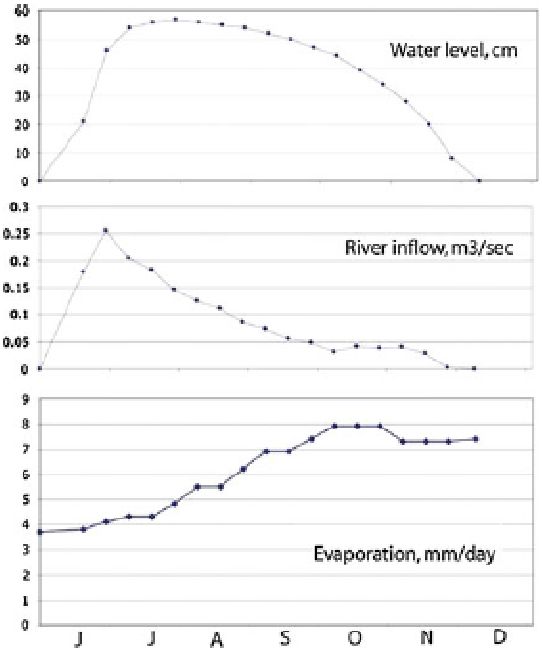

Fig. 5 Hydrology of a seasonally flooded floodplain in the middle of the Okavango Delta including **a** water depth, **b** river inflow, and **c** evaporation rates (from Ramberg et al. 2006b)

the Delta. This, however, is not the case. There are no significant water off-takes in the Delta. Although hydrological inputs have changed throughout decades, there are indications that the effects are attributed to long-term climatic variability (Tyson et al. 2002). Importantly, the relationship between hydrological inputs (inflow from the Okavango River and local rainfall) and outflow from the system has not changed during the analyzed period (Wolski et al. 2006). The dramatic reduction in outflows is simply a magnification of the not so dramatic reduction in inputs. This partly results from the fact that the actual flooding in the Delta integrates wetness conditions in the system occurring during several previous years, and a dry phase was observed since 1989. A recovery, however, appears to be occurring since 1997, with the outlook towards wetter conditions and larger floods in the Delta in future years.

Carbon sequestration

There is not a clear understanding about the rate at which atmospheric carbon is sequestered in tropical wetlands compared to temperate and boreal wetlands. On the one hand, tropical wetlands are generally more productive. On the other hand, higher temperatures in the tropics could lead to more rapid decomposition of that productivity. Overall carbon sequestration rates estimated from boreal, temperate, and tropical wetlands range from 8 to 480 g-C m^{-2} year^{-1} (Table 2). The range of 20–140 g-C m^{-2} year^{-1} reported by Mitra et al. (2005) for wetlands is meant to include wetlands in all climates but cross-climate comparisons have been few and difficult to carry out. The highest rate of carbon sequestration in Table 2 was estimated to be 480 g-C m^{-2} year^{-1} for a highly productive *Cyperus papyrus* tropical wetland in Uganda (Saunders et al. 2007) while Page et al. (2004) estimated carbon sequestration of only 94 g-C m^{-2} year^{-1} over the past 500 years in the upper meter of a core from a tropical Indonesian peatland. Some of this range may be due to different techniques used for these estimates.

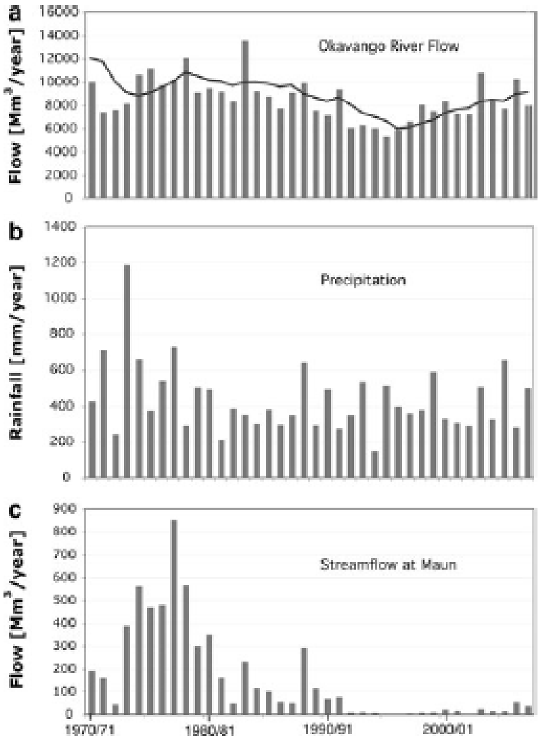

Fig. 6 Hydrologic flows at Okavango Delta for 1970–71 to 2007–08 including **a** Okavango River flow into the Delta at Mohembo, Botswana; **b** precipitation; and **c** streamflow at downstream of Okavango at Maun, Botswana

Table 2 Carbon sequestration in wetlands (partially from Mitsch and Gosselink 2007)

Wetland type	g-C m^{-2} $year^{-1}$	Reference
General average for peatlands	12–25	Malmer (1975)
General range for wetlands	20–140	Mitra et al. (2005)
Peatlands (North America)	29	Gorham (1991)
Peatlands (Alaska and Canada)	8–61	Ovenden (1990)
Boreal peatlands	15–26	Turunen et al. (2002)
Temperate peatlands	10–46	Turunen et al. (2002)
Thoreau's Bog, Massachusetts	90	Hemond (1980)
Tropical papyrus wetland, Kenya	160	Jones and Humphries (2002)
Tropical papyrus wetlands, Uganda	480	Saunders et al. (2007)
Created temperate marshes, Ohio	180–190	Anderson and Mitsch (2006)
Prairie pothole wetlands, North America		Euliss et al. (2006)
Restored (semi-permanently flooded)	305	
Reference wetlands	83	
Tropical peatland, Indonesia	56 (for 24,000 year) 94 (for last 500 year)	Page et al. (2004)
Flow-through freshwater wetlands		Bernal and Mitsch (2008a)
Ohio (temperate)	124–160	
Costa Rica (humid tropical)	250–260	

We are currently investigating soil carbon sequestration at a number of tropical and temperate wetlands in Costa Rica using similar sampling techniques and radiometric dating of the soil cores with ^{137}Cs measurements. Early results comparing carbon sequestration in one of the Costa Rican wetlands with a similar wetland in temperate zone Ohio, first reported by Bernal and Mitsch (2008a), are summarized here. Tropical soil cores were taken from a 112-ha wetland slough at EARTH University campus in the humid tropics of Costa Rica. That wetland is dominated by the swamp palm *Raphia taedigera* Mart., but it also has a diverse woody canopy and numerous herbaceous understory plants (see Mitsch et al. 2008 for site description). Soil cores were also extracted in a similar fashion from Old Woman Creek (OWC), a 56-ha freshwater flow-through temperate wetland on the Lake Erie coastline in Ohio, USA, during the same month. Two composite cores consisted of three sediment cores spaced within 40 cm were taken in each wetland. Soil core layers were analyzed by gamma spectroscopy and organic and inorganic carbon contents were determined as described by Bernal and Mitsch (2008b).

The Ohio temperate wetland (OWC) peak ^{137}Cs concentration indicated an accumulation of 16–18 cm of sediments in the last 42 years, whereas the Costa Rican EARTH University wetland (EA) accumulated 30–38 cm in that same period of time (Fig. 7). The sediment mass accumulation was actually higher at the temperate wetland compared to the tropical wetland (28.7 vs. 26.3 tons ha^{-1} $year^{-1}$) but the average carbon content for the tropical wetland (111 gC/kg soil) was double that of the temperate wetland (54 gC/kg soil). From these results, it was estimated that the temperate wetland accumulated 142 g-C m^{-2} $year^{-1}$, while the tropical wetland accumulated 80% more carbon at 255 g-C m^{-2} $year^{-1}$. The sequestration rate at our tropical site is considerably higher than rates generally estimated for boreal peatlands and most temperate wetlands summarized in Table 2. Jones and Humphries (2002) and Saunders et al. (2007) used eddy covariance techniques to estimate sequestration rates of 160 and 480 g-C m^{-2} $year^{-1}$ respectively, from permanent *Cyperus papyrus* swamps in tropical East Africa. Our tropical rate is intermediate between those two numbers.

These preliminary results using identical field and laboratory techniques in tropical and temperate wetlands with similar hydrologic (slow-flowing sloughs) conditions suggest but do not prove that

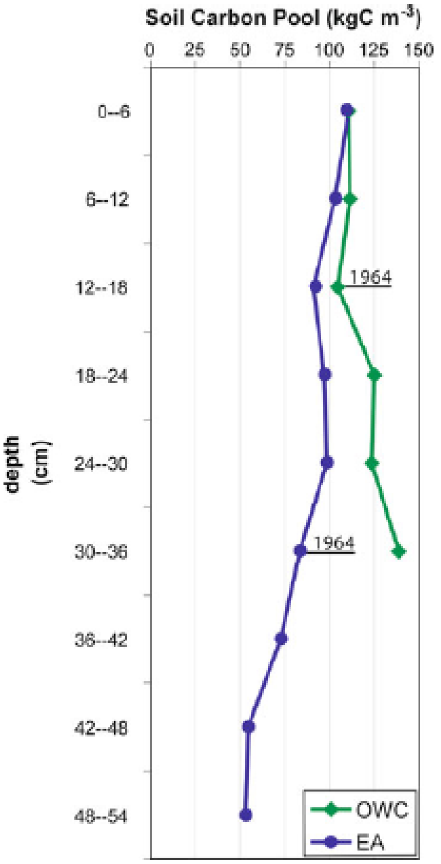

Fig. 7 Soil carbon density (from three composite cores) in hydrologically similar flow-through wetlands in humid temperate Ohio (OWC = Old Woman Creek) and humid tropical Costa Rica (EA = EARTH University). Each wetland was sampled in 2006. Date 1964 indicates depth of maximum ^{137}Cs reading that in turn indicates peak global nuclear testing year of 1964

humid tropical wetlands sequester more carbon than do similar wetlands in the temperate zone. More samples will be taken in both Costa Rica and Ohio to validate this conclusion. The conversion of these permanently wet wetlands in the humid tropics to seasonally flooded wetlands with a shift in the ITCZ might lead to more carbon oxidation and less carbon sequestration.

Methane emissions

Methane emissions are one of the most important connections between wetlands and climate change yet relatively little is known about the current and potential importance of methane emissions from tropical wetlands. Wetlands, when rice paddies are included in their definition, have been estimated to emit 33–37% of global methane (CH_4) emissions to the earth's atmosphere (Megonigal et al. 2004, Whalen 2005; Table 3). Bartlett and Harriss (1993) determined that tropical wetlands emitted about 60% of the methane from all natural wetlands, close to the estimate by Megonigal et al. (2004) in Table 3. Using satellite remote sensing, Bergamaschi et al. (2007) estimated that while extratropical regions (30–90°) of the world emitted 42.5 Tg–CH_4/year, tropical wetlands produced more than three times the methane at 138 Tg–CH_4/year, or 76% of the total wetland methane emissions. Melack et al. (2004) used satellite microwave remote sensing and habitat-specific methane emission rates published by Devol et al. (1990) that ranged from 38 (open water) to 243 (aquatic macrophytes) mg-C m^{-2} day^{-1} to estimate the emissions of methane from the Amazon River Basin alone of 22 Tg–C/year.

Recent discoveries that aerobic tropical forests emit methane (Frankenberg et al. 2005; Keppler et al. 2006) have led some to suggest that we do not know as much as we thought about wetland methane emissions in the tropics. Bergamaschi et al. (2007) speculated that as a result of these discoveries methane emission estimates from tropical wetlands may "have been overestimated."

There is the question of how methane emissions from wetlands affect climate but a more important question might be how climate change could affect

Table 3 Estimates of annual fluxes of methane from wetlands and other sources, Tg–CH_4/year (from Mitsch and Gosselink 2007)

Sources	Megonigal et al. (2004)	Whalen (2005)
Natural wetlands	115	145
Tropics	65	
Northern latitude	40	
Others	10	
Other natural sources	45	45
Anthropogenic		
Rice paddies	60	80
Other	315	330
Total sources	535	600

methane emissions from wetlands in the future. While these questions have been frequently asked for boreal peatlands, few studies have looked at the effects climate and hydrologic changes would have on methane emissions from tropical wetlands if, for example, the ITCZ were to shift in its seasonal movements.

Most of the methane emission studies to date have been in peatlands (bogs and fens) and freshwater marshes. Researchers in boreal wetlands found deep ponds to have higher methane flux rates than other wetland types, neutral fens to have higher rates than acid fens and bogs, and freshwater swamps and marshes to generate more methane than do coastal salt marshes and mangroves. Whalen's (2005) estimates (Table 3) suggest that tropical and subtropical wetlands may have higher rates of methane production than originally believed. Sorrell and Boon (1992) found methane emissions in Australian billabongs of about 32–60 mg-C m^{-2} day^{-1}. Delaune and Pezeshki (2003) reported methane emissions of $\sim$7 to over 600 mg-C m^{-2} day^{-1} in subtropical Louisiana freshwater marshes with the greatest methane emissions occurred in the summer months. Hadi et al. (2005) measured methane emissions from tropical peatlands in Indonesia and found only 12–53 mg-C m^{-2} day^{-1}, with the highest number from cultivated paddy fields. Shindell et al. (2004) simulated a global climate model (GCM) with double CO_2 conditions and found that methane emissions rose 78%, with most of the increased from existing tropical wetlands.

We have been investigating the effects of climate and hydrologic conditions on methane emissions in the tropics for several years in Costa Rica. There are two distinct biomes in Costa Rica—a wet rain forest biome on the eastern (Caribbean) side, and wet-dry tropical forests/savannahs in western (Pacific) side. The humid tropics of Eastern Costa Rica are influenced year-round by the ITCZ, which does not move very far north and south in this region compared to other parts of the world (Fig. 3). The wet-dry conditions of Western Costa Rica, while mostly caused by the orographic influences of Guanacaste, Tilarán, Central, and Talamanca mountains that pass through the center of Central America (Kohlmann et al. 2008), create conditions that are similar to regions in Africa and elsewhere where there is major monsoonal movement of the ITCZ. In the humid tropics of eastern Costa Rica, we have been measuring methane emissions in two sites: the EARTH University La Reserva wetland described above that is now surrounded by secondary forest growth after restoration of grazing lands; and a small wetland in a tropical rain forest at La Selva Biological Station in the Sarapiqui watershed in the north-central portion of the country. In western Costa Rica, we are measuring methane emissions from wetlands at the Palo Verde Biological Field Station in the Tempisque watershed, where there is a significant wet-dry pulsing season. The two wetland sites in the humid tropics—EARTH and La Selva—have average (± SE) precipitation of 3,460 ± 750 and 4,337 ± 520 mm/year, respectively, (Fig. 8a, b).

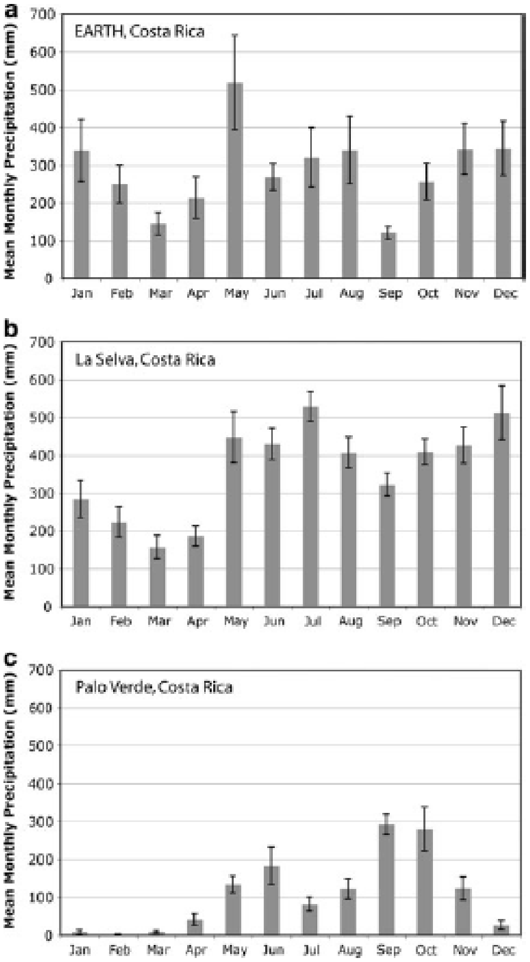

Fig. 8 Precipitation patterns (ave ± SE) at three methane emission study sites in Costa Rica: **a** EARTH University in humid tropics ($n = 8$ year; 1996–2005). **b** La Selva in rain forest in humid tropics ($n = 15$ year; 1992–2006), and **c** Palo Verde in seasonally wet tropics ($n = 10$ year; 1996–2006)

Precipitation is decidedly seasonal at the Palo Verde site in western Costa Rica with the total amount (1,307 ± 271 mm/year; Fig. 8c) about one-third of the precipitation of the humid sites.

Methane is being measured in each of the three wetlands using 12 non-steady-state gas chambers constructed of polyvinyl chloride (PVC) pipe and a fitted plastic cover in methods similar to those described in Altor and Mitsch (2006, 2008). Methane samples were collected over three periods (summer 2006, winter 2007, and spring 2007) in each of the three wetlands over soil (fixed chambers) and water (floating chambers). There were no significant differences in mean methane emissions within each wetland site for intermittently flooded and permanently flooded conditions (Fig. 9); however, the seasonally pulsed Palo Verde wetland had significantly ($\alpha = 0.05$) higher mean methane emissions than did the La Selva or EARTH wetlands in the humid tropics. In fact the average methane emission rate for the seasonally flooded Palo Verde wetlands of 1,080 mg-C m^{-2} day^{-1} is far in excess of the range of 30–440 mg-C m^{-2} day^{-1} reported by Mitsch and Wu (1995) and Whalen (2005) for tropical wetlands. The methane emissions from the humid tropics wetlands in our study are 120 and 278 mg-C m^{-2} day^{-1} for EARTH and La Selva wetlands, respectively, (Fig. 9), within this previously published range for tropical wetlands.

The seasonally flooded Palo Verde wetland experiences a slight lag between peak wetland water depths and precipitation. Wetland water depths were low in the summer 2006 (1.0 ± 0.4 and 17 ± 3 cm) and highest in the winter 2007 (25 ± 1 and 56 ± 2 cm) for intermittently and permanently flooded areas, respectively). During spring 2007 as is typical, the wetland was completely dry (Fig. 10a). Methane emissions from Palo Verde are not significantly different in seasons with the exception of the intermittently flooded site during winter 2007 wet season and the permanently flooded site during the summer 2006 moist season (Fig. 10b). Methane emissions are highest during times when the water depth is between 15 and 30 cm. When water depths are shallower, methane oxidation may be occurring in the soils that can become aerated at the surface. When water depth is above this range, methane oxidation may be occurring in the water column. Jauhiainen et al. (2005) saw a similar pattern of decreasing methane emissions with water depth from an ombrotrophic tropical peatland in Indonesia. In that study they determined that the overall methane emission rate was less than 3.7 mg-C m^{-2} day^{-1}, a flux two orders of magnitude lower than the rates measured in our mineral-rich wetlands in Costa Rica. It is also possible that methane emissions are lower during deepwater periods because losses by ebullition occur frequently then and are notoriously difficult to measure by the chamber studies as we used here (Walter et al. 2006).

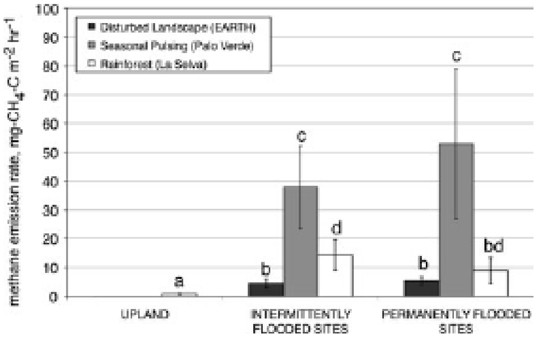

Fig. 9 Methane emissions from three sets of measurements, summer 2006 to spring 2007, in uplands, intermittently flooded wetlands and permanently flooded wetlands at 3 study sites in Costa Rica

The upland areas adjacent to the wetlands produced no methane emissions except for the uplands at

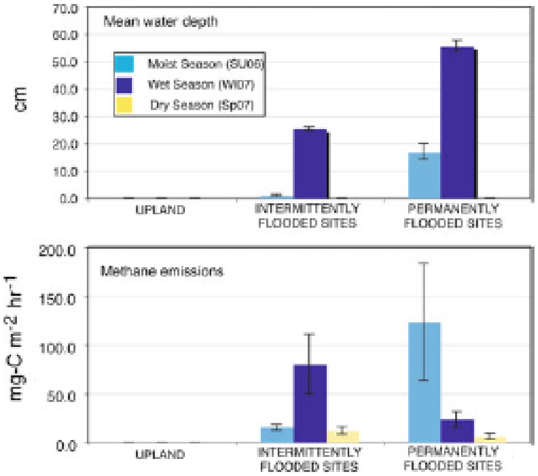

Fig. 10 Seasonal patterns at Palo Verde wetland, Costa Rica, for summer 2006 through spring 2007: **a** mean water depth during measurements, and **b** methane emissions. Measurements are for uplands, intermittently flooded wetlands, and permanently flooded wetlands

La Selva tropical rain forest site. The mean upland methane rate there was 19 mg-C m^{-2} day^{-1} (Fig. 9). This small methane emission is most likely due to the moist rain forest landscape with its constantly wet soils where methane emissions have been found to be significant (Keppler et al. 2006).

Our preliminary results suggest that wetlands with pulsing hydrology typical of the monsoonal wet-dry cycles may have higher methane emissions than those wetlands that are continuously wet. If tropical wetlands were to transition from permanently flooded conditions and 3,000 mm/year of precipitation to seasonal flooding with 1,500 mm/year of precipitation, as could occur if the ITCZ were to shift its seasonal patterns, much higher methane emissions might result.

Fire

Fire significantly affects subtropical and seasonally flooded tropical wetlands such as the Florida Everglades and the Okefenokee Swamp in southeastern USA (see Forward), and the Okavango Delta in northern Botswana during their dry season. These fires represent a major reintroduction of carbon stored in the wetland plants and soils back into the atmosphere. If fire frequency changes in these seasonally flooded wetlands, the release of stored carbon could be much more significant than any slower releases caused by minor changes in water level.

In the Okavango Delta, floodplain fires, which occur just before floodplain flooding, are more frequent and more important ecologically than are upland fires (Heinl et al. 2007; Fig. 11). At the Okavango Delta, an average of 15% of the floodplain burns each year (Heinl et al. 2006), representing a 6.6 year return interval. No increase in fire was reported over the period 1989–2003 (Heinl et al. 2007) nor is there any evidence that fires are more frequent in this seasonally flooded wetland because of climate change. Any significant shift in the flooding pulse would change the potential for fire frequency changes and dramatic changes in the ecosystem. In Heinl et al.'s (2006, 2007) 15 year study, 60% of the floodplains burned from two up to ten times.

Most fires in the Okavango take place in the two dry periods that fall between the rain pulse of summer that start in September and the seasonal flooding pulse that often reaches the delta as late as May (winter). During these two dry periods thunderstorms are uncommon and most fires are man-made (Cassidy 2003, Heinl 2005). There are several reasons for these man-made fires including: to improve the quality of grazing for wildlife and facilitate their viewing by tourists; to improve hunting; to improve access for fishing; to improve in the quality of thatching grass, reeds and papyrus that all are commonly utilized by villagers; and to construct fire breaks.

Fig. 11 Fire has a significant role in carbon cycling and vegetation dynamics on the floodplains of the Okavango Delta (photo January 18, 2007 by WJ Mitsch)

On the seasonally flooded floodplains there is a positive correlation between mean frequency of flooding and the frequency of fires up to a level of seven flooding years and three fires (Ramberg et al. 2009) after which the fire frequency drops. These trends are readily explained by the increase of macrophyte primary production in the floodplains caused by higher flooding frequency and the resulting higher fuel load as a determinant for fire frequency (Heinl et al. 2006); fire is less likely where flood frequency is greater than 7 years in fifteen because the increased wetness reduces the possibility of burning.

In the Okavango Delta area there are no long lasting differences in plant biodiversity between areas that have been burnt compared to those with a long period without fires (Heinl 2005) but records of burning only go back 15 years. Fires in Africa and many other tropical parts of the world have been prevalent for several 100,000 years and the biota that now exists in areas with high fire frequencies is adapted to this. Fires will however start new plant successions beginning with annual and pioneer species that after a few years are replaced by short lived perennials and after about 10 years woody plants are taking over. The highest species diversity on a larger scale is often found where there are a number of fire patches of different age.

Conclusions: tropical wetlands and climate change

Climate change could affect tropical wetlands in four distinct ways: changes of hydrologic pulses from upstream; changes in local precipitation patterns; changes in temperature/humidity and subsequent evapotranspiration patterns; and sea level and coastal storm influences for coastal wetlands. Changes in tropical wetlands will be most dramatically seen in wetlands that depend on the migration of the ITCZ such as the Okavango Delta and less in wetlands that are found in the continuously wet humid tropics. A critical question is whether tropical, hydrologically stable wetlands will expand if the ITCZ were to shift or (and perhaps more likely) climate change would convert tropical humid wetlands into seasonally flooded types with distinct dry–wet periods. Patterns of methane generation from tropical wetlands could be initially higher if hydroperiods change from continually flooded to pulsing. Carbon oxidation by peat exposure and fire in tropical wetlands will clearly increase with decreased precipitation or flooding, partially because of large storage of fuel in the peat. Humid tropical wetlands provide a significant yet often overlooked sink for carbon, due to both the high productivity but also the wet environment that protects peat from oxidation. Questions that we pose that still need to be answered include:

- If climate change affects the dynamics of the inter-tropical convergence zone (ITCZ), will hydrology and biochemistry of tropical wetlands be affected and to what extent?
- What are the planetary roles of tropical wetlands in global carbon cycling, particularly in carbon sequestration and methane emissions?
- If hydrologic conditions in the tropics shift, what are the global implications of less (or more) methane emissions, fires and other carbon oxidations or reductions in tropical wetlands?

Any changes in the ITCZ could have dramatic effects on the carbon dynamics and productivity of tropical wetlands. Wetlands found in monsoonal climates seasonally affected by the ITCZ may emit more methane than do permanently wet humid tropical wetlands; fires and subsequent release of CO_2 are more frequent there as well.

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