

Environmental controls of temporal and spatial variability in CO₂ and CH₄ fluxes in a neotropical peatland

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Abstract

Tropical peatlands play an important role in the global storage and cycling of carbon (C) but information on carbon dioxide (CO₂) and methane (CH₄) fluxes from these systems is sparse, particularly in the Neotropics. We quantified short and long-term temporal and small scale spatial variation in CO₂ and CH₄ fluxes from three contrasting vegetation communities in a domed ombrotrophic peatland in Panama. There was significant variation in CO₂ fluxes among vegetation communities in the order *Campnosperma panamensis* > *Raphia taedigera* > *Cyperus*. There was no consistent variation among sites and no discernible seasonal pattern of CH₄ flux despite the considerable range of values recorded (e.g. −1.0 to 12.6 mg m^{−2} h^{−1} in 2007). CO₂ fluxes varied seasonally in 2007, being greatest in drier periods (300–400 mg m^{−2} h^{−1}) and lowest during the wet period (60–132 mg m^{−2} h^{−1}) while very high emissions were found during the 2009 wet period, suggesting that peak CO₂ fluxes may occur following both low and high rainfall. In contrast, only weak relationships between CH₄ flux and rainfall (positive at the *C. panamensis* site) and solar radiation (negative at the *C. panamensis* and *Cyperus* sites) was found. CO₂ fluxes showed a diurnal pattern across sites and at the *Cyperus* sp. site CO₂ and CH₄ fluxes were positively correlated. The amount of dissolved carbon and nutrients were strong predictors of small scale within-site variability in gas release but the effect was site-specific. We conclude that (i) temporal variability in CO₂ was greater than variation among vegetation communities; (ii) rainfall may be a good predictor of CO₂ emissions from tropical peatlands but temporal variation in CH₄ does not follow seasonal rainfall patterns; and (iii) diurnal variation in CO₂ fluxes across different vegetation communities can be described by a Fourier model.

Keywords: carbon dioxide, methane, nutrient gradient, Panama, peatland, tropical

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Introduction

Tropical peatlands store and release quantities of carbon (C) that are of significant importance to the global C cycle (Page *et al.*, 2011). Current estimates of tropical C stores are 89 Gt C, or 15–19% of the estimated global C stored in peatlands (Page *et al.*, 2011). Tropical peatlands are therefore potentially significant sources of C emissions under future climate change scenarios, which generally predict increased temperatures (Giorgi, 2005; Baettig *et al.*, 2007; IPCC, 2007; Couwenberg *et al.*, 2010). However, the predicted regional variation in changes in rainfall, with rainfall expected to decrease in parts of the Neotropics, has significant implications for the water balance of wetlands.

Temporal variation in carbon dioxide (CO₂) and methane (CH₄) fluxes from peatlands depends on various factors including hydrology, soil and air temperature and dominant vegetation type. In northern

peatlands, there is evidence of strong diurnal, seasonal and interannual trends in emissions which are linked to variation in temperature and the activity of the vegetation (Oechel *et al.*, 1993; Whiting & Chanton, 1993; Thomas *et al.*, 1996; Clair *et al.*, 2002; Turetsky *et al.*, 2002; Ding *et al.*, 2005; Coursolle *et al.*, 2006). The higher temperatures in tropical peatlands increase decomposition rates (Kadlec & Reddy, 2001; Couwenberg *et al.*, 2010), although annual fluctuations in soil and air temperature are smaller than in boreal and northern peatlands (Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009), with the result that temperature is less important in determining temporal variation in CO₂ and CH₄ fluxes. However, some studies have shown that variations of only a few degrees centigrade are sufficient to affect gas fluxes (Hirano *et al.*, 2009). In tropical peatlands, hydrology (Hadi *et al.*, 2005; Hashimoto *et al.*, 2007; Jauhiainen *et al.*, 2008; Strack *et al.*, 2008; Couwenberg *et al.*, 2010), substrate availability and associated links with the dominant vegetation type (Updegraff *et al.*, 1995; Scanlon & Moore, 2000; Wright & Reddy, 2007; Wright *et al.*, 2011) are the foremost factors influencing CO₂ and CH₄ fluxes

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to the atmosphere. The hydrological status of tropical peatlands is often primarily influenced by rainfall, and strong seasonal trends in CO₂ and CH₄ fluxes may be associated with seasonal variation in precipitation (Hashimoto *et al.*, 2007) as this influences water table depth and substrate moisture status (Jaenicke *et al.*, 2010). During the dry season, the water table may fall well below the peat surface and this generally increases CO₂ emissions and reduces CH₄ fluxes (Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a, b; Jaenicke *et al.*, 2010).

In addition to abiotic controls on heterotrophic respiration, surface vegetation has an important role in controlling CO₂ and CH₄ evolution and influences temporal variation in gas production *via* several processes, including input of fresh organic material from dead roots (Hanson *et al.*, 2000; Personeni & Loiseau, 2004; Crow & Wieder, 2005) and release of photoassimilates as root exudates into the peat profile. These inputs supply the microbial community with labile substrate, increasing the production and evolution of both CO₂ and CH₄ (Joabsson *et al.*, 1999; Schwendenmann & Veldkamp, 2006; Klumpp *et al.*, 2007; Konnerup *et al.*, 2011). Furthermore, root respiration *per se* provides a direct source of CO₂ which contributes up to 50% of that released from tropical forests (Crow & Wieder, 2005; Schwendenmann & Veldkamp, 2006; Metcalfe *et al.*, 2008; Van Haren *et al.*, 2010). Recent evidence also shows that mycorrhizal respiration contributes substantially to surface CO₂ fluxes (Nottingham *et al.*, 2011). Roots may also influence redox potential, and hence CH₄ emissions, by releasing O₂ into the surrounding substrate (Fritz *et al.*, 2011).

Below-ground impacts of plants on CO₂ and CH₄ fluxes are, in part, linked to the rate of photosynthesis (Schwendenmann & Veldkamp, 2006; Konnerup *et al.*, 2011). Hence, if net primary production (NPP) increases, the extent to which plants influence CO₂ and CH₄ production, for example, by providing labile substrates for respiration through leaf litter inputs, root exudation and rhizodeposition or influencing the O₂ status of the soil (Lu *et al.*, 2000; Schaefer *et al.*, 2009; Chen *et al.*, 2010; Fritz *et al.*, 2011; Drake *et al.*, 2012), is likely to be enhanced, potentially resulting in greater release of these gases to the atmosphere. Plants growing in tropical peatlands are likely to have a higher NPP during the dry season than the wet season due to a combination of decreased cloud cover and increased solar radiation, lower wind speed and higher air temperatures (Nemry *et al.*, 1999; Schuur, 2003; Mohamed *et al.*, 2004; Huete *et al.*, 2006; Saleska *et al.*, 2007), although the development of water stress may decrease NPP in peatlands experiencing substantial water table drawdown. Previous studies of tropical and subtropical wetlands have shown a strong seasonal (wet and dry)

influence on soil CO₂ and CH₄ fluxes; thus, CO₂ fluxes were greater during the dry season and lower during the wet season (Jauhiainen *et al.*, 2005; Schedlbauer *et al.*, 2010), whereas the reverse applied for CH₄ (Biswas *et al.*, 2007; Grand & Gaidos, 2010). These trends were particularly evident in tropical wetlands which exhibited pronounced water table drawdown during the dry season compared to those which were inundated throughout the annual cycle.

The substrate lability and nutrient status strongly influences decomposition rates and gas release (Bridgman & Richardson, 1992; Cheesman *et al.*, 2010; Grover & Baldock, 2010; Wright *et al.*, 2011). Greater concentrations of labile C, N and P are generally associated with high initial rates of OM loss and greater CO₂ and CH₄ production (Bridgman & Richardson, 1992; Charman *et al.*, 1999; Battle & Golladay, 2007; Chanton *et al.*, 2008; Sjögersten *et al.*, 2011). The most labile fraction is generally water soluble and rapidly leaches from the litter, particularly if the water table is above the peat surface (Yule & Gomez, 2009; Wright *et al.*, 2013). However, as labile fractions, for example, cellulose are broken down (Choi *et al.*, 2006; Williams & Yavitt, 2010) they may also contribute substantially to CO₂ and CH₄ production (Wright *et al.*, 2011).

As noted previously, various factors influence CO₂ and CH₄ fluxes from tropical peatlands, resulting in strong temporal variability. It is important to understand how the fluxes of these key global warming gases are influenced by environmental conditions over both short and longer timescales to provide accurate representations of the control mechanisms for use in models of CO₂ and CH₄ fluxes under predicted future climatic scenarios. In the Neotropics, CO₂ and CH₄ fluxes from peat surfaces vary greatly depending on the dominant vegetation community (Nahlik & Mitsch, 2011; Sjögersten *et al.*, 2011; Wright *et al.*, 2011), probably due to a combination of the influence of vegetation on environmental factors affecting gas fluxes and direct plant influences on system function such as root exudates and aeration of peat (Van Haren *et al.*, 2010). However, the extent of the temporal variation within different vegetation communities is poorly understood. On a larger scale, there are substantial discrepancies between top-down estimates of CH₄ efflux using inverse modelling and bottom-up estimates using process-based models in the Neotropics (Mikaloff Fletcher *et al.*, 2004a, b; Bergamaschi *et al.*, 2007, 2009; Meirink *et al.*, 2008) suggesting that our current understanding of CH₄ emissions from the region is incomplete.

In situ measurements of surface gas fluxes of CO₂ and CH₄ in the San San Pond Sak peatland in Panama, meteorological data and peat C, N and P status were used to test the hypotheses that:

- 1 surface gas fluxes vary among sites within the peatland depending on the dominant vegetation type.
- 2 CO₂ and CH₄ fluxes vary seasonally in response to variation in rainfall, solar radiation and relative humidity.
- 3 diurnal variation in CO₂ and CH₄ fluxes follows the daily rhythm of net primary production by the surface vegetation.
- 4 greater labile substrate and nutrient availability result in greater surface emissions of CO₂ and CH₄.

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, Republic of Panama. 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 southeast of the Rio Changuinola, within which seven distinct phasic plant communities have been identified (Phillips *et al.*, 1997). These form roughly concentric rings (*cf.* Wright *et al.*, 2011 for map and further details); three of these communities were examined in this study. The nearby town of Bocas del Toro, Isla Colon, ca. 10 km from the peatland, has a mean annual (1992–2001) temperature of 27 °C and precipitation of 3209 mm (Estadística Panameña, 2001). Rainfall continues throughout the year with no pronounced dry season, although rainfall is generally lower between February–April (140 mm month⁻¹, based on data from 2007 to 2009) and September–October (160 mm month⁻¹; 2007–2009 data) compared to the rest of the year (265 mm month⁻¹; 2007–2009 data).

Study sites

The three communities examined spanned a strong N, P and K nutrient gradient (Troxler, 2007; Sjögersten *et al.*, 2011; Cheesman *et al.*, 2012) which included a relatively nutrient-rich (0.96 ± 0.040 mg P g⁻¹) site dominated by *Raphia taedigera* (a canopy-forming palm), an intermediate site (0.68 ± 0.057 mg P g⁻¹) dominated by *Camposperma panamensis* (an evergreen canopy-forming hardwood tree species) and a nutrient-poor site (0.40 ± 0.041 mg P g⁻¹) dominated by *Cyperus* sp. (a mat-forming ca. 1 m tall sedge).

All sites were freshwater, with the water table typically being at the peat surface ±20 cm (E. L. Wright, personal observation). The *R. taedigera* site was monodominant (Sjögersten *et al.*, 2011) with a limited understorey, with large amounts of leaf litter on the peat surface. Its microtopography was characterized by shallow pools of water and raised areas densely covered by pneumatophores under the canopies of the palm trees. The *C. panamensis* site was also monodominant but had a denser understorey as more light penetrated its canopy. Its microtopography was dominated by 'knees' of roots interspersed with small hollows which pooled during and after

rainfall events. The *Cyperus* sp. site was the most species-diverse site, but the vegetation was short and confined mainly to small shrubby islands. The understorey and areas between the shrubby islands consisted almost exclusively of *Cyperus* sp., as reflected by their lower microtopography.

The carbon content of the peat was high (490–500 mg g⁻¹) and the pH of the surface peat was comparable at all sites (3.8, 3.9 and 4.0, respectively, for the *R. taedigera*, *C. panamensis* and *Cyperus* sites; Sjögersten *et al.*, 2011). The texture of peat varied between the interior (coarse) and edge (fine) of the peatland (Phillips *et al.*, 1997; Wright *et al.*, 2011), indicating greater decomposition and/or differences in the source of litter. The peat was shallower at the edge of the peatland than in the interior (ca. 2 m under *R. taedigera*, 4 m under *C. panamensis* and 8 m under *Cyperus* sp. (Phillips *et al.*, 1997); peat at the *Cyperus* site contained a dense mat of decaying roots. Peat chemistry differed among sites, as carbohydrate content was greatest in the coarser peat found in the interior of the peatland and lowest in the fine peat at the *R. taedigera* site. Marked differences in pore water chemistry among vegetation communities were also evident as dissolved carbon and nitrogen concentrations were higher at the *R. taedigera* site than at the two sites closer to the centre of the peatland (Wright *et al.*, 2011). The peat at the *R. taedigera* site contained 1.8 mg g⁻¹ of aluminium (Al) and 4.7 mg g⁻¹ of iron (Fe) while at the *Cyperus* sp. site the levels were lower at 0.6 and 1.2 mg g⁻¹ for Al and Fe respectively (Hamdan *et al.*, 2012). This may result in contrasting suppression of methanogenesis (Teh *et al.*, 2008). The contrasting environment at the sites is reflected by shifts in the microbial community composition across the nutrient gradient (Troxler *et al.*, 2012).

Gas and peat sampling and analysis

Long-term variation. Fluxes of CO₂ and CH₄ from the soil surface were measured for five 2 × 2 m plots at each site along the transect. Replicate plots were at least 20 m apart and divided into two subplots; gas fluxes were measured in each subplot. All vegetation, fallen branches and emerging seedlings were removed before commencing gas flux measurements. Gas samples were collected on the 21st day of each month at the *C. panamensis* and *Cyperus* sp. sites and the 22nd day at the *R. taedigera* site between February and November 2007, excluding October. Samples were collected between 10:00 hours and 2:00 hours local time using the closed chamber technique (Denmead, 2008). The headspace was ca. 10 cm in height and 810 cm² in area with rounded corners, giving a total volume of 7.8 dm³, and was sealed to the peat surface using a flexible plastic skirt weighed down with metal chain to minimize peat and root disturbance. Additional measurements of surface gas fluxes were made at all three sites in July and August 2009 and at the *Cyperus* sp. site in February 2009. At these time, samples were collected using a 0.45 dm³ headspace, ca. 10 cm in height, which was lightly pressed into the peat surface to a depth of ca. 0.3 cm to ensure a tight seal. Air in the headspace was mixed prior to collecting a 25 ml sample through a Subaseal using a hypodermic needle and syringe. Samples collected after 0, 2, 10 and 20 min were injected into evacuated 12 ml exetainers for transport to the laboratory.

Some studies have shown that the static chamber approach underestimates CO₂ fluxes relative to 'open flow' chamber systems when CO₂ fluxes are >600 mg CO₂ m⁻² h⁻¹, while at lower gas fluxes increasing CO₂ concentration in the head space does not significantly affect the rate of CO₂ diffusion from the soil (e.g. Norman *et al.*, 1997). Other studies (e.g. Bekku *et al.*, 1997) found no significant difference in estimates of CO₂ flux between static, closed dynamic and open flow systems in an experiment using a known CO₂ flux. In our study, the increase in concentration in the head space was linear in almost all cases; when flux was nonlinear, only the first three data points were used to calculate flux. Furthermore, the gas fluxes in our study were well below 600 mg CO₂ m⁻² h⁻¹ (i.e. below the range where CO₂ accumulation is likely to influence estimates of flux obtained using the static chamber method; Norman *et al.*, 1997). A recent study comparing CO₂ fluxes from peat measured using closed static and closed dynamic chambers (Heinemeyer & McNamara, 2011) showed no significant difference between these methods over shorter incubation periods and concluded that an incubation period of ca. 15 min provides good quality data using the static chamber approach. In addition, as the peat soils examined in Panama were always saturated or flooded the potential problem of changes in the diffusion gradient in the head space was negligible (Davidson *et al.*, 2002). On the basis that the fluxes were <600 mg CO₂ m⁻² h⁻¹, linearity was checked for all measurements, the peat was saturated and the incubation times were relatively short, we conclude that CO₂ release was not underestimated.

All gas samples were analysed by gas chromatography (GC 2014; Shimadzu, Milton Keynes, UK) using a 1 ml sampling loop and a molecular sieve column; CO₂ concentration was determined by thermal conductivity and CH₄ by flame ionization.

Diurnal gas fluxes. To quantify the diurnal trends for CO₂ and CH₄ fluxes, five 1 × 1 m plots were established at all sites, separated by a distance of at least 5 m. Samples were taken in February 2009 at the *Cyperus* sp. site and during August 2009 for all three sites. Sampling began in the afternoon of Day 1 and continued into Day 2, with samples being collected at 16:00, 18:30, 22:00, 07:30, 09:30 and 13:00 h local time. The 18:30 and 07:30 h time points occurred after sunset and sunrise, respectively. For the diurnal measurement, gas sampling was made using the smaller head spaces as described above.

Spatial variability in gas fluxes in relation to microtopography and peat chemistry. A detailed survey of peat properties was carried out for the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites during August and September 2009. At each site, a 10 m² grid containing nine sampling points was established. Peat temperature at 10 cm depth at the time of sampling at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites was 26.4, 26.0 and 26.5 °C, respectively, while air temperature measured 100 cm above the ground surface was 27.0, 24.0 and 33.0 °C. The water table at the time of sampling was at the peat surface, but the microtopography at each site resulted in

shallow hollows being submerged in ca. 5 cm of water while hummocks were ca. 5 cm above the water table.

Surface gas fluxes were collected using the same headspace as described under the diurnal sampling section. If the water table was above the peat surface, the depth of standing water and the height of hummocks protruding above the water table was recorded using a ruler. If there was no standing water at the point of headspace sampling, water samples were taken from standing water within 20 cm of the headspace if available. Samples were filtered and frozen before analysis of total dissolved organic C (DOC), dissolved N (DN) and dissolved P (DP). DOC and DN was analysed using a TOC-V/TN analyser (Shimadzu Corp, Kyoto, Japan). DP was measured using standard molybdate colorimetry with an absorbance wavelength of 880 nm following reduction using ascorbic acid.

A 10 × 10 × 10 cm sample of the surface (0–10 cm) peat directly under the headspace was collected and placed in a plastic bag, stored at 4 °C and processed within 2 days of collection. Living roots were removed before air-drying the samples at 26 °C. The dried samples were then ball milled. Total C (TC) and total N (TN) was determined by automated combustion (Flash EA 1112 Series, CE Instruments Ltd, UK). Total P (TP) was determined by ashing at 550 °C for 3 h and dissolution in 1 M H₂SO₄ with P detection as described above.

Climatic variables

Data for rainfall, air temperature and solar radiation were sourced from the weather station at the Smithsonian Research Institute on Isla Colon. Environmental conditions were recorded at 15-min intervals using a rain gauge (CS700; Campbell Scientific Inc, Utah, USA), a temperature and relative humidity probe (CS215; Campbell Scientific Inc), and a pyranometer for solar radiation (LI200X; Campbell Scientific Inc). Meteorological data were processed to determine mean monthly air temperature and relative humidity and cumulative rainfall and solar radiation during the 28-day period preceding each gas sampling event. Observational data of the state of the water table was collected at the time of sampling.

Data analysis

Data for CO₂ and CH₄ fluxes were tested for normality using the Shapiro–Wilk's test and transformed to meet the assumptions of normality if needed. To test for significant differences between sites, we used residual maximum likelihood with site, time and their interactions as fixed effects and sampling location nested within plot as the random effect. Relationships between gas fluxes and environmental factors for (i) each measurement date; and (ii) between gas fluxes and peat chemistry were analysed by regression analysis. Diurnal fluxes were analysed using repeated measures ANOVA for each site, with time as the fixed effect. Site differences were evaluated using SED's (SE of the difference). The percentage of variance explained by the statistical models presented is referred to as σ^2 in the text and figures (a perfect model fit is $\sigma^2 = 100$). All statistical analyses were performed using Genstat version 11 (Lawes Agricultural Trust, Rothamsted Experimental Station).

Results

Long term variation in gas fluxes

CO_2 . The effect of sampling date on surface CO_2 flux was significant ($P < 0.001$; Fig. 1a–c) and pronounced. In 2007, mean values declined from a maximum in February and March to a minimum in June and July for all sites; this was followed by an increase during the rest of the observation period. The lowest recorded flux in 2007 was $59 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ at the *Cyperus* sp. site in June and the highest was $402 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ at the *C. panamensis* site in February.

CO_2 fluxes varied between sampling sites ($P < 0.05$), although the variation among sites were less than the variation over time (based on the SE of the difference; SEDs for the CO_2 fluxes were 26.1 and $45.2 \text{ mg m}^{-2} \text{ h}^{-1}$ for Site and Time respectively). Fluxes were consistently greatest at the *C. panamensis* site except in November 2007 and July 2009, followed by the *R. taedigera* and *Cyperus* sp. sites. Differences between sites were less pronounced during June and July 2007 when fluxes were much lower than at other times of year. CO_2 fluxes were lower in July and August 2007 than in the equivalent

months in 2009 for all sites ($F_{1, 46} = 31.31$, $P < 0.001$). The highest mean CO_2 flux was recorded at the *C. panamensis* site in August 2009 ($520 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), closely followed by the *Cyperus* sp. site ($506 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in the same month. The greatest CO_2 flux at the *R. taedigera* site ($431 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) was again in 2009, but in July rather than August.

CH_4 . No significant variation in surface CH_4 fluxes between sites ($P = 0.4$) and no discernible seasonal trends were detected in 2007, although the influence of sampling date was significant (SED $2.56 \text{ mg m}^{-2} \text{ h}^{-1}$; $P < 0.05$; Fig. 1d–f), possibly because values $>45 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ were recorded at the *R. taedigera* and *C. panamensis* sites in August 2009. With the exception of these exceptionally high values, CH_4 fluxes were typically $<13 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ and ranged from -0.88 to $12.63 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at the *R. taedigera* site, -0.88 to $3.63 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at the *C. panamensis* site, and -1.06 to $3.10 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at the *Cyperus* sp. site.

Variation in environmental conditions. Cumulative monthly rainfall, cumulative monthly solar radiation and mean air temperature did not differ significantly

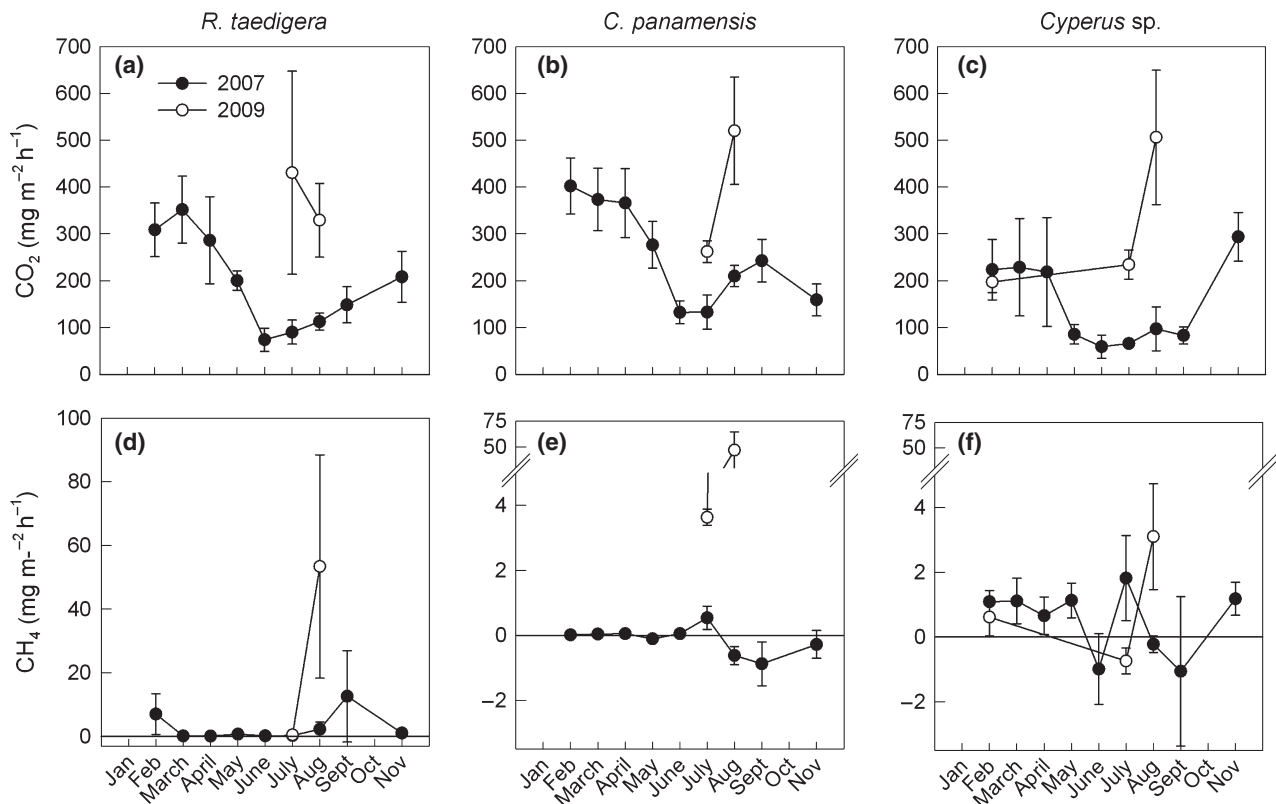


Fig. 1 CO_2 (a–c) and CH_4 (d–f) fluxes between February and November 2007 (excluding October) for *Raphia taedigera* (a, d) *Camposperma panamensis* (b, e) and *Cyperus* sp. (c, f). Means \pm SE are shown ($n = 5$). CO_2 statistical summary: Time, $F_{8, 187} = 14.27$, $P < 0.001$, Site, $F_{2, 27} = 5.15$, $P < 0.05$, Time*Site: $F_{16, 187} = 1.59$, $P = 0.1$. CH_4 statistical summary: Time, $F_{8, 203} = 2.34$, $P < 0.05$, Site, $F_{2, 24} = 0.98$, $P = 0.4$, Time*Site, $F_{16, 203} = 0.96$, $P = 0.5$.

between 2007 and 2009 (Fig. 2a–c), while monthly mean values for relative humidity were generally greater in 2009 ($P < 0.05$; Fig. 2d). Monthly mean air temperature was highest ($>26^{\circ}\text{C}$) between April and October and lowest ($<26^{\circ}\text{C}$) between November and March ($P < 0.05$). Cumulative monthly solar radiation also varied seasonally, with peaks in February, March and September ($P = 0.056$). Monthly values for mean relative humidity and cumulative rainfall showed no significant seasonal variation.

Water levels responded quickly to rainfall and fell to >10 cm below the peat surface during periods of low rainfall (February to April 2007) at all sites. Similarly, during the periods of extremely high rainfall in November 2007 and August 2009, the water level rose 10–20 cm above the peat surface. Indeed, during the diurnal measurements at the *R. taedigera* site, heavy overnight rainfall resulted in a 20 cm rise in the water level.

Influence of environmental factors on surface gas fluxes. Strong positive polynomial relationships (*R. taedigera* $P = 0.002$; *C. panamensis* $P < 0.001$; *Cyperus* sp. $P < 0.001$) between the surface CO_2 fluxes in 2007 and cumulative rainfall during the 28-day period preceding sampling were observed at all sites (Fig. 3). These rela-

tionships remained significant, or approached significance, at the *R. taedigera*, *C. panamensis* and *Cyperus* sites ($P < 0.05$, $P = 0.075$ and $P < 0.01$ respectively) when the data from July and August 2009 were included in the model, although the proportion of variance explained decreased (Fig. 3). Solar radiation (monthly mean or cumulative total), relative humidity and air temperature at the time of sampling had no significant effect on surface CO_2 fluxes at all sites.

None of the meteorological factors examined significantly affected CH_4 flux at the *R. taedigera* site (Table 1), whereas fluxes at the *C. panamensis* site were positively related to air temperature ($P < 0.05$; Fig. 4; Table 1). The CH_4 flux at the *Cyperus* sp. site was negatively correlated with cumulative solar radiation (near significant regression $P = 0.07$); Table 1; data not shown).

Diurnal variation in gas fluxes

No significant diurnal variation in CO_2 flux was detected for the *R. taedigera* site ($P = 0.4$; Fig. 5a), in contrast to the *C. panamensis* and *Cyperus* sp. sites ($P < 0.05$; $P < 0.001$; Fig. 5b, c). Fluxes at the *C. panamensis* and *Cyperus* sp. sites increased from a minimum at 07:30 h to a maximum at 16:00 h. CO_2 fluxes at the *Cyperus* sp. site in February 2009 followed a similar

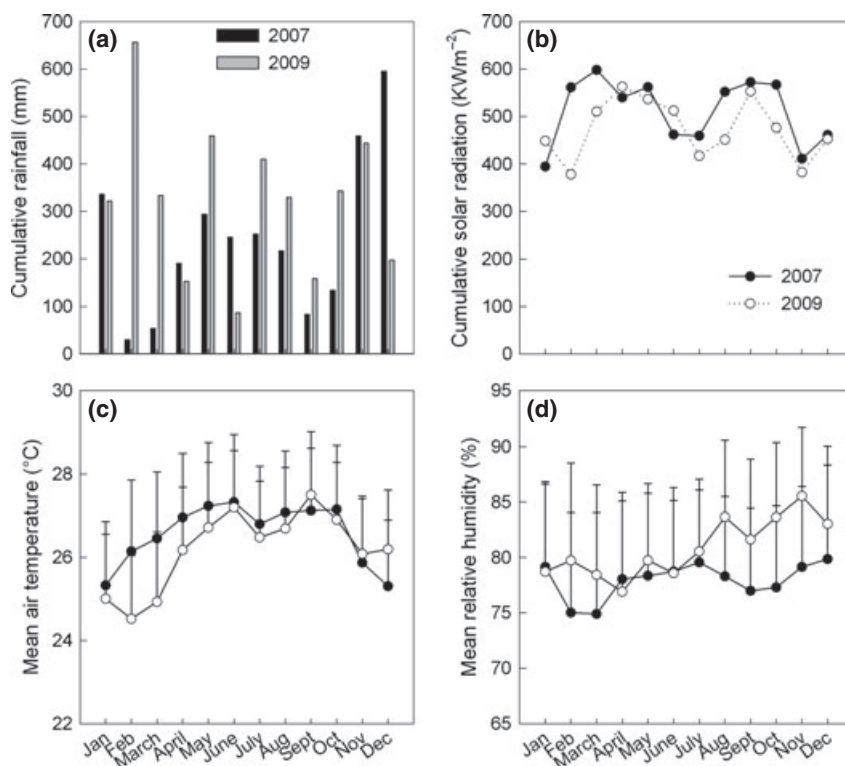


Fig. 2 Seasonal timecourses for (a) cumulative monthly rainfall, (b) cumulative monthly solar radiation, (c) mean daily air temperature and (d) mean relative humidity. Monthly mean SE are shown for air temperature and relative humidity.

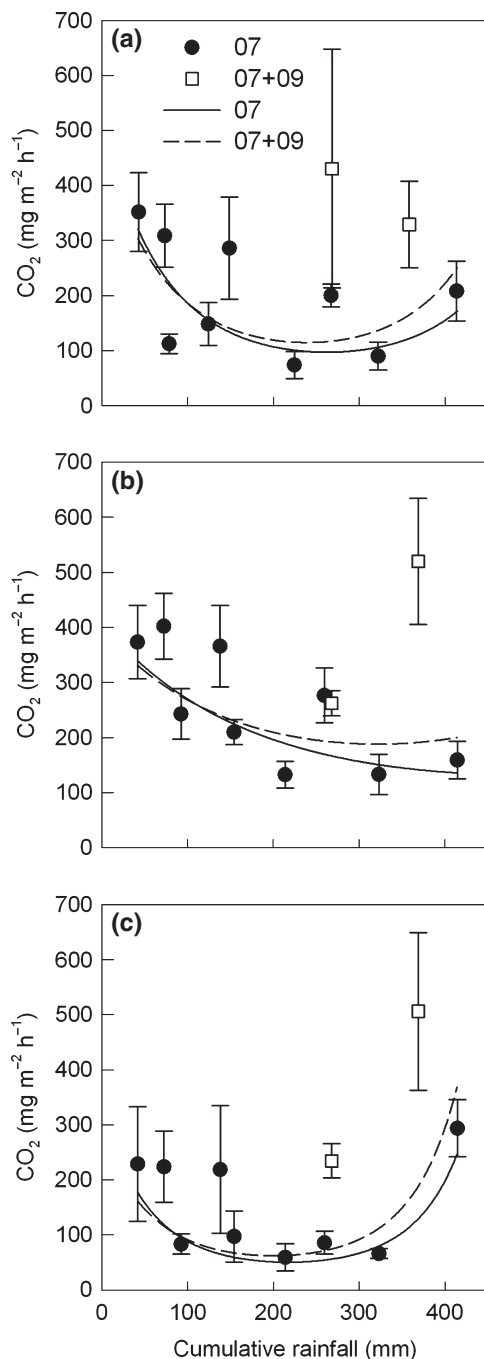


Fig. 3 Regression between CO_2 flux and cumulative rainfall during the 28-day period preceding sample collection for (a) *Raphia taedigera*, (b) *Campnosperma panamensis* and (c) *Cyperus* sp. Data collected in 2007 (filled circles) and 2009 (during July and August) (unfilled circles) are shown as the mean \pm SE. Polynomial regressions and the variance accounted are shown both for data from 2007 only (solid line) and 2007 and 2009 data combined (dashed line). Polynomial regression analysis summary: (a) 2007: $F_{2, 43} = 7.28$, $P < 0.01$, $\sigma^2 = 22.6$; 2007 + 2009: $F_{2, 51} = 3.24$, $P < 0.05$, $\sigma^2 = 8.1$; (b) 2007: $F_{2, 44} = 7.61$, $P < 0.01$, $\sigma^2 = 23.1$; 2007 + 2009: $F_{2, 50} = 2.74$, $P = 0.075$, $\sigma^2 = 6.5$; (c) 2007: $F_{2, 40} = 5.72$, $P < 0.01$, $\sigma^2 = 19.1$; 2007 + 2009: $F_{2, 46} = 6.34$, $P < 0.01$, $\sigma^2 = 18.8$.

Table 1 Results of linear regressions for CH_4 for each site and environmental factor

	Environmental factor	df	F	P	σ^2
<i>R. taedigera</i>	Air temperature	1, 50	0.44	0.5	ns
	24-h rainfall	1, 50	0.77	0.4	ns
	24-h solar radiation	1, 50	2.19	0.1	ns
	28-day solar radiation	1, 50	0.61	0.4	ns
	Relative humidity	1, 50	0.04	0.8	ns
<i>C. panamensis</i>	Air temperature	1, 50	0.03	0.9	ns
	28-day rainfall	1, 50	5.64	<0.05	8.5
	24-h solar radiation	1, 50	4.06	<0.05	5.8
	28-day solar radiation	1, 50	4.30	<0.05	6.2
	Relative humidity	1, 50	8.93	<0.05	13.7
<i>C. panamensis</i> -restricted data*	Air temperature	1, 47	0.04	0.8	ns
	28-day rainfall	1, 47	3.48	0.07	5.0
	24-h solar radiation	1, 47	0.87	0.4	ns
	28-day solar radiation	1, 47	8.39	0.4	ns
	Relative humidity	1, 47	0.82	0.4	ns
<i>Cyperus</i> sp.	Air temperature	1, 47	0.00	1.0	ns
	24-h rainfall	1, 49	2.21	0.1	ns
	24-h solar radiation	1, 49	0.13	0.7	ns
	28-day solar radiation	1, 49	3.42	0.07	4.7
	Relative humidity	1, 49	0.03	0.9	Ns

Significant effects are shown in bold and marginally significant results (i.e. >0.05 but <0.10) are italicized. σ^2 is shown for regressions with $P < 0.1$; ns indicates nonsignificant regressions.

*Excluding extreme CH_4 values at the *C. panamensis* site.

diurnal time-course, although not significant, to that observed in August 2009 (Fig. 5c). However, peak fluxes were substantially lower in February than in August ($P < 0.001$; Fig. 5c). Overall, variation in CO_2 fluxes over 24 h was well described by a Fourier model (Fig. 6a).

No significant diurnal variation in CH_4 fluxes was found for any of the sites examined (Fig. 5d–f). Fluxes at the *R. taedigera* site were highly variable with most fluxes ranging were between 1 and 3 $\text{mg m}^{-2} \text{h}^{-1}$. CH_4 fluxes at the *Cyperus* sp. site were low, with a small peak of 0.61 $\text{mg m}^{-2} \text{h}^{-1}$ at 13:00 h. At the *C. panamensis* site, CH_4 fluxes were lowest before 13:00 h, with a peak at 22:00 h.

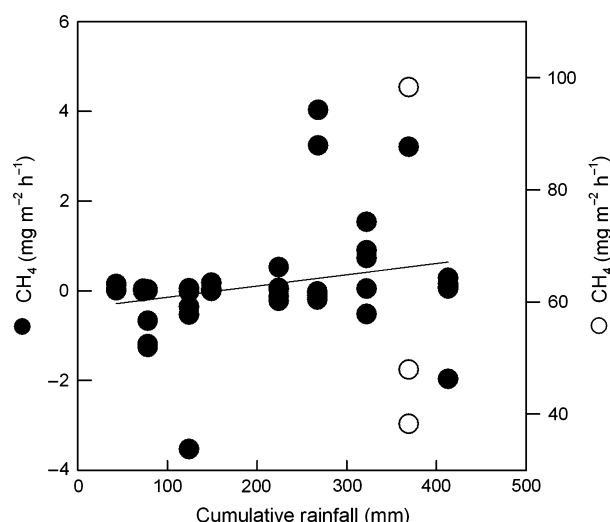


Fig. 4 Correlation between CH_4 flux and cumulative rainfall at the *Campnosperma panamensis* site during 2007 and 2009. Open points show extreme values and solid points indicate all data $< 30 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$. The relevant statistics are shown in Table 1.

In parallel with the long-term measurements, variation among sites were smaller than variation over time for both CO_2 and CH_4 fluxes (SEDs for the CO_2 fluxes were 48.2 and $68.2 \text{ mg m}^{-2} \text{ h}^{-1}$ and SEDs for the CH_4 fluxes were 0.67 and $0.95 \text{ mg m}^{-2} \text{ h}^{-1}$ for Site and Time, respectively).

Interestingly, there was a strong positive linear relationship between diurnal variation in CO_2 and CH_4 fluxes at the *Cyperus* site (Fig. 6b) but not at the other two sites. Despite substantial variation in solar radiation, air temperature and rainfall during the sampling period (Fig. 7) only a relatively weak relationship between air temperature and CO_2 efflux was found ($F_{1,113} = 11.42$; $P < 0.001$; $\sigma^2 = 8.4$, data not shown), while none of the meteorological variables could predict diurnal variation in CH_4 .

Spatial variation in surface gas release in relation to microtopography and peat chemistry

The microtopography was a significant predictor of CO_2 release at all three sites. Specifically, submerged areas had greater emissions of CO_2 (Fig. 8). Within-site variation in CO_2 fluxes site was governed by the DOC concentration at the *R. taedigera* and the C : P or N : P ratio at the *C. panamensis* sites, respectively (Fig. 9a–b), while none of the measured parameters correlated with CO_2 fluxes at the *Cyperus* sp. site. CH_4 emissions increased with DOC concentrations at the *C. panamensis* site (Fig. 9c), but peat chemistry did not explain the spatial variation in CH_4 emissions at either the *R. taedi-*

gera or *Cyperus* sp. sites. There was no relationship among total peat C, N or P content and gas release at any site.

Discussion

The two forested sites showed overall greater CO_2 effluxes during periods of low rainfall than the interior sedge-dominated site (Fig. 1a–c; Fig. 5a–c). The differing magnitude and range of CO_2 fluxes among vegetation communities may be linked to differing contributions of root respiration to surface CO_2 fluxes between the three vegetation communities examined (Whiting & Chanton, 1993; Thomas *et al.*, 1996; Crow & Wieder, 2005) and/or the lability of the peat (Wright *et al.*, 2011) as well as fresh litter inputs (Yule & Gomez, 2009; Wright *et al.*, 2013). However, as respiration by autotrophic and heterotrophic organisms was not separated in this study, this influence cannot be fully evaluated (Nottingham *et al.*, 2011). In contrast to the CO_2 fluxes, CH_4 fluxes did not vary among vegetation communities suggesting that limitation in CH_4 production (e.g. substrate availability, redox conditions) and oxidation (e.g. position of the water table) was not strongly influenced by the dominant vegetation community. Taken together, data support hypothesis 1 (which predicts that the vegetation community control gas release) with respect to CO_2 fluxes but not in the case of CH_4 fluxes.

Seasonal variation in CO_2 fluxes in the San San Pond Sak peatland was strongly linked to rainfall (Figs 1 and 3). The high CO_2 efflux during periods of low rainfall is comparable that reported for other tropical peatland systems (Chimner & Ewel, 2004; Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a; Hirano *et al.*, 2009) during the dry season when water table falls below the peat surface which enhances air-filled porosity, greater pore connectivity and reduce gas transport limitation (Updegraff *et al.*, 1995; Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009; Schedlbauer *et al.*, 2010). Furthermore, dry season weather condition (Meir *et al.*, 2008) may support greater gross primary productivity, as has been shown elsewhere on terra firma in the tropics (Huete *et al.*, 2006; Saleska *et al.*, 2007), and hence greater root respiration rates. However, Hirano *et al.* (2009) also reported that CO_2 efflux from hummocks in drained swamp forests increased during periods when rainfall and the water table were high, suggesting additional controls of CO_2 emissions. In parallel with these findings, greater CO_2 release was associated with flooded hollows in San San Pond Sak (Fig. 8). Increased litterfall associated with rainstorms and consequent increases in the availability of labile substrate as these leach from the litter material (Schreeg *et al.*, 2013; Wright *et al.*, 2013) may

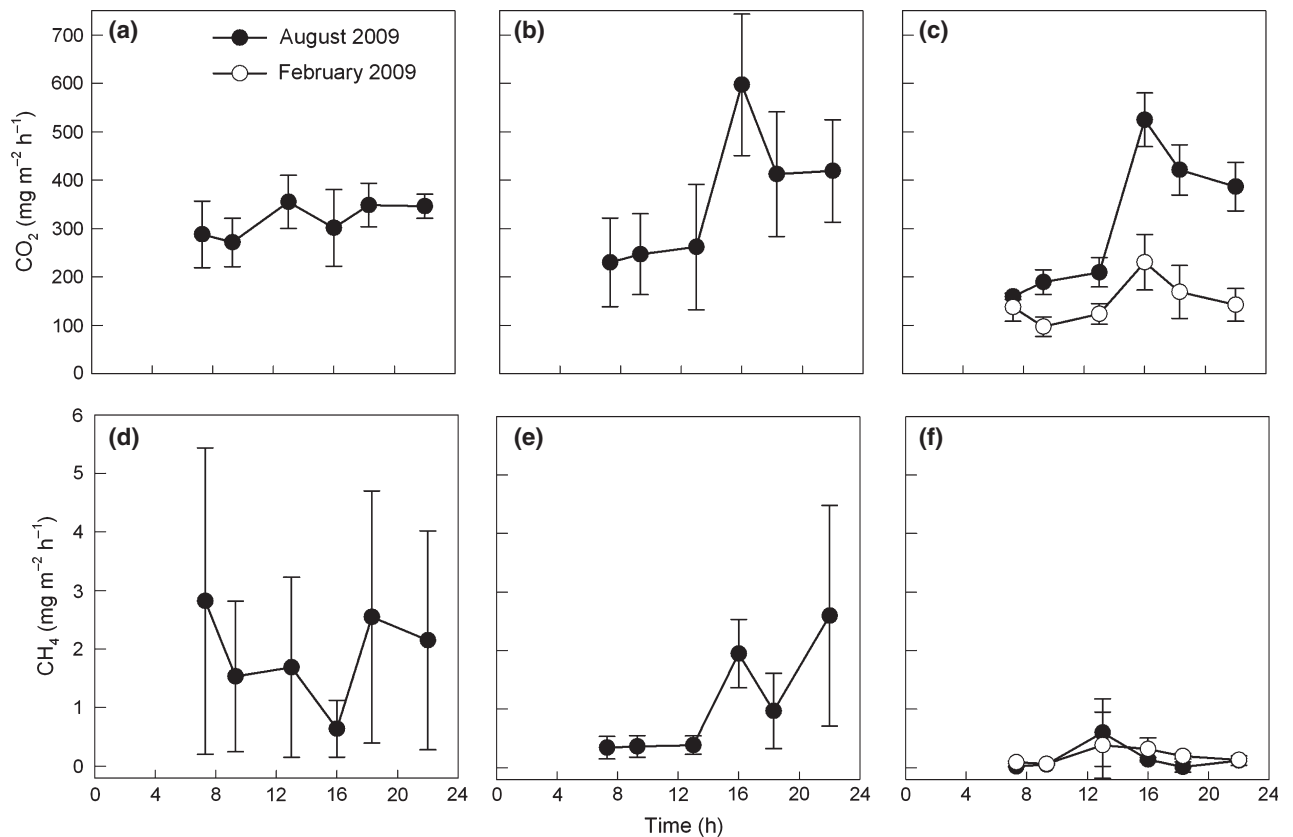


Fig. 5 Diurnal CO_2 fluxes at the (a) *Raphia taedigera* and (b) *Campnosperma panamensis* sites in August 2009 and (c) the *Cyperus* sp. site in February and August 2007. Mean values \pm SE are shown ($n = 5$). Summary of repeated measures ANOVA: (a) $F_{5, 25} = 0.90$, $P = 0.4$; (b) $F_{5, 28} = 7.34$, $P < 0.05$; (c) August: $F_{5, 28} = 24.92$, $P < 0.001$; February: $F_{5, 29} = 1.44$, $P = 0.3$; Month: $F_{1, 59} = 165.52$, $P < 0.001$. Diurnal timecourses of CH_4 fluxes at the (d) *R. taedigera* and (e) *C. panamensis* sites in August 2009 and (f) at the *Cyperus* sp. site in February and August 2007. Mean values \pm SE of the mean are shown ($n = 5$). Summary of repeated measures ANOVA: $F_{5, 29} = 0.52$, $P = 0.7$; $F_{5, 28} = 2.57$, $P = 0.2$; August: $F_{5, 29} = 1.14$, $P = 0.4$; February: $F_{5, 29} = 1.44$, $P = 0.3$; Month: $F_{5, 59} = 0.49$, $P = 0.6$.

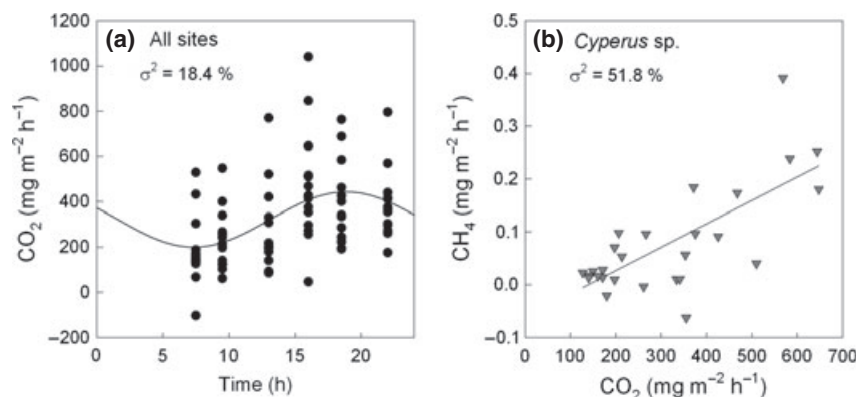


Fig. 6 (a) Fourier model describing temporal variation in CO_2 fluxes across all three vegetation communities over a diurnal cycle ($F_{3, 84} = 7.31$, $P < 0.001$; $\text{CO}_2 = 321.3 + 121.6 \times \sin(2\pi(\text{Time}-13.1)/23.01)$) and (b) positive linear relationship between CH_4 and CO_2 at the *Cyperus* sp. site ($F_{1, 27} = 30.06$; $P < 0.001$; note that one extreme value was removed prior to the statistical analysis).

explain the high CO_2 efflux during periods of high rainfall. It is also possible that rainfall events may oxygenate the surface peat. As polynomial relationships were

found at all three sites, the link between rainfall and CO_2 might provide a useful tool for predicting CO_2 fluxes in forested tropical peatlands (Fig. 3).

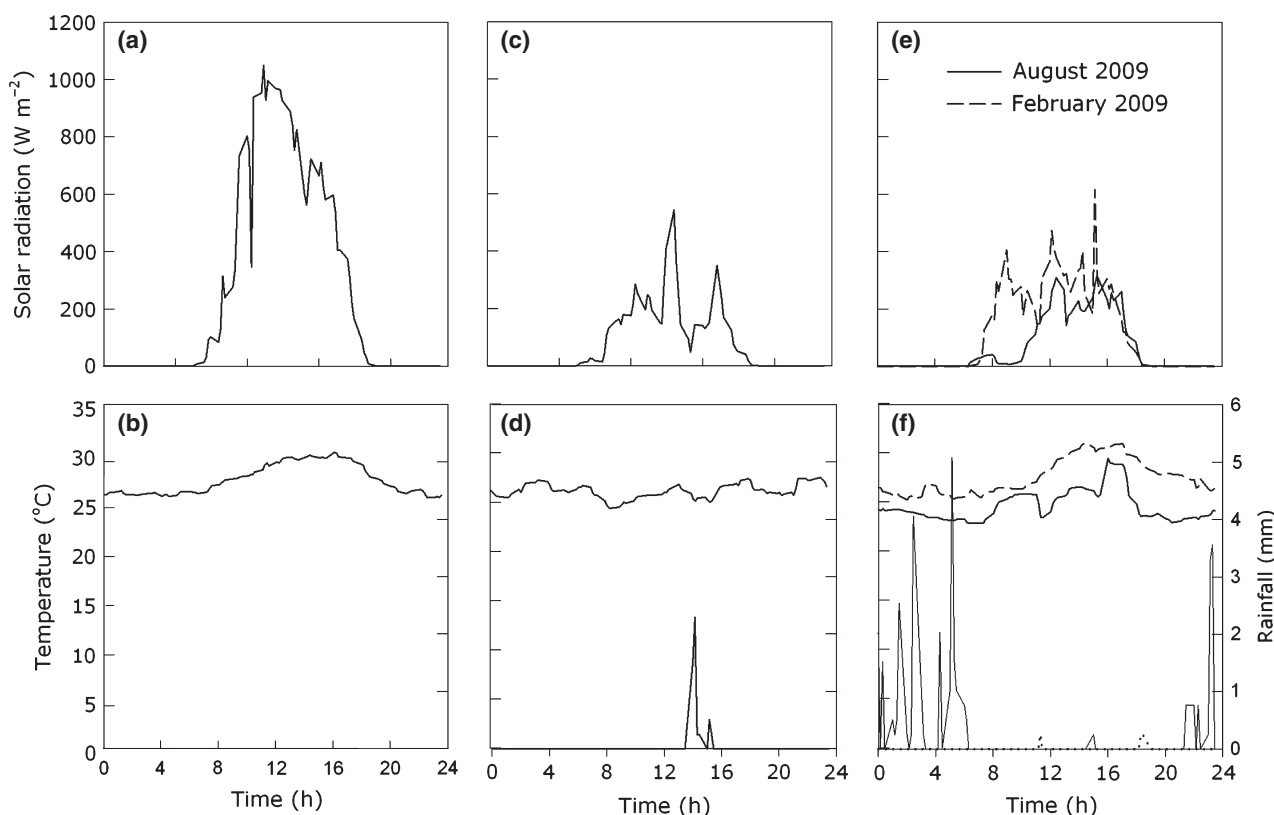


Fig. 7 Diurnal timecourses of solar radiation (a, c, e), air temperature (b, d, f) and rainfall (b, d, f) compiled from measurements made at 15 min intervals during the 24-h gas flux sampling periods for *Raphia taedigera* (a, b), *Camposperma panamensis* (c, d) *Cyperus* sp. (e, f) in February and August 2009.

The lack of relationship between rainfall and CH₄ emissions in the permanently inundated San San Pond Sak peatland contrasts sharply with the strong seasonal variation in CH₄ efflux reported for a tropical peatland further east in Panama which experience a pronounced dry season (Keller, 1990 as cited by Walter & Heimann, 2000). There might therefore be marked differences in annual CH₄ emissions from wetlands within the region in response to rainfall, linked to low fluctuation in methanogenic and/or methanotrophic communities throughout the year in areas that do not experience pronounced dry seasons. The study by Keller (1990) was used to validate tropical CH₄ emissions in a process-based model by Walter & Heimann (2000), which has been subsequently used to estimate CH₄ emissions in South America (e.g. Bergamaschi *et al.*, 2007, 2009). Rainfall patterns in the Neotropics are highly variable and it will be important to determine whether CH₄ emissions from peatlands follow rainfall patterns at multiple sites. This is particularly important given the discrepancies in CH₄ emission identified using inverse modelling (e.g. Mikaloff Fletcher *et al.*, 2004a, b; Meirink *et al.*, 2008).

The San San Pond Sak wetland generally acted as a CH₄ source, with fluxes typically ranging between 0 and 2 mg m⁻² h⁻¹, comparable to values for other tropical peatlands. For example, Jauhiainen *et al.* (2005) reported mean CH₄ effluxes of 0.16 mg m⁻² h⁻¹ in Central Kalimantan, Indonesia, while Inubushi *et al.* (2005) reported 3.66 mg m⁻² h⁻¹ for a swamp forest in Indonesia. The negative fluxes recorded during some months at the *C. panamensis* and *Cyperus* sp. sites confirm those reported by Melling *et al.* (2005a) for a forested peatland in Sarawak, Malaysia (−0.0061 to 0.0112 mg CH₄ m⁻² h⁻¹). The highly variable and occasionally high CH₄ emissions (Fig. 1d–f) may have resulted from ebullition (Ueda *et al.*, 2000), suggesting that this represents a potentially important emission pathway in tropical peatlands in addition to diffusive efflux of CH₄. However, the high emissions of methane might also reflect localized hot spots of CH₄ production, that is, sites within the peat where conditions are optimal for methanogens. Similarly, high CH₄ emissions (e.g. >40 mg CH₄ m⁻² h⁻¹) have been reported for wetlands in Costa Rica (Nahlik & Mitsch, 2011) and Panama (Keller, 1990 cited in Walter & Heimann, 2000).

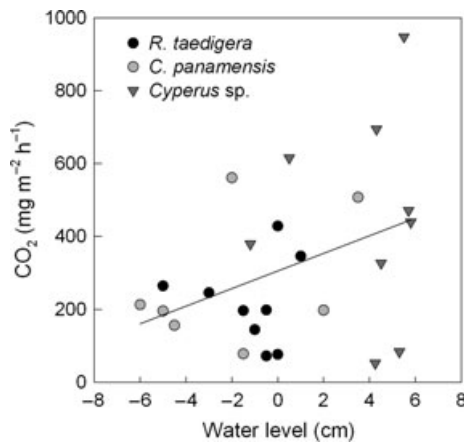


Fig. 8 Relationship between CO_2 flux and the level of the water table in relation to the peat surface for the *Raphia taedigera*, *Campnosperma panamensis* and *Cyperus* sp. sites ($F_{1, 24} = 4.20$, $P = 0.052$). Positive values (cm) indicate the distance between the water table and the top of individual hummocks while negative values indicate the depth between the water table and the submerged peat surface in hollows.

Increased concentrations of labile C produced by root exudates have been shown to strongly increase methane production (Lu *et al.*, 2000) and the lability of peat has proven to be a strong predictor of variation in methane production through depth profiles (Wright *et al.*, 2011). However, the net release of CH_4 may be strongly limited by methane consumption, for example, in the oxic surface layers of peatlands (Hornibrook *et al.*, 2009; Laing *et al.*, 2010). The higher *in situ* CH_4 effluxes at depth compared to the surface reported for some tropical peatlands (Inubushi *et al.*, 1998; Melling *et al.*, 2005a; Wright *et al.*, 2011) might also reflect methane consumption (Teh *et al.*, 2005). In addition, a sufficiently low redox potential is needed for CH_4 production to occur (Yu *et al.*, 2007). Flooded soil conditions often result in low redox potential, but O_2 inputs by roots can strongly influence the redox values for peat soils (Wolf *et al.*, 2007; Fritz *et al.*, 2011). At this stage, it is not possible to identify the degree to which these interacting processes control CH_4 release at the tropical peatland site examined in this study. Indeed, it

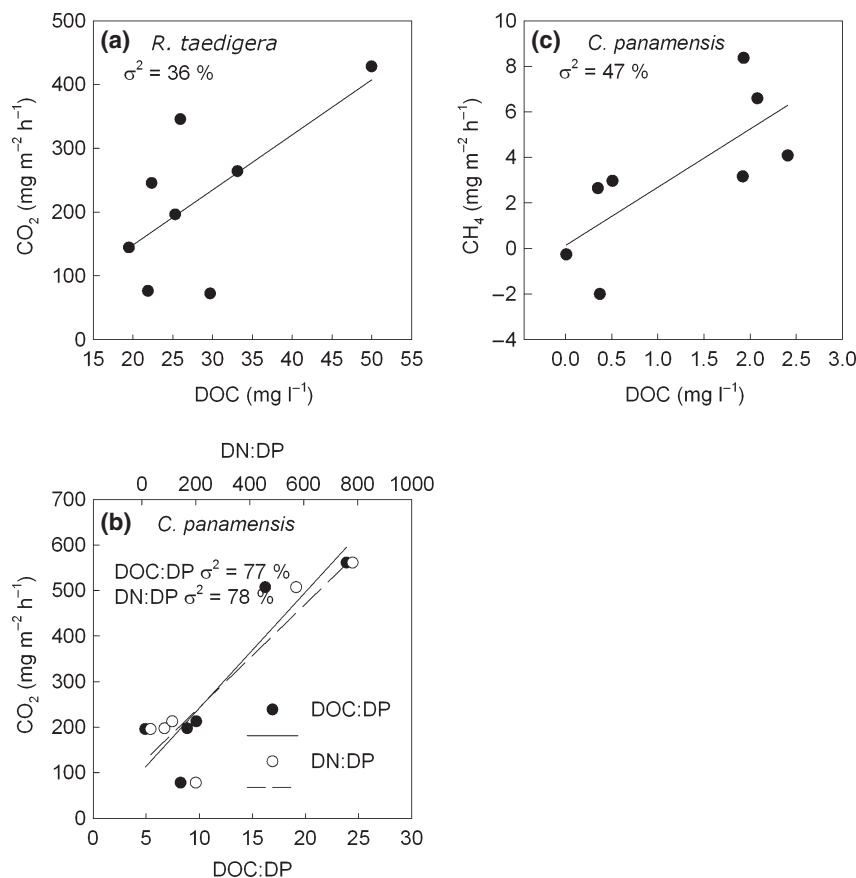


Fig. 9 Relationship between (a) CO_2 flux and dissolved organic C (DOC) concentration at the *Raphia taedigera* site ($F_{1, 7} = 4.87$, $P = 0.07$), (b) CO_2 flux and the ratio between dissolved organic C (DOC) and dissolved P (DP) ($F_{1, 5} = 17.95$, $P < 0.05$) and DP and dissolved nitrogen (DN) at the *Campnosperma panamensis* site ($F_{1, 5} = 18.86$, $P < 0.05$), (c) CH_4 flux and dissolved C (DOC) concentration at the *C. panamensis* site ($F_{1, 7} = 7.32$, $P < 0.05$).

is possible that strong CH₄ oxidation might mask potential temporal or spatial trends in CH₄ production, although this requires further investigation. Hence, regarding hypothesis 2, which predicts that rainfall, solar radiation and relative humidity controls gas release, we are able to support this notion for CO₂ fluxes which showed a strong relationship with rainfall, but not in the case of CH₄ fluxes.

Substantial diurnal variation in CO₂ fluxes occurred at the *C. panamensis* and *Cyperus* sp. sites, where values rose sharply during the morning to a maximum in mid-afternoon before declining again overnight (Fig. 5b, c). The positive correlation between diurnal CO₂ efflux and air temperature suggests that the overnight decrease in temperature reduced decomposition rate (Oechel *et al.*, 1993, 2000; Hirano *et al.*, 2009) and/or decreased root respiration (Atkin & Tjoelker, 2003). While root respiration is influenced by soil temperature, it is also affected by the rate of photosynthesis and the rate and distance of transport of photoassimilate to the roots (Tang *et al.*, 2005). Pressurization and convective flow within plant tissue has been shown for *Cyperus* sp. (Konnerup *et al.*, 2011) which may explain the diurnal variation found at the *Cyperus* sp. site. Although little is known regarding maximum CO₂ efflux resulting from root respiration in tropical wetland species, studies focusing on species from other biomes have shown that the timing of maximum root respiration varies between ca. 12:00 and 21:00 h (Kutsch *et al.*, 2001; Tang *et al.*, 2005; Wang *et al.*, 2005; Jia *et al.*, 2006; Bahn *et al.*, 2009). This corresponds well with the modelled peak in CO₂ fluxes at ca. 19:00 h in San San Pond Sak (Fig. 6a). In addition to direct effects on CO₂ fluxes *via* root respiration, roots may exude both photoassimilates and O₂, stimulating microbial activity in the peat (Joabsson *et al.*, 1999; Singh, 2001; Crow & Wieder, 2005; Ding *et al.*, 2005; Fritz *et al.*, 2011). Although considerable variation was found among sites regarding their diurnal CO₂ release, the temporal variation over the 24-h cycle was greater than that found among sites, in parallel to the strong seasonal variability in CO₂ fluxes.

In contrast to recent studies showing strong diurnal variation in CH₄ fluxes driven by the photosynthetic activity of the dominant vegetation (Hatala *et al.*, 2012) and soil temperature (Gažovič *et al.*, 2010), no significant diurnal variation in flux was found at any of the study sites, although the trend towards differing emission patterns might have proved significant with greater replication. Indeed, significant variation in CH₄ fluxes during the course of the day has been reported from tropical wetlands in Costa Rica (Nahlik & Mitsch, 2011). Specifically, the dominant vegetation type may affect CH₄ efflux by providing substrates for methanogenic bacteria (Joabsson *et al.*, 1999; Sotta *et al.*, 2004)

and a pathway for CH₄ produced within the peat profile to the atmosphere following transport from roots to shoots (Nouchi *et al.*, 1990; Watson *et al.*, 1997; Nisbet *et al.*, 2009). In our study, there was no significant diurnal or seasonal variation in CH₄ fluxes that could be related to variation in weather conditions and by inference linked to variation in NPP. However, to test the question whether the activity of the vegetation influences the CH₄ efflux in the San San Pond Sak peatland fully, in line with findings in more northern wetlands (Whiting and Chanton 1993), further studies of the relative importance of vegetation effects on substrate supply and peat oxygenation and methane oxidation processes are required. Indeed, the results presented here reflect ebullition and diffusive CH₄ efflux but do not include CH₄ released through the vegetation; it is probable that this pathway also contributed to CH₄ efflux in San San Pond Sak. Konnerup *et al.* (2011) presented evidence for CH₄ evolution from *Cyperus* species. Although no equivalent information is available for *C. panamensis* and *R. taedigera*, methane emissions from trees have been shown in both temperate and tropical wetlands (Gauci *et al.*, 2010; Pangala *et al.*, 2013), suggesting that the methane effluxes reported here may represent only part of the net emissions of CH₄. We are hence able to support hypothesis 3, which states that gas fluxes will follow the circadian rhythm of the net primary production with respect to CO₂ flux but not for CH₄. However, we do not feel able to reject this hypothesis without data accounting for CH₄ oxidation and the vegetation emission pathway.

As within-site spatial variability in CO₂ and CH₄ fluxes was correlated with the availability of dissolved C, N or P at the *R. taedigera* and *C. panamensis* sites (Fig. 9), but not with total C, N and P in the peat, data support hypothesis 4, which predicts that greater labile substrate and nutrient availability result in greater surface emissions. Hence, leaching of labile compounds from recently fallen litter (Yule & Gomez, 2009; Schrege *et al.*, 2013; Wright *et al.*, 2013) or root exudates (Ström *et al.*, 2005) may be of particular importance for gas production.

In conclusion, temporal variability in CO₂ was greater than variation among vegetation communities. Contrasting controls of gas release in relation to peat chemistry, together with the distinct patterns in CO₂ efflux among communities, highlights the importance of carefully considering the forest diversity found in tropical peatlands when assessing their C balance. Interestingly, the variability in CH₄ flux from the peat surface appeared largely independent both seasonal, diurnal as well as meteorological conditions and variation in peat C and nutrient status. The lack of a seasonal pattern in CH₄ emissions suggests different controls to

the Varzeas in the Amazon and peatlands experiencing a stronger dry seasons (Bartlett & Harriss, 1993). Hence, care needs to be taken when modelling CH₄ fluxes in from wetlands in the region. Also we found potential for high CH₄ emissions suggesting that Neotropical peatlands may contribute strongly to regional CH₄ emissions. In contrast, there was a strong polynomial relationship between long-term variation in CO₂ fluxes and monthly rainfall while diurnal variation followed a Fourier model, providing potential tools for predicting long and short term temporal variation in CO₂ fluxes from tropical peatlands.

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