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

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Abstract

Tropical wetlands are not included in Earth system models, despite being an important source of methane (CH₄) and contributing a large fraction of carbon dioxide (CO₂) 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 CO₂ and CH₄ emissions, with exceptionally large fluxes in Southeast Asia and the Neotropics. By upscaling short-term measurements, we calculate that approximately 90 ± 77 Tg CH₄ year⁻¹ and 4540 ± 1480 Tg CO₂ year⁻¹ are released from tropical wetlands globally. CH₄ fluxes are greater from mineral than organic soils, whereas CO₂ fluxes do not differ between soil types. The high CO₂ and CH₄ 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 (CO₂) emissions from these ecosystems. For example, 1–3% of annual fossil fuel emissions or 355–855 Mt C year⁻¹ 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 (CH₄) each year, accounting for two thirds of global emissions from wetlands [e.g., Richey et al., 2002; Jauhiainen 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 × 10⁶ km², while models predict a much larger range (1.3–38.8 × 10⁶ km²) [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 CO₂ and CH₄.

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The rate of increase in CH\textsubscript{4} concentration in the atmosphere has varied during the past three decades reassuming its increase after 2006 to ca. 6 Tg CH\textsubscript{4} y\textsuperscript{-1} [Kirschke et al., 2013]; with tropical wetlands playing a major role in the renewed increase of atmospheric CH\textsubscript{4} [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\textsubscript{4} 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\textsubscript{4} flux measurements [Riley et al., 2011].

Our rudimentary understanding of CH\textsubscript{4} emissions in the tropics is underlined by the discrepancy between emissions of CH\textsubscript{4} from the surface of wetlands and the high concentrations of this gas in the tropical

| Wetland Type | Description | Area (km\textsuperscript{2}) |
|--------------|-------------|-----------------------------|
| 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 flooded areas along rivers or lakes showing considerable variation in vegetation cover. In the Amazon flood plain two separate systems are defined *Varzea forests* which are fed by muddy rivers and *Igapo forests* located in blackwater and clearwater tributaries | 715,000 |

*For this review we have limited data to forested systems.*

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$_4$ 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$_4$ 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$_4$ 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$_4$ emissions [Bridgham et al., 2013; Melton et al., 2013] use estimates of tropical CH$_4$ fluxes from a small number of review papers [e.g., Matthews and Fung, 1987; Aselmann and Crutzen, 1989; Bartlett and Harris, 1993] that estimated CH$_4$ emissions from a limited number of measurements. It is therefore not surprising that outputs from wetland models that estimate current CH$_4$ emissions from tropical areas vary widely, with values between 85 ± 7 and 184 ± 11 Tg CH$_4$ year$^{-1}$ [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$_2$ and CH$_4$ 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$_2$ and CH$_4$ 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$_2$ and CH$_4$ 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$_2$ and CH$_4$ 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 ($\text{half time} = \ln(2)/k$) 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$_{\text{total}}$ and NPP$_{\text{canopy}}$ 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$_{\text{total}} = 2.27 \times \text{NPP}_{\text{canopy}}$. NPP$_{\text{canopy}}$ 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$_{\text{total}}$.

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$_{\text{total}}$ 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 g C m$^{-2}$ yr$^{-1}$, at the higher end of the range reported for the tropics. In Kalimantan, mean accumulation rates were estimated to be 31–77 g C m$^{-2}$ yr$^{-1}$ [Dommain et al., 2011] and 94 g C m$^{-2}$ yr$^{-1}$ [Moore et al., 2013], while comparable values of 39–85 g C m$^{-2}$ yr$^{-1}$ have been reported for Peruvian Amazon peatlands [Lähteenoja et al., 2009] and 43–55 g C m$^{-2}$ 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 g C m$^{-2}$ yr$^{-1}$, at the upper end of range of long-term C accumulation rates.
Carbon accumulation is also substantial in depositional sedimentary floodplain systems. Moreira-Turcq et al. [2004] suggested a rate of 100 g C m$^{-2}$ yr$^{-1}$ for the varzea of the Amazon, while Devol et al. [1984] suggested a rate of 44 g C m$^{-2}$ 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 g C m$^{-2}$ 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 132–198 g C m$^{-2}$ 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 g C m$^{-2}$ 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 g C m$^{-2}$ yr$^{-1}$ [Robinson and Moore, 1999; Turunen and Turunen, 2003; Sannel and Kuhry, 2009], while accumulation rates in Finland were between 15 and 35 g C m$^{-2}$ 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 1000–1300 g C m$^{-2}$ yr$^{-1}$ [Nebel et al., 2001] and NPP of 1100 g C m$^{-2}$ yr$^{-1}$ [Chimner and Ewel, 2005]. Our calculations of NPP$_{total}$ (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 g C m$^{-2}$ yr$^{-1}$ in a forested wetland in Puerto Rico [Frangi and Lugo, 1985], while the lowest recorded value was 430 g C m$^{-2}$ yr$^{-1}$ in a floodplain forest in Australia [Payntner, 2005]. NPP$_{total}$ was significantly greater in tropical wetlands on organic soils (mean ± SE: 1206 ± 93 g C m$^{-2}$ yr$^{-1}$) than on mineral soils (mean ± SE: 880 ± 77 g C m$^{-2}$ 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% yr$^{-1}$) than in equivalent temperate and boreal systems (55 and 45% 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 CO$_2$ or simultaneous release of both CO$_2$ and CH$_4$. Measurements of daily, monthly, and seasonal variation in gas fluxes show that specific wetlands can switch between production of mainly CO$_2$ and a greater contribution of 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 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 CO$_2$ emissions and one on 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 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 CO$_2$ from forested tropical wetlands vary greatly, with reported values ranging between 30 and 4055 mg m$^{-2}$ 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 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$_{\text{total}}$$^a$ (g C m$^{-2}$ yr$^{-1}$) | Reference                      |
|----------------------------|-------------------------------------|-----------|-----------------------------------------------|-------------------------------|
| Puerto Rico                | Pterocarpus officinalis forest       | Organic   | 1277                                          | Easse and Aide [1999]          |
| Luquillo, Puerto Rico      | Flood plain palm forest             | Organic   | 616                                           | Frangi and Lugo [1998$^{b}$]   |
| Puerto Rico                | Prestoea montana 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                | Pterocarpus officinalis forest, Mayaguez | Organic | 1600                                          | Alvarez-Lopez [1990]          |
| Puerto Rico                | Pterocarpus officinalis forest, Patillas | Organic | 1351                                          | Alvarez-Lopez [1990]          |
| Guadeloupe                 | Pterocarpus officinalis forest, Dorado | Mineral | 997                                           | Guadeloupe [1990]              |
| Guadeloupe                 | Pterocarpus officinalis swamp forest | Organic   | 1476                                          | Miegot and Imbert [2012]       |
| Guadeloupe                 | Pterocarpus officinalis swamp forest | Organic   | 1606                                          | Miegot and Imbert [2012]       |
| Panana                     | 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, Tahuampa        | 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                                           | Toror 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]         |
| 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 Mimosa pigra     | Mineral   | 430                                           |Payntner [2005]                |
| Australia                  | Flood plain forest, Melaleuca spp.—Mangrove, northeastern Queensland | Mineral | 470                                           | Duke [1982]                   |
| Australia                  | Melaleuca spp. forest, Magela flood plain | Mineral | 350                                           | Finlayson et al. [1993]       |
| Australia                  | Melaleuca 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, Eugenia 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, P16              | Organic   | 783                                           | Brady [1997]                  |
| Sumatra, Indonesia         | Peat swamp forest, P19              | Organic   | 624                                           | Brady [1997]                  |
| Sumatra, Indonesia         | Peat swamp forest, P112             | Organic   | 624                                           | Brady [1997]                  |
| Yela, Micronesia          | Peat swamp forest                   | Organic   | 1689                                          | Chimner and Ewel [2005]        |
| Yewuk, Micronesia         | Peat swamp forest                   | Organic   | 1716                                          | Chimner and Ewel [2005]        |

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$^a$NPP$_{\text{total}}$ is based on conversion of NPP$_{\text{canopy}}$ using NPP$_{\text{total}} = 2.27 \times $NPP$_{\text{canopy}}$ [Molhi et al., 2011], where total NPP was not reported.

$^b$Data from 1980.
regions were highly variable and affected by local conditions. Interestingly, the greater range of CO₂ around this mean will arise from current poor understanding of tropical wetland area from organic soil (Figure 2a) was related to the area covered by peatlands. Substantial additional uncertainty of 8.22 and 6.10 mg CH₄ m⁻² h⁻¹ found in tropical wetlands have also been observed in subtropical wetland systems. A maximum emission of 19 mg CH₄ m⁻² h⁻¹ 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 CH₄ m⁻² h⁻¹ from forested floodplains in South Africa [Otter and Scholes, 2000]. In contrast, maximum CH₄ fluxes from flooded temperate and boreal peatlands are lower, ranging between 10 and 14 mg CH₄ m⁻² h⁻¹.

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 CO₂ 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 CO₂ m⁻² h⁻¹) 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 CO₂ fluxes to pantropical wetland areas suggests a release of approximately 4540 ± 1480 Tg CO₂ year⁻¹ (mean ± standard deviation (SD)). This calculation is based on the simplistic assumption that the CO₂ 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 CO₂ fluxes between tropical wetlands on organic and mineral soils (P > 0.05; Figure 1a). Furthermore, there was no systematic variation in CO₂ efflux among wetland types (P > 0.05; Figure 2c).

### 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

|                | Organic                      | Mineral                     |
|----------------|------------------------------|-----------------------------|
| **Fluxes (g C m⁻² 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                        |
| CO₂ efflux | −875.1 (481.3; 17)          | −901.4 (728.0; 18)        |
| CH₄ efflux | −40.1 (66.1; 15)             | −54.0 (52.1; 29)            |
| DOC | −75.5 (17; 2)                | −120 (n/d; 1)               |
| **Pools (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)               |

*Negative values indicate C losses from the ecosystem.

**From Richey et al. [2002], Moore et al. [2011], and Moore et al. [2013].**

4.2. Methane

Estimated fluxes of CH₄ from peatlands are typically several orders of magnitude lower than those for CO₂ (Table 4). Indeed, CH₄ emissions are undetectable in some peatlands and uptake from the atmosphere might occur instead. Reported CH₄ fluxes vary among wetland types (F₃,₄₂ = 6.77, P < 0.001), ranging from −0.1 to 40 mg CH₄ m⁻² h⁻¹; 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, 1999; Nahlik and Mitsch, 2011; Wright et al., 2011]. CH₄ fluxes in Southeast Asian forested peatlands were typically lower (<2 mg CH₄ m⁻² h⁻¹), while the highest, albeit variable, fluxes were reported for the Neotropics (F₃,₄₂ = 12.88; P < 0.001; Figure 2e). For example, fluxes from peatlands in Panama ranged between −5.35 and 143 mg CH₄ m⁻² h⁻¹ (Table 4 [Wright et al., 2011]), highlighting the potential for very high CH₄ fluxes and marked temporal variability. The highest average CH₄ emissions were from wetlands on mineral soils (F₃,₄₂ = 6.97, P < 0.05), with mean fluxes of 8.22 and 6.10 mg CH₄ m⁻² h⁻¹ 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 CH₄ m⁻² h⁻¹ 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 CH₄ m⁻² h⁻¹ from forested floodplains in South Africa [Otter and Scholes, 2000]. In contrast, maximum CH₄ fluxes from flooded temperate and boreal peatlands are lower, ranging between 10 and 14 mg CH₄ m⁻² h⁻¹.
Table 4. Carbon Dioxide (CO₂) and Methane (CH₄) Fluxes From Tropical Wetlands Showing the Mean Fluxes[a] and (Ranges) if Available

| Location                      | Type                      | Soil Type | CO₂ Efflux (mg m⁻² h⁻¹) | CH₄ Efflux (mg m⁻² h⁻¹) | Reference                  |
|-------------------------------|---------------------------|-----------|--------------------------|--------------------------|-----------------------------|
| Kalimantan, Indonesia        | Forested peatland         | Organic   | na                       | 510 ± 180 (146–843)      | Inubushi et al. [1998]       |
| Kalimantan, Indonesia        | Secondary forest          | Organic   | 317–950                  | 0.18 ± 0.06 (0–1)        | Inubushi et al. [2003]       |
| Kalimantan, Indonesia        | Forested peatland         | Organic   | 513                      | 0.19                     | Hirano et al. [2009]         |
| Kalimantan, Indonesia        | Secondary forest          | Organic   | 395 (183–4055)           | 0.50 (0–3.33)            | Hadi et al. [2001]           |
| Kalimantan, Indonesia        | Forested peatland         | Organic   | 399 ± 36 (50–550)        | 0.16 ± 0.65 (–0.1–0.35)  | Jauhiainen et al. [2005]     |
| Kalimantan, Indonesia        | Forested peatland         | Organic   | 563 (79–1580)            | na                       | Sundari et al. [2012]        |
| Sumatra, Indonesia           | Forested peatland         | Organic   | 380 ± 55                 | 0.89 ± 0.48              | Furukawa et al. [2005]       |
| Sumatra, Indonesia           | Forested peatland         | Organic   | 278 ± 16                 | 1.21 ± 1.36              | Furukawa et al. [2005]       |
| Sumatra, Indonesia           | Forested peatland         | Organic   | 376 ± 107                | 0.77 ± 0.27              | Furukawa et al. [2005]       |
| Malaysia                     | Forested peatland         | Organic   | 905 (366–1953)           | na                       | Melling et al. [2005a]       |
| Malaysia                     | Forested peatland         | Organic   | 12.8 (0.125)             | 0.0029 (–0.006–0.011)    | Melling et al. [2005b]       |
| Malaysia                     | Forested peatland         | Organic   | 444                      |                          | Murayama and Bakar [1996]    |
| Thailand                     | Forest peatland           | Organic   | 1.12 ± 2.7 (0.19–12.6)   |                          | Ueda et al. [2000]           |
| Micronesia                   | Forested peatland         | Organic   | 396 ± 36 (340–402)       | na                       | Chinner [2004]               |
| Maui, Hawaii                  | Montane peatland          | Organic   | 285 ± 75                 |                          | Chinner [2004]               |
| Bocas del Toro, Panama       | Forested peatland         | Organic   | 212 (11–1694)            | 23 (–5.35–143)           | Wright et al. [2011]         |
| Bocas del Toro, Panama       | Forested peatland         | Organic   | 238 (62–801)             | 17 (–3.35–98.3)          | Wright et al. [2011]         |
| Bocas del Toro, Panama       | Open peatland             | Organic   | 259 (7–950)              | 31 (–6.40–7.88)          | Wright et al. [2011]         |
| Colon, Panama                | Forested peatland         | Organic   | na                       | 14.4 (0–48)              | Keller [1990]                |
| Kalimantan, Indonesia        | Forested peatland         | Organic   | na                       |                          | Pangala et al. [2013]        |
| Ka’au, Hawaii                | Montane swamp             | Organic   | 127 ± 47                 | na                       | Chinner [2004]               |
| Orinoco Llanos, Venezuela    | Palm swamp                | Organic   | 30 (17–54)               | na                       | Bracho and San José [1990]   |
| Sumatra, Indonesia           | Forested floodplain       | Mineral   | 410 ± 35                 | na                       | All et al. [2006]            |
| Sumatra, Indonesia           | Forested floodplain       | Mineral   | 884 ± 212                | na                       | All et al. [2006]            |
| Ka’au crater, Hawaii         | Forested floodplain       | Mineral   | na                       | 5.25 ± 0.42 (2.08–14.17) | Grand and Gaidos [2010]      |
| La Selva, Costa Rica         | Flooded forest            | Mineral   | 23.3 ± 14.6              | na                       | Nahlik and Mitsch [2011]     |
| La Selva, Costa Rica         | Flooded forest            | Mineral   | 40.4 ± 13.1              | na                       | Nahlik and Mitsch [2011]     |
| Earth wetlands, Costa Rica   | Secondary forest          | Mineral   | 5.7 ± 1.4                | na                       | Nahlik and Mitsch [2011]     |
| Earth wetlands, Costa Rica   | Secondary forest          | Mineral   | 4.5 ± 0.78               | na                       | Nahlik and Mitsch [2011]     |
| Orinoco, Venezuela           | Forested floodplain       | Mineral   | 4.6                      | na                       | Smith et al. [2000]          |
| Orinoco, Venezuela           | Forested floodplain       | Mineral   | 10.7 (0–78)              | na                       | Smith and Lewis [1992]       |
| Orinoco, Venezuela           | Forested floodplain       | Mineral   | 12.8 (0.125–95.3)        | na                       | Smith and Lewis [1992]       |
| Orinoco, Venezuela           | Forested floodplain       | Mineral   | 7.27 (0–68.7)            | na                       | Smith and Lewis [1992]       |
| Orinoco, Venezuela           | Forested floodplain       | Mineral   | 10.3 (0–114)             | na                       | Smith and Lewis [1992]       |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 4.6 (0.24–31.7)          | na                       | Devol et al. [1988]          |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 1.88 (0–8.33)            | na                       | Wassmann et al. [1992]       |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 2.29 ± 0.54 (0.014–47.3) | na                       | Devol et al. [1990]          |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 8 ± 1.12                 | na                       | Bartlett et al. [1988]       |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 5.25 ± 0.83              | na                       | Bartlett et al. [1990]       |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 237                      | 0.1                      | Richey et al. [1988]         |
| Amazon river, Brazil         | Forested floodplain       | Mineral   | 36                       | 7.5                      | Richey et al. [1988]         |
| Itu, Negro river, Brazil     | Forested floodplain       | Mineral   | 375                      | 1.9                      | Belger et al. [2011]         |
| Araca, Negro river, Brazil   | interfluvial wetland      | Mineral   | 583                      | 2.5                      | Belger et al. [2011]         |
| Pantanal, Brazil             | Floodplain                | Mineral   | na                       | 5.9 ± 13.1 (0.042–91.1)  | Manzini and Alvala [2007]    |
| Pantanal, Brazil             | Floodplain                | Mineral   | 554                      | 5.8                      | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 444                      | 2.9                      | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 507                      | 2.9                      | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 317                      | 8.6                      | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 364                      | 8.6                      | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 428                      | 11.5272                  | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 586                      | 11.5                     | Hamilton et al. [1995]       |
| Pantanal, Brazil             | Floodplain                | Mineral   | 1062                     | 17.3                     | Hamilton et al. [1995]       |
| Congo river basin, Congo     | Flooded forest            | Mineral   | na                       | 4.41                     | Tathy et al. [1992]          |

[a] 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 CO₂ or CH₄ from the peat, and negative CH₄ fluxes indicate CH₄ oxidation in the peat. na, not available.
Indeed, when comparing the estimated CH₄ fluxes from tropical wetland to CH₄ fluxes to higher-latitude wetland (e.g., subarctic and boreal; mean fluxes 4.7 and 3.0 mg CH₄ m⁻² h⁻¹, respectively) and other types of wetlands (e.g., bog and fens; mean fluxes 4.0 and 3.9 mg CH₄ m⁻² h⁻¹, respectively), mean tropical CH₄ fluxes are higher [Turetsky et al., 2014].

Simple upscaling of short-term measurements to the pantropics suggests that approximately 91.6 ± 77 Tg CH₄ year⁻¹ (mean ± SD) is released from tropical wetlands, assuming that the CH₄ 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 CH₄ 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 important to acknowledge the importance of tree stems and canopies for CH₄ 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 CH₄ budgets. Additionally, tropical rivers represent an important source of CH₄ to the atmosphere with recent estimates of CH₄ emissions from rivers in the Amazon basin amounting to 0.40 to 0.58 Tg C year⁻¹ which should be considered in the context of tropical CH₄ emissions [Sawakuchi et al., 2014].

The much lower emissions of CH₄ relative to CO₂ suggest that only a small component of net C losses result from CH₄ release. However, given its greater global warming potential compared to CO₂ [Meehl et al., 2007], CH₄ 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.
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 CO₂ and CH₄ emissions from wetlands (Figure 2 and Table 4), in which environmental conditions are important in determining the proportions released as CO₂ and CH₄. For example, drainage of peatland for agriculture results in substantial CO₂ emissions, whereas wetlands, in which environmental conditions are maintained, often result in high CO₂ and CH₄ emissions from wetlands. Drainage of peatland for agriculture results in high CO₂ and CH₄ emissions, whereas wetlands, in which environmental conditions are maintained, often result in high CO₂ and CH₄ emissions from wetlands.

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 NPPtotal (Table 2) and from the different litter fractions (Table 3) provided comparable results for organic soils (1206 g C m⁻² yr⁻¹ for NPPtotal and NPPcombined, respectively). As the data set for NPPtotal 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 CO₂ and CH₄ efflux) are likely to decompose fully, contributing to the substantial CO₂ and CH₄ 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.

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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 g C m⁻² yr⁻¹ with fluxes being estimated to be 2.2, 11.0, and 20.4 g C m⁻² yr⁻¹ for Africa, America, and Asia, respectively. Estimates of carbon exports of 8.5 g C m⁻² 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 g C m⁻² 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 CH₄ fluxes about an order of magnitude smaller than CO₂ 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\textsubscript{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\textsubscript{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\textsubscript{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, Jauhiainen et al. [2012] concluded that up to 80% of the CO\textsubscript{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\textsubscript{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\textsubscript{total} from peat forming wetlands is comparable to lowland rainforest, but that NPP\textsubscript{total} from wetlands on mineral soils are lower. Decomposition rates in the wetland systems were generally lower (approximately 900 and 1350 g C m\textsuperscript{-2} yr\textsuperscript{-1} for wetlands and lowland forests, respectively). Together with the higher NPP\textsubscript{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\textsubscript{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\textsubscript{4} emissions, particularly in the Neotropics, might partially explain the high atmospheric CH\textsubscript{4} concentrations reported for tropical regions [Mikaloff Fletcher et al., 2004a, 2004b; Meirink et al., 2008]. The growing body of recent data for CO\textsubscript{2} and CH\textsubscript{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].

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