

Contribution of subsurface peat to CO₂ and CH₄ fluxes in a neotropical peatland

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Abstract

Tropical peatlands play an important role in the global carbon cycling but little is known about factors regulating carbon dioxide (CO₂) and methane (CH₄) fluxes from these ecosystems. Here, we test the hypotheses that (i) CO₂ and CH₄ are produced mainly from surface peat and (ii) that the contribution of subsurface peat to net C emissions is governed by substrate availability. To achieve this, *in situ* and *ex situ* CO₂ and CH₄ fluxes were determined throughout the peat profiles under three vegetation types along a nutrient gradient in a tropical ombrotrophic peatland in Panama. The peat was also characterized with respect to its organic composition using ¹³C solid state cross-polarization magic-angle spinning nuclear magnetic resonance spectroscopy. Deep peat contributed substantially to CO₂ effluxes both with respect to actual *in situ* and potential *ex situ* fluxes. CH₄ was produced throughout the peat profile with distinct subsurface peaks, but net emission was limited by oxidation in the surface layers. CO₂ and CH₄ production were strongly substrate-limited and a large proportion of the variance in their production (30% and 63%, respectively) was related to the quantity of carbohydrates in the peat. Furthermore, CO₂ and CH₄ production differed between vegetation types, suggesting that the quality of plant-derived carbon inputs is an important driver of trace gas production throughout the peat profile. We conclude that the production of both CO₂ and CH₄ from subsurface peat is a substantial component of the net efflux of these gases, but that gas production through the peat profile is regulated in part by the degree of decomposition of the peat.

Keywords: carbon, methane, nutrient gradient, Panama, peatland, solid state ¹³C CPMAS NMR, tropical

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Introduction

Tropical peatlands are known to have considerable significance in the global carbon (C) cycle (Page *et al.*, 2011; Vegas-Vilaruba *et al.*, 2010), but the sink strength of tropical peatlands is under increasing threat from changes in land use and climate (Couwenberg *et al.*, 2010). In areas of the tropics which are expected to experience reduced rainfall and more prolonged drought (Meehl *et al.*, 2007), peatlands may become less important sources of atmospheric methane (CH₄). However, this would be offset by greatly increased rates of aerobic decomposition and carbon dioxide (CO₂) release, with the result that their combined global warming potential would increase (Hirano *et al.*, 2009; Couwenberg *et al.*, 2010; Sjögersten *et al.*, 2010). It is

also plausible that old C stored deep in the peat profile would be metabolized if climatic conditions become more favourable for decomposition, as has been reported for northern peatlands (e.g. Dorrepaal *et al.*, 2009). In tropical environments, a substantial draw down of the water table would be required to impact deep peat layers.

Considerable variation in C fluxes occurs between vegetation types in tropical wetland systems (Melling *et al.*, 2005a, b; Sjögersten *et al.*, 2010), suggesting that C inputs from the vegetation (Sebacher *et al.*, 1985; Joabsson & Christensen, 2001; Konnerup *et al.*, 2010) are strong drivers of C fluxes in these systems. However, it is not known if these differences in C fluxes result mainly from surface processes or are maintained throughout the peat profile. Tropical peatlands may reach depths of up to 15 m (Phillips *et al.*, 1997; Page *et al.*, 1999, 2004; Shimada *et al.*, 2001; Hope *et al.*, 2005). To date, most studies of C fluxes from such systems

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have focused on surface fluxes of CO₂ and CH₄ (e.g. Jauhainen *et al.*, 2005; Hirano *et al.*, 2007; Sjögersten *et al.*, 2010), but little is known about the factors influencing the production and emission of these gases. Greater CH₄ production at depth (at least down to 50 cm) than in surface peat has been noted in peatlands in Sarawak, Malaysia (Inubushi *et al.*, 1998) and CH₄ production at 80 cm depth has been found to vary over several orders of magnitude between vegetation types (Melling *et al.*, 2005a).

Paleoecological studies of the Changuinola peat deposit on the Caribbean coast of western Panama demonstrated variation in the dominant peat-forming vegetation over a period of ca. 4500 years and changes in peat structure with depth (Phillips *et al.*, 1997). These observations suggest that the degree of peat decomposition and properties vary not only over the surface of peatlands (Sjögersten *et al.*, 2010) but also with depth, as has also been shown in higher latitude peatlands (Krull *et al.*, 2004; Forbes *et al.*, 2009; Grover & Baldock, 2010). In these systems, there is a trend for higher aliphatic to carbohydrate ratios (commonly used to indicate the degree of decomposition; Baldock & Preston, 1995) and more aromatic compounds to be found at depth, consistent with an increasing degree of decomposition with depth. Such changes in peat composition with depth have implications for microbial degradation of C stored in peatlands; for example, Grover & Baldock (2010) demonstrated a link between peat substrate quality and mass loss, with lower decomposition rates being found in the deeper peat deposits. Indeed, the supply of labile C limits heterotrophic microbial activity in the surface layers of tropical, subtropical and boreal peatlands (Miyajima *et al.*, 1997; Bergman *et al.*, 1999; Wright *et al.*, 2009), with implications for the production of CO₂ and CH₄ throughout the peat profile.

In northern peatlands, there is good evidence that the contribution of old C from depths ≥ 4 m to surface gas efflux is low (Charman *et al.*, 1994, 1999; Chanton *et al.*, 1995, 2008; Garnett & Hardie, 2009). In agreement with this observation, microbial activity in tropical peatlands has been shown to decline with depth based on studies of microbial enzyme activity (Jackson *et al.*, 2009), although it is unclear how this translates into CO₂ and CH₄ effluxes from different peat layers formed under contrasting vegetation types. Furthermore, root activity impacts on CO₂ and CH₄ fluxes throughout the peat profile by influencing belowground O₂ supplies (e.g. Dinsmore *et al.*, 2009; Fritz *et al.*, 2011) and substrate inputs (e.g. Laing *et al.*, 2010), and by allowing rapid transport of CH₄ through the roots to the surface, thereby avoiding oxidation within the peat profile (e.g. Purvaja *et al.*, 2004; Chen *et al.*, 2010). In northern peatlands, CH₄ production has been associated with distinct

subsurface peat layers, with emissions being much lower for the intervening layers (Laing *et al.*, 2010; Shoemaker & Schrag, 2010). In addition to such vertical variation in gas production, spatial variability in nutrient availability (Koelbener *et al.*, 2010) and forest composition controls gas transport (Konnerup *et al.*, 2010) and shapes microbial activity in the surface peat layers in tropical peatlands. Gas fluxes vary substantially between vegetation types (Chimner, 2004; Melling *et al.*, 2005a,b; Sjögersten *et al.*, 2010), in parallel with the substantial variation between species with respect to gas transport demonstrated recently in tropical wetland plants (Konnerup *et al.*, 2010). Together, this evidence points towards substantial variation in gas production throughout the profile in relation to variation in substrate availability and the physiochemical environment.

In this paper, we explore variation in peat properties and associated gas fluxes throughout the profile at three sites in a neotropical peatland with distinct vegetation communities to test the hypotheses that: (i) CO₂ and CH₄ are produced mainly from surface peat and; (ii) the contribution of subsurface peat to net C emissions is governed by substrate availability. To test these hypotheses, CO₂ and CH₄ fluxes from different peat layers were measured both *in situ* and *ex situ* in an ombrotrophic domed tropical coastal peatland in western Panama. Gas fluxes were then correlated with substrate composition throughout the peat profile determined using solid state ¹³C cross-polarization magic-angle spinning nuclear magnetic resonance (CPMAS NMR).

Materials and methods

Site description

The San San Pond Sak peatland is a 164 km² mosaic of freshwater and marine-influenced wetlands in Bocas del Toro Province on the Caribbean coast of western Panama (Cohen & Stack, 1996). Recognized internationally as a site of special scientific interest (Ramsar site #611), it includes the significant 80 km² Changuinola peat deposit, an ombrotrophic domed peatland to the south east of Changuinola river.

The oldest deposits in the Changuinola peatland are estimated to have been formed 4000–4500 years ago and are >8 m deep in the central areas (Phillips *et al.*, 1997). Peat at the edges of the peatland is younger and ca. 2 m deep. The vegetation communities which formed the peat have shifted spatially over time, meaning that C inputs and environmental conditions at specific locations have differed greatly (Phillips *et al.*, 1997). The texture of the peat varies between the interior, where it is predominantly coarse to a depth of 2–4 m and dominated by roots in the surface layers, to the edges where the peat has a fine texture throughout the profile (Phillips *et al.*,

1997), indicating greater decomposition and/or differences in the source of litter.

Seven distinct phasic plant communities cover the peatland in approximately concentric rings (Phillips *et al.*, 1997). Starting from the periphery, these communities have been designated as (i) *Rhizophora mangle* mangrove swamp, (ii) mixed back mangrove swamp, (iii) *Raphia taedigera* palm swamp, (iv) mixed forest swamp, (v) *Campnosperma panamensis* forest swamp, (vi) sawgrass/stunted forest swamp and (vii) *Myrica-Cyrilla* bog-plain. Nutrient levels in the peat and plant tissue vary greatly between vegetation communities and are generally low in the interior and higher towards the edge of the peatland (Troxler, 2007; Sjögersten *et al.*, 2010). Previous work has shown that the low nutrient content in the interior is reflected by lower microbial biomass C:N and C:P ratios and upregulation of the activity of extracellular enzymes involved in nutrient acquisition (Sjögersten *et al.*, 2010). Furthermore, *in situ* CO₂ and CH₄ fluxes did not appear to reflect nutrient availability, while drained surface peat samples exhibited lower CO₂ production in material from the interior than sites closer to the edge of the peatland (Sjögersten *et al.*, 2010).

The nearby town of Bocas del Toro, Isla Colon, ca. 10 km from the peatland, has a mean annual temperature of 27 °C with low intra-annual variability and a mean annual precipitation of 3209 mm between 1992 and 2001 (Estadística Panameña, 2001). Rainfall is continuous throughout the year with no pronounced dry season, although there are two distinct periods of lower rainfall (February–April and September–October). The water table is generally at the surface of the peatland throughout the year, with no distinct period of draw

down. Mean peat temperature 10 cm below the surface is ca. 25 °C and shows little intra-annual variation (E. L. Wright *et al.*, unpublished data).

Experimental programme

Two approaches were used to investigate peat characteristics and CO₂ and CH₄ fluxes throughout the profile: (i) *in situ* monitoring of fluxes from the surface and at three depths within the profile and; (ii) *ex situ* incubation of peat from different depths.

Depth profiles of gas fluxes and peat cores were collected along a ca. 2.7 km transect across the peatland for three of the phasic communities identified by Phillips *et al.* (1997). The three communities examined were located near the edge of the peatland (82°24'6.17"W, 9°25'29.50"N), half-way to the central bog plain (82°24'22.61"W, 9°25'13.48"N), and at the edge of the central bog plain (82°24'47.70"W, 9°24'44.31"N) (Fig. 1). The sampling sites were dominated by the following species: *R. taedigera* (Palmae) (palm swamp), *C. panamensis* (Anacardiaceae) (forest swamp) and *Cyperus* sp. (Cyperaceae) (sawgrass plain; cf. Sjögersten *et al.* (2010) for further details of locations and vegetation composition).

In situ gas flux measurements

In situ gas fluxes were determined for the peat surface and at depths of 30, 60 and 100 cm to determine the contribution of surface and deeper peat layers to net CO₂ and CH₄ emissions. Measurements were made for all sites in July 2009, representing the onset of a period of increased rainfall, and August

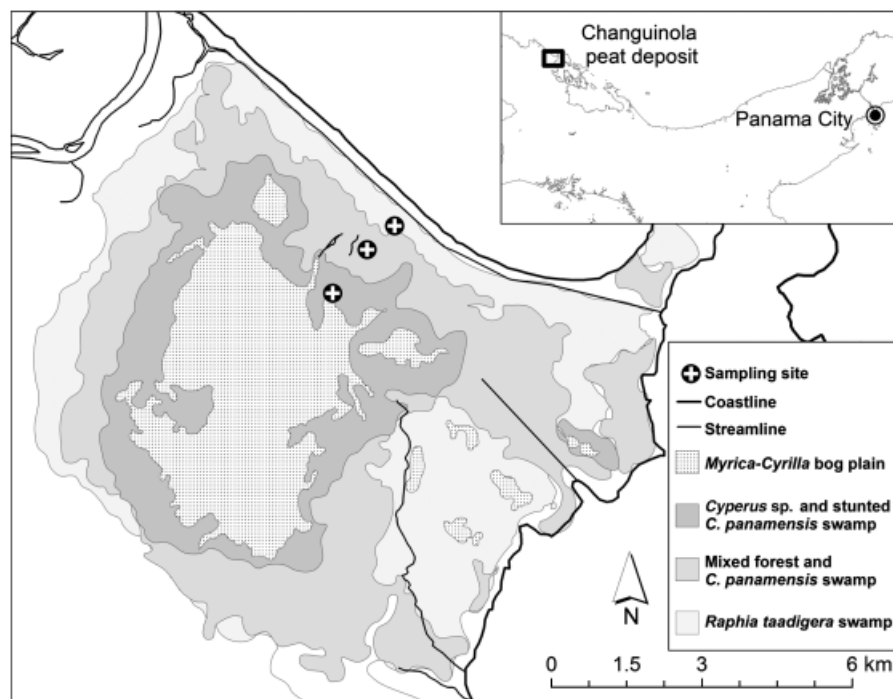


Fig. 1 Map of the Changuinola peat deposit, a portion of the San San Pond Sak wetland, in Western Panama. The dominant vegetation zones (reworked from Phillips *et al.*, 1997) and locations of the three sampling sites are shown; the *Raphia taedigera* site is closest to the coast, followed by the *Campnosperma panamensis* site and the *Cyperus* sp. site towards the centre of the peatland.

2009. Sampling locations at each site were located in four replicated blocks spaced at 20–30 m intervals with four gas sampling depths. The distance between sampling tubes within each block was 50 cm. The total number of plots was 48, comprising three vegetation types, four sampling depths and four replicates. In this method, the gas samples collected from the tubes to estimate gas fluxes are assumed to originate from a vertical column below the sampling tube. However, a proportion of the measured gas flux is likely to have originated from a wider area around the base of the tubes, possibly resulting in overestimation of the true gas production.

In situ gas fluxes were measured using diffusion tubes constructed from 5 cm diameter drainage pipes, open at both ends to allow gas emitted from the peat horizon at the bottom of the tube to migrate up through the water column within the tube. The tubes were inserted using a 3.8 cm diameter borer, which was pushed into the peat to the correct depth before inserting the sample tube over the borer. The tubes protruded 30 cm above the peat surface. When the borer was removed from inside the diffusion tubes, these were emptied of peat but filled rapidly with water. The diffusion tubes were covered with ventilated caps to allow gas exchange with the external atmosphere and ensure leaf material did not enter the tubes; they were then left to equilibrate for eight months. Gas samples were collected by attaching a 5 cm tall opaque head space to the diffusion tubes, giving a total volume of 0.69 dm³; a small fan ensured mixing of the head space air. Twenty-five milliliter samples of air were collected *via* a Suba-Seal[®] (Fisherbrand, Loughborough, UK) using a syringe 0, 2, 10 and 20 min after fitting the head space before transferring these to prepared 12 mL vacuumed exetainers (Labco, High Wycombe, UK). Surface gas samples were collected using a 10 cm tall head space with a volume of 0.45 dm³ placed directly on the peat surface at times 0 and 10 min; the sampling time was adjusted to account for the smaller head space (Yao *et al.*, 2009). All samples were shipped to the University of Nottingham for CO₂ and CH₄ analysis. As an overpressure was injected into the vials, it was easy to detect any loss of sample during transport; samples were discarded when this occurred (<2%). The samples from each head space were checked for linearity before the gas flux calculations.

Concurrently with removal of the peat cores in November 2007, surface CO₂ and CH₄ fluxes were measured in the field for comparison with the *ex situ* data. The sampling technique described above was again used, but with a larger head space volume of 7.8 dm³. Before sampling, the vegetation was carefully removed from the plots where necessary (mainly at the interior *Cyperus* site) by severing it at ground level, while roots and pneumatophores were left in place; removal of the above-ground vegetation may have resulted in underestimation of CH₄ and CO₂ emissions. Air samples (25 mL) were again collected using a syringe 0, 2, 10 and 20 min after placing the head space on the peat surface (Sjögersten *et al.*, 2010). Samples were taken from five plots situated at least 20 m apart for all three sites close to where the peat cores were collected and the diffusion tubes were installed. The depth of the water table was recorded within each diffusion tube relative to the ground surface using a ruler, and peat temperature was measured using a digital thermometer inserted to 10 cm depth in each block.

CO₂ and CH₄ concentrations were analysed simultaneously using a gas chromatograph (GC-2014, Shimadzu, Milton Keynes, UK) fitted with a flame ionizing detector for CH₄ and a thermal conductivity detector for CO₂. The GC was fitted with a 1 mL sample loop and a molecular sieve column.

Peat coring for ex situ measurements

Four 1 m long cores were taken at all three sampling sites, one of which was subsequently extended to a depth of 2 m; each core was located at least 20 m from neighbouring cores. The cores were taken using a simplified lightweight 7.6 cm internal diameter piston corer (Fisher *et al.*, 1992) designed to remove intact undisturbed cores using a vacuum to minimize compaction and ensure that the sampled material remained in the corer during recovery. After collection, the cores were kept upright and stored overnight at 4 °C. On the day after sampling, the cores were subdivided into 10 cm segments which were capped to avoid oxidation of the peat. The segments were allowed to settle and equilibrate at 24 °C for 2 h before sampling. Because of the disturbance of the loose surface layer, the 0–30 cm horizon was regarded as one mixed segment for determination of peat properties and separate 10 cm long surface cores were collected in the field.

Ex situ CO₂ and CH₄ flux measurements

CO₂ and CH₄ fluxes from each core segment were measured by head space analysis at 24 °C and as close to the *in situ* water content as possible. As removal of up to 2 m of hydraulic head increased the diffusion rate of gas through the peat, the *ex situ* gas flux measurements must be regarded as maximum potential rates. Owing to the disturbance of the 0–30 cm layer, CO₂ and CH₄ fluxes from this layer were not included in the analysis; instead, the separately collected 0–10 cm surface peat cores were used to determine surface CO₂ and CH₄ fluxes. Gas sampling was achieved by fitting a head space as described previously and immediately flushing this with nitrogen gas for 20 s to avoid oxidation of the peat; the core segments were left to stabilize for 30 min before sampling. Samples were collected 0 and 10 min after fitting the head space and injected into exetainers as described above. Gas fluxes from the *ex situ* sampling analyses were expressed on both a mass and land area basis to evaluate gas production in relation to: (i) the mass of peat (i.e. mass based) and (ii) the net contribution of each peat layer to surface fluxes (i.e. area based). Cumulative fluxes through the peat profile (single cores to a depth of ca. 2 m) were calculated from the *ex situ* measurements by summing the fluxes from each peat layer.

Determination of peat characteristics

Redox potential was determined for each core segment using a KDCMPtB11 redox probe (Thermo Electron Corporation, Altrincham, UK) before gas sampling. The probe was carefully inserted ca. 3 cm into the peat and allowed to stabilize for 5 min before completing the measurement. Note that redox potential is hard to determine accurately in *ex situ* heterogeneous samples hence these results must be treated with some caution. After determining gas fluxes, the individual segments of the peat cores were mixed and roots and organic fragments

>1 mm were removed. Living roots were separated by their colour and condition and all recovered material was rinsed in deionized water and air-dried. Moisture content was calculated for fresh subsamples by gravimetric loss after 70 h at 70 °C, while pH was determined using a 2:1 fresh peat:deionized water ratio and glass electrode. Bulk density (BD) was determined by recording the fresh weight of each 10 cm peat segment and calculating its dry weight using a wet-dry weight conversion factor based on the moisture content of a subsample from each segment. BD was calculated by dividing the dry peat weight by the sample volume. Organic matter content was estimated from loss on ignition (LOI) after ashing 250 mg of ground air-dried material at 550 °C for 4 h in borosilicate scintillation vials. Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were measured in water samples collected using 10 cm long Rhizon samplers constructed from hydrophilic porous polymer with a pore diameter of ca. 0.1 µm to exclude soil particles (Rhizosphere Research Products, Wageningen, The Netherlands). Samples were frozen during storage and transport and were subsequently analysed using a TOC-V/TN analyser (Shimadzu Corp, Kyoto, Japan). The total C content of the samples was measured by combustion and gas chromatography using a Flash EA1112 (Thermo Scientific, Waltham, MA, USA) total element analyser.

Solid state ^{13}C CPMAS NMR spectroscopy

Solid state ^{13}C NMR spectroscopy was used to determine the proportions of aliphatic, carbohydrate and aromatic C (Baldock & Preston, 1995). Peat samples were taken from 0 to 10, 90 to 100 and 170 to 190 cm depth (the depth of the deepest sample varied slightly between sites), while at the sawgrass site samples from 50 to 60 cm depth were also analysed. None of these samples contained macroscopic charcoal which, if present at high concentrations, can influence the measurement. NMR spectra were obtained using a DSX200 spectrometer (Bruker, Coventry, UK) equipped with double-bearing probes for cross polarization and magic angle spinning. The resonance frequency for ^{13}C was 50 MHz and the sample was spun at the magic angle with a speed of 7 kHz. The contact time and relaxation delay for the cross polarization technique were 2.0 ms and 3.0 s, respectively, with 20000 scans accumulated for high-power ^1H decoupling. All spectra were determined at ambient temperature and processed with a line-broadening factor of 50 Hz. Chemical shifts were calibrated using an external sample of tetrakis(trimethylsilyl)silane. The CP method, although sensitive, tends to overestimate the proportion of aliphatic C, although this effect is pronounced only in materials with a high proportion of polyaromatic C such as lignite and coal (Love *et al.*, 1992). This effect should not be significant for peat, which has only 5–10% aromatic C, most of which is not polyaromatic. The NMR-derived C concentration was calculated based on the total C content of the peat.

Statistical analysis

The results were analysed using Genstat version 13 (Lawes Agricultural Trust, Rothamsted Experimental Station, UK). *In*

situ CO_2 and CH_4 fluxes were analysed using a repeated measures ANOVA structure with site, depth and time as fixed effects. As significant interactions with time were found, the effects of site and depth were analysed separately for each month. *Ex situ* CO_2 and CH_4 flux measurements and peat properties were analysed using two separate ANOVAs. The first analysis included the replicated samples to a depth of 1 m for all three sites, with site and depth as fixed effects, while the second tested for depth effects for the three 2 m deep cores (i.e. one from each site). Because of the disturbance of the top 0–30 cm of the cores, the mean values for additional 10 cm deep surface cores collected for all sites were used as the '5 cm' depth point in the analysis. Mean values and standard errors of the mean are reported. All data were tested for normality and transformed if necessary to meet the normality assumption in the ANOVA. Statements made in the Results section are underpinned by statistical summaries presented in the figure legends. Owing to the unreplicated nature of the solid state ^{13}C CPMAS NMR data, only limited statistical analysis could be carried out for these results.

Results

Peat properties

Gravimetric moisture content was extremely high throughout the profile, ranging from 89 to 99% (Fig. 2a). pH ranged from 3.5 to 4.5 (Fig. 2b) and was highest in the surface peat layer, decreased sharply at 40 cm depth, and then remained relatively constant through the profile apart from at the *C. panamensis* site, where pH increased slowly from the surface minimum to a depth of 1 m. The peat was generally weakly reduced throughout the profile (Fig. 2c), with mean redox potentials for the entire profile of 282, 335 and 356 mV at the *R. taedigera*, *C. panamensis* and *Cyperus* sites, respectively.

LOI was generally extremely high, ranging between 82% and 99%, except for distinct layers of higher ash content at depths of 110–140 and 150 cm at the *R. taedigera* and *C. panamensis* sites (Fig. 2d). Dry BD was very low and always $<0.09 \text{ g cm}^{-3}$ (Fig. 2e). The BD of the surface peat (0–10 cm) was lowest at the *Cyperus* site (ca. 0.02 g cm^{-3}), but the values for depths of 10–120 cm were generally similar, ranging from 0.03 to 0.05 g cm^{-3} at all sites, although a marked increase was apparent between 120 and 140 cm at the *R. taedigera* and *C. panamensis* sites. The peak in BD at the *R. taedigera* site corresponded to a much lower LOI and a high pH for the same depth.

Root dry biomass did not vary significantly with depth within the upper 100 cm and was close to zero at depths >110 cm (Fig. 2f). The values were greatest at the *Cyperus* site for depths between 0 and 65 cm, with maximum values of ca. 360 g m^{-2} . However, at greater

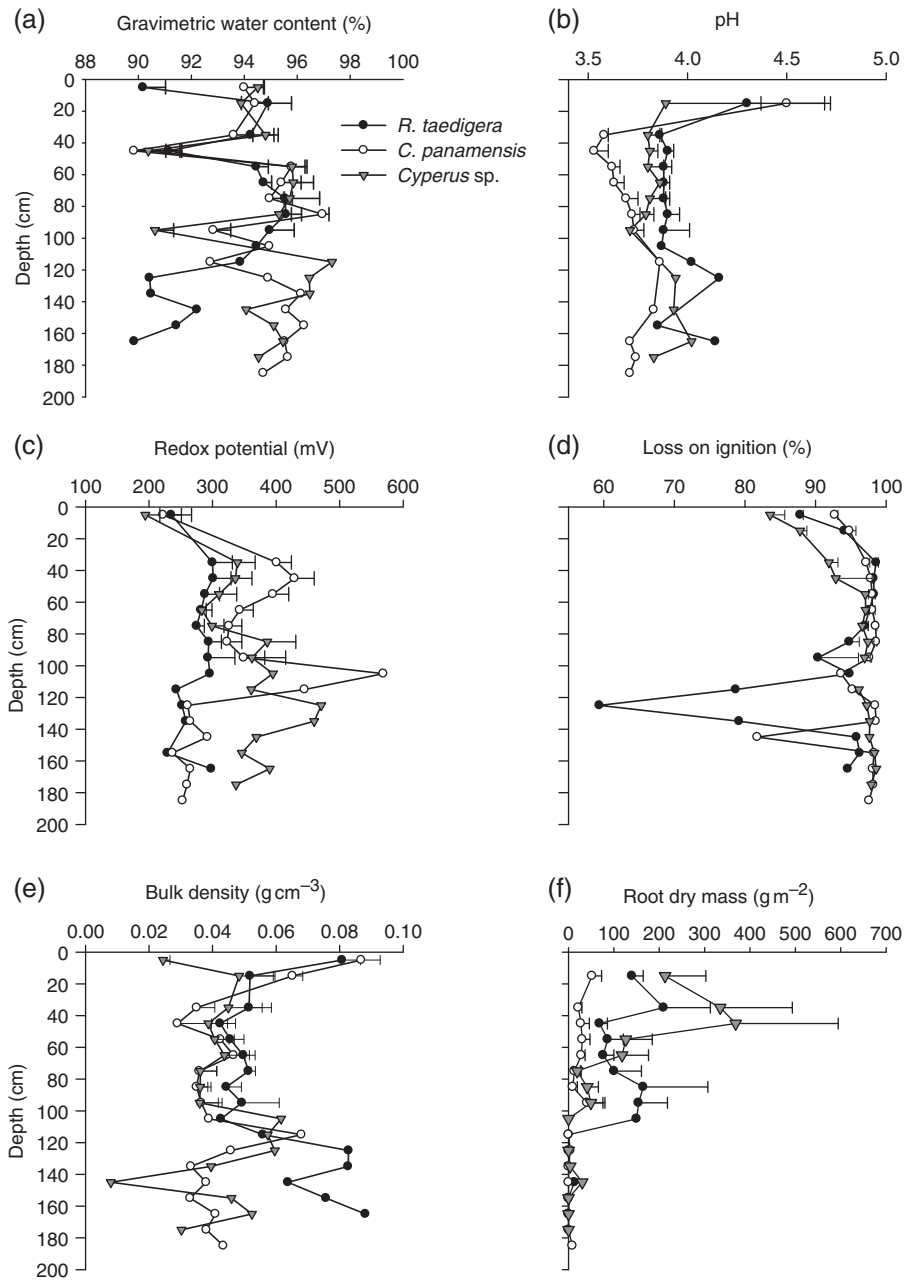


Fig. 2 Profiles of peat properties to a depth of 2 m for each site; $n = 5$ for 0–10 cm, $n = 4$ for 10–100 cm and $n = 1$ for 100–200 cm. Single standard errors of the mean are shown for depths of 0–100 cm. ANOVA outputs to a depth of 100 cm are: (a) gravimetric soil moisture content, Depth: $F_{8,108} = 7.32$, $P < 0.001$; Site: $F_{2,108} = 4.18$, $P = 0.019$; Site \times Depth: $F_{16,108} = 8.31$, $P < 0.001$; (b) pH, Depth: $F_{8,84} = 5.62$, $P < 0.001$; Site: $F_{2,84} = 29.13$, $P < 0.001$; Site \times Depth: $F_{16,84} = 1.05$, $P = 0.422$; (c) redox potential, Depth: $F_{8,110} = 10.63$, $P < 0.001$; Site: $F_{2,110} = 9.78$, $P < 0.001$; Site \times Depth: $F_{16,110} = 1.36$, $P = 0.180$; (d) loss on ignition, Depth: $F_{8,109} = 12.73$, $P < 0.001$; Site: $F_{2,109} = 11.46$, $P < 0.001$; Site \times Depth: $F_{16,109} = 2.35$, $P < 0.01$; (e) bulk density, Depth: $F_{8,110} = 6.28$, $P < 0.001$; Site: $F_{2,110} = 11.36$, $P < 0.001$ and Site \times Depth: $F_{16,110} = 4.12$, $P < 0.001$ and (f) root biomass, Depth: $F_{7,95} = 1.60$, $P = 0.15$; Site: $F_{2,95} = 2.79$, $P = 0.11$; Depth \times Site: $F_{14,95} = 1.44$, $P = 0.16$. Single cores ($n = 1$ at each site) 15–185 cm, Depth: $F_{16,47} = 1.96$, $P = 0.056$.

depths (75–105 cm), root biomass was greatest at the *R. taedigera* site, although the values were distinctly lower (150 g m^{-2}) than in the surface layers at the *Cyperus* site. Root biomass was consistently lowest for *C. panamensis* throughout the profile.

The concentrations of DOC and TDN varied significantly among sites, with the highest concentrations being recorded at the *R. taedigera* site and the lowest at the *Cyperus* site (Fig. 3). Neither DOC nor DN varied significantly with depth.

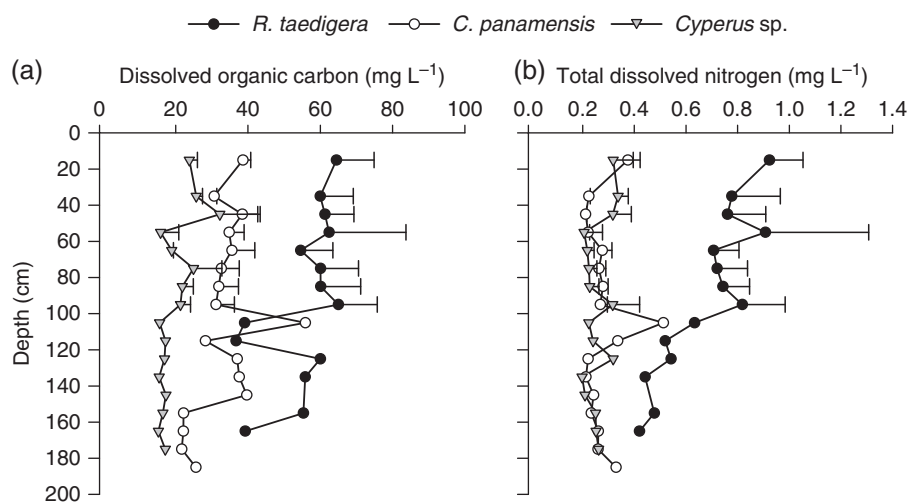


Fig. 3 Profiles of dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) to a depth of 2 m for each site; $n = 4$ for 10–100 cm, $n = 1$ for 100–200 cm. Single standard errors of the mean are shown for depths of 0–100 cm, ANOVA summaries to a depth of 100 cm are: (a) DOC, Depth: $F_{7,95} = 0.30$, $P = 0.95$; Site: $F_{2,95} = 56.20$, $P < 0.001$; Site \times Depth: $F_{14,95} = 0.21$, $P = 0.99$; (b) DN, Depth: $F_{7,95} = 0.44$, $P = 0.88$; Site: $F_{2,95} = 69.79$, $P < 0.001$; Site \times Depth: $F_{14,95} = 0.45$, $P = 0.95$.

Solid state CPMAS ^{13}C NMR spectroscopy

Clear changes in peat chemistry with depth were observed (Table 1; Fig. 4). The marked increase in the ratio of aromatic C to carbohydrate and distinct decreases in the relative intensity of chemical shifts associated with polysaccharide resonances at 106, 72 and 64 ppm indicate carbohydrate decay. By contrast, the ratio of carbohydrates to aliphatic compounds showed no clear trend with depth. Another distinct trend at all sites was a decrease in the methoxyl to aromatic C ratio with depth.

The most pronounced difference between sites was the greater quantity of carbohydrates found throughout the profile at the *Cyperus* site. Overall, the mean proportion of labile C present as carbohydrate (spectral range 50–110 ppm) averaged across the entire profiles for all three sites was 21%. The values were greatest at the *Cyperus* site, near the centre of the peatland (25%), followed by the *C. panamensis* and *R. taedigera* sites (19% and 18%, respectively).

In the aromatic region of the spectrum, peaks at 135, 148 and 153 ppm are assigned to C bound to oxygen and/or other C atoms in the stable part of the aromatic lignin structure (Fig. 4). This component of the lignin structure remained unaltered with respect to depth in all cores, indicating that the aromatic C in lignin is stable.

In situ fluxes of CO_2 and CH_4

CO_2 fluxes did not vary significantly between sites or with depth when the combined data for all sites sampled in July 2008 were analysed (Fig. 5a–c). How-

ever, in August, CO_2 fluxes (Fig. 5d–f) were greatest for the surface horizon at all three sites, ranging from 320–500 $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$. Fluxes from the surface layer were two to three-fold higher than at 30 cm or greater depths and the values were comparable for all sites. The contrasting patterns for CO_2 fluxes between months are reflected by the significant Month \times Depth interaction ($F_{3,67} = 3.97$; $P < 0.05$) resulting from the greatly increased surface efflux in August at the *C. panamensis* and *Cyperus* sites.

There was no significant difference in CH_4 fluxes among sites in July (Fig. 6a–c), although a significant depth effect was found across all three sites, with emissions being greatest 30 cm below the surface. CH_4 fluxes were very low at depths > 30 cm at the *R. taedigera* and *C. panamensis* sites, but detectable fluxes were apparent at 60 and 100 cm at the *Cyperus* site. In August, CH_4 fluxes were greatest from the surface layer at the *R. taedigera* and *C. panamensis* sites and values for the deeper layers were very low (Fig. 6d–f). However, no significant variation with depth was found for the *Cyperus* site and the flux from the surface layer was much lower than at the other two sites. The influence of time on the depth distribution of CH_4 fluxes was significant (Month \times Depth: $F_{3,76} = 5.79$; $P = 0.002$).

At the time of sampling in July and August 2008, neither water table nor substrate temperature varied significantly among sites. Cumulative rainfall during the preceding month was also similar, being 322 and 362 mm in July and August, respectively. The water table tended to be just below the peat surface (average of 8 cm) at the *R. taedigera* site and just above the surface (average of 6 cm) at the two sites closer to the interior of

Table 1 Composition of material from peat cores collected from three contrasting vegetation communities based on ¹³C solid state CPMAS NMR

Site	Depth (cm)	C (mg g ⁻¹)	Aliphatic (0–50)		Methoxyl (50–60)		Carbohydrate (60–90)		Carbohydrate + Aliphatic lignin (90–110)		Aromatic lignin (110–160)		Carboxyl-Carbonyl (160–200)		Methoxyl/Aromatic		Aromatic/Aliphatic		Carbohydrate/Aliphatic		Aromatic/Carbohydrate																																																																																		
			236 (43.8)	177 (31.2)	94 (24.3)	168 (34.6)	183 (34.7)	172 (32.7)	107 (25.3)	86 (17.2)	150 (27.4)	160 (28.8)	23 (4.8)	38 (6.6)	33 (8.6)	35 (7.3)	35 (6.7)	30 (5.7)	39 (9.1)	60 (11.9)	40 (7.4)	39 (7.0)	117 (24.0)	130 (22.9)	104 (27.0)	142 (29.2)	125 (23.7)	116 (22.0)	183 (43.2)	227 (45.4)	159 (29.1)	149 (26.8)	54 (11.0)	147 (25.9)	109 (28.3)	74 (15.3)	118 (22.3)	127 (24.0)	43 (10.1)	86 (17.2)	117 (21.4)	124 (22.4)	35 (7.2)	38 (6.6)	15 (3.9)	35 (7.3)	39 (7.3)	49 (9.3)	26 (6.1)	17 (3.3)	51 (9.4)	50 (9.0)	0.44	0.26	0.28	0.41	0.24	0.26	0.60	0.29	0.25	0.27	0.23	0.83	1.16	0.44	0.64	0.73	0.40	1.00	0.78	0.50	0.73	1.11	0.85	0.68	0.67	1.71	2.63	1.06	0.93	0.46	1.13	1.05	0.52	0.94	1.09	0.23	0.83	1.16	0.44	0.64	0.73	0.40	1.00	0.78	0.50	0.73	1.11	0.85	0.68	0.67	1.71
<i>Raphia taedigera</i>	5	489	236 (43.8)	177 (31.2)	94 (24.3)	168 (34.6)	183 (34.7)	172 (32.7)	107 (25.3)	86 (17.2)	150 (27.4)	160 (28.8)	23 (4.8)	38 (6.6)	33 (8.6)	35 (7.3)	35 (6.7)	30 (5.7)	39 (9.1)	60 (11.9)	40 (7.4)	39 (7.0)	117 (24.0)	130 (22.9)	104 (27.0)	142 (29.2)	125 (23.7)	116 (22.0)	183 (43.2)	227 (45.4)	159 (29.1)	149 (26.8)	54 (11.0)	147 (25.9)	109 (28.3)	74 (15.3)	118 (22.3)	127 (24.0)	43 (10.1)	86 (17.2)	117 (21.4)	124 (22.4)	35 (7.2)	38 (6.6)	15 (3.9)	35 (7.3)	39 (7.3)	49 (9.3)	26 (6.1)	17 (3.3)	51 (9.4)	50 (9.0)	0.44	0.26	0.28	0.41	0.24	0.26	0.60	0.29	0.25	0.27	0.23	0.83	1.16	0.44	0.64	0.73	0.40	1.00	0.78	0.50	0.73	1.11	0.85	0.68	0.67	1.71	2.63	1.06	0.93																						
<i>Campnosperma panamensis</i>	5	566	177 (31.2)	94 (24.3)	168 (34.6)	183 (34.7)	172 (32.7)	107 (25.3)	86 (17.2)	150 (27.4)	160 (28.8)	23 (4.8)	38 (6.6)	33 (8.6)	35 (7.3)	35 (6.7)	30 (5.7)	39 (9.1)	60 (11.9)	40 (7.4)	39 (7.0)	117 (24.0)	130 (22.9)	104 (27.0)	142 (29.2)	125 (23.7)	116 (22.0)	183 (43.2)	227 (45.4)	159 (29.1)	149 (26.8)	54 (11.0)	147 (25.9)	109 (28.3)	74 (15.3)	118 (22.3)	127 (24.0)	43 (10.1)	86 (17.2)	117 (21.4)	124 (22.4)	35 (7.2)	38 (6.6)	15 (3.9)	35 (7.3)	39 (7.3)	49 (9.3)	26 (6.1)	17 (3.3)	51 (9.4)	50 (9.0)	0.44	0.26	0.28	0.41	0.24	0.26	0.60	0.29	0.25	0.27	0.23	0.83	1.16	0.44	0.64	0.73	0.40	1.00	0.78	0.50	0.73	1.11	0.85	0.68	0.67	1.71	2.63	1.06	0.93																							
<i>Cyperus sp.</i>	5	501	177 (31.2)	94 (24.3)	168 (34.6)	183 (34.7)	172 (32.7)	107 (25.3)	86 (17.2)	150 (27.4)	160 (28.8)	23 (4.8)	38 (6.6)	33 (8.6)	35 (7.3)	35 (6.7)	30 (5.7)	39 (9.1)	60 (11.9)	40 (7.4)	39 (7.0)	117 (24.0)	130 (22.9)	104 (27.0)	142 (29.2)	125 (23.7)	116 (22.0)	183 (43.2)	227 (45.4)	159 (29.1)	149 (26.8)	54 (11.0)	147 (25.9)	109 (28.3)	74 (15.3)	118 (22.3)	127 (24.0)	43 (10.1)	86 (17.2)	117 (21.4)	124 (22.4)	35 (7.2)	38 (6.6)	15 (3.9)	35 (7.3)	39 (7.3)	49 (9.3)	26 (6.1)	17 (3.3)	51 (9.4)	50 (9.0)	0.44	0.26	0.28	0.41	0.24	0.26	0.60	0.29	0.25	0.27	0.23	0.83	1.16	0.44	0.64	0.73	0.40	1.00	0.78	0.50	0.73	1.11	0.85	0.68	0.67	1.71	2.63	1.06	0.93																							

Functional groups associated with specific spectral ranges (ppm) are shown as NMR-derived C concentrations in the samples (mg g⁻¹); values in brackets are the proportion (%) of each C fraction based on total C content. The concentration ratios between functional groups are shown to illustrate their relative distribution within the peat profiles. Values represent single measurements for each depth at each site.

the peatland (Table 2). However, rainfall during the 24 h period preceding sampling rapidly and substantially affected the height of the water table by up to 10–15 cm (E. L. Wright, personal observation).

Ex situ CO₂ and CH₄ emissions

Peat from the *C. panamensis* and *Cyperus* sites tended to respire more rapidly to a depth of ca. 40 cm than that from the *R. taedigera* site when expressed on a unit peat mass basis, with a maximum CO₂ production of ca. 0.07 mg CO₂ g⁻¹ h⁻¹ for both the *C. panamensis* and *Cyperus* sites (Fig. 7a). Below that depth, CO₂ fluxes at the *R. taedigera* site were greater than at the *C. panamensis* and *Cyperus* sites, with a peak of 0.075 mg CO₂ g⁻¹ h⁻¹ at 55 cm depth. There was a second peak in CO₂ emissions between 120 and 150 cm at all three sites. CO₂ production expressed on a unit land area basis was greatest for *R. taedigera* in the top 1 m of peat, reflecting the higher BD of peat at this site (Figs. 7c and 2e). CO₂ fluxes peaked at 120–160 cm depth at all sites, with maximum values of ca. 370, 280 and 230 mg CO₂ m⁻² h⁻¹ being obtained for *C. panamensis*, *R. taedigera* and *Cyperus*, respectively (Fig. 7c).

CH₄ fluxes expressed on a peat dry mass basis were significantly greater for the *R. taedigera* and *Cyperus* sites at depths of 0–130 cm (Fig. 7b), with maximum recorded fluxes of 0.0010 and 0.0018 mg CH₄ g⁻¹ h⁻¹, respectively. When expressed per unit land area, CH₄ fluxes were significantly greater at the *R. taedigera* and *Cyperus* sites than at the *C. panamensis* site, with a maximum value of ca. 7 mg CH₄ m⁻² h⁻¹ being recorded at the *R. taedigera* site (Fig. 7d).

Cumulative CO₂ fluxes (i.e. the sum of fluxes measured from the individual 10 cm segments in the *ex situ* study) to a depth of 1.6 m were, respectively, 2600, 2400 and 2200 mg CO₂ m⁻² h⁻¹ for the *R. taedigera*, *C. panamensis* and *Cyperus* sites. Cumulative CH₄ fluxes showed greater variation among sites, being greatest for *R. taedigera* followed by *Cyperus* and *C. panamensis* (39, 26 and 11 mg CH₄ m⁻² h⁻¹, respectively). Cumulative CO₂ and CH₄ fluxes were an order of magnitude greater than the surface fluxes measured at the time of coring. Surface CO₂ and CH₄ fluxes measured at the same sites in November 2007 were 202 ± 46, 104 ± 54 and 289 ± 44 mg CO₂ m⁻² h⁻¹, and 1.03 ± 0.87, -0.27 ± 0.39 and 1.12 ± 0.39 mg CH₄ m⁻² h⁻¹ for the *R. taedigera*, *C. panamensis* and *Cyperus* sites, respectively.

Percentage moisture content and BD of the peat at each site and depth examined accounted for 33% and 26%, respectively, of the variation in CO₂ fluxes (Fig. 8a and b), with CO₂ fluxes being greater for peat with a high moisture content and low BD. In contrast, CH₄ fluxes were not correlated with either moisture content

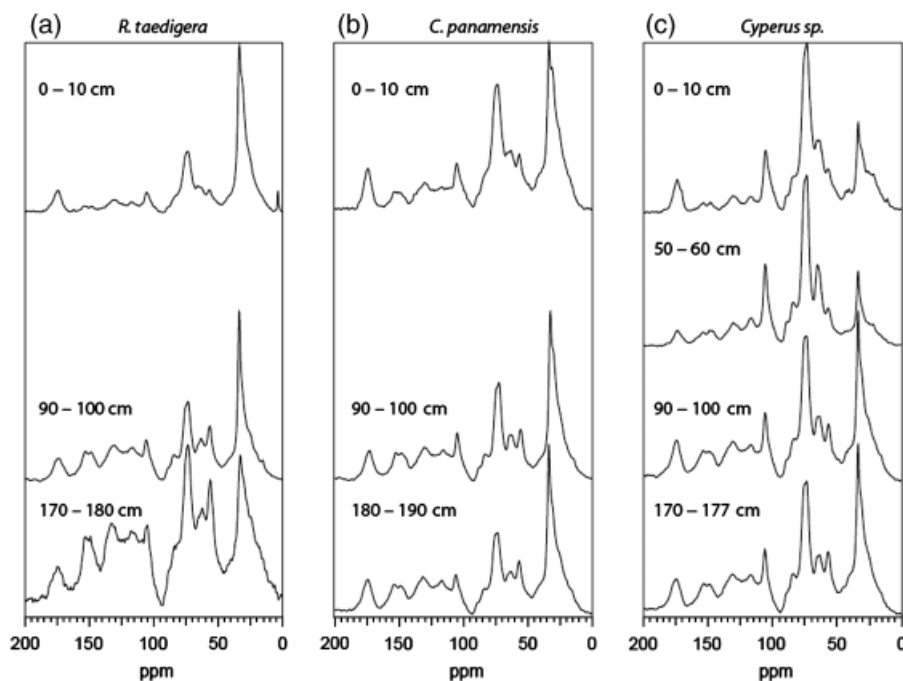


Fig. 4 ^{13}C solid state MAS NMR spectra for depths of 0–10, 50–60*, 90–100 and 170–180 cm for: (a) *R. taedigera*; (b) *C. panamensis* and (c) *Cyperus* sp. **Cyperus* site only.

or BD (data not shown). Redox potential, root biomass, DOC and TDN did not contribute significantly to the observed variation in CO_2 and CH_4 fluxes.

In addition to the relationship between CO_2 fluxes and the physical properties of the peat, there were strong positive relationships between CO_2 and CH_4 fluxes and the quantity of labile C present in the peat (Fig. 9). CO_2 emissions were most strongly predicted by the ratio of carbohydrate to aliphatic functional groups (indicating the degree of decomposition), accounting for 30% of the variance, while 63% of the variation in CH_4 fluxes was attributable to the concentration of carbohydrates (60–90 ppm) in the peat.

Discussion

In contrast to SE Asia (Couwenberg *et al.*, 2010), the *in situ* and *ex situ* measurements both show clearly that the deeper peat layers may contribute substantially to the net efflux of CO_2 from the peatland examined here. The *in situ* measurements showed that subsurface CO_2 production made a greater contribution to net CO_2 emissions from the top 30 cm in August than in July (Fig. 5). This shift in CO_2 emissions suggests the occurrence of strong temporal variability despite the permanently high water table and stable peat temperature, in sharp contrast to findings in SE Asia where fluctuations in the water table were the main driver of temporal variation in CO_2 fluxes (Jauhiainen *et al.*, 2005; Melling

et al., 2005a,b; Hirano *et al.*, 2007). Measurements extending over longer time periods and with greater temporal resolution are needed to establish the factors controlling temporal variability in CO_2 fluxes in the San San Pond Sak peatland.

The high cumulative CH_4 efflux from the *ex situ* peat cores highlights the potential for substantial emissions of this potent greenhouse gas from tropical peatlands, although the relatively low *in situ* net emissions from the peat surface in July, despite substantial production at a depth of 30 cm (Fig. 6), suggests strong oxidation of CH_4 in the surface peat. In August, CH_4 emissions from the surface peat were much greater and within the upper range of values reported for SE Asian peatlands (Couwenberg *et al.*, 2010). This suggests that the peatland can switch rapidly from being a weak to a strong source of CH_4 and highlights that, as for CO_2 , strong variation in CH_4 emission can occur without variation in the water table or peat temperature. The depth distribution of CO_2 and CH_4 fluxes did not vary greatly among sites, suggesting that gas production does not depend directly on the properties of distinct vegetation communities, such as the nutrient status of the litter produced (Troxler, 2007; Sjögersten *et al.*, 2010).

The large *ex situ* gas fluxes relative to the *in situ* fluxes may well reflect the slow gas diffusion through the water-saturated peat profile *in situ*. High gas concentrations at depth in peat profiles have been recorded previously in tropical peatlands (e.g. Inbushi *et al.*,

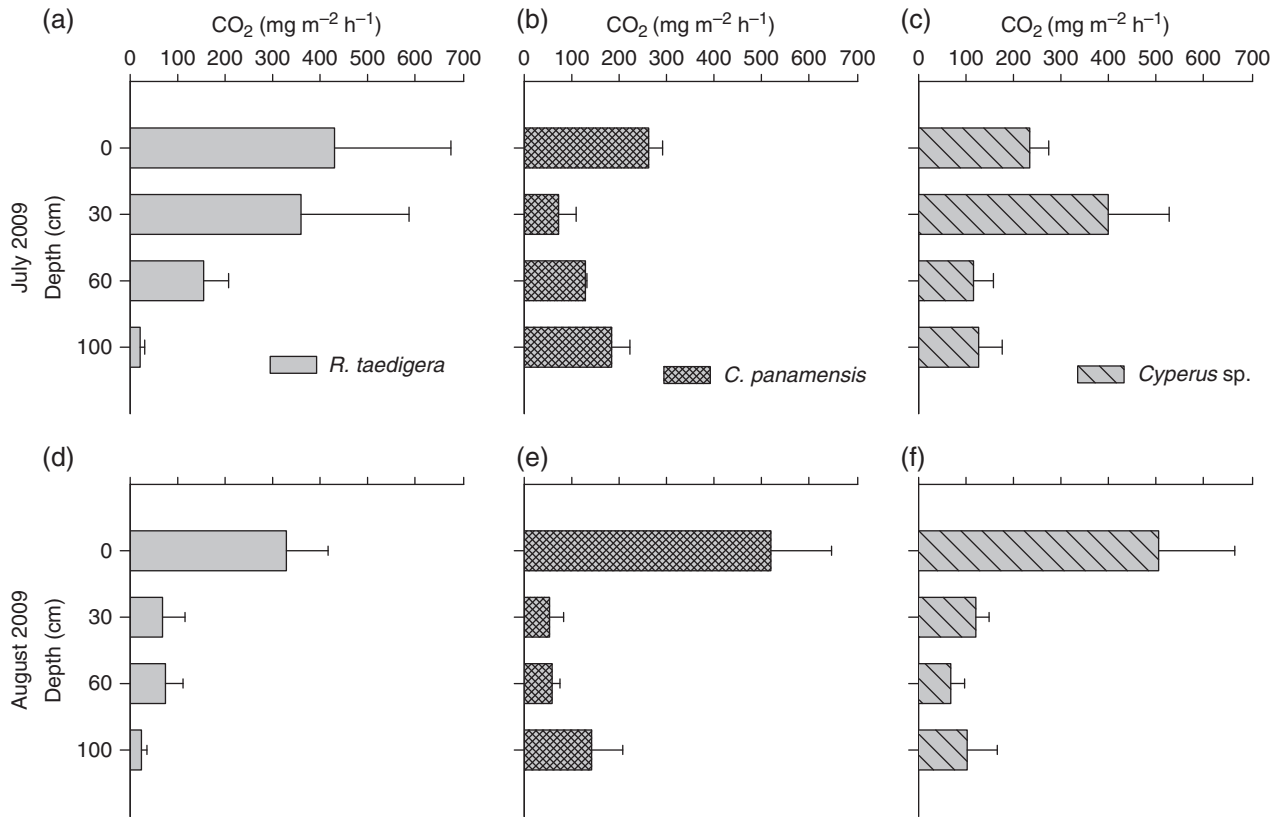


Fig. 5 Mean *in situ* CO₂ fluxes during July (a–c) and August 2009 (d–f) at the *R. taedigera*, *C. panamensis* and *Cyperus* sites. Fluxes shown for specific depths represent gas production from the base of the sampling tube up to that depth in the profile. Single standard errors of the mean are shown ($n = 4$). ANOVA summaries for July are: Depth, $F_{3,32} = 0.79$, $P = 0.52$; Site, $F_{2,32} = 0.23$, $P = 0.79$, and for August are: Depth, $F_{3,42} = 18.43$, $P < 0.001$; Site, $F_{2,42} = 0.49$, $P = 0.62$.

1998; Melling *et al.*, 2005a). The *ex situ* fluxes reported here should therefore be interpreted as potential fluxes following removal of the hydraulic head, rather than a measure of the actual contribution of individual peat layers to surface emissions. The release of CH₄ from deep peat layers to the atmosphere is likely to be mediated both by the dominant vegetation (Joabsson & Christensen, 2001) and ebullition, which is known to be an important transport mechanism for the release of CH₄ in northern peatlands (Comas *et al.*, 2007).

The high *in situ* CO₂ fluxes in August suggest substantial losses of C from the peatland if extrapolated to an annual timescale. Such large C losses must be balanced by similarly high gross net primary productivity to maintain the C accumulation rates estimated by Phillips *et al.* (1997). High tree basal areas have been reported for the *R. taedigera* and *C. panamensis* sites (Sjögersten *et al.*, 2010), but further work on their productivity and C allocation is needed to determine the C balance of the peatland. Indeed, substantial below ground inputs of labile C from the trees might be an important contributor to the high *in situ* CO₂ and CH₄ fluxes, analogous to the reports of strong direct

controls of gas production by the vegetation in northern peatlands (Joabsson & Christensen, 2001).

The strong relationship between C fluxes and peat composition (Fig. 9) suggests that CO₂ and CH₄ production were substrate-limited to a depth of 2 m as fluxes of these gases depend on the type and quantity of carbohydrates present. The greater CO₂ and CH₄ fluxes in the surface peat at the *Cyperus* sites (Fig. 7) are likely to be related to the greater quantities of carbohydrates in the peat. The greater lability of peat at the *Cyperus* site is reflected by its higher microbial biomass C content and extracellular enzyme activity (e.g. cellobiohydrolase, xylanase, glucosidase) in the surface peat compared with sites closer to the edge of the peatland (Sinsabaugh *et al.*, 2008; Sjögersten *et al.*, 2010). The accumulation of deep carbohydrate-rich peat at the *Cyperus* sites may reflect nutrient limitation of the heterotrophic microbial community, resulting in slow decomposition and preservation of carbohydrates (Phillips *et al.*, 1997; Sjögersten *et al.*, 2010). In contrast, the *R. taedigera* peat had relatively high CH₄ release despite low carbohydrate concentrations; however, this site has higher substrate nutrient levels (Sjögersten *et al.*, 2010).

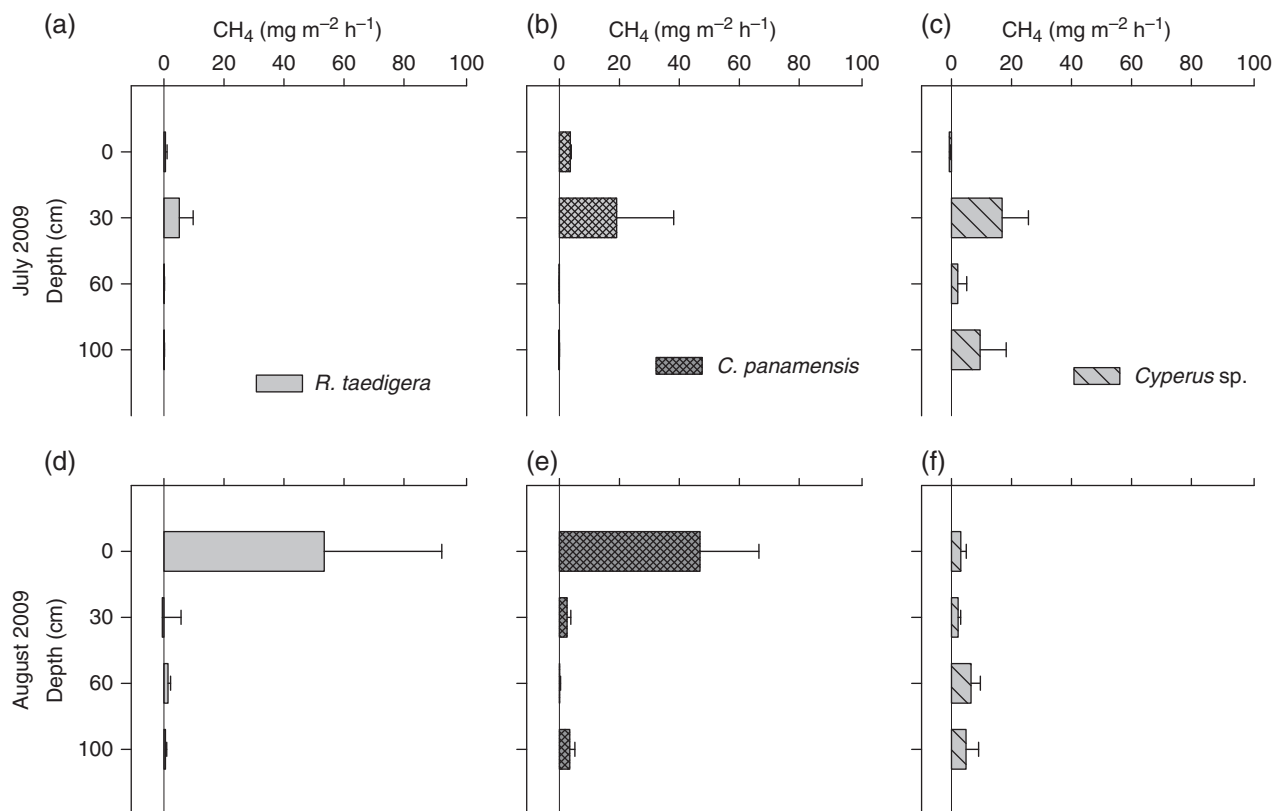


Fig. 6 Mean *in situ* CH₄ fluxes during July (a–c) and August 2009 (d–f) at the *R. taedigera*, *C. panamensis* and *Cyperus* sites. The fluxes shown for specific depths represent gas production from the base of the sampling tube up to that depth in the profile. Single standard errors of the mean are shown ($n = 4$). ANOVA summaries for July were: Depth, $F_{3,37} = 4.55$, $P < 0.05$; Site, $F_{2,37} = 0.48$, $P = 0.63$, and for August were Depth, $F_{3,46} = 6.45$, $P < 0.01$; Site, $F_{2,46} = 0.37$, $P = 0.70$.

Table 2 Water table and peat temperature for all sites measured concurrently with the *in situ* gas sampling ($n = 4$)

	Water table (cm) July	Water table (cm) August	Soil temperature (°C) July	Soil temperature (°C) August
<i>Raphia taedigera</i>	-13.9 ± 0.7	-2.3 ± 1.4	25.2 ± 0.3	25.8 ± 0.9
<i>Camposperma panamensis</i>	6.8 ± 0.6	1.3 ± 2.1	24.8 ± 0.2	25.0 ± 0
<i>Cyperus</i> sp.	5.2 ± 0.3	10.0 ± 1.3	26.6 ± 0.7	27.2 ± 2.2

Means and SEM are shown. Negative values indicate depth of water table below the ground surface.

and DOC and TDN concentrations, which may contribute to the overall higher emissions from this site. The *R. taedigera* site exhibited the greatest cumulative CO₂ and CH₄ emissions per unit land area to a depth of ca. 1.6 m due to the combination of the high lability and slightly greater density of the peat.

Approximately 30% of the peat C in San San Pond Sak was present in the form of carbohydrate compounds which are considered to be readily accessible for microbial degradation. The solid state ¹³C NMR results clearly indicate progressive decay of carbohydrates relative to lignin with depth at all three sites, as indicated by the systematic decrease of the carbohydra-

te:lignin ratio (Fig. 4; Table 1) and the decreasing methoxyl:aromatic ratio resulting from microbial cleavage of aromatic methoxyl moieties (Vane *et al.*, 2003). Compared with other peatlands (Krull *et al.*, 2004; Grover & Baldock, 2010), the proportion of carbohydrates (at chemical shifts 60–110 ppm) in the surface peat was low (117–183 mg g⁻¹), while the proportion of aliphatic C (at chemical shifts 0–50 ppm) was comparatively high (107–236 mg g⁻¹) (Table 1). This suggests either a rapid initial loss of carbohydrates and that the surface peat material was already depleted of labile C, or that aliphatic C is an important component of the C inputs. The relative decay of lignin and cellulose there-

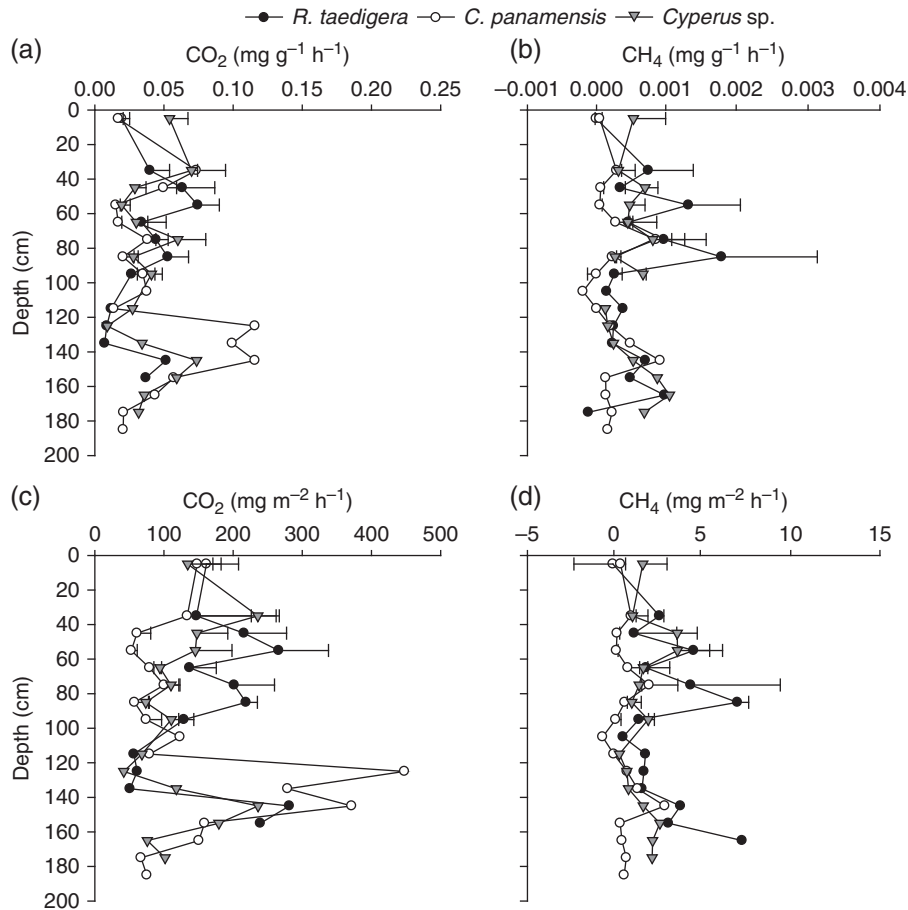


Fig. 7 Fluxes of CO₂ (a, c) and CH₄ (b, d) expressed on the basis of peat mass (a, b) and land surface area (c, d) throughout the profile. Single standard errors of the mean are shown for depths ≤ 100 cm ($n = 5$ for 0–10 cm and $n = 4$ for 10–100 cm). Values for depths > 100 cm are unreplicated. ANOVA summaries for 5–95 cm were: (a) Depth: $F_{7,83} = 3.78$, $P = 0.002$; Site: $F_{2,83} = 3.49$, $P < 0.05$; Site \times Depth: $F_{14,83} = 3.71$, $P < 0.001$; (b) Depth: $F_{7,85} = 1.51$, $P = 0.18$; Site: $F_{2,85} = 4.38$, $P < 0.05$; Site \times Depth: $F_{14,85} = 1.36$, $P = 0.20$; (c) Depth: $F_{7,83} = 1.65$, $P = 0.138$; Site: $F_{2,83} = 10.13$, $P < 0.001$; Site \times Depth: $F_{14,83} = 1.92$, $P < 0.05$; (d) Depth: $F_{7,85} = 1.42$, $P = 0.21$; Site: $F_{2,85} = 6.29$, $P < 0.01$; Site \times Depth: $F_{14,85} = 1.62$, $P = 0.10$. ANOVA summaries for 5–185 cm (one core from each site) were: (a) Depth: $F_{16,53} = 1$, $P < 0.05$; (b) Depth: $F_{16,55} = 0.93$, $P = 0.5$; (c) Depth: $F_{16,53} = 1.24$, $P = 0.28$; (d) Depth: $F_{16,55} = 0.89$, $P = 0.59$.

fore provides a more reliable measure of decomposition than ratios involving aliphatic compounds, as has also been shown for subtropical (Orem & Hatcher, 1986; Krull *et al.*, 2004), alpine (Grover & Baldock, 2010) and subarctic communities (Sjöggersten *et al.*, 2003).

The higher cellulose content of peat at the *Cyperus* site is comparable to the shifts in the organic chemistry of peat with depth and between peatland vegetation communities found in domed peat deposits in Sarawak, Malaysia (Calvert *et al.*, 1991). In Sarawak, the highest cellulose content was associated with peat under herbaceous vegetation, while deeper peat and peat formed from woody vegetation showed strong signals from lignin (Calvert *et al.*, 1991; Orem *et al.*, 1996). Deep peat layers in tropical bogs in Kalimantan, Borneo have undergone substantial microbial degradation (Dehmer,

1993), suggesting that it is peat located closer to the surface that contributes most to gas emissions. Peat from San San Pond Sak produced both CO₂ and CH₄ to a depth of 2 m *ex situ* and the values did not decline strongly with depth, indicating that the peat was relatively labile throughout this depth range. The NMR data indicate that decomposition was lower than that of surface peats in Indonesia which had a low carbohydrate content (9%; Orem *et al.*, 1996). The NMR data and high gas fluxes suggest that peat in San San Pond Sak is labile to greater depth than in SE Asia (Orem *et al.*, 1996; Melling *et al.*, 2005a). We speculate that the permanently high water table in the wetland examined here limits decomposition to a greater extent than in SE Asia, where greater draw-down of the water table occurs (e.g. Jauhainen *et al.*, 2005).

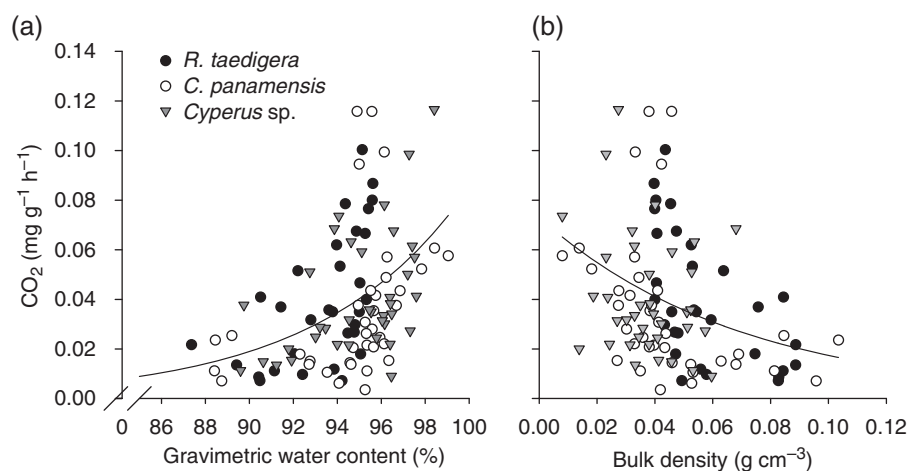


Fig. 8 Relationship between CO_2 flux and (a) percentage moisture content; $F_{1,114} = 58.06$, $P < 0.001$ and (b) bulk density of peat, $F_{1,115} = 41.14$, $P < 0.001$.

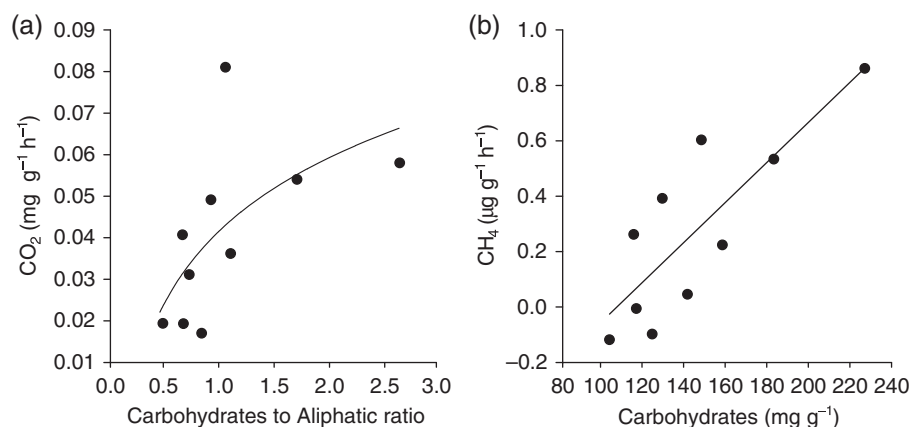


Fig. 9 Relationship between *ex situ* CO_2 fluxes and: (a) the ratio between carbohydrates and aliphatic C (log-linear regression: $F_{1,8} = 4.85$, $P = 0.059$, variance explained 30%); and (b) the carbohydrate content of the peat (linear regression: $F_{1,8} = 16.40$, $P < 0.01$, variance explained 63%).

With respect to the relationships between CO_2 fluxes, BD and soil moisture content (Fig. 8), we speculate that these reflect to some extent either substrate lability, i.e. the relatively low density peat at the *Cyperus* site tended to be more carbohydrate-rich, or that supplies of O_2 and labile DOC (Charman *et al.*, 1994) to depth through highly permeable peat stimulated respiration. However, the measured profiles for DOC (Fig. 3) did not provide reliable predictions of gas production. The density of peat was generally low and within the range reported for tropical peatlands (Shimada *et al.*, 2001; Page *et al.*, 2004; Lahteenoja *et al.*, 2009). It is also interesting to note that BD did not change consistently with depth to 2 m. Similarly, BD was low throughout the profile in peatlands in Kalimantan to a depth of 9 m and in some peats in the Amazon to depths of 4.9 m (Page *et al.*, 2004; Lahteenoja *et al.*, 2009). These observations suggest that

low BD may be an important feature of tropical peatlands compared with the denser peat found at depth in temperate and boreal peatlands (Laiho *et al.*, 2004; Danevčič *et al.*, 2010).

Redox potential did not explain the variation in CO_2 and CH_4 fluxes from peat cores from the San San Pond Sak peatland. Similarly, spatial variation in CO_2 and CH_4 fluxes under field conditions have been found to be independent of redox potential (Ueda *et al.*, 2000; Chimner & Ewel, 2004; Hadi *et al.*, 2005), suggesting that other soil properties, such as nutrient status, are more important drivers (Wright & Reddy, 2001; Hadi *et al.*, 2005; Yu *et al.*, 2007). However, the relatively high redox potentials observed throughout the profile to a depth of 2 m and the high root biomass down to ca. 110 cm (Fig. 2) may have been at least partly responsible for the large gas production in the subsurface peat (Figs.

5–7; Bergman *et al.*, 1999; Metcalfe *et al.*, 2007; Yu *et al.*, 2007, Seo & Dehaune 2010).

Climate change predictions for Panama suggest an increase in air temperature of up to 3.5 °C and a reduction in precipitation (Meehl *et al.*, 2007), potentially lowering water tables in the peatland. As water table draw-down has been shown to increase CO₂ emissions from SE Asian peatlands (Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009), it is plausible that any reduction in water table resulting from climate change would increase CO₂ emissions from San San Pond Sak, a view supported by the increased CO₂ fluxes from experimentally drained surface peat from the site (Sjögersten *et al.*, 2010). The potential fluxes of CO₂ and CH₄ to a depth of 2 m (Fig. 7) suggest that the deeper layers of peatlands may contribute substantially to increased CO₂ and CH₄ emissions in response to elevated temperature (Hirano *et al.*, 2009; Long *et al.*, 2010). Draw-down of the water table would reduce the extent of the anaerobic microsites in the upper 30 cm of the peat profile that currently are most active in producing CH₄ (Fig. 6). The combined effect of the lower quality of peat at depth (Table 1) and a thicker surface layer of aerated peat where oxidation of CH₄ takes place would be likely to reduce CH₄ emissions from this neotropical peatland.

In conclusion, detailed knowledge of the processes affecting gas production from deep peat layers is essential to predict how climate change will affect the net fluxes of CO₂ and CH₄ from tropical peatlands. Moreover, it is clear that deeper peat layers have the potential to lose C rapidly, and that variation in peat quality and BD within the profile associated with contrasting vegetation communities in tropical peatlands is important in determining CO₂ and CH₄ production. There is currently a dearth of information regarding the sources of CO₂ and CH₄ within peat profiles, the environmental constraints on the release of the gases produced and the influence of vegetation type on both the production and release of these gases. Further work, including radiocarbon dating of DOC, CO₂ and CH₄ gases and more intensive measurements of gas emissions in relation to the role of the vegetation and abiotic variables is needed to fill the knowledge gaps which currently limit our ability to predict CO₂ and CH₄ emissions from neotropical peatlands. Such studies are vital in view of the substantial land areas occupied by such systems and their considerable potential contribution to future climate change.

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