



## LJMU Research Online

**Sjögersten, S, Black, CR, Evers, SL, Hoyos-Santillan, J, Wright, EL and Turner, BL**

**Tropical wetlands: A missing link in the global carbon cycle?**

<http://researchonline.ljmu.ac.uk/id/eprint/4224/>

### Article

**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Sjögersten, S, Black, CR, Evers, SL, Hoyos-Santillan, J, Wright, EL and Turner, BL (2014) Tropical wetlands: A missing link in the global carbon cycle? GLOBAL BIOGEOCHEMICAL CYCLES, 28 (12). pp. 1371-1386. ISSN 0886-6236**

LJMU has developed **LJMU Research Online** for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact [researchonline@ljmu.ac.uk](mailto:researchonline@ljmu.ac.uk)

<http://researchonline.ljmu.ac.uk/>

## RESEARCH ARTICLE

10.1002/2014GB004844

## Key Points:

- Released from tropical wetlands are 90 Tg CH<sub>4</sub> year<sup>-1</sup> and 3860 Tg CO<sub>2</sub> year<sup>-1</sup>
- CH<sub>4</sub> emissions were greatest from mineral soils
- NEP appears greater in peat-forming wetlands than on mineral soil

## Correspondence to:

S. Sjögersten,  
Sofie.Sjogersten@nottingham.ac.uk

## Citation:

Sjögersten, S., C. R. Black, S. Evers, J. Hoyos-Santillan, E. L. Wright, and B. L. Turner (2014), Tropical wetlands: A missing link in the global carbon cycle?, *Global Biogeochem. Cycles*, 28, 1371–1386, doi:10.1002/2014GB004844.

Received 5 MAR 2014

Accepted 4 OCT 2014

Accepted article online 8 OCT 2014

Published online 4 DEC 2014

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

## Tropical wetlands: A missing link in the global carbon cycle?

Sofie Sjögersten<sup>1</sup>, Colin R. Black<sup>1</sup>, Stephanie Evers<sup>2</sup>, Jorge Hoyos-Santillan<sup>1</sup>, Emma L. Wright<sup>1</sup>, and Benjamin L. Turner<sup>3</sup>

<sup>1</sup>School of Biosciences, University of Nottingham, Nottingham, UK, <sup>2</sup>School of Biosciences, University of Nottingham, Kuala Lumpur, Malaysia, <sup>3</sup>Smithsonian Tropical Research Institute, Panama City, Panama

**Abstract** Tropical wetlands are not included in Earth system models, despite being an important source of methane (CH<sub>4</sub>) and contributing a large fraction of carbon dioxide (CO<sub>2</sub>) emissions from land use, land use change, and forestry in the tropics. This review identifies a remarkable lack of data on the carbon balance and gas fluxes from undisturbed tropical wetlands, which limits the ability of global change models to make accurate predictions about future climate. We show that the available data on in situ carbon gas fluxes in undisturbed forested tropical wetlands indicate marked spatial and temporal variability in CO<sub>2</sub> and CH<sub>4</sub> emissions, with exceptionally large fluxes in Southeast Asia and the Neotropics. By upscaling short-term measurements, we calculate that approximately 90 ± 77 Tg CH<sub>4</sub> year<sup>-1</sup> and 4540 ± 1480 Tg CO<sub>2</sub> year<sup>-1</sup> are released from tropical wetlands globally. CH<sub>4</sub> fluxes are greater from mineral than organic soils, whereas CO<sub>2</sub> fluxes do not differ between soil types. The high CO<sub>2</sub> and CH<sub>4</sub> emissions are mirrored by high rates of net primary productivity and litter decay. Net ecosystem productivity was estimated to be greater in peat-forming wetlands than on mineral soils, but the available data are insufficient to construct reliable carbon balances or estimate gas fluxes at regional scales. We conclude that there is an urgent need for systematic data on carbon dynamics in tropical wetlands to provide a robust understanding of how they differ from well-studied northern wetlands and allow incorporation of tropical wetlands into global climate change models.

### 1. Introduction

Tropical wetlands play an important role in the global carbon (C) cycle [Page *et al.*, 2011]. Currently, they are under considerable pressure from agriculture [Houghton, 2012] resulting in substantially increased carbon dioxide (CO<sub>2</sub>) emissions from these ecosystems. For example, 1–3% of annual fossil fuel emissions or 355–855 Mt C year<sup>-1</sup> in Indonesia alone [Hooijer *et al.*, 2010] are estimated to originate from tropical peatlands. Undisturbed tropical wetlands emit between 85 and 184 Tg of methane (CH<sub>4</sub>) each year, accounting for two thirds of global emissions from wetlands [e.g., Richey *et al.*, 2002; Jauhainen *et al.*, 2005; Hooijer *et al.*, 2006; Nahlik and Mitsch, 2011; Melton *et al.*, 2013].

The dominant wetland ecosystems in the tropics are forested peatlands, swamps, and floodplains (Table 1) [Aselmann and Crutzen, 1989]. Of these, only peatlands accumulate substantial C deposits (between 0.5 and 11 m deep) [Phillips *et al.*, 1997; Page *et al.*, 1999; Shimada *et al.*, 2001; Hope *et al.*, 2005; Page *et al.*, 2011; Lähteenoja *et al.*, 2012]. However, controls on the formation of deep peats in the tropics are not well understood. As expected from their capacity for C accumulation, tropical peatlands comprise a significant proportion of terrestrial C: an estimated 89 Gt C or 19% of the C stored in peatlands worldwide [Page *et al.*, 2011]. Accumulation of C in tropical peatlands is under threat from land use and climate change, which can transform tropical wetlands into C sources [Furukawa *et al.*, 2005; Laiho, 2006; Meehl *et al.*, 2007; Hooijer *et al.*, 2010].

There are considerable uncertainties regarding the spatial extent of tropical wetlands (Figure 1). Observational data suggest that tropical wetland areas range between 2.8 and 6.0 × 10<sup>6</sup> km<sup>2</sup>, while models predict a much larger range (1.3–38.8 × 10<sup>6</sup> km<sup>2</sup>) [Melton *et al.*, 2013]. Uncertainties regarding the relative distribution of tropical wetland types are even larger; areal estimates of different wetland types are presented in Table 1 [Aselmann and Crutzen, 1989; Page *et al.*, 2011]. Given the contrasting environmental conditions associated with these different wetland types (e.g., peat accumulation and nutrient-poor conditions in peatlands and seasonal variation in the degree of inundation in floodplain systems), tropical wetlands are not only expected to differ in C accumulation as peat but also their release of CO<sub>2</sub> and CH<sub>4</sub>.

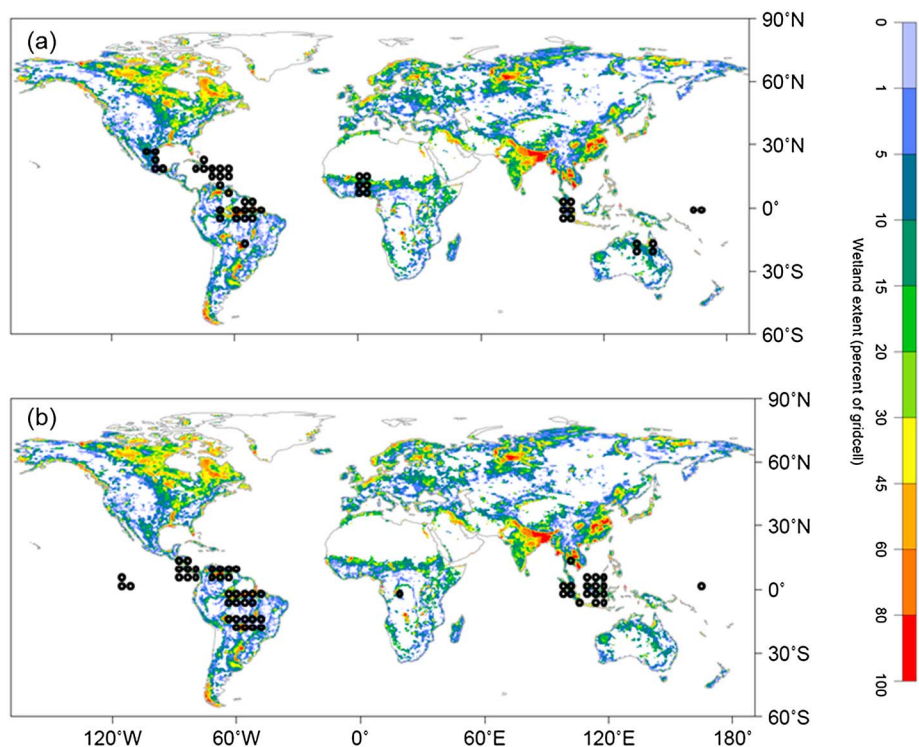
**Table 1.** Description of Wetland Types<sup>a</sup>

Wetland Type	Description	Area (km <sup>2</sup> )
Swamps	Forested freshwater wetlands on waterlogged or inundated soils where little or no peat accumulation takes place. For this review we have limited data to forested system.	230,000
Peatlands	Peat producing wetlands in moist climates where organic materials have accumulated over long periods.	441,000
Floodplains	Periodically follower areas along rivers or lakes showing considerable variation in vegetation cover. In the Amazon flood plain two separate systems are defined <i>Varzea forests</i> which are fed by muddy rivers and <i>Igapo forests</i> located in blackwater and clearwater tributaries	715,000

<sup>a</sup>For this review we have limited data to forested systems.

The rate of increase in CH<sub>4</sub> concentration in the atmosphere has varied during the past three decades reassuming its increase after 2006 to ca. 6 Tg CH<sub>4</sub> y<sup>-1</sup> [Kirschke et al., 2013]; with tropical wetlands playing a major role in the renewed increase of atmospheric CH<sub>4</sub> [IPCC, 2013]. The magnitude of this increase has been observed to differ depending on whether the estimate is based on a top-down (atmospheric inversion models) or a bottom-up (process-based models; adding up independently estimated flux components) analytical approach. Higher estimates have been reported using the bottom-up approach, where the estimates of fluxes from natural wetlands carry an uncertainty of at least 50% [Kirschke et al., 2013]. The uncertainty in the bottom-up approach of the CH<sub>4</sub> emissions from wetlands is mainly due to the lack of a reliable estimate of the global extent of wetlands [Melton et al., 2013] and to the scarcity of wetland CH<sub>4</sub> flux measurements [Riley et al., 2011].

Our rudimentary understanding of CH<sub>4</sub> emissions in the tropics is underlined by the discrepancy between emissions of CH<sub>4</sub> from the surface of wetlands and the high concentrations of this gas in the tropical



**Figure 1.** The wetland map is based on remotely sensed inundation data and GIEMS refers to the Global Inundation Extent from Multi-Satellites; the GIEMS inundation data set is plotted as the mean annual maximum value across between 1993 and 2004 [Melton et al., 2013]. (a) The spatial distribution of NPP data sets (data in Table 2) and (b) greenhouse gas flux data sets (data in Table 4).

atmosphere [Melack *et al.*, 2004; Miller *et al.*, 2007; Bergamaschi *et al.*, 2009; Bloom *et al.*, 2010]; with CH<sub>4</sub> emissions from top-down and bottom-up approaches differing the most in tropical South America [Kirschke *et al.*, 2013]. Addressing this knowledge gap is of particular importance as models predict a global increase in CH<sub>4</sub> emissions of 77%, due largely to increased emissions from existing tropical wetlands in response to increasing temperatures [Shindell *et al.*, 2004]. The model used by Shindell *et al.* [2004] calculates CH<sub>4</sub> emissions based on relationships between temperature, water table depth, and net primary productivity (NPP). Some progress has been made in testing these relationships [Walter and Heimann, 2000], but data are limited, particularly regarding NPP and temperature responses; such issues must be considered in greater detail [Farmer *et al.*, 2012].

Several existing wetland modeling tools may be suitable for application to tropical peatlands and some might be useful in Earth system models [Farmer *et al.*, 2012]. However, the inclusion of tropical wetlands in such models is hampered by a lack of suitable data to validate them. Current models of global CH<sub>4</sub> emissions [Bridgham *et al.*, 2013; Melton *et al.*, 2013] use estimates of tropical CH<sub>4</sub> fluxes from a small number of review papers [e.g., Matthews and Fung, 1987; Aselmann and Crutzen, 1989; Bartlett and Harriss, 1993] that estimated CH<sub>4</sub> emissions from a limited number of measurements. It is therefore not surprising that outputs from wetland models that estimate current CH<sub>4</sub> emissions from tropical areas vary widely, with values between  $85 \pm 7$  and  $184 \pm 11$  Tg CH<sub>4</sub> year<sup>-1</sup> [Melton *et al.*, 2013]. Without appropriate data on C dynamics from undisturbed tropical wetlands, it will be difficult to predict how degradation of these systems will impact on global climate. Key input data needed to model C dynamics in tropical wetlands are aboveground and belowground net primary productivity (NPP), litter input and decay, and information on soil properties, including nutrient status, and hydrology [Farmer *et al.*, 2012]. Good quality CO<sub>2</sub> and CH<sub>4</sub> flux data, i.e., data accounting for temporal and spatial variability in fluxes are also needed to evaluate model predictions and close the gap between top down and bottom up modeling approaches [Farmer *et al.*, 2012].

Compared to the more intensively studied boreal and temperate peatlands, tropical peatlands are poorly understood with respect to the controls on decomposition and C storage; the C sink strength of tropical peatlands therefore remains poorly quantified [Dommain *et al.*, 2011]. However, tropical wetlands have common characteristics, such as high mean annual temperature with little seasonal variation, high rainfall, generally high hydraulic conductivity at the surface in the case of peatlands, and the presence of overstorey rainforest providing the main input of organic matter [Page *et al.*, 1999; Sjögersten *et al.*, 2010; Lähteenoja and Page, 2011; Wright *et al.*, 2011]. Carbon accumulation in ecosystems is determined by the balance between inputs and output. In high-latitude wetlands, the main control of C accumulation is slow decomposition of recalcitrant litter inputs, often *Sphagnum* spp., in cold wet soils [Clymo, 1984], whereas the situation in the tropics is less well understood. In contrast to cold regions, temperature is unlikely to be a major factor in limiting decomposition. The recalcitrance of litter inputs is less constrained as they are produced from different plant tissue types and plant species. Chimner and Ewel [2005] suggested that relatively slow root decomposition may be instrumental in the formation of tropical peat, implying that root production rate is important in determining C balance. However, the relationship between NPP and long-term C storage within tropical wetlands has not been explored.

We calculated current C balances for a wide range of tropical wetlands by compiling data for long-term net C accumulation rates and CO<sub>2</sub> and CH<sub>4</sub> emissions from flooded tropical wetlands/peatlands. It was anticipated that C accumulation rates would be greater in tropical than in temperate and boreal peatlands, but that CO<sub>2</sub> and CH<sub>4</sub> emissions would be high due to the substantial inputs of fresh litter and stable high temperatures. The hypothesis that C accumulation in tropical peatlands is driven by slow decomposition rather than high NPP was tested by comparing decomposition rates and NPP with tropical wetlands that do not accumulate peat.

## 2. Methods

### 2.1. Data Collation

The Web of Knowledge and Google Scholar were used to collate information on CO<sub>2</sub> and CH<sub>4</sub> fluxes, peat depth, NPP, and C accumulation from the relevant published literature using the following search terms:

Tropical, Amazon, Pantanal, Africa, Southeast Asia, peatlands, wetlands, methane, peat, carbon dioxide, biomass, litter, NPP, and root. Based on the references obtained, all relevant original research pertaining to forested tropical wetland areas was used to identify additional references. We consider only freshwater wetlands.

To assess litter decomposition rates, a data set of decay constants ( $k$ ) was compiled for different litter types from in situ decomposition in tropical and subtropical wetlands, with high  $k$  values corresponding to more rapid decay. Half times (half time =  $\ln(2)/k$ ) were calculated for different tissue types.

## 2.2. Data Processing and Analysis

We used two approaches to estimate NPP, (i) by summing C inputs and (ii) by using a conversion between litter production and total NPP. To construct a C balance for wetlands on organic and mineral soil, using the first approach, plant production was estimated by summing leaf litterfall, reproductive litterfall (flowers, fruit, and seed), branch litterfall, other litter (e.g., chaff), wood increment, and fine root production. No data were found for coarse woody debris or coarse root production. Published data for litter production were generally presented as mass of material, for conversion to C inputs a 50% C content was assumed [Wright *et al.*, 2013]. We assumed that data for some of the litter pools needed for estimating NPP this way would be limited. Therefore, we used our second approach for estimating NPP. This was based on a linear relationship between  $NPP_{total}$  and  $NPP_{canopy}$  reported for lowland rainforest [Malhi *et al.*, 2011], and we chose this approach since data availability for canopy litter production in tropical wetlands was the most regularly measured component of the C inputs. The relationship was used to estimate NPP based on the assumption that  $NPP_{total} = 2.27(NPP_{canopy})$ .  $NPP_{canopy}$  was calculated as leaf litter + reproductive litterfall + branch litterfall + other litter again assuming a C content of 50% to convert litterfall to C inputs. Net ecosystem production (NEP) was calculated by subtracting total C losses (in the form of average gaseous losses as  $CO_2$  and  $CH_4$  and aquatic losses as dissolved organic carbon (DOC) across all sites from which data were available) from the substrate from  $NPP_{total}$ .

Calculations of NEP were separated between the organic and mineral soil components, and estimates of heterotrophic respiration were based on upscaling of short-term in situ ground surface flux measurements to the annual scale to enable comparison with litter inputs. The measurements of surface  $CO_2$  flux combine both autotrophic and heterotrophic respiration; as measurements were largely collected during the daytime period, this may have introduced bias within the data. Furthermore, collection of flux data during different seasons may also have influenced the balance between C inputs and output (inputs were based on litterfall data normally collected over an annual cycle). Potential data limitations are highlighted in the discussion.

Tests for significant differences in  $CO_2$  and  $CH_4$  fluxes and  $NPP_{total}$  between tropical wetland types (e.g., peat forming versus wetlands on mineral soil) and geographical regions were conducted using an unbalanced analysis of variance (ANOVA).  $CO_2$  and  $CH_4$  flux data were square root and log transformed, respectively, to meet the normality assumption of ANOVA. All statistical analysis was carried out using GENSTAT version 15. To assess the impacts of data gaps in the C balance, we carried out a sensitivity analysis calculating potential errors associated with particular data gaps relative to the total C inputs using existing studies from either tropical wetlands or tropical lowland rainforest system.

## 3. Carbon Accumulation

Carbon accumulates in both mineral and peat-forming tropical wetlands and a wide range of peat accumulation rates have been reported for tropical peatlands; for example, Chimner and Ewel [2005] estimated accumulation on the island of Kosrae in Micronesia to be  $300 \text{ g C m}^{-2} \text{ yr}^{-1}$ , at the higher end of the range reported for the tropics. In Kalimantan, mean accumulation rates were estimated to be  $31\text{--}77 \text{ g C m}^{-2} \text{ yr}^{-1}$  [Dommain *et al.*, 2011] and  $94 \text{ g C m}^{-2} \text{ yr}^{-1}$  [Moore *et al.*, 2013], while comparable values of  $39\text{--}85 \text{ g C m}^{-2} \text{ yr}^{-1}$  have been reported for Peruvian Amazon peatlands [Lähteenoja *et al.*, 2009] and  $43\text{--}55 \text{ g C m}^{-2} \text{ yr}^{-1}$  in Panamanian peatlands (J. Hoyos, unpublished data, 2014). Furthermore, peat accumulation rates appear to be greater in coastal lowland peatlands than in inland peatlands [Dommain *et al.*, 2011]. Hirano *et al.* [2009] reported that net ecosystem C production (NEP) in a drained peatland forest in Kalimantan ranged from  $296$  to  $594 \text{ g C m}^{-2} \text{ yr}^{-1}$ , at the upper end of range of long-term C accumulation rates.

Carbon accumulation is also substantial in depositional sedimentary flood plain systems. *Moreira-Turcq et al.* [2004] suggested a rate of  $100 \text{ g C m}^{-2} \text{ yr}^{-1}$  for the varzea of the Amazon, while *Devol et al.* [1984] suggested a rate of  $44 \text{ g C m}^{-2} \text{ yr}^{-1}$  based on depositional systems connected to the Amazon for only 6 months of the year. In Lake Rawa Danau, West Java, Indonesia, sedimentary deposition of organic C was lower at  $11.75 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Flux data are lacking for C inputs into the Bengal delta plain, even though this region may represent an important store given the high outflow of sediments with C contents ranging between 0.05 and 1.4% [*Datta et al.*, 1999].

Carbon accumulation rates in boreal and temperate peatlands are generally lower than in the tropics, although substantial variation occurs depending on peatland type, with values as high as  $132\text{--}198 \text{ g C m}^{-2} \text{ yr}^{-1}$  being recorded for bogs in the USA [*Craft et al.*, 2008]. However, lower peat accretion rates are also common; for example, rates close to  $21 \text{ g C m}^{-2} \text{ yr}^{-1}$  were reported in Scotland [*Anderson*, 2002] and Canada [*Roulet et al.*, 2007]. Accumulation rates in boreal peatlands are generally lower than in temperate and tropical peatlands. For example, accumulation rates in boreal peatlands in Canada range between  $6$  and  $22 \text{ g C m}^{-2} \text{ yr}^{-1}$  [*Robinson and Moore*, 1999; *Turunen and Turunen*, 2003; *Sannel and Kuhry*, 2009], while accumulation rates in Finland were between  $15$  and  $35 \text{ g C m}^{-2} \text{ yr}^{-1}$  [*Turunen et al.*, 2002; *Ukonmaanaho et al.*, 2006]. In summary, C accumulation rates are, with a few exceptions, greatest in the tropics and decrease with latitude.

The high long-term C accumulation in tropical peatlands may be driven by their high mean NPP, with aboveground biomass production of  $1000\text{--}1300 \text{ g C m}^{-2} \text{ yr}^{-1}$  [*Nebel et al.*, 2001] and NPP of  $1100 \text{ g C m}^{-2} \text{ yr}^{-1}$  [*Chimner and Ewel*, 2005]. Our calculations of  $\text{NPP}_{\text{total}}$  (Table 2) and existing data from *Nebel et al.* [2001] and *Chimner and Ewel* [2005] suggest that C inputs from NPP are generally high in tropical wetlands, although there is considerable variability among wetland types. Maximum values for NPP based on litterfall data were  $1929 \text{ g C m}^{-2} \text{ yr}^{-1}$  in a forested wetland in Puerto Rico [*Frangi and Lugo*, 1985], while the lowest recorded value was  $430 \text{ g C m}^{-2} \text{ yr}^{-1}$  in a floodplain forest in Australia [*Payntner*, 2005].  $\text{NPP}_{\text{total}}$  was significantly greater in tropical wetlands on organic soils (mean  $\pm$  SE:  $1206 \pm 93 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) than on mineral soils (mean  $\pm$  SE:  $880 \pm 77 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) ( $F_{1,49} = 7.15$ ;  $P = 0.01$ ; Table 2). These high rates of productivity generally yield large C stocks, but pool sizes are poorly quantified (Table 3).

A further important aspect of C inputs to tropical wetlands is a more rapid root turnover rate ( $70\% \text{ yr}^{-1}$ ) than in equivalent temperate and boreal systems ( $55$  and  $45\% \text{ yr}^{-1}$ , respectively) [*Gill and Jackson*, 2000; *Chimner and Ewel*, 2005]. This observation suggests that C inputs from root turnover might contribute significantly to the high C accumulation rates in tropical wetlands, but data for root production are scarce (Table 3).

#### 4. Carbon Dioxide and Methane Fluxes From Tropical Swamps

Depending on prevailing environmental conditions, primarily the oxygen content and redox potential of the peat, microbial degradation of organic material in wetlands can induce the release of predominantly  $\text{CO}_2$  or simultaneous release of both  $\text{CO}_2$  and  $\text{CH}_4$ . Measurements of daily, monthly, and seasonal variation in gas fluxes show that specific wetlands can switch between production of mainly  $\text{CO}_2$  and a greater contribution of  $\text{CH}_4$  [*Hadi et al.*, 2005; *Jauhiainen et al.*, 2005; *Melling et al.*, 2005a, 2005b; *Wright et al.*, 2013]. Only a few studies have addressed temporal variability in gas fluxes in tropical peatlands, although strong seasonal variation in  $\text{CH}_4$  fluxes has been reported in floodplain wetlands in the Amazon [e.g., *Devol et al.*, 1988; *Bartlett et al.*, 1990]. Gas fluxes can also vary strongly among vegetation types, which in turn are linked to nutrient status [*Wright et al.*, 2013]. Given the diversity of forest types present on tropical wetland soils, this provides a substantial degree of variability. Information on fluxes is almost entirely lacking for many geographical regions; for example, we identified only two papers on  $\text{CO}_2$  emissions and one on  $\text{CH}_4$  emissions from African wetlands. No data were found for gas fluxes from peatlands in the Amazon basin despite their vast spatial extent ( $150,000 \text{ km}^2$ ) [*Lähteenoja et al.*, 2009], although detailed data exist from the floodplains in the region [*Bartlett et al.*, 1988, 1990; *Crill et al.*, 1988; *Devol et al.*, 1988, 1990].

##### 4.1. Carbon Dioxide

Fluxes of  $\text{CO}_2$  from forested tropical wetlands vary greatly, with reported values ranging between  $30$  and  $4055 \text{ mg m}^{-2} \text{ h}^{-1}$  (Table 4). The lowest values were reported for a palm swamp in Venezuela [*Bracho and San José*, 1990], while values were greatest for a forested peatland in Kalimantan, Indonesia [*Melling et al.*, 2005a]. The majority of available data on  $\text{CO}_2$  fluxes from forested tropical wetlands are from Southeast Asian

**Table 2.** Net Primary Productivity Based on Litterfall Data in a Range of Forested Tropical Wetlands

Region, Country	Forest Type, Site Name	Soil Type	NPP <sub>total</sub> <sup>a</sup> (g C m <sup>-2</sup> yr <sup>-1</sup> )	Reference
Puerto Rico	<i>Pterocarpus officinalis</i> forest	Organic	1277	Easse and Aide [1999]
Luquillo, Puerto Rico	Flood plain palm forest	Organic	616	Frangi and Lugo [1998] <sup>b</sup>
Puerto Rico	<i>Prestoea montana</i> forest	Organic	1929	Frangi and Lugo [1985]
Veracruz, Mexico	Forested wetlands, Apompal	Organic	1056	Mata et al. [2012]
Veracruz, Mexico	Forested wetlands, Mancha	Organic	1101	Mata et al. [2012]
Veracruz, Mexico	Forested wetlands, Chica	Organic	1691	Mata et al. [2012]
Veracruz, Mexico	Forested wetlands, Cienaga	Mineral	1566	Mata et al. [2012]
Veracruz, Mexico	Forested wetlands, Salado	Organic	1419	Mata et al. [2012]
Puerto Rico	<i>Pterocarpus officinalis</i> forest, Mayaguez	Organic	1600	Alvarez-Lopez [1990]
Puerto Rico	<i>Pterocarpus officinalis</i> forest, Patillas	Organic	1351	Alvarez-Lopez [1990]
Puerto Rico	<i>Pterocarpus officinalis</i> forest, Dorado	Mineral	987	Alvarez-Lopez [1990]
Guadeloupe	<i>Pterocarpus officinalis</i> swamp forest	Organic	1476	Miegot and Imbert [2012]
Guadeloupe	<i>Pterocarpus officinalis</i> swamp forest	Organic	1606	Miegot and Imbert [2012]
Guadeloupe	<i>Pterocarpus officinalis</i> swamp forest	Organic	1189	Miegot and Imbert [2012]
Panama	Riverine forest	Mineral	1318	Golley et al. [1975]
Peru	Flood plain forest, high restinga	Mineral	796	Nebel et al. [2001]
Peru	Flood plain forest, low restinga	Mineral	810	Nebel et al. [2001]
Peru	Flood plain forest, <i>Tahuampa</i>	Mineral	787	Nebel et al. [2001]
Orinoco Llanos, Venezuela	Palm swamp forest, flood-prone	Organic	560	San-José et al. [2010]
Orinoco Llanos, Venezuela	Palm swamp forest, flood plain	Organic	2438	San-José et al. [2010]
Brazil	Swamp forest	Mineral	647	Terror et al. [2011]
Pantanal, Brazil	Flooded forest	Mineral	1021	Haase [1999]
Manaus, Brazil	Swamp forest, Igapo	Organic	772	Adis et al. [1979]
Manaus, Brazil	Flood plain forest	Mineral	726	Franken et al. [1979]
Manaus, Brazil	Swamp forest	Organic	760	Franken et al. [1979]
Para, Brazil	Swamp forest	Organic	976	Klinge [1978]
Para, Brazil	Flood plain forest	Mineral	193	Klinge [1978]
Para, Brazil	Swamp forest	Organic	874	Silva and Lobo [1982]
Para, Brazil	Flood plain forest	Mineral	976	Silva and Lobo [1982]
Para, Brazil	Flood plain forest	Mineral	1566	Cattanio et al. [2004]
Amazonia	Floodplain forest, varzea, 40 year old	Mineral	1190	Naiman [2005]
Amazonia	Floodplain forest, varzea, 80 year old	Mineral	1680	Naiman [2005]
Australia	Flood plain forest <i>Mimosa pigra</i>	Mineral	430	Payntner [2005]
Australia	Flood plain forest, <i>Melaleuca</i> spp.—Mangrove, northeastern Queensland	Mineral	470	Duke [1982]
Australia	<i>Melaleuca</i> spp. forest, Magela flood plain	Mineral	350	Finlayson et al. [1993]
Australia	<i>Melaleuca</i> spp forest, Magela flood plain	Mineral	750	Finlayson [1988]
Ivory coast	Water logged forest, VG	Mineral	919	Devineau [1976]
Ivory coast	Riverine forest, TR6	Mineral	783	Devineau [1976]
Ivory coast	Riverine forest, gallery, MS	Mineral	965	Devineau [1976]
Ivory coast	Riverine forest, gallery, TR4	Mineral	704	Devineau [1976]
Ivory coast	Riverine forest, gallery, BD	Mineral	874	Devineau [1976]
Ivory coast	Riverine forest, gallery, TR2	Mineral	602	Devineau [1976]
Malaysia, Tasek Bera	Riverine forest, <i>Eugenia</i> swamp	Organic	1039	Furtado et al. [1980]
Sumatra, Indonesia	Peat swamp forest, PS3	Organic	1351	Brady [1997]
Sumatra, Indonesia	Peat swamp forest, SE6	Organic	829	Brady [1997]
Sumatra, Indonesia	Peat swamp forest, PI6	Organic	783	Brady [1997]
Sumatra, Indonesia	Peat swamp forest, PI9	Organic	624	Brady [1997]
Sumatra, Indonesia	Peat swamp forest, PI12	Organic	624	Brady [1997]
Yela, Micronesia	Peat swamp forest	Organic	1689	Chimner and Ewel [2005]
Yewak, Micronesia	Peat swamp forest	Organic	1716	Chimner and Ewel [2005]

<sup>a</sup>NPP<sub>total</sub> is based on conversion of NPP<sub>canopy</sub> using  $NPP_{total} = 2.27 * NPP_{canopy}$  [Malhi et al., 2011], where total NPP was not reported.

<sup>b</sup>Data from 1980.

peatlands, but these tend to be disturbed by human activity, making it difficult to assess regional variation in CO<sub>2</sub> losses from tropical peatlands. We found no significant differences in CO<sub>2</sub> efflux among geographical regions ( $P > 0.05$ ; Figure 2b), although data are absent or very limited for some regions, including both Africa and the Amazon basin, which limits the strength of any conclusions. CO<sub>2</sub> emission rates tended to be greater in tropical peatlands (Table 4) than in temperate and boreal systems [Silvola et al., 1996; Clair et al., 2002;

**Table 3.** Fluxes and Pools of C in Tropical Wetlands on Organic Peat Soil and Mineral Soils; Values are Mean (Standard Deviation; *n*), *n*/d Refers to No Data, References in Addition to Those in Table 1 as Listed Below<sup>a</sup>

	Organic		Mineral	
	Fluxes ( $\text{g C m}^{-2} \text{yr}^{-1}$ )			
Reproductive litter	71.7	(62.6; 17)	73.6	(44.8; 10)
Leaves	333.3	(95.7; 17)	281.2	(86.1; 17)
Fine woody litter	104.9	(51.2; 16)	90.5	(34.1; 9)
Coarse wood	155.0	(183.8; 2)	n/d	
Live wood increment	379.8	(71.7; 2)	547.9	(323.4; 6)
Other litter	28.6	(14.0; 12)	29.0	(2.0; 2)
Fine root production	112.1	(140.3; 7)	n/d	
CO <sub>2</sub> efflux	-875.1	(481.3; 17)	-901.4	(728.0; 18)
CH <sub>4</sub> efflux	-40.1	(66.1; 15)	-54.0	(52.1; 29)
DOC <sup>b</sup>	-75.5	(17; 2)	-120	(n/d; 1)
	Pools ( $\text{kg C m}^{-2}$ )			
Leaves	n/d		0.6	(n/d; 1)
Wood	12.4	(4.5; 3)	17.1	(8.2; 4)
Forest floor litter	1.2	(0.9; 8)	0.3	(0.1; 3)
Downed logs	0.8	(n/d; 2)	n/d	
Fine roots	1.9	(2.2; 13)	2.4	(1.7; 5)

<sup>a</sup>Negative values indicate C losses from the ecosystem.<sup>b</sup>From Richey *et al.* [2002], Moore *et al.* [2011], and Moore *et al.* [2013].

Bubier *et al.*, 2003; Crow and Wieder, 2005; Makiranta *et al.*, 2009], although fluxes within specific tropical regions were highly variable and affected by local conditions. Interestingly, the greater range of CO<sub>2</sub> emissions from flooded forested tropical peatlands [e.g., Hadi *et al.*, 2005; Melling *et al.*, 2005b] were within the same range (i.e., approximately 1000 mg CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>) as those found for tropical peatlands with substantially lowered water tables (up to 1 m below the peat surface) [Couwenberg *et al.*, 2010]. Upscaling the CO<sub>2</sub> fluxes to pantropical wetland areas suggests a release of approximately 4540 ± 1480 Tg CO<sub>2</sub> year<sup>-1</sup> (mean ± standard deviation (SD)). This calculation is based on the simplistic assumption that the CO<sub>2</sub> flux from mineral soil (Figure 2a) is related to the area covered by swamps and floodplains (Table 1), and the flux from organic soil (Figure 2a) was related to the area covered by peatlands. Substantial additional uncertainty around this mean will arise from current poor understanding of tropical wetland area [Melton *et al.*, 2013; Lähteenoja *et al.*, 2009]. Despite the general accumulation of organic matter in tropical peatlands, there was no significant difference in CO<sub>2</sub> fluxes between tropical wetlands on organic and mineral soils ( $P > 0.05$ ; Figure 1a). Furthermore, there was no systematic variation in CO<sub>2</sub> efflux among wetland types ( $P > 0.05$ ; Figure 2c).

#### 4.2. Methane

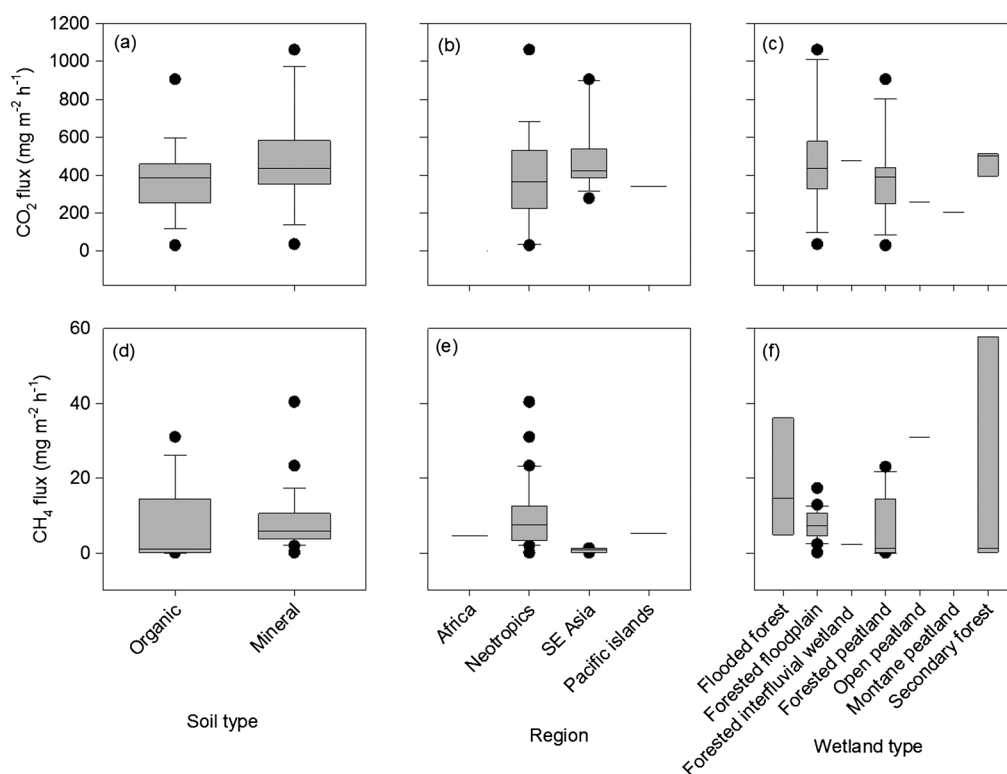
Estimated fluxes of CH<sub>4</sub> from peatlands are typically several orders of magnitude lower than those for CO<sub>2</sub> (Table 4). Indeed, CH<sub>4</sub> emissions are undetectable in some peatlands and uptake from the atmosphere might occur instead. Reported CH<sub>4</sub> fluxes vary among wetland types ( $F_{5,42} = 6.77$ ,  $P < 0.001$ ), ranging from -0.1 to 40 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup>; the highest values were recorded across a range of wetland systems (Figure 2f), including forested peatland and floodplain ecosystems [Keller, 1990; Devol *et al.*, 1998, 1990; Nahlik and Mitsch, 2011; Wright *et al.*, 2011]. CH<sub>4</sub> fluxes in Southeast Asian forested peatlands were typically lower (<2 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup>), while the highest, albeit variable, fluxes were reported for the Neotropics ( $F_{3,42} = 12.88$ ;  $P < 0.001$ ; Figure 2e). For example, fluxes from peatlands in Panama ranged between -5.35 and 143 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup> (Table 4 [Wright *et al.*, 2011]), highlighting the potential for very high CH<sub>4</sub> fluxes and marked temporal variability. The highest average CH<sub>4</sub> emissions were from wetlands on mineral soils ( $F_{1,42} = 6.97$ ,  $P < 0.05$ ), with mean fluxes of 8.22 and 6.10 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup> in mineral and organic soils, respectively (Figure 2d). The high emissions found in tropical wetlands have also been observed in subtropical wetland systems. A maximum emission of 19 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup> was found in a subtropical forested floodplain in Australia [Boon *et al.*, 1997], which is comparable to fluxes in swamp forests in the Everglades, USA, [Bartlett and Harriss, 1993] and 77 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup> from forested floodplains in South Africa [Otter and Scholes, 2000]. In contrast, maximum CH<sub>4</sub> fluxes from flooded temperate and boreal peatlands are lower, ranging between 10 and 14 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup>



**Table 4.** Carbon Dioxide (CO<sub>2</sub>) and Methane (CH<sub>4</sub>) Fluxes From Tropical Wetlands Showing the Mean Fluxes<sup>a</sup> and (Ranges) if Available

Location	Type	Soil Type	CO <sub>2</sub> Efflux(mg m <sup>-2</sup> h <sup>-1</sup> )	CH <sub>4</sub> Efflux(mg m <sup>-2</sup> h <sup>-1</sup> )	Reference
Kalimantan, Indonesia	Forested peatland	Organic	na	1.1 ± 0.61	<i>Inubushi et al.</i> [1998]
Kalimantan, Indonesia	Secondary forest	Organic	501 ± 180 (146–843)	0.18 ± 0.06 (0–1)	<i>Inubushi et al.</i> [2003]
Kalimantan, Indonesia	Forested peatland	Organic	317–950	na	<i>Hirano et al.</i> [2009]
Kalimantan, Indonesia	Secondary forest	Organic	513	0.19	<i>Hadi et al.</i> [2001]
Kalimantan, Indonesia	Secondary forest	Organic	395 (183–4055)	0.50 (0–3.33)	<i>Hadi et al.</i> [2005]
Kalimantan, Indonesia	Forested peatland	Organic	399 ± 36 (50–550)	0.16 ± 0.65 (–0.1–0.35)	<i>Jauhainen et al.</i> [2005]
Kalimantan, Indonesia	Forested peatland	Organic	563 (79–1580)	na	<i>Sundari et al.</i> (2012)
Sumatra, Indonesia	Forested peatland	Organic	380 ± 55	0.89 ± 0.48	<i>Furukawa et al.</i> [2005]
Sumatra, Indonesia	Forested peatland	Organic	278 ± 16	1.21 ± 1.36	<i>Furukawa et al.</i> [2005]
Sumatra, Indonesia	Forested peatland	Organic	376 ± 107	0.77 ± 0.27	<i>Furukawa et al.</i> [2005]
Malaysia	Forested peatland	Organic	905 (366–1953)	na	<i>Melling et al.</i> [2005a]
Malaysia	Forested peatland	Organic	na	0.0029 (–0.006–0.011)	<i>Melling et al.</i> [2005b]
Malaysia	Forested peatland	Organic	444		<i>Murayama and Bakar</i> [1996]
Thailand	Forest peatland	Organic	na	1.12 ± 2.7 (0.19–12.6)	<i>Ueda et al.</i> [2000]
Micronesia	Forested peatland	Organic	396 ± 36 (340–402)	na	<i>Chimner</i> [2004]
Mauim, Hawaii	Montane peatland	Organic	285 ± 75		<i>Chimner</i> [2004]
Bocas del Toro, Panama	Forested peatland	Organic	212 (11–1694)	23 (–5.35–143)	<i>Wright et al.</i> [2011]
Bocas del Toro, Panama	Forested peatland	Organic	238 (62–801)	17 (–3.53–98.3)	<i>Wright et al.</i> [2011]
Bocas del Toro, Panama	Open peatland	Organic	259 (7–950)	31 (–6.40–7.88)	<i>Wright et al.</i> [2011]
Colon, Panama	Forested peatland	Organic	na	14.4 (0–48)	<i>Keller</i> [1990]
Kalimantan, Indonesia	Forested peatland	Organic	na		<i>Pangala et al.</i> [2013]
Ka'au, Hawaii	Montane swamp	Organic	127 ± 47	na	<i>Chimner</i> [2004]
Orinoco Llanos, Venezuela	Palm swamp	Organic	30 (17–54)	na	<i>Bracho and San José</i> [1990]
Sumatra, Indonesia	Forested floodplain	Mineral	410 ± 35	na	<i>Ali et al.</i> [2006]
Sumatra, Indonesia	Forested floodplain	Mineral	884 ± 212	na	<i>Ali et al.</i> [2006]
Ka'au crater, Hawaii	Forested floodplain	Mineral	na	5.25 ± 0.42 (2.08–14.17)	<i>Grand and Gaidos</i> [2010]
La Selva, Costa Rica	Flooded forest	Mineral	na	23.3 ± 14.6	<i>Nahlik and Mitsch</i> [2011]
La Selva, Costa Rica	Flooded forest	Mineral	na	40.4 ± 13.1	<i>Nahlik and Mitsch</i> [2011]
Earth wetlands, Costa Rica	Secondary forest	Mineral	na	5.7 ± 1.4	<i>Nahlik and Mitsch</i> [2011]
Earth wetlands, Costa Rica	Secondary forest	Mineral	na	4.5 ± 0.78	<i>Nahlik and Mitsch</i> [2011]
Orinoco, Venezuela	Forested floodplain	Mineral	na	4.6	<i>Smith et al.</i> [2000]
Orinoco, Venezuela	Forested floodplain	Mineral	na	10.7 (0–78)	<i>Smith and Lewis</i> [1992]
Orinoco, Venezuela	Forested floodplain	Mineral	na	12.8 (0.125–95.3)	<i>Smith and Lewis</i> [1992]
Orinoco, Venezuela	Forested floodplain	Mineral	na	7.27 (0–68.7)	<i>Smith and Lewis</i> [1992]
Orinoco, Venezuela	Forested floodplain	Mineral	na	10.3 (0–114)	<i>Smith and Lewis</i> [1992]
Amazon river, Brazil	Forested floodplain	Mineral	na	4.6 (0.24–31.7)	<i>Devol et al.</i> [1988]
Amazon river, Brazil	Forested floodplain	Mineral	na	1.88 (0–8.33)	<i>Wassmann et al.</i> [1992]
Amazon river, Brazil	Forested floodplain	Mineral	na	2.29 ± 0.54 (0.014–47.3)	<i>Devol et al.</i> [1990]
Amazon river, Brazil	Forested floodplain	Mineral	na	8 ± 1.12	<i>Bartlett et al.</i> [1988]
Amazon river, Brazil	Forested floodplain	Mineral	na	5.25 ± 0.83	<i>Bartlett et al.</i> [1990]
Amazon river, Brazil	Forested floodplain	Mineral	237	0.1	<i>Richey et al.</i> [1988]
Amazon river, Brazil	Forested floodplain	Mineral	36	7.5	<i>Richey et al.</i> [1988]
Itu, Negro river, Brazil	Forested	Mineral	375	1.9	<i>Belger et al.</i> [2011]
Araca, Negro river, Brazil	interfluvial wetland				
	Forested	Mineral	583	2.5	<i>Belger et al.</i> [2011]
Pantanal, Brazil	interfluvial wetland				
	Floodplain	Mineral	na	5.9 ± 13.1 (0.042–91.1)	<i>Marani and Alvala</i> [2007]
Pantanal, Brazil	Floodplain	Mineral	554	5.8	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	444	2.9	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	507	2.9	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	317	8.6	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	364	8.6	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	428	11.5272	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	586	11.5	<i>Hamilton et al.</i> [1995]
Pantanal, Brazil	Floodplain	Mineral	1062	17.3	<i>Hamilton et al.</i> [1995]
Congo river basin, Congo	Flooded forest	Mineral	na	4.41	<i>Tathy et al.</i> [1992]

<sup>a</sup>Error is standard deviation. As the fluxes reported here are from studies extending over different time periods, they should be used for indicative purposes to illustrate the range of fluxes in tropical wetlands. The forested tropical wetlands shown in the table were not managed. Positive fluxes represent a release of CO<sub>2</sub> or CH<sub>4</sub> from the peat, and negative CH<sub>4</sub> fluxes indicate CH<sub>4</sub> oxidation in the peat. na, not available.



**Figure 2.** Box plots comparing (a–c)  $\text{CO}_2$  and (d–f)  $\text{CH}_4$  fluxes from different: (Figures 2a and 2d) soil types, (Figures 2b and 2e) regions, and (Figures 2c and 2f) wetland types. The box plots show the lowest and highest observations and the lowest, median, and upper quartiles as well as values which may be considered as outliers. The statistics describing these results are reported in the text.

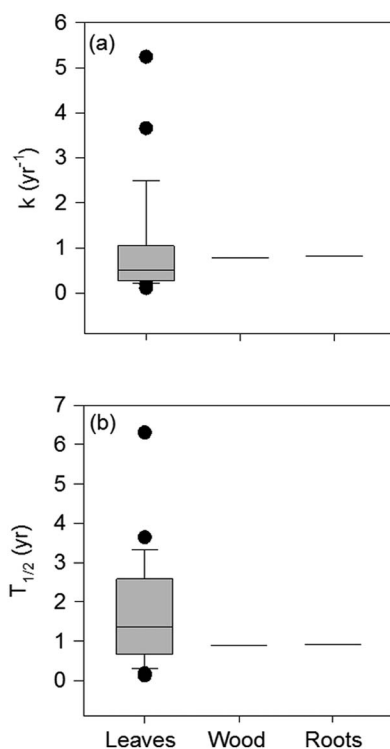
[Couwenberg *et al.*, 2010, and references therein]. Indeed, when comparing the estimated  $\text{CH}_4$  fluxes from tropical wetland to  $\text{CH}_4$  fluxes to higher-latitude wetland (e.g., subarctic and boreal; mean fluxes 4.7 and 3.0  $\text{mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ , respectively) and other types of wetlands (e.g., bog and fens; mean fluxes 4.0 and 3.9  $\text{mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ , respectively), mean tropical  $\text{CH}_4$  fluxes are higher [Turetsky *et al.*, 2014].

Simple upscaling of short-term measurements to the pantropics suggests that approximately  $91.6 \pm 77 \text{ Tg CH}_4 \text{ year}^{-1}$  (mean  $\pm$  SD) is released from tropical wetlands, assuming that the  $\text{CH}_4$  flux from mineral soil (Figure 2d) is related to the area covered by swamps and floodplains (Table 1), and the flux from organic soil (Figure 2d) was related to the area covered by peatlands. Our estimates of  $\text{CH}_4$  emissions from the peat surface of tropical wetlands are within the lower range of fluxes predicted by models [Melton *et al.*, 2013]. In this context, it is important to acknowledge the importance of tree stems and canopies for  $\text{CH}_4$  release [Pangala *et al.*, 2013]. This pathway was not included in our calculations, which are therefore likely to underestimate actual fluxes. It will be important to include stem fluxes in future  $\text{CH}_4$  budgets. Additionally, tropical rivers represent an important source of  $\text{CH}_4$  to the atmosphere with recent estimates of  $\text{CH}_4$  emissions from rivers in the Amazon basin amounting to 0.40 to 0.58  $\text{Tg C year}^{-1}$  which should be considered in the context of tropical  $\text{CH}_4$  emissions [Sawakuchi *et al.*, 2014].

The much lower emissions of  $\text{CH}_4$  relative to  $\text{CO}_2$  suggest that only a small component of net C losses result from  $\text{CH}_4$  release. However, given its greater global warming potential compared to  $\text{CO}_2$  [Meehl *et al.*, 2007],  $\text{CH}_4$  emissions at the upper end of the reported emissions range from tropical wetlands are still important from the perspective of radiative forcing.

## 5. Balance Between Carbon Inputs and Outputs

The high C effluxes presented above clearly suggest that most of the substantial quantity of C entering wetland systems eventually decomposes and does not contribute to accumulation of C in soil. This is also illustrated by the high litter decay constants ( $k$ ) and short half times (mean 1.6 year) for in situ litter

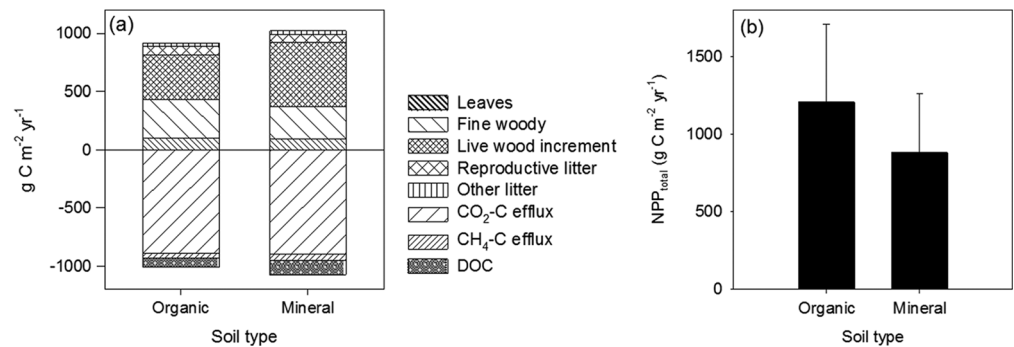


**Figure 3.** Box plots showing (a) litter decay constants for different tissue types reported in the literature and (b) calculated half times for different tissue types. Data are from in situ decomposition in tropical or subtropical wetlands. Given the small sample size for wood and roots ( $n = 2$ ), only the median values are shown in the graph. The box plots show the lowest and highest observations and the lower, median, and upper quartiles, as well as observations which may be considered as outliers. The statistics describing these results are reported in the text. (Values are from Furtado *et al.* [1980], Irmiler and Furch [1980], Frangi and Lugo [1985], Brady [1997], Rejmankova [2001], Del Valle-Arango [2003], Gamage and Asaeda [2005], Chimner and Ewel [2005], Troxler and Childers [2009], and Yule and Gomez [2009]).

decomposition in tropical and subtropical wetlands (Figure 3). Carbon accumulation in tropical wetlands is therefore attributable to the relatively small residual fraction compared to the much larger inputs (litter and root exudates) and outputs (heterotrophic respiration and DOC leaching) of C. This ultimately results in high  $\text{CO}_2$  and  $\text{CH}_4$  emissions from wetlands (Figure 2 and Table 4), in which environmental conditions are important in determining the proportions released as  $\text{CO}_2$  and  $\text{CH}_4$ . For example, drainage of peatland for agriculture result enhances heterotrophic respiration and large  $\text{CO}_2$  losses from SE Asian peatlands ( $172 \text{ Tg C yr}^{-1}$  [Hooijer *et al.*, 2006]) amounting to 12% of C losses arising from deforestation and degradation on the tropics ( $1.4 \text{ Pg year}^{-1}$  [Houghton, 2012]). In addition, the compilation of  $\text{CH}_4$  emissions suggests that the low  $\text{CH}_4$  emissions from wetlands in Southeast Asia reported by Couwenberg *et al.* [2010] are not representative of tropical wetlands globally (Figure 2 and Table 4). It is clear that various natural tropical wetland systems, including peatlands, are potentially significant sources of both  $\text{CH}_4$  and  $\text{CO}_2$  emissions.

Although  $k$  values for leaf litter decay were high, they differed among tree species and tissue types: the highest and lowest values reported for leaf tissue are, respectively,  $5.64$  and  $0.11 \text{ year}^{-1}$  (Figure 3). The corresponding values for wood and roots are within the same range as for leaf tissue, but only one study appears to have examined in situ wood and root decay in tropical wetlands [Chimner and Ewel, 2005]. Decay constants  $>1$  for some leaf litter types illustrate that some components of the litter input are likely to decompose fully, contributing to the substantial  $\text{CO}_2$  and  $\text{CH}_4$  efflux from tropical wetlands. Based on the existing limited data for different tissue types, it is currently impossible to ascertain whether specific tissue types degrade more slowly than others. However, the low decay constants for leaf litter reported in some studies (Figure 3) clearly indicate that leaf materials, as well as wood and roots, contribute to peat formation. As wood and roots were important components for plant biomass production (approximately 50 and 10%, respectively [Chimner and Ewel, 2005]), information on their decay rates is needed to establish the relative contribution of tissue types to peat formation.

Based on the compilation of litter production and C loss data (Tables 2 and 3), C balances were constructed for two types of tropical wetlands: those that are peat-forming, and those occurring on mineral soils (Figure 4). Carbon inputs estimated as  $\text{NPP}_{\text{total}}$  (Table 2) and from the different litter fractions (Table 3) provided comparable results for organic soils ( $1206$  and  $1185 \text{ g C m}^{-2} \text{ yr}^{-1}$  for  $\text{NPP}_{\text{total}}$  and  $\text{NPP}_{\text{combined}}$ , respectively). As the data set for  $\text{NPP}_{\text{total}}$  was based on a larger number of studies, we used this to calculate NEP. Mean C losses from the soil in the form of respiration (autotrophic and heterotrophic losses and  $\text{CO}_2$  and  $\text{CH}_4$  fluxes combined) and DOC losses for organic soils were lower for organic soils ( $991 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) than for mineral soils ( $1075 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). In contrast,  $\text{NPP}_{\text{total}}$  was greater in wetlands with organic soils ( $1206 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) than for those with mineral soils ( $880 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). This resulted in NEP of  $215$  and  $-195 \text{ g C m}^{-2} \text{ yr}^{-1}$  for organic and mineral soils, respectively. The estimated NEP is within the range of the long-term C accumulation in tropical peatlands, which ranged between  $30$  and  $300 \text{ g C m}^{-2} \text{ yr}^{-1}$  (see above), but is lower than reported by Hirano *et al.* [2007], who recorded NEP values of  $310$ ,  $380$ , and  $600 \text{ g C m}^{-2} \text{ yr}^{-1}$  in three consecutive years in a drained peat swamp forest and a papyrus swamp in Uganda (approximately  $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$  [Saunders *et al.*, 2012]).



**Figure 4.** (a) Comparison of mean C inputs and outputs in tropical wetlands on organic and mineral soil, respectively. Note that the number of observations used for the means is highly variable (cf. Table 3). There are also some important gaps in the comparison of the C balance between wetlands on organic and mineral soils, namely root (fine and coarse) production and coarse woody litter fall due to lack of data; (b) estimated C inputs ( $NPP_{total}$ ) from fine litterfall data sets (data in Table 3) separated between wetlands on organic and mineral soil.

These balances suggest that positive NEP values are reflected by peat accumulation. However, the negative NEP for wetlands on mineral soils clearly indicates that the data must be used with caution; indeed, reliable estimates of NEP cannot be calculated from actual litter production due to the severe limitations in the available database. More specifically, we found only seven studies of fine root production, all on peat soils, and none containing data on coarse root production; these components of the C cycle are therefore not included in Figure 4. This is a major concern, given their potentially large contribution to the overall C budget. Based on *Chimner and Ewel* [2005], fine root production amounted to approximately 11% of total plant production in a tropical peatland forest, while *Malhi et al.* [2011] estimated that coarse root production contributed approximately 7% to total plant production in tropical rainforest on mineral soil. Similarly, very few references report data for woody growth, which might represent a large flux of C in tropical wetlands (Table 3). Data from *Chimner and Ewel* [2005] suggest that this might introduce an error of 25–30% in estimates of plant production. Omission of belowground and wood increment data from calculations of C balance may therefore lead to underestimations of C inputs of approximately 40–50%.

Similar problems exist with organic C data for fluvial soils. *Ting-Hsuan et al.* [2012] present data for overall regional trends of C export from tropical rivers suggesting that fluvial C losses from tropical rivers are  $8.3 \text{ g C m}^{-2} \text{ yr}^{-1}$  with fluxes being estimated to be 2.2, 11.0, and  $20.4 \text{ g C m}^{-2} \text{ yr}^{-1}$  for Africa, America, and Asia, respectively. Estimates of carbon exports of  $8.5 \text{ g C m}^{-2} \text{ yr}^{-1}$  from the Amazon were presented by *Richey et al.* [1988]. However, these studies do not isolate the contribution from wetlands. Data from *Moore et al.* [2013], including TOC losses of 63 and  $97 \text{ g C m}^{-2} \text{ yr}^{-1}$  from intact and disturbed peat swamp forests, respectively, in Kalimantan, suggest a potentially notable contribution of fluvial C losses from NEP calculations for peatland systems in Southeast Asia (approximately 10% increased C losses compared to the above calculations of gaseous losses and 22% compared with local accumulation rates). However, any available TOC or DOC data are integrated over large areas [*Richey et al.*, 2002; *Moore et al.*, 2011, 2013], in contrast to the measurement of litter production and C gas release. Furthermore, high variability of temporal fluvial C in relation to flood and rain events [e.g., *Bass et al.*, 2011], combined with a low number of high-resolution temporal studies, also contribute to the limitations of aquatic C estimates. Given the limited available data, DOC fluxes appear to be of the same order of magnitude as CH<sub>4</sub> fluxes about an order of magnitude smaller than CO<sub>2</sub> losses (Figure 4 and Table 3). Although variation in the reported DOC flux data was substantial between organic and mineral soils systems (60%), the limitations of the available data mean that it is not possible to test whether this is a systematic difference.

Data availability was better for fine litterfall from the canopy, which was used in to calculate  $NPP_{total}$ . However, the relationship between  $NPP_{total}$  and  $NPP_{canopy}$  established for lowland rainforests may not be applicable to forested wetlands and may also differ between ombrotrophic and minerotrophic wetlands. Indeed, covariation between nutrient availability, forest composition, and peat depth/organic chemistry [*Phillips et al.*, 1997; *Sjögersten et al.*, 2010] suggests that nutrient availability may provide a strong control of C cycling in tropical wetlands. Care is therefore needed when interpreting these data.

Bearing in mind the data limitation noted above,  $NPP_{total}$  appeared to be greater in tropical peatlands than in systems that were not accumulating peat ( $F_{1,48} = 7.15$ ;  $P = 0.01$ ; Figure 4b). Data for litterfall and C effluxes were often not available for the same wetland systems, making it difficult to make valid comparisons of C inputs and outputs. Furthermore, the time frame for soil respiration measurements was highly variable, and there were neither long-term data sets on soil  $CO_2$  efflux nor diurnal variation with respect to plant-mediated gas transport [Pangala et al., 2013]. As a result, comparison of C inputs, which tend to be estimated on an annual basis, and the temporally discrete point measurements of  $CO_2$  emissions are unbalanced, which is likely to introduce a large error in the estimated NEP.

To assess the C budget of tropical wetlands fully, there is also an urgent need to separate autotrophic and heterotrophic respiration. Based on studies of an *Acacia* plantation on peat soil, Jauhainen et al. [2012] concluded that up to 80% of the  $CO_2$  efflux from tropical peatlands might originate from root respiration, while work in well-drained tropical forests suggests that root respiration could account for 25–50% of the total soil  $CO_2$  efflux [Nottingham et al., 2010].

Comparison of our tentative C budgets for tropical wetlands with tropical forest on well-drained soils [Malhi et al., 2011] shows that  $NPP_{total}$  from peat forming wetlands is comparable to lowland rainforest, but that  $NPP_{total}$  from wetlands on mineral soils are lower. Decomposition rates in the wetland systems were generally lower (approximately 900 and 1350 g C m<sup>-2</sup> yr<sup>-1</sup> for wetlands and lowland forests, respectively). Together with the higher  $NPP_{total}$  in wetlands on organic peat soils, this suggests that C accumulation in tropical peatlands is driven by a combination of lower decomposition rates and higher NPP.

## 6. Conclusions

Our metaanalysis suggests that greenhouse gas fluxes from tropical wetlands are high, with  $CH_4$  emissions being highest from mineral soils, although data quality is variable, with substantial data gaps for some regions (Figure 1). NEP was greater in peat-forming wetlands than on mineral soils, but missing data for key components of the C balance again add significant uncertainty to our estimates of NEP.

The high  $CH_4$  emissions, particularly in the Neotropics, might partially explain the high atmospheric  $CH_4$  concentrations reported for tropical regions [Mikaloff Fletcher et al., 2004a, 2004b; Meirink et al., 2008]. The growing body of recent data for  $CO_2$  and  $CH_4$  fluxes from a range of tropical wetlands should be utilized in global wetland models, setting a challenge for the modeling community. However, our ability to assess the role of tropical wetlands in the global C cycle is limited by severe gaps in current understanding of net C inputs (with very limited data on root inputs and woody growth) and outputs (data are largely lacking on DOC losses and separation of autotrophic and heterotrophic respiration), presenting field researchers with an equally important challenge. Without such data, we cannot assess how these ecosystems influence global climate and how their role in the global C cycle may be impacted by future change in land use and climate [Melton et al., 2013].

### Acknowledgments

The project was supported by a University of Nottingham New Investigator grant. Emma Wright received a PhD scholarship from the UK Biotechnology and Biological Sciences Research Council. Jorge Hoyos received funding for a PhD scholarship from CONACYT, Mexico. The data used for this literature review are available in the published literature.

### References

- Adis, J., K. Furch, and U. Irmeler (1979), Litter production of Central-Amazonian blackwater inundation forest, *Trop. Ecol.*, *20*, 236–245.
- Ali, M., D. Taylor, and K. Inubushi (2006), Effects of environmental variations on  $CO_2$  efflux from a tropical peatland in eastern Sumatra, *Wetlands*, *26*, 612–618.
- Alvarez-Lopez, J. A. (1990), Ecology of *Pterocarpus officinalis* forested wetlands in Puerto Rico, in *Ecosystems of the World, 15 Forested Wetlands*, edited by A. E. Lugo, M. Brinson, and S. Brown, pp. 251–265, Elsevier, Netherlands.
- Anderson, D. E. (2002), Carbon accumulation and C/N ratios of peat bogs in North West Scotland, *Scott. Geogr. J.*, *118*, 323–341.
- Aselmann, I., and P. J. Crutzen (1989), Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions, *J. Atmos. Chem.*, *8*, 307–358.
- Bartlett, K. B., and R. C. Harriss (1993), Review and assessment of methane emissions from wetlands, *Chemosphere*, *26*, 261–320.
- Bartlett, K. B., P. M. Crill, D. I. Sebach, R. C. Harriss, J. O. Wilson, and J. M. Melack (1988), Methane flux from the central Amazonian floodplain, *J. Geophys. Res.*, *93*, 1574–1582.
- Bartlett, K. B., P. M. Crill, J. A. Bonassi, J. E. Richey, and R. C. Harriss (1990), Methane flux from Central Amazonian floodplains: Emission during rising water, *J. Geophys. Res.*, *95*, 16,733–16,788.
- Bass, A. M., M. I. Bird, M. J. Liddell, and P. N. Nelson (2011), Fluvial dynamics of dissolved and particulate organic carbon during periodic discharge events in a steep tropical rainforest catchment, *Limnol. Oceanogr.*, *56*, 2282–2292.
- Belger, L., B. R. Forsberg, and J. M. Melack (2011), Carbon dioxide and methane emissions from interfluvial wetlands in the upper Negro River basin, Brazil, *Biogeochemistry*, *105*, 171–183.
- Bergamaschi, P., et al. (2009), Inverse modeling of global and regional  $CH_4$  emissions using SCIAMACHY satellite retrievals, *J. Geophys. Res.*, *114*, D22301, doi:10.1029/2009JD012287.

- Bloom, A. A., P. I. Palmer, A. Fraser, D. S. Reay, and C. Frankenberg (2010), Large-scale controls of methanogenesis inferred from methane and gravity spaceborne data, *Science*, **327**, 322–325.
- Boon, P. I., A. Mitchell, and K. Lee (1997), Effects of wetting and drying on methane emissions from ephemeral floodplain wetlands in southeastern Australia, *Hydrobiologia*, **357**, 73–87.
- Bracho, R., and J. San José (1990), Energy fluxes in a morichal (swamp palm community) at the Orinoco Llanos, Venezuela: Microclimate, water vapour and CO<sub>2</sub> exchange, *Photosynthetica*, **24**, 468–494.
- Brady, M. A. (1997), Organic material dynamics of coastal peat deposits in Sumatra, Indonesia, PhD thesis, The Univ. of British Columbia, Canada.
- Bridgman, S. D., H. Cadillo-Quiroz, J. K. Keller, and Q. Zhong (2013), Methane emissions from wetlands: Biogeochemical, microbial and modelling perspectives from local to global scales, *Global Change Biol.*, **19**, 1325–1346.
- Bubier, J. L., G. Bhatia, T. R. Moore, N. T. Roulet, and P. M. Lafleur (2003), Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada, *Ecosystems*, **6**, 353–367.
- Cattanio, J. H., A. B. Anderson, J. S. Rombold, and D. C. Nepstad (2004), Phenology, litterfall, growth, and root biomass in a tidal floodplain forest in the Amazon estuary, *Rev. Bras. Bot.*, **27**, 703–712.
- Chimner, R. A. (2004), Soil respiration rates of tropical peatlands in Micronesia and Hawaii, *Wetlands*, **24**, 51–56.
- Chimner, R. A., and K. C. Ewel (2005), A tropical freshwater wetland: II. Production, decomposition and peat formation, *Wetlands Ecol. Manage.*, **13**, 671–684.
- Clair, T. A., P. Arp, T. R. Moore, M. Dalva, and F. R. Meng (2002), Gaseous carbon dioxide and methane, as well as dissolved organic carbon losses from a small temperate wetland under a changing climate, *Environ. Pollut.*, **116**, S143–S148.
- Clymo, R. S. (1984), The limits to peat bog growth, *Philos. Trans. R. Soc. London, Ser. B*, **303**, 605–654.
- Couwenberg, J., R. Dommain, and H. Joosten (2010), Greenhouse gas fluxes from tropical peatlands in south-east Asia, *Global Change Biol.*, **16**, 1715–1732.
- Craft, C., C. Washburn, and A. Parker (2008), Latitudinal trends in organic carbon accumulation in temperate freshwater peatlands, in *Wastewater Treatment, Plant Dynamics and Management in Constructed and Natural Wetlands*, pp. 23–31, Springer Science + Business Media BV, New York.
- Crill, P. M., K. B. Bartlett, R. C. Harriss, J. M. Melack, S. MacIntyre, L. Lesack, and L. Smith-Morrill (1988), Tropospheric methane from an Amazonian floodplain lake, *J. Geophys. Res.*, **93**, 1564–1570, doi:10.1029/JD093iD02p01564.
- Crow, S. E., and R. K. Wieder (2005), Sources of CO<sub>2</sub> emission from a northern peatland: Root respiration, exudation, and decomposition, *Ecology*, **86**, 1825–1834.
- Datta, D. K., L. P. Gupta, and V. Subramian (1999), Distribution of C, N and P in the sediments of the Ganges ± Brahmaputra ± Meghna river system in the Bengal Basin, *Org. Geochem.*, **30**, 75–82.
- Del Valle-Arango, J. I. (2003), Descomposición de la hojarasca fina en bosques pantanosos del pacífico colombiano, *Interciencia*, **28**, 148–153.
- Devineau, J. L. (1976), Données préliminaires sur la litière e al chute feuilles dans quelque forestières semi-décidues de la moyenne Côte d'Ivoire, *Oecol. Plant.*, **11**, 375–395.
- Devol, A. H., T. M. Zaret, and B. R. Forsberg (1984), Sedimentary organic matter diagenesis and its relation to the carbon budget of tropical Amazon floodplain lakes, *Verh. Int. Verein. Theor. Angew. Limnol.*, **22**, 1299–1304.
- Devol, A. H., J. E. Richey, W. A. Clark, and S. L. King (1988), Methane emissions to the troposphere from the Amazon floodplain, *J. Geophys. Res.*, **93**, 1583–1492, doi:10.1029/JD093iD02p01583.
- Devol, A. H., J. E. Richey, B. R. Forsberg, and L. A. Martinelli (1990), Seasonal dynamics in methane emissions from the Amazon River floodplain to the troposphere, *J. Geophys. Res.*, **95**, 16,417–16,426, doi:10.1029/JD095iD10p16417.
- Dommain, R., J. Couwenberg, and H. Joosten (2011), Development and carbon sequestration of tropical peat domes in south-east Asia: Links to post-glacial sea-level changes and Holocene climate variability, *Quat. Sci. Rev.*, **30**, 999–1010.
- Duke, N. C. (1982), Mangrove litterfall data from Hinchbrook Island, north-eastern Australia, Australian Institute of Marine Science Data Report Coastal Studies Series, Townsville, Australia.
- Easse, A. M., and T. M. Aide (1999), Patterns of litter production across a salinity gradient in a *Pterocarpus officinalis* tropical wetland, *Plant. Ecol.*, **145**, 307–315.
- Farmer, J., R. Matthews, J. U. Smith, P. Smith, and B. K. Singh (2012), Assessing existing peatland models for their applicability for modelling greenhouse gas emissions from tropical peat soils, *Curr. Opin. Environ. Sustainability*, **3**, 339–349.
- Finlayson, C. M. (1988), Productivity and nutrient dynamics of seasonally inundated floodplains in the Northern Territory, in *Northern Australia: Progress and Prospects*, Floodplains Res., vol. 2, edited by D. Wade-Marshall and P. Loveday, pp. 58–83, ANU Press, Canberra, Australia.
- Finlayson, C. M., I. D. Cowie, and B. J. Bailey (1993), Biomass and litter dynamics in a Melaleuca forest on a seasonally inundated floodplain in tropical, northern Australia, *Wetlands Ecol. Manage.*, **2**, 177–188.
- Frangi, J. L., and A. E. Lugo (1985), Ecosystem dynamics of a subtropical floodplain forest, *Ecol. Monogr.*, **55**, 351–369.
- Frangi, J. L., and A. E. Lugo (1998), A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after hurricane Hugo, *Biotropica*, **30**, 339–348.
- Franken, M., U. Irmeler, and H. Klinge (1979), Litterfall in inundation, riverine and terra firme forest of Central Amazonia, *Trop. Ecol.*, **20**, 225–235.
- Furtado, J. I., S. Verghese, K. S. Liew, and T. H. Lee (1980), Litter production in a freshwater swamp forest Tasek Bera, Malasia, in *Tropical Ecology and Development. Proceedings of the Vth International Symposium of Tropical Ecology*, edited by J. I. Furtado, pp. 815–822, International Society of Tropical Ecology, Kuala Lumpur, Malaysia.
- Furukawa, Y., K. Inubushi, M. Ali, A. M. Itang, and H. Tsuruta (2005), Effect of changing groundwater levels caused by land-use changes on greenhouse gas fluxes from tropical peat lands, *Nutr. Cycling Agroecosyst.*, **71**, 81–91.
- Gamage, N. P. D., and T. Asaeda (2005), Decomposition and mineralization of *Eichhornia crassipes* litter under aerobic conditions with and without bacteria, *Hydrobiologia*, **541**, 13–27.
- Gill, R. A., and R. B. Jackson (2000), Global patterns of root turnover for terrestrial ecosystems, *New Phytol.*, **147**, 13–31.
- Golley, F. B., J. T. McGinnis, R. G. Clements, G. I. Child, and M. J. Duever (1975), *Mineral Cycling in a Tropical Moist Forest Ecosystem*, Univ. Georgia.
- Grand, M., and E. Gaidos (2010), Methane emission from a tropical wetland in Ka'au Crater, O'ahu, Hawaii, *Pac. Sci.*, **64**, 57–72.
- Haase, R. (1999), Litterfall and nutrient return in seasonally flooded and non-flooded forest of the Pantanal, Mato Grosso, Brazil, *For. Ecol. Manage.*, **117**, 129–147.
- Hadi, A., M. Haridi, and K. Inubushi (2001), Effect of land-use change on the microbial population and emission of greenhouse gasses, *Micro. Environ.*, **16**, 79–86.

- Hadi, A., K. Inubushi, Y. Furukawa, E. Purnomo, M. Rasmadi, and H. Tsuruta (2005), Greenhouse gas emissions from tropical peatlands of Kalimantan, Indonesia, *Nutr. Cycling Agroecosyst.*, **71**, 73–80.
- Hamilton, S. K., S. J. Sippel, and J. M. Melack (1995), Oxygen depletion and carbon dioxide and methane production in waters of the Pantanal wetland of Brazil, *Biogeochemistry*, **30**, 115–141.
- Hirano, T., H. Segah, T. Harada, S. Limin, T. June, R. Hirata, and M. Osaki (2007), Carbon dioxide balance of a tropical peat swamp forest in Kalimantan, Indonesia, *Global Change Biol.*, **13**, 412–425.
- Hirano, T., J. Jauhiainen, T. Inoue, and H. Takahashi (2009), Controls on the carbon balance of tropical peatlands, *Ecosystems*, **12**, 873–887.
- Hooijer, A., M. Silvius, H. Wosten, and S. Page (2006), PEAT-CO<sub>2</sub>: Assessment of CO<sub>2</sub> emissions from drained peatlands in SE Asia, Delft Hydraulics Report Q3943, 36 p.
- Hooijer, A., S. Page, J. G. Canadell, M. Silvius, J. Kwadijk, H. Wosten, and J. Jauhiainen (2010), Current and future CO<sub>2</sub> emissions from drained peatlands in Southeast Asia, *Biogeosciences*, **7**, 1505–1514.
- Hope, G., U. Chokkalingam, and S. Anwar (2005), The stratigraphy and fire history of the Kutai Peatlands, Kalimantan, Indonesia, *Quat. Res.*, **64**, 407–417.
- Houghton, R. A. (2012), Carbon emissions and the drivers of deforestation and forest degradation in the tropics, *Curr. Opin. Environ. Sustainability*, **4**, 1–7.
- Inubushi, K., A. Hadi, M. Okazaki, and K. Yonebayashi (1998), Effect of converting wetland forest to sago palm plantations on methane gas flux and organic carbon dynamics in tropical peat soil, *Hydrol. Process.*, **12**, 2073–2080.
- Inubushi, K., Y. Furukawa, A. Hadi, E. Purnomo, and H. Tsuruta (2003), Seasonal changes of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes in relation to land-use change in tropical peatlands located in coastal area of South Kalimantan, *Chemosphere*, **52**, 603–608.
- IPCC (2013), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by T. F. Stocker et al., Cambridge Univ. Press, Cambridge, U. K., and New York.
- Irmiler, U., and K. Furch (1980), Weight, energy, and nutrient changes during the decomposition of leaves in the emersions phase of Central-Amazonian inundation forests, *Pedobiologia*, **20**, 18–130.
- Jauhiainen, J., H. Takahashi, J. E. P. Heikkinen, P. J. Martikainen, and H. Vasanders (2005), Carbon fluxes from a tropical peat swamp forest floor, *Global Change Biol.*, **11**, 1788–1797.
- Jauhiainen, J., A. Hooijer, and S. E. Page (2012), Carbon dioxide emissions from an Acacia plantation on peatland in Sumatra Indonesia, *Biogeosciences*, **8**, 8270–9302.
- Keller, M. (1990), Biological sources and sinks of methane in tropical habitats and tropical atmospheric chemistry, Cooperative thesis 126, Princeton Univ., Princeton, N. J.
- Kirschke, S., et al. (2013), Three decades of global methane sources and sinks, *Nat. Geosci.*, **6**, 813–823.
- Klinge, H. (1978), Litter production in tropical ecosystems, *Malay. Nat. J.*, **30**, 415–422.
- Lähteenoja, O., and S. Page (2011), High diversity of tropical peatland ecosystem types in the Pastaza-Maranon basin, Peruvian Amazonia, *J. Geophys. Res.*, **116**, G02025, doi:10.1029/2010JG001508.
- Lähteenoja, O., K. Ruokolainen, L. Schulman, and M. Oinonen (2009), Amazonian peatlands: An ignored C sink and potential source, *Global Change Biol.*, **15**, 2311–2320.
- Lähteenoja, O., Y. R. Reátegui, M. Räsänen, D. D. C. Torres, M. Oinonen, and S. Page (2012), The large Amazonian peatland carbon sink in the subsiding Pastaza-Marañón foreland basin, Peru, *Global Change Biol.*, **18**, 164–178.
- Laiho, R. (2006), Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels, *Soil Biol. Biochem.*, **38**, 2011–2024.
- Makiranta, P., R. Laiho, H. Fritze, J. Hytonen, J. Laine, and K. Minkinen (2009), Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity, *Soil Biol. Biochem.*, **41**, 695–703.
- Malhi, Y., C. Doughty, and D. Galbraith (2011), The allocation of ecosystem net primary productivity in tropical forests, *Philos. Trans. R. Soc., B*, **366**, 3225–3245.
- Marani, L., and P. C. Alvala (2007), Methane emissions from lakes and floodplains in Pantanal, Brazil, *Atmos. Environ.*, **41**, 1627–1633.
- Mata, D. I., P. Moreno-Casasola, and C. Madero-Vega (2012), Litterfall of tropical forested wetlands of Veracruz in the coastal floodplains of the Gulf of Mexico, *Aquat. Bot.*, **98**, 1–11.
- Matthews, E., and I. Fung (1987), Methane emissions from natural wetlands: Global distribution, area and environmental characteristics of sources, *Global Biogeochem. Cycles*, **1**, 61–86.
- Meehl, G. A., et al. (2007), Global climate projections, in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon et al., Cambridge Univ. Press, Cambridge, U. K., and New York.
- Meirink, J. F., P. Bergamaschi, and M. C. Krol (2008), Four-dimensional variational data assimilation for inverse modelling of atmospheric methane emissions: Analysis of SCIAMACHY observations, *J. Geophys. Res.*, **113**, D17301, doi:10.1029/2007JD009740.
- Melack, J. M., L. L. Hess, M. Gastil, B. R. Forsberg, S. K. Hamilton, I. B. T. Lima, and E. L. M. Novo (2004), Regionalization of methane emissions in the Amazon Basin with microwave remote sensing, *Global Change Biol.*, **10**, 530–544.
- Melling, L., R. Hatano, and K. J. Goh (2005a), Methane fluxes from three ecosystems in tropical peatland of Sarawak, Malaysia, *Soil Biol. Biochem.*, **37**, 1445–1453.
- Melling, L., R. Hatano, and K. J. Goh (2005b), Soil CO<sub>2</sub> flux from three ecosystems in tropical peatland of Sarawak, Malaysia, *Tellus Ser. B-Chem. Phys. Met.*, **57**, 1–11.
- Melton, J. R., et al. (2013), Present state of global wetland extent and wetland methane modelling: Conclusion from a model inter-comparison project (WETCHIMP), *Biogeosciences*, **10**, 753–788, doi:10.5194/bg-10-753-2013.
- Miegot, J., and D. Imbert (2012), Phenology and production of litter in a *Pterocarpus officinalis* (Jacq.) swamp forest of Guadeloupe (Lesser Antilles), *Aquat. Bot.*, **101**, 18–27.
- Mikaloff Fletcher, S. E., P. P. Tans, L. M. Bruhwiler, J. B. Miller, and M. Heimann (2004a), CH<sub>4</sub> sources estimated from atmospheric observations of CH<sub>4</sub> and its <sup>13</sup>C/<sup>12</sup>C isotopic ratios: 1. Inverse modeling of source processes, *Global Biogeochem. Cycles*, **18**, GB4004, doi:10.1029/2004GB002224.
- Mikaloff Fletcher, S. E., P. P. Tans, L. M. Bruhwiler, J. B. Miller, and M. Heimann (2004b), CH<sub>4</sub> sources estimated from atmospheric observations of CH<sub>4</sub> and its <sup>13</sup>C/<sup>12</sup>C isotopic ratios: 2. Inverse modeling of CH<sub>4</sub> fluxes from geographical regions, *Global Biogeochem. Cycles*, **18**, GB4005, doi:10.1029/2004GB002224.
- Miller, J. B., L. V. Gatti, M. T. S. d'Amelio, A. M. Crowell, E. J. Dlugokencky, P. Bakwin, P. Artaxo, and P. P. Tans (2007), Airborne measurements indicate large methane emissions from the eastern Amazon basin, *Geophys. Res. Lett.*, **34**, L10809, doi:10.1029/2006GL029213.

- Moore, S., V. Gauci, C. D. Evans, and S. E. Page (2011), Fluvial organic carbon losses from a Bornean blackwater river, *Biogeosciences*, *8*, 901–909.
- Moore, S., C. D. Evans, S. E. Page, M. H. Garnett, T. G. Jones, C. Freeman, A. Hooijer, A. J. Wiltshire, S. H. Limin, and V. Gauci (2013), Deep instability of deforested tropical peatlands revealed by fluvial organic carbon fluxes, *Nature*, *493*, 660–663.
- Moreira-Turcq, P., J. M. Jouanneau, B. Turcq, P. Seyler, O. Weber, and J. L. Guyot (2004), Carbon sedimentation at Lago Grande de Curuai, a floodplain lake in the low Amazon region: Insights into sedimentation rates, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *214*, 27–40.
- Murayama, S., and Z. A. Bakar (1996), Decomposition of tropical peat soils, 2. Estimation of in situ decomposition by measurement of CO<sub>2</sub> flux, *Jpn. Agric. Res. Q.*, *30*, 153–158.
- Nahlik, A. M., and W. J. Mitsch (2011), Methane emissions from tropical freshwater wetlands located in different climatic zones of Costa Rica, *Global Change Biol.*, *17*, 1321–1334.
- Naiman, R. J. (2005), *Riparia: Ecology, Conservation, and Management of Streamside Communities*, 140 pp., Academic Press, Mass.
- Nebel, G., J. Dragsted, and A. S. Vega (2001), Litterfall, biomass and net primary production in flood plain forests in the Peruvian Amazon, *For. Ecol. Manage.*, *150*, 93–102.
- Nottingham, A. T., B. L. Turner, K. Winter, M. G. A. van der Heijden, and E. V. J. Tanner (2010), Arbuscular mycorrhizal mycelial respiration in a moist tropical forest, *New Phytol.*, *186*, 957–967.
- Otter, L. B., and M. C. Scholes (2000), Methane sources and sinks in a periodically flooded South African savanna, *Global Biogeochem. Cycles*, *14*, 97–111.
- Page, S. E., J. O. Rieley, Ø. W. Shotyk, and D. Weiss (1999), Interdependence of peat and vegetation in a tropical peat swamp forest, *Philos. Trans. R. Soc., B*, *354*, 1885–1897.
- Page, S. E., J. O. Rieley, and C. J. Banks (2011), Global and regional importance of the tropical peatland carbon pool, *Global Change Biol.*, *17*, 798–818.
- Pangala, S. R., S. Moore, E. R. C. Hornibrook, and V. Gauci (2013), Trees are major conduits for methane egress from tropical forested wetlands, *New Phytol.*, *197*, 524–531.
- Payntner, Q. (2005), Evaluating the impact of a biological control agent *Carmentis mimosae* on the woody wetland weed *Mimosa pigra* in Australia, *J. Appl. Ecol.*, *42*, 1054–1062.
- Phillips, S., G. E. Rouse, and R. M. Bustin (1997), Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panama, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *128*, 301–338.
- Rejmankova, E. (2001), Effect of experimental phosphorus enrichment on oligotrophic tropical marshes in Belize, Central America, *Plant Soil*, *236*, 33–53.
- Richey, J. E., A. H. Devol, S. C. Wofsy, R. Victoria, and M. N. Riberio (1988), Biogenic gases and the oxidation and reduction of carbon in Amazon River and floodplain waters, *Limnol. Oceanogr.*, *33*, 551–561.
- Richey, J. E., J. M. Melack, A. K. Aufdenkampe, V. M. Ballester, and L. L. Hess (2002), Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO<sub>2</sub>, *Nature*, *416*, 617–620.
- Riley, W. J., Z. M. Subin, D. M. Lawrence, S. C. Swenson, M. S. Torn, L. Meng, N. M. Mahowald, and P. Hess (2011), Barriers to predicting changes in global terrestrial methane fluxes: Analyses using CLM4Me, a methane biogeochemistry model integrated in CESM, *Biogeosciences*, *8*, 1925–1953, doi:10.5194/bg-8-1925-2011.
- Robinson, S. D., and T. R. Moore (1999), Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada, *Global Biogeochem. Cycles*, *13*, 591–601.
- Roulet, N. T., P. M. Lafleur, P. J. H. Richard, T. R. Moore, E. R. Humphreys, and J. Bubier (2007), Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, *Global Change Biol.*, *13*, 397–411.
- San-José, J., R. Montes, M. Angel Mazorra, E. Aguirre Ruiz, and N. Matute (2010), Patterns and carbon accumulation in the inland water-land palm ecotone (morichal) across the Orinoco lowlands, South America, *Plant Ecol.*, *206*, 361–374.
- Sannel, A. B. K., and P. Kuhry (2009), Holocene peat growth and decay dynamics in sub-arctic peat plateaus, west-central Canada, *Boreas*, *38*, 13–24.
- Saunders, M. J., F. Kansiime, and M. B. Jones (2012), Agricultural encroachment: Implications for carbon sequestration in tropical African wetlands, *Global Change Biol.*, *18*, 1312–1321.
- Sawakuchi, H. O., D. Bastviken, A. O. Sawakuchi, A. V. Krusche, M. V. R. Ballester, and J. E. Richey (2014), Methane emissions from Amazonian Rivers and their contribution to the global methane budget, *Global Change Biol.*, *9*, 2829–2840.
- Shimada, S., H. Takahashi, A. Haraguchi, and M. Kaneko (2001), The carbon content characteristics of tropical peats in Central Kalimantan, Indonesia: Estimating their spatial variability in density, *Biogeochemistry*, *53*(3), 249–267.
- Shindell, D. T., B. P. Walter, and G. Faluvegi (2004), Impacts of climate change on methane emissions from wetlands, *Geophys. Res. Lett.*, *31*, L21202, doi:10.1029/2004GL021009.
- Silva, M. F. F., and M. G. A. Lobo (1982), Nota sobre decomposição de matéria orgânica em floresta de terra firme, várzea e igapó, *Bol. Mus. Para. Emílio Goeldi (S Bot)*, *1*, 111–158.
- Silvola, J., J. Alm, J. Ahlholm, H. Nykanen, and P. J. Martikainen (1996), CO<sub>2</sub> fluxes from peat in boreal mires under varying temperature and moisture conditions, *J. Ecol.*, *84*, 219–228.
- Sjögersten, S., A. W. Cheesman, O. Lopez, and B. L. Turner (2010), Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland, *Biogeochemistry*, *104*, 147–163.
- Smith, L. K., and W. M. Lewis (1992), Methane emissions from the Orinoco River floodplain, Venezuela. ASLO 92, Aquatic Science Meeting, Santa Fe, NM, February 9–14.
- Smith, L. K., W. M. Lewis, J. P. Chanton, G. Cronin, and S. K. Hamilton (2000), Methane emissions from the Orinoco River floodplain, Venezuela, *Biogeochemistry*, *51*, 113–140.
- Sundari, S., T. Hirano, H. Yamada, and L. S. Kusin (2012), Effect of ground water level on soil respiration in tropical peat swamp forests, *J. Agric. Meteorol.*, *68*, 121–134.
- Tathy, J. P., B. Cros, R. A. De Imas, A. Marengo, J. Servant, and M. Labal (1992), Methane emissions from flooded forest in Central Africa, *J. Geophys. Res.*, *97*, 6159–6168, doi:10.1029/90JD02555.
- Terror, V. L., H. C. de Sousa, and A. Rodrigues Kozovit (2011), Produção, decomposição e qualidade nutricional da serapilheira foliar em uma floresta paludosa de altitude, *Acta Bot. Bras.*, *25*, 113–121.
- Ting-Hsuan, H., F. Yu-Han, P. Pei-Yi, and A. C. Chen-Tung (2012), Fluvial carbon fluxes in tropical rivers, *Curr. Opin. Environ. Sustainability*, *4*, 162–169.
- Troxler, T., and D. L. Childers (2009), Litter decomposition promotes differential feedbacks in an oligotrophic southern Everglades wetland, *Plant Ecol.*, *200*, 69–82.



- Turetsky, M. R., et al. (2014), A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands, *Global Change Biol.*, *20*, 2183–2197, doi:10.1111/gcb.12580.
- Turunen, C., and J. Turunen (2003), Development history and carbon accumulation of a slope bog in oceanic British Columbia, Canada, *Holocene*, *13*, 225–238.
- Turunen, J., E. Tomppo, K. Tolonen, and A. Reinikainen (2002), Estimating carbon accumulation rates of undrained mires in Finland—Application to boreal and subarctic regions, *Holocene*, *12*, 69–80.
- Ueda, S., C. S. U. Go, T. Yoshioka, N. Yoshida, E. Wada, T. Miyajima, A. Sugimoto, N. Boontanon, P. Vijarnsorn, and S. Boonprakub (2000), Dynamics of dissolved O<sub>2</sub>, CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O in a tropical coastal swamp in southern Thailand, *Biogeochemistry*, *49*, 191–215.
- Ukonmaanaho, L., T. M. Nieminen, N. Rausch, A. Cheburkin, G. Le Roux, and W. Shotyk (2006), Recent organic matter accumulation in relation to some climatic factors in ombrotrophic peat bogs near heavy metal emission sources in Finland, *Global Planet. Change*, *53*, 259–268.
- Walter, B. P., and M. Heimann, (2000), A process-based, climate-sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate, *Global Biogeochem. Cycles*, *14*, 745–765, doi:10.1029/1999GB001204.
- Wassmann, R., U. G. Thein, M. J. Whiticar, H. Rennenbergh, W. Seiler, and W. J. Junk (1992), Methane emissions from the Amazon floodplain: characterization of production and transport, *Global Biogeochem. Cycles*, *6*, 3–13.
- Wright, E. L., C. Black, B. L. Turner, and S. Sjögersten (2013), Environmental controls of temporal and spatial variability in CO<sub>2</sub> and CH<sub>4</sub> fluxes in a neotropical peatland, *Global Change Biol.*, *19*, 3775–3789.
- Wright, E., C. R. Black, A. W. Cheesman, T. Drage, D. Large, B. L. Turner, and S. Sjögersten (2011), Contribution of subsurface peat to CO<sub>2</sub> and CH<sub>4</sub> fluxes in a neotropical peatland, *Global Change Biol.*, *17*, 2867–2881.
- Yule, C. M., and L. N. Gomez (2009), Leaf litter decomposition in a tropical peat swamp forest in Peninsular Malaysia, *Wetlands Ecol. Manage.*, *17*, 231–241.