

Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland

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Abstract Biogeochemical properties, including nutrient concentrations, carbon gas fluxes, microbial biomass, and hydrolytic enzyme activities, were determined along a strong nutrient gradient in an ombrotrophic peatland in the Republic of Panama. Total phosphorus in surface peat decreased markedly along a 2.7 km transect from the marginal *Raphia taedigera* swamp to the interior sawgrass swamp, with similar trends in total nitrogen and potassium. There were parallel changes in the forest structure: basal area decreased dramatically from the margins to the interior, while tree diversity was greatest at sites with extremely low concentrations of readily-exchangeable phosphate. Soil microbial biomass concentrations declined in parallel with nutrient concentrations, although microbes consistently contained a large proportion (up to 47%) of the total soil phosphorus. Microbial C:P and N:P ratios and hydrolytic enzyme

activities, including those involved in the cycles of carbon, nitrogen, and phosphorus, increased towards the nutrient-poor wetland interior, indicating strong below-ground nutrient limitation. Soil CO₂ fluxes and CH₄ fluxes did not vary systematically along the nutrient gradient, although potential soil respiration determined on drained soils was lower from nutrient-poor sites. Soil respiration responded strongly to drainage and increased temperature. Taken together, our results demonstrate that nutrient status exerts a strong control on above and below-ground processes in tropical peatlands with implications for carbon dynamics and hence long term development of such ecosystems.

Keywords Carbon · Enzymes · Forest diversity · Methane · Microbial biomass · Nitrogen · Peat · Phosphorus · Soil respiration · Tropical wetland

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Introduction

Tropical wetlands provide a range of ecosystem services, including ground water recharge, conservation of biodiversity, the removal of excess nutrients from surface waters, and the sequestration and storage of atmospheric carbon (e.g., Silvius and Giesen 1996; Jaenicke et al. 2008). However, they are under increasing threat from changes in land use and climate (Chimner and Ewel 2004; Day et al. 2008; Wosten et al. 2008; Keddy et al. 2009).

The inaccessible nature of tropical peatlands has meant that few detailed investigations have been carried out on their formation, ecology, and function (but see Phillips et al. 1997; Page et al. 1999). This limits our ability to predict the consequences of increased direct and indirect anthropogenic pressures upon them (Phillips 1998; Limpens et al. 2008; Langner and Siegert 2009).

The humid tropics contain a substantial proportion (~13%) of global peatlands, mostly associated with coastal systems (Maltby and Immerzi 1993; Rieley et al. 1997; Hoekman 2007; Jaenicke et al. 2008). Tropical peatlands include self emergent ombrotrophic systems (Andriess 1988) that are hydrologically isolated due to doming (Belyea and Baird 2006). In such peatlands, the processes of vegetation succession, peat accumulation, and transport of dissolved material from the wetland interior (Winston 1994; Phillips et al. 1997), lead to the formation of distinct concentric vegetation communities. The peats formed in these systems tend to be deep (>20 m in some places; Anderson 1983; Page et al. 1999) and, because they are formed from the roots and woody debris produced by swamp forests, to be relatively heterogeneous and low density (Shimada et al. 2001; Chimner and Ewel 2004).

In contrast to Southeast Asian wetlands, where most studies of ombrotrophic tropical peatlands have occurred to date, information on Central American wetlands is derived in large part from studies of calcareous minerotrophic wetlands in Belize and Mexico, in which productivity is limited strongly by phosphorus availability (e.g., Johnson and Rejmankova 2005). However, many wetlands in the region are not calcareous and the nutrient status of these systems remains poorly understood. Links between vegetation diversity and peat properties have been found in wetlands in both Southeast Asia (Page et al. 1999) and Central and South America, including Belize, Mexico, and Venezuela (Johnson and Rejmankova 2005; Vegas-Vilarrubia and Laseras 2008; Moreno-Casasola et al. 2009), which suggests that edaphic properties, in conjunction with hydrological processes, can drive diversity in tropical wetlands (Ferreira and Stohlgren 1999; Lopez and Kursar 2007; Rodriguez-Gonzalez et al. 2008). This is likely to have important implications for the carbon cycle, because peat properties (Bachoon and Jones 1992; Bridgman and Richardson 1992; Keller et al. 2006)

and vegetation type (Chimner and Ewel 2004) exert strong controls on carbon storage and greenhouse gas fluxes from tropical and subtropical wetlands.

Here we report detailed information on tree diversity and biogeochemical properties, including nutrient concentrations, carbon gas fluxes, and microbial properties, along a strong nutrient gradient in a large peatland on the Caribbean coast of the Republic of Panama. This domed peatland is characterized by clear shifts in vegetation composition with distance from the peatland interior (Phillips et al. 1997) that correspond to marked changes in soil nutrients (Troxler 2007). Our aim was to strengthen the understanding of this ecosystem by quantifying changes in soil nutrients and forest community composition, and assessing their influence on below-ground processes linked to the carbon cycle.

Methods

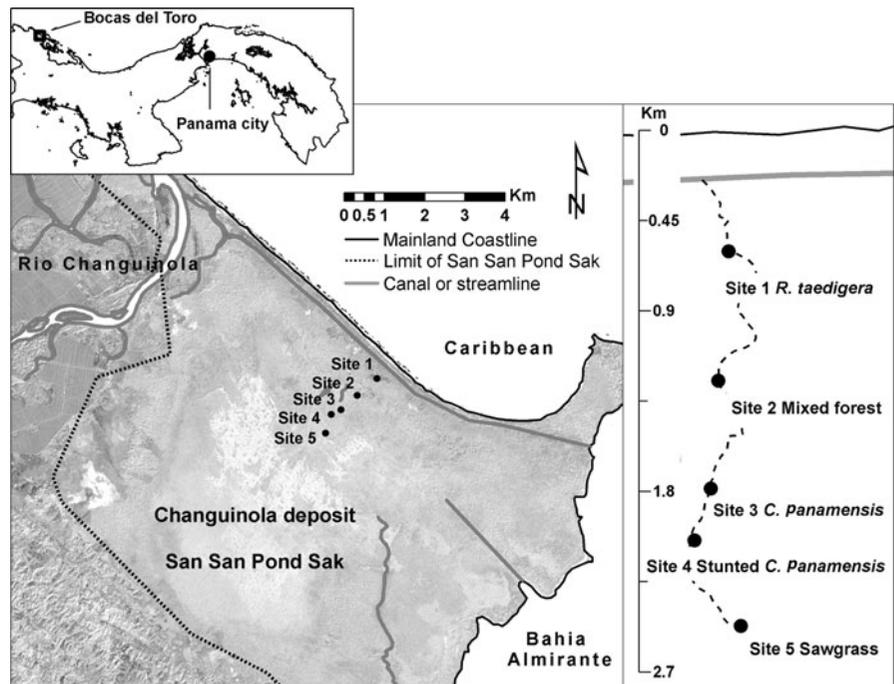
Site description

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 (Fig. 1). The oldest deposits within the Changuinola peat system are estimated to have been formed 4000–5000 years ago and vary from ~2 m at the wetland exterior to >8 m deep in the central areas of the peatland (Phillips et al. 1997).

Seven distinct phasic plant communities have been identified in the peatland (Phillips et al. 1997). These form roughly concentric rings that, from the periphery, have been designated as: (i) *Rhizophora mangle* mangrove swamp, (ii) mixed species back-mangrove swamp, (iii) *Raphia taedigera* palm swamp, (iv) mixed-species forest swamp, (v) *Camposperma panamensis* forest swamp, (vi) sawgrass/stunted forest swamp, (vii) *Myrica-Cyrilla* bog-plain.

The nearby town of Bocas del Toro, Isla Colon, approximately 10 km from the peatland, has a mean annual temperature of 27°C and a mean annual precipitation of 3209 mm (calculated from data for the years 1992–2001; Estadística Panameña 2001).

Fig. 1 Map of the study area showing the location of the San San Pond Sak peatland in Panama. The right panel shows the study transect. The locations of the five research sites (Site 1–5) are marked both in the overview and the inset. The map is based upon a panchromatic Landsat 7 Enhanced Thematic Mapper (ETM) + scene



Rainfall is relatively continuous throughout the year with no pronounced dry season, although there are two distinctive periods of lower rainfall (February–April and September–October). Samples in this study were collected during February 2007.

Study transect

We established five study sites with distinct differences in vegetation community along a 2.7 km transect into the central area of the peatland (Phillips et al. 1997; Troxler 2007). All sites were freshwater. The vegetation zones were defined as follows (letters in parentheses indicate the corresponding vegetation zone indentified by Phillips et al. 1997 as defined above):

- Site 1. *Raphia taedigera* swamp (zone iii)
- Site 2. Mixed-species forest swamp (zone iv)
- Site 3. *Camposperma panamensis* forest swamp (zone v)
- Site 4. Stunted *C. panamensis* forest with a sawgrass (*Cyperus* sp.) understorey (zone vi)
- Site 5. Sawgrass (*Cyperus* sp.) swamp with occasional stunted *C. panamensis* (this site was on the edge of the central bog-plain) (zone vi-vii).

At each site we established permanent plots to census vegetation and for soil and gas flux sampling (described below).

Vegetation census

To quantify forest structure and species diversity, we established a permanent 20 m × 50 m (0.1 ha) census plot at each study site, in which all stems ≥10 cm diameter at breast height were measured, mapped, and tagged. The clumping growth form of *R. taedigera* means that basal area for this species is likely to be a slight overestimation. Voucher samples of all species were collected and their identities verified at the National Herbarium at the University of Panama (<http://www.up.ac.pa:8080/Herbario/inicio.php>) following nomenclature by Tropics.org (Missouri Botanical Garden, www.tropics.org). The Shannon diversity index was calculated for each plot using EstimateS (Colwell 2005).

Gas flux sampling and analysis

Fluxes of CO₂ and CH₄ from the soil surface were measured in five 2 m × 2 m plots at each site along the transect in close proximity to the forest census

plots (i.e., within the same vegetation type and <300 m away from the associated census plot). Plots for gas sampling were at least 20 m apart and each was divided into two subplots, with gas flux measurements made in each subplot. Values from the pair of subplots were averaged prior to statistical analysis. Gas flux samples were collected during 3 days in February 2007 with stable clear weather conditions and low wind speed. The soil temperature averaged 25°C at the time of sampling and did not vary significantly among sites or over time. Samples were collected between 10 am and 2 pm using the closed chamber technique (Denmead 2008). Headspace areas were 810 cm² and *ca.* 10 cm high, with a total volume of 7.8 dm³. To minimize soil and root disturbance the headspace was sealed at the ground surface by a flexible plastic ‘skirt’ weighed down with a metal chain. The air in the head space was mixed prior to collecting a 25 ml air sample through a suba seal using a hypodermic needle and syringe. Samples were collected after 0, 2, 10, and 20 min, and injected into evacuated 12 ml exetainers for transport to the laboratory. Samples were analyzed by gas chromatography (GC 2014, Shimadzu, Milton Keynes, UK) with a 1 ml sampling loop, a molecular sieve column, and detection of CO₂ by thermal conductivity and CH₄ by flame ionization.

Potential soil respiration

To determine potential soil respiration, blocks of surface peat were collected from each plot in parallel with the peat samples collected for the nutrient analysis (described below). At the time of sampling the water table was either at the soils surface or just below (maximum 10 cm depth). The blocks were trimmed to 5 cm × 5 cm surface area and 10 cm depth and then allowed to drain to field capacity for 24 h at 35°C to simulate the maximum air temperature recorded under the tree canopy in the peatland. The flux of CO₂ was then determined by placing the peat samples in air tight container with suba seals inserted in the lids as sampling ports. The volume inside the container excluding the peat was 0.46 dm³. Following mixing of the air in the head space a 25 ml sample was collected at the start of the incubation and then again after 10 min. The collection of two samples over time eliminated problems with under-pressure in the relatively small head space. The

assumption of linearity during the 10 min sampling period was supported by the field data. Samples were stored and analyzed for CO₂ concentration as described above.

Soil sampling

Surface soil samples were collected for biogeochemical characterization (i.e., total elements, extractable nutrients, microbial nutrients, and hydrolytic enzyme activities) by cutting blocks of peat (10 × 10 × 10 cm) adjacent to the plots used for gas sampling. Soils were transported to the laboratory (~4 h) and stored at 4°C prior to analysis. Bulk density was determined on a minimum of three separate intact cores per site (7.5 cm diameter, 0–10 cm depth). The majority of the roots were removed by hand prior to analysis, although fine roots inevitably remained in some samples. Moisture content was determined by drying subsamples of soil at 105°C for 24 h. Soil pH was determined using a glass electrode in a 1:1 ratio of fresh soil to deionized water.

Extractable nutrients

Dissolved organic carbon and nitrogen fractions were extracted by shaking 40 g of fresh soil in 75 mL of 0.5 M K₂SO₄ for 1 h. Extracts were centrifuged (8000g, 15 min) and dissolved organic carbon determined after a five-fold dilution by automated combustion and gas chromatography on a TOC-VCSH analyzer (Shimadzu, Columbia, MD). Ammonium and nitrate were determined by automated colorimetry using a Lachat Quickchem 8500 flow injection analyzer (Hach Ltd, Loveland, CO). Ammonium was determined by automated colorimetry at 660 nm following reaction with phenolate, while nitrate was determined at 520 nm following cadmium-catalyzed reduction to nitrite and reaction with sulfanilamide at pH 8.5. Total nitrogen was determined in the extracts by alkaline persulfate oxidation (Cabrera and Beare 1993) overnight at 80°C in sealed glass tubes, with detection as nitrate by automated colorimetry as described above. Dissolved organic nitrogen was calculated as the difference between total nitrogen and the sum of ammonium and nitrate.

Readily-exchangeable phosphate was determined by extraction with anion exchange membranes (AEM) using a method based on that described by

Myers et al. (1999). Soil (20 g fresh weight) was shaken for 24 h with 80 ml deionized water and five anion-exchange resin strips (1 × 4 cm; manufactured by BDH Prolabo and distributed by VWR International, Lutterworth, Leicestershire, UK). The strips were rinsed in deionized water and the phosphate recovered by shaking for 1 h in 50 ml of 0.25 M H₂SO₄. Phosphate was determined in the acid solution at 880 nm following online neutralization and automated molybdate colorimetry using a flow injection analyzer (Lachat Quickchem 8500, Hach Ltd, Loveland, CO).

Total element concentrations

Subsamples of each soil were air-dried on shallow trays at ambient laboratory temperature (10 days at approximately 22°C), ground in a ball mill, and then stored in sealed vials at ambient laboratory temperature and humidity prior to determination of total element concentrations. Total carbon and nitrogen were determined by combustion and gas chromatography using a Flash NC1112 Soil Analyzer (CE Elantech, Lakewood, NJ). Total calcium, phosphorus, and potassium were determined by digestion of 200 mg soil in 2 ml of concentrated HNO₃ under pressure in sealed PTFE vials at 180°C (PDS-6 Pressure Digestion System, Loftfields Analytical Solutions, Neu-Eichenberg, Germany) followed by analysis of diluted samples by inductively-coupled plasma optical-emission spectrometry (ICP–OES) using an Optima 2100 (Perkin-Elmer Inc., Shelton, CT). All total element concentrations were corrected for residual moisture in the air-dried sample.

Soil microbial biomass nutrients

Carbon and nitrogen contained within soil microbial biomass was estimated by CHCl₃ fumigation and 0.5 M K₂SO₄ extraction using a correction factor of 2.64 to account for unrecovered biomass carbon (Vance et al. 1987) and 1.85 to account for unrecovered biomass nitrogen (Brookes et al. 1985). Microbial phosphorus was determined by extraction with anion-exchange membranes; soils were extracted as described above for available phosphate, but with the addition of 0.5 ml of hexanol (Myers et al. 1999). Fumigation-released phosphorus was calculated as

the difference between phosphate determined in fumigation and unfumigated samples. We did not correct values for unrecovered biomass, since the correction factors used for CHCl₃ fumigation (e.g., Brookes et al. 1982) gave microbial phosphorus values that exceeded the total soil phosphorus. We therefore assume that phosphorus released by hexanol fumigation provides a reasonable approximation of the microbial phosphorus concentration in these soils.

Hydrolytic enzyme assays

We measured the activity of seven enzymes involved in the release of carbon, nitrogen, and phosphorus from organic compounds. Assays were conducted using methylumbelliferone-linked fluorogenic substrates (Marx et al. 2001). Enzymes (and substrates) were:

- (i) Cellobiohydrolase (4-methylumbelliferyl β-D-cellobiopyranoside)
- (ii) β-Xylanase (4-methylumbelliferyl β-D-xylopyranoside)
- (iii) α-Glucosidase (4-methylumbelliferyl α-D-glucopyranoside)
- (iv) β-Glucosidase (4-methylumbelliferyl β-D-glucopyranoside)
- (v) *N*-acetyl-β-glucosaminidase (4-methylumbelliferyl *N*-acetyl-β-D-glucosaminide)
- (vi) Phosphomonoesterase (4-methylumbelliferyl phosphate)
- (vii) Phosphodiesterase (bis-(4-methylumbelliferyl) phosphate)

Samples were stored for 1 week at 4°C prior to analysis. This was not expected to significantly influence activity based on previous studies of tropical mineral soils, which indicated that activities were relatively stable for up to 2 weeks of refrigerated storage (Turner and Romero 2010). On the day of the assay, 2 g soil (dry weight basis) was added to 200 ml of 1 mM NaN₃ and stirred for 10 min. Aliquots (50 μl) of soil suspension were dispensed into a 96-well microplate containing 100 μl of 200 μM substrate (100 μM final concentration in the assay mixture) and 50 μl of sodium acetate–acetic acid buffer adjusted to pH 4.0 (the approximate mean soil pH). Microplates were incubated at 30°C for either 30 min (β-glucosidase, *N*-acetyl-β-glucosaminidase, phosphomonoesterase, phosphodiesterase) or 4 h (other enzymes)

dependent on activity. Following incubation, 50 μl of 0.5 M NaOH was added to terminate the reaction and fluorescence was determined immediately on a Fluostar Optima spectrofluorometer (BMG Labtech, Offenburg, Germany).

Data analysis

Significant differences between sites were tested using analysis of variance (ANOVA) after variables that did not fulfill the normality assumption (as determined by visual inspection of quantile–quantile plots and Shapiro-Wilks test to assess the normality of the residuals) were log, square, or square root transformed. Significant differences between means were analyzed using least significant difference (LSD) at the 5% confidence level. Relationships between dependent and independent variables were tested using backwards elimination stepwise regression, with only significant regressions reported. All statistical analysis was performed in Genstat version 10.1 (Lawes Agricultural Trust, Rothamsted Experimental Station). Due to the high spatial variability in the wetland we set $P = 0.1$ as the limit for reporting the statistics from the data analysis.

Concentrations of total elements and microbial nutrients are reported both on a mass and an area basis. This was done to account for the variation in bulk density among sites (data shown below) and hence the amounts of nutrients per surface area. This is essential when considering the availability of nutrients to plants and when comparing among soils of markedly different bulk density. The extractable nitrogen and phosphorus were expressed on an area basis, since nutrient availability per surface area is most relevant from a plant perspective.

Results

Vegetation survey

The five study sites contained 16 tree species, including two palms. Tree species diversity (Shannon diversity index) ranged from 1.13 at site 1 (*R. taedigera*) to 1.90 at site 4 (stunted *C. panamensis*). Site 1 contained the lowest estimated stem density (106 stems ha^{-1}), but the highest estimated basal area (103 $\text{m}^2 \text{ha}^{-1}$) (Table 1). The highest estimated stem density was at site 4 (529 stems ha^{-1}) and the lowest basal area was recorded at site 5 (sawgrass; 5 $\text{m}^2 \text{ha}^{-1}$) (Table 1). Only *C. panamensis* was present at all five study sites and made the greatest contribution to the basal area at sites 2–5 (40–88%; Table 2). The basal area at site 1 was dominated completely by *R. taedigera* (>99% of the basal area).

There was a negative relationship between the total basal area and tree species diversity ($R^2 = 87.9$, $F_3 = 30.0$, $P < 0.05$), with the highest basal area at sites 1 and 3, both of which were dominated by a single species (*R. taedigera* and *C. panamensis*, respectively; Table 2).

Peat chemical and physical properties

Water content and bulk density varied in parallel across the peatland, with the greatest water content and lowest bulk density in the wetland interior (Table 3). Although significant, the changes in pH of the surface peat were not substantial, ranging from 3.7 to 4.0 (Table 3).

Total element concentrations expressed on a mass basis differed significantly among sites for phosphorus

Table 1 Estimated number of stems, species diversity (Shannon index) and basal area for trees ≥ 10 cm diameter at breast height at each of five sites across the sampling transect in the San San Pond Sak peatland, Panama

Site	Forest type	Individuals (stems ha^{-1})	Shannon index	Basal area ($\text{m}^2 \text{ha}^{-1}$)
Site 1	<i>Raphia taedigera</i>	106	1.13	103
Site 2	Mixed forest	317	1.73	13
Site 3	<i>Camposperma panamensis</i>	212	1.53	26
Site 4	Stunted <i>C. panamensis</i>	529	1.90	10
Site 5	Sawgrass	423	1.83	5

Table 2 Contribution to the total basal area (%) of trees species for individuals ≥ 10 cm diameter at breast height at five sites across the sampling transect in the San San Pond Sakpeatland, Panama, with the species contributing the greatest proportion of the basal area indicated in *bold*

Species	Site 1	Site 2	Site 3	Site 4	Site 5
<i>Alchornea latifolia</i> Sw.	0.3	0.6			
<i>Ardisia</i> sp.		1.0	0.2		
<i>Camposperma panamensis</i> Standl.	0.2	38.7	70.0	54.4	87.9
<i>Cassipourea elliptica</i> (Sw.) Poir.		25.0	1.8		
<i>Chrysobalanus icaco</i> L.				16.0	
<i>Clusia cf. rosea</i> Jacq.		1.1	0.9		
<i>Cyrilla racemiflora</i> L.				9.7	5.0
<i>Drypetes standleyi</i> G.L. Webster		1.0	13.0	16.9	1.4
<i>Euterpe precatoria</i> Mart.		10.0	0.4		
<i>Ficus brevibracteata</i> W.C. Burger	0.3				
<i>Ficus costaricana</i> (Liebm.) Miq.		0.3			
<i>Ficus maxima</i> Mill.	0.2				
<i>Ficus</i> sp.		0.3			
<i>Myrica mexicana</i> Humb. & Bonpl. ex Willd.				2.1	5.7
<i>Raphia taedigera</i> (Mart.) Mart.	98.9				
<i>Symphonia globulifera</i> L. f.		21.7	13.6	0.4	

(a consistent decline towards the interior) and calcium (highest concentrations at site 3) (Table 3). However, all elements differed significantly among sites when concentrations were expressed on a area basis. The most marked changes were for potassium (four-fold) and phosphorus (seven-fold) between site 1 (*R. taedigera* swamp) and site 5 (sawgrass) (Table 3). Specifically, total phosphorus declined from 7.31 ± 0.31 to 1.10 ± 0.11 g m⁻². The carbon and nitrogen concentrations expressed on a area basis declined towards the wetland interior by approximately two to three-fold (Table 3), although the greatest calcium concentrations was measured at site 3 (*C. panamensis*).

There were marked changes in C:P and N:P ratios along the study transect (Fig. 2). Values for C:P increased from 518 ± 38 at site 1 (*R. taedigera*) to 1313 ± 107 at site 5 (sawgrass), while N:P increased from 25 ± 3 to 67 ± 10 at the same sites. However, the C:N ratio did not vary significantly among sites (18.6–21.1; Fig. 2).

The patterns seen in total nitrogen and phosphorus were reflected in significant site differences in extractable (plant-available) nutrients (Fig. 3), with a general decline in the concentrations of inorganic nitrogen and readily-exchangeable phosphate towards the interior

of the peatland ($F_4 = 3.5$, $P < 0.05$ and $F_4 = 28.2$, $P < 0.001$, respectively). The trend in inorganic nitrogen was driven by a significant decrease in nitrate (lower concentrations towards the peatland interior), whereas ammonium concentrations did not vary significantly across the transect (data not shown). There was a noticeable low concentration of readily-exchangeable phosphate at site 2, despite a relatively high total phosphorus concentration (Fig. 3). There was a strong positive correlation between total phosphorus and readily-exchangeable phosphate ($R^2 = 0.48$, $F_{1,18} = 23.1$, $P < 0.001$), although total nitrogen was not correlated with inorganic nitrogen ($P > 0.1$). There was also a significant positive regression describing the co-variation in exchangeable phosphate and nitrate ($R^2 = 0.47$, $F_{1,3} = 22.5$, $P < 0.001$).

Organic carbon and organic nitrogen extractable in K₂SO₄ varied significantly among sites ($F_4 = 3.9$, $P < 0.05$), although the pattern along the transect differed from that of inorganic nitrate and exchangeable phosphate (Fig. 3). The extractable organic carbon and organic nitrogen concentrations were lowest at sites 3 and 4 (dominated by *C. panamensis*) and highest at sites 2 and 5 (mixed forest and sawgrass, respectively).

Table 3 Chemical and physical properties of surface peat (0–10 cm) at five sites across the sampling transect in the San San Pond Sak peatland, Panama

Site	pH	Gravimetric moisture		Bulk density (g cm ⁻³)	Total elements								
		(g g ⁻¹)	(g cm ⁻³)		C (mg C g ⁻¹)	N (kg N m ⁻²)	P (mg P g ⁻¹)	Ca (g Ca m ⁻²)	K (mg K g ⁻¹)				
1	3.8 ± 0.03	6.4 ± 0.1	0.076 ± 0.004	490 ± 19.6	3.75 ± 0.15	23.8 ± 2.23	0.182 ± 0.017	0.957 ± 0.040	7.31 ± 0.31	1.07 ± 0.05	8.21 ± 0.39	0.36 ± 0.03	2.76 ± 0.25
2	3.7 ± 0.03	5.6 ± 0.6	0.078 ± 0.007	481 ± 13.4	3.75 ± 0.10	25.8 ± 1.63	0.201 ± 0.013	0.659 ± 0.028	5.14 ± 0.22	0.90 ± 0.26	7.00 ± 2.07	0.33 ± 0.04	2.61 ± 0.29
3	3.9 ± 0.04	6.7 ± 0.2	0.075 ± 0.007	489 ± 8.4	3.68 ± 0.06	26.6 ± 1.53	0.200 ± 0.011	0.668 ± 0.057	5.02 ± 0.43	2.30 ± 0.23	17.27 ± 1.71	0.26 ± 0.03	1.96 ± 0.25
4	4.0 ± 0.04	10.4 ± 1.0	0.040 ± 0.003	497 ± 11.8	2.00 ± 0.05	26.4 ± 1.7	0.106 ± 0.007	0.565 ± 0.059	2.27 ± 0.24	1.33 ± 0.27	5.36 ± 1.09	0.30 ± 0.05	1.19 ± 0.20
5	4.0 ± 0.10	14.1 ± 0.9	0.028 ± 0.002	502 ± 10.5	1.39 ± 0.03	25.0 ± 2.0	0.069 ± 0.006	0.395 ± 0.041	1.10 ± 0.11	0.75 ± 0.15	2.08 ± 0.41	0.26 ± 0.047	0.74 ± 0.13
<i>F</i>	6.6	25.8	21.6	158.7	33.9	77.9	19.40	19.40	18.5				16.9
<i>P</i>	<0.001	<0.001	<0.001	NS	<0.001	NS	<0.001	<0.001	<0.001	<0.001	<0.001	NS	<0.001
LSD (5%)	0.2	2.1	0.017	0.26	0.034	0.83	0.066	0.066	3.89				0.68

Values are the mean ± standard error of five replicate samples apart from the bulk density values, which were *n* = 8 at sites 1, 3 and 5 and *n* = 3 at sites 2 and 4. Significant differences between sites are indicated by *F* and *P* values and least significant differences (LSD, 5%). Total element concentrations are expressed on a mass and area basis. NS, not significant

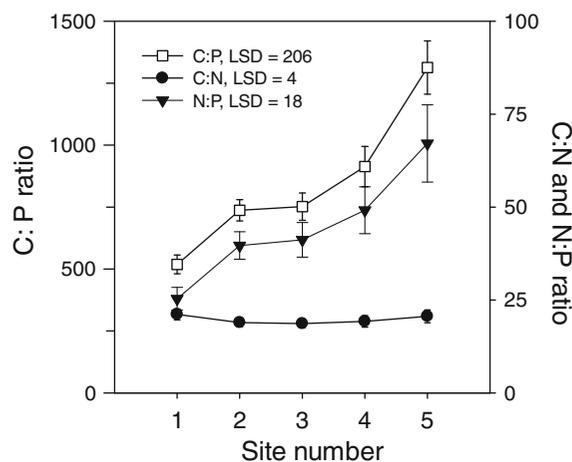


Fig. 2 Total element ratios for carbon to nitrogen, carbon to phosphorus, and nitrogen to phosphorus in surface peat (0–10 cm) at five sites across the sampling transect in the San San Pond Sak peatland, Panama. The ratios are derived from data presented in Table 2. Values are the mean ± standard error of five replicate samples, with the least significant differences (LSD; 5%) shown

Microbial nutrients

Microbial carbon, nitrogen, and phosphorus concentrations varied significantly among sites, being highest in the peatland margin and decreasing towards the peatland interior (Table 4). The differences were approximately two-fold for microbial carbon and five-fold for microbial nitrogen and phosphorus. There were significant differences among sites in microbial C:N and C:P ratios ($F_4 = 10.2$, $P < 0.001$ and $F_4 = 10.2$, $P < 0.001$, respectively), but not in the microbial N:P ratio, despite the marked changes in the soil N:P ratios (Fig. 4). Microbial C:N ratios were relatively constant between sites 1 and 4, but increased markedly at site 5 (sawgrass).

The microbial biomass contained between 32 and 47% of the total soil phosphorus, with the proportion increasing towards the peatland interior (Table 4). In contrast, microbial nitrogen accounted for only 1.8–3.8% of the total soil nitrogen, with values decreasing towards the peatland interior (Table 4). Thus, the microbial biomass contained a larger proportion of the phosphorus but a smaller proportion of the nitrogen at nutrient-poor sites compared to nutrient-rich sites. Microbial phosphorus was strongly correlated with total soil phosphorus ($R^2 = 0.87$, $F_{1,23} = 160.1$, $P < 0.001$), but microbial nitrogen

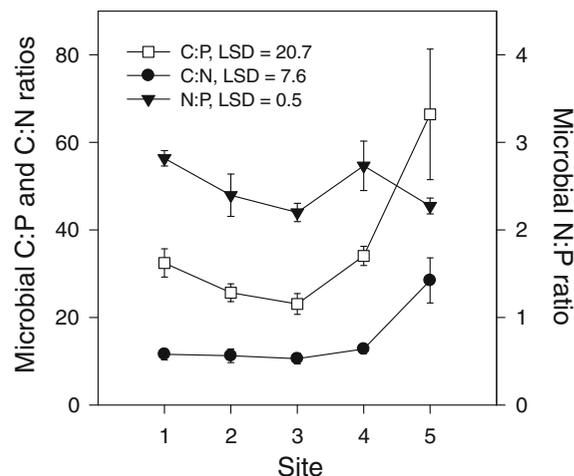


Fig. 4 Microbial carbon to nitrogen, carbon to phosphorus, and nitrogen to phosphorus ratios in surface peat (0–10 cm) at five sites across the sampling transect in the San San Pond Sak peatland, Panama. Values are the mean \pm standard error of five replicate samples, with the least significant differences (LSD; 5%) shown

202.3 ± 22.2 nmol MU g^{-1} soil min^{-1} at site 5 (Fig. 5). However, there was a noticeable increase in phosphatase activity at site 2 (mixed forest), which corresponded with the extremely low concentration of readily-exchangeable phosphate at this site (Figs. 3, 5). The activity of *N*-acetyl β -glucosaminidase and the four enzymes involved in the carbon cycle increased markedly at site 5 (site effect $F_4 = 15.6$, $P < 0.001$). For example, *N*-acetyl β -glucosaminidase increased from 3.55 ± 1.86 nmol MU g^{-1} soil min^{-1} at site 1 to 34.3 ± 16.3 nmol MU g^{-1} soil min^{-1} at site 5 (Fig. 5). For the carbon enzymes, the activity of β -glucosidase (5.88 – 39.9 nmol MU g^{-1} soil min^{-1}) showed a strong increase in the interior sites ($F_4 = 15.2$, $P < 0.001$) and was much greater than the activities of cellobiohydrolase, β -xylanase, and α -glucosidase (Fig. 5), although the activity of these enzymes were also highest at site 5 (site effect $F_4 = 5.6$, $P < 0.01$; $F_4 = 21.8$, $P < 0.001$; $F_4 = 13.6$, $P < 0.001$ for cellobiohydrolase, β -xylanase, and α -glucosidase, respectively)

Carbon gas fluxes

Potential soil respiration differed significantly between sites ($F_4 = 5.2$, $P < 0.01$), being greatest at site 1 (*R. taedigera*) and least at site 4 (stunted

C. panamensis) (Fig. 6a). However, this was not reflected directly in the surface CO_2 fluxes measured in the field (Fig. 6b), for which there were no significant differences among sites ($P > 0.1$), and as for potential respiration the greatest CO_2 efflux measured was from site 3 (*C. panamensis*) rather than from site 1 (*R. taedigera*). There was an order of magnitude greater soil respiration in response to drainage and elevated temperature compared to field measurements (Fig. 6a, b). Methane fluxes measured in the field differed significantly among sites ($F_4 = 28.33$, $P < 0.001$), with high CH_4 efflux at site 1 (*R. taedigera*) and site 5 (sawgrass), but low or negative fluxes at the other three sites (Fig. 6c).

Effect of nutrient availability on the tree community and microbial properties

Tree community

There was a strong ($R^2 = 0.81$) negative relationship between readily-exchangeable phosphate and tree species diversity described by the Shannon diversity index ($F_{1,3} = 17.8$, $P < 0.05$), with lowest diversity in plots with the highest exchangeable phosphate. Similarly, nitrate accounted for a substantial proportion of the variance in species diversity ($R^2 = 0.71$; $F_{1,3} = 10.8$, $P < 0.05$), but did not explain any additional variation when phosphate and nitrate were fitted together. In addition, there was a strong positive relationship ($R^2 = 0.87$, $F_{1,3} = 26.81$, $P < 0.05$ (log-transformed basal area)) between readily-exchangeable phosphate and tree basal area. Again, nitrate was correlated to basal area ($F_{1,3} = 8.84$, $P = 0.059$ (log-trans basal area)), but explained less variation ($R^2 = 0.63$) than readily-exchangeable phosphate and did not explain additional variation compared to exchangeable phosphate alone when the two variables were fitted together. Tree species diversity and tree basal area did not explain variation in either CO_2 or CH_4 fluxes ($P > 0.1$).

Microbial properties

There was a strong positive linear relationship between potential soil respiration and microbial carbon ($R^2 = 0.58$, $F_{1,18} = 27.7$, $P < 0.001$), although CO_2 fluxes were less strongly related to microbial carbon in the field: 25.2% of the variation

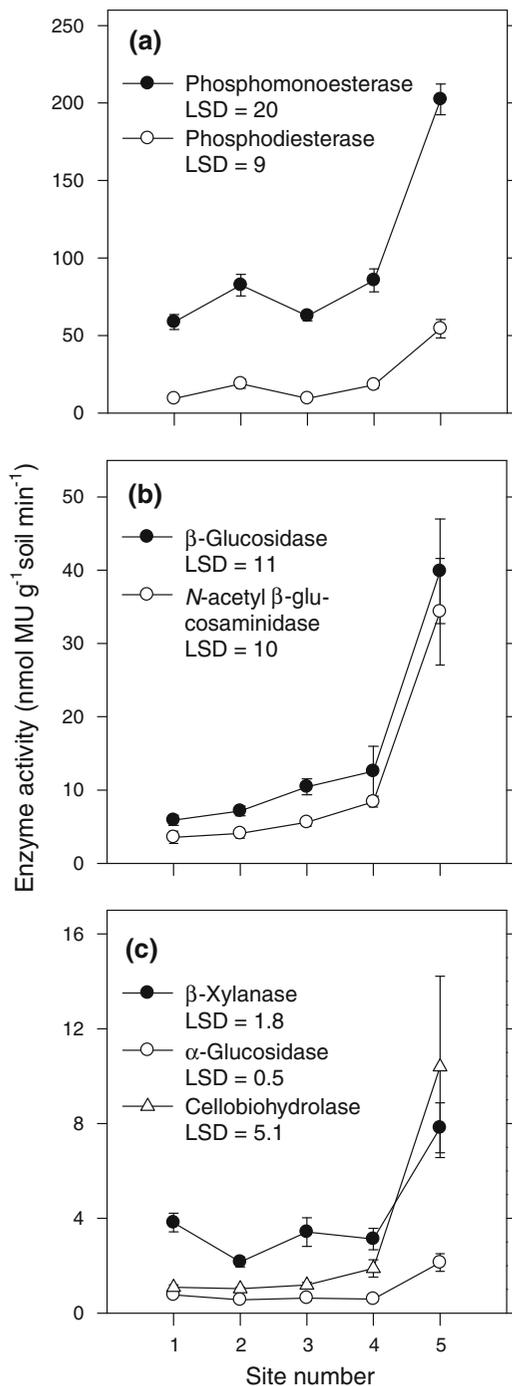


Fig. 5 Hydrolytic enzyme activities in surface peat (0–10 cm) expressed on the basis of microbial carbon: **a** phosphatases, **b** β-glucosidase and *N*-acetyl β-glucosaminidase, and **c** β-xylanase, α-glucosidase, and cellobiohydrolase, at five sites across the sampling transect in the San San Pond Sak peatland, Panama. Values are the mean ± standard error of five replicate samples, with the least significant differences (LSD; 5%) shown

in field-measured CO₂ flux was attributed to moisture content and microbial carbon ($F_{1,18} = 5.04$, $P < 0.05$). There was a strong positive linear relationship between the microbial C:P ratio and CH₄ production in the field, with the microbial C:P ratio explaining 68% of the variation in the CH₄ fluxes ($F_{1,23} = 51.3$, $P < 0.001$). The microbial nutrient status (i.e. C:P and C:N ratio's) was a strong predictor of the activity of all enzymes (Table 5). In addition, the availability of dissolved carbon, nitrogen and phosphorus also explained some of the variation in the activity of all enzymes (Table 5). Total soil C:P ratio's absorbed variation in β-Glucosidase and *N*-acetyl β-glucosaminidase.

Discussion

Tree community

Tree diversity in the San San Pond Sak peatland was low compared to surrounding lowland forests on mineral soils, which typically contain >100 species ha⁻¹ and are characterized by extremely high β-diversity (e.g., Pyke et al. 2001). Low diversity tree communities are typical of Central American wetlands (Keogh et al. 1999; Ellison 2004; Ramberg et al. 2006; Lopez and Kursar 2007). For example, the low diversity in San San Pond Sak is similar to that in forested wetlands in Mexico (Shannon index 1.95; Moreno-Casasola et al. 2009) and lowland forest swamp in Costa Rica (Shannon index 1.99–2.56; Webb and Peralta 1998).

The basal area in the *R. taedigera* swamp (site 1) was high (103 m² ha⁻¹, but note that this was a slight overestimation due to the multi-stemmed growth form) compared to previous reports of tropical forest swamps, including 80 m² ha⁻¹ in French Guiana (Koponen et al. 2004) and 63–58 m² ha⁻¹ in Kalimantan, Indonesia (Page et al. 1999). In contrast, basal areas at the interior sites (5 and 10 m² ha⁻¹, although the lowest value was from the sawgrass site lacking a continuous forest canopy) are low in comparison to the lower range reported from other sites, including 22 m² ha⁻¹ in seasonally flooded evergreen forest in Brazil (Haase 1999) and 29 m² ha⁻¹ in fresh water swamps in Micronesia (Allen et al. 2005). The differences in basal area among sites with contrasting nutrient availability

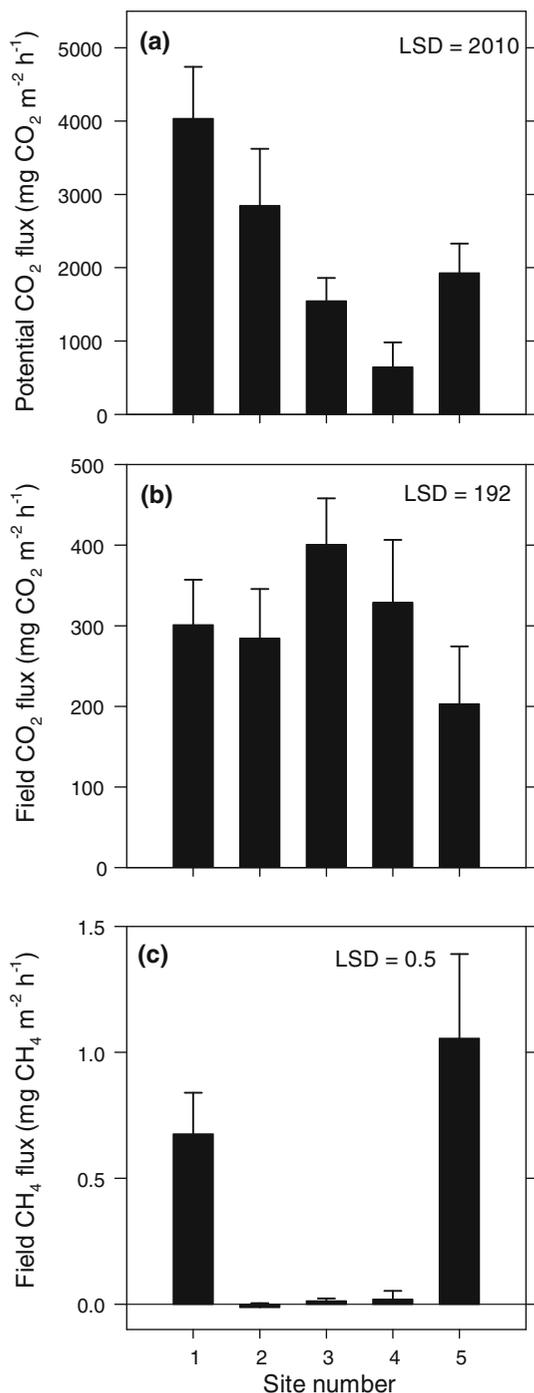


Fig. 6 Carbon fluxes from surface peat (0–10 cm) at five sites across the sampling transect in the San San Pond Sak peatland, Panama: **a** potential CO₂ flux from incubated samples, **b** CO₂ fluxes in the field, **c** CH₄ fluxes in the field. Values are the mean ± standard error of five replicate samples, with the least significant differences (LSD; 5%) shown

presented here were generally greater than changes in tree basal reported previously on contrasting mineral soils types (Allen et al. 2005) or under different flooding regimes (Koponen et al. 2004).

Within the peatland, species composition and basal area changed markedly over a relatively short distance and in parallel with considerable changes in nutrient status. This confirms previous reports (Phillips et al. 1997; Troxler 2007) and suggests that the nutrient gradient from the edge to the interior of the peatland exerts a strong control on the tree community. Low nutrients may contribute to the dwarfing of the trees and the sparse canopy, although this requires experimental confirmation. In contrast, the high basal area in the *R. taedigera* swamp and the relatively high concentrations of available nutrients there suggest that available phosphate and inorganic nitrogen concentrations are sufficient to maintain a relatively high productivity at that site. Strong edaphic controls of wetland vegetation communities were reported previously for the lower Orinoco delta plain of Venezuela, where species composition changed >80% among swamp forests, mangroves, and meadows, in response to a 10 km acidity gradient (Vegas-Vilarrubia and Laseras 2008).

We used a series of measurements to assess nutrient status within the San San Pond Sak peatland, including the concentrations of total and extractable nutrients, microbial biomass nutrients, and hydrolytic enzyme activities. These all indicated a marked decline in nutrient availability per unit area from the peatland margin to the interior sawgrass swamp, which we attribute to the doming of the peatland (i.e., the increased distance from the underlying mineral substrate) and gradual loss of nutrients dissolved in the soil solution as it move through the low density peat material as ground water and surface flow from the central areas to the edges of the wetland (Ingram 1982).

Several nutrients showed clear declines towards the center of the peatland, although most evidence points to phosphorus as being the key limiting nutrient. For example, the relatively high soil N:P ratios and the high proportion of the total phosphorus in microbial biomass across the entire transect indicate relatively low availability of phosphorus compared to nitrogen. The sawgrass swamp in particular exhibits clear evidence of extremely low phosphorus availability,

Table 5 Results from stepwise regression analysis showing the significance of the overall model describing a range of soil microbial enzyme activities (data shown in Fig. 5), the amount for variance attributed to it, and the significance of the fitted variables

Enzyme	Fitted variables	<i>F</i>	<i>t</i>	<i>P</i>	<i>R</i> ²
Cellobiohydrolase	Overall model	24.17		<0.001	82.8
	Microbial C		−6.00	<0.001	
	Microbial N		5.12	<0.001	
	Microbial C:N		7.38	<0.001	
	DOC		−4.28	<0.001	
	DON		2.96	<0.01	
α -Glucosidase	Overall model	57.52		<0.001	82.5
	Microbial C:N		6.96	<0.001	
	Total dissolved N		2.89	<0.01	
β -Glucosidase	Overall model	33.25		<0.001	72.9
	C:P (total)		5.25	<0.001	
	Total dissolved N		1.98	0.06	
<i>N</i> -acetyl β -glucosaminidase	Overall model	61.33		<0.001	88.3
	C:P (total)		4.04	<0.001	
	Microbial C:P		4.36	<0.001	
	Total dissolved N		2.48	<0.05	
Phosphodiesterase	Overall model	104.74		<0.001	92.8
	Microbial C:P		8.54	<0.001	
	Exchangeable P		−4.28	0.005	
	Total dissolved N		7.16	<0.001	
Phosphomonoesterase	Overall model	62.60		<0.001	88.5
	Microbial C:N		5.57	<0.001	
	Total dissolved N		6.57	<0.001	
	Exchangeable P		−3.34	<0.01	
β -Xylanase	Overall model	10.50		<0.001	44.2
	Microbial C:N		2.01	0.06	
	Dissolved organic N		1.74	0.09	

as indicated both by the high soil C:P and N:P ratios, negligible exchangeable phosphate, high microbial C:P ratios, and the marked increase in phosphatase enzyme activity compared to other sites. In this context it is important to note the contrasting patterns in soil nutrients when expressing these on a per mass vs a per area basis: It is clear that some nutrients does not change on a per mass basis along the transects but the amounts of nutrients potentially available to the plants (i.e. per area) change markedly. Readily-exchangeable phosphate was the strongest predictor of basal area and species diversity of the forest. Furthermore, leaf tissue N:P ratio's >16 suggests that the vegetation in the peatland is P limited (Troxler 2007) as a consequence of the low P availability. In contrast, nitrogen availability appeared to be the most important driver of the forest structure in Indonesian peatlands (Widyatmoko and Burgman 2006). Further work is therefore needed

on nutrient turnover through litter inputs and decomposition to fully understand how nutrient availability impacts ecosystem function in this peatland.

Of particular interest in terms of below-ground nutrient status was that a considerable proportion of the total soil phosphorus was contained within the microbial biomass. This occurred at all sites and suggests that the microbial community exerts a strong control on phosphorus availability in the peatland, with intense competition between plants and microbes for available phosphorus. In contrast, a large proportion of the soil nitrogen is stabilized in organic matter and therefore is not available to microbes. High rates of leaching of phosphorus from litter material and subsequent assimilation by the microbial community have been demonstrated previously (Qiu et al. 2002; Battle and Golladay 2007). The microbial biomass declined markedly towards

the peatland interior, yet contained a relatively constant and low microbial N:P ratio at all sites. This suggests a constraint on the stoichiometry of these nutrients in microbial biomass in the peatland, as reported recently in a meta-analysis of soil microbial nutrients in mineral soils (Cleveland and Liptzin 2007). A caveat is that the microbial nutrient concentrations almost certainly included a contribution from fine roots that were not removed prior to fumigation, leading to an overestimation of microbial nutrients.

The activities of all hydrolytic enzymes investigated increased towards the centre of the peatland in parallel with the decline in nutrient concentrations, while the microbial biomass concentration per surface area declined. Enzymes involved in the cycling of phosphorus and nitrogen respond strongly to changes in the availability of these nutrients, both in mineral soils (Olander and Vitousek 2000; Allison et al. 2007) and wetlands (e.g., Bragazza et al. 2006; Rejmánková and Macek 2008; Penton and Newman 2008), indicating a shift in resources allocation to increased enzyme activity to maintain metabolic rates. Similar rates of phosphatase activity were also reported from Malaysian peat swamps (Jackson et al. 2009).

There were also marked changes in activity from the edge to the interior of the peatland for enzymes involved in the degradation of long-chain plant-derived polymeric molecules (i.e., cellobiohydrazase, *N*-acetyl- β -glucosaminidase, β -glucosidase). As these enzymes are induced by the presence of substrate, this perhaps indicates a change in the carbon chemistry of the peat, although the increase in *N*-acetyl- β -glucosaminidase activity may indicate either an increased microbial investment in nitrogen acquisition (Olander and Vitousek 2000; Bragazza et al. 2006) or increased fungal activity (Miller et al. 1998) in the interior of the peatland. β -Xylanase is linked to more slowly decomposing material, but differences in its activity among sites were relatively small. Interestingly, compared to finding in temperate peatlands (Bragazza et al. 2006), the activity of phosphatase, β -glucosidase and *N*-acetyl- β -glucosaminidase were several orders of magnitude lower in our study system.

The marked changes in nutrient status of below-ground organisms and species composition of the forest canopy are likely to influence the carbon cycle

(Raich et al. 2007; Troxler 2007). Indeed, potential soil respiration determined on drained samples in the current study showed a clear link to nutrient status. This was not reflected in the pattern of CO₂ flux in the field, however, suggesting that variables other than nutrient status, such as root respiration (Chimner 2004; Metcalfe et al. 2007) or water table fluctuations (Jauhiainen et al. 2005), regulate the net CO₂ efflux from the peat surface. The CO₂ flux rates were within the range of those measured from lowland forested swamps on deep peat in central Kalimantan, Indonesia (ca. 850 mg CO₂ m⁻² h⁻¹; Jauhiainen et al. 2005), Sarawak, Malaysia (366–1954 mg CO₂ m⁻² h⁻¹; Melling et al. 2005a, b), and Micronesia (32–381 mg CO₂ m⁻² h⁻¹; Chimner 2004). Methane fluxes measured here were several orders of magnitude lower than CO₂ fluxes and varied markedly among sites. The highest CH₄ fluxes from site 1 (*R. taedigera*) and site 5 (sawgrass swamp) are comparable to fluxes reported in the literature from Kalimantan (e.g., 0.35–2 mg CH₄ m⁻² h⁻¹; Furukawa et al. 2005; Hadi et al. 2005; Jauhiainen et al. 2005), while the lowest CH₄ fluxes at the three intermediate sites in the current study (*C. panamensis* and mixed forest) are comparable to those reported for Sarawak wetlands (maximum rates of 11.2 μ g CO₂ m⁻² h⁻¹; Melling et al. 2005a, b). Our results suggest that CH₄ fluxes have high spatial variability in peatland systems and vary in response to differences in the water table (Inubushi et al. 2005; Hadi et al. 2005; Jauhiainen et al. 2005) and substrate availability (Bachoon and Jones 1992) to a greater extent than CO₂ fluxes. Seasonal variability in gas fluxes has been shown in tropical peatlands (e.g. Hadi et al. 2005) and it is likely that both the CH₄ and CO₂ fluxes in the San San Pond Sak wetland will fluctuate between the drier and wetter periods of the year. Further detailed studies at a range of temporal scales are therefore required to assess the temporal stability of the spatial differences in gas fluxes in the peatland shown here as well as the mechanisms driving them.

As warming and drainage during the laboratory incubation increased CO₂ production from surface peat by an order of magnitude compared to field fluxes, this demonstrates that the carbon storage potential of the system may be sensitive to climate warming and/or a lowering of the water table (Brady 1997; Inubushi et al. 2005; Hadi et al. 2005; Jauhiainen et al. 2005). However, this may be regulated to some extent by the apparent strong

nutrient limitation of below-ground processes in the peatland interior, as found in subtropical wetlands (Bachoon and Jones 1992; Battle and Golladay 2007; Wright et al. 2009). Further experimental studies are needed to assess whether microbial activity in this ombrotrophic peatland is limited by nutrients or labile carbon or indeed the environmental conditions. In summary, our results revealed marked changes in nutrient status across a relatively short distance in this tropical peatland, which appear to exert a strong control on both above and below ground organisms. In particular, phosphorus limitation appears to be extreme in the peatland interior. Nutrient status therefore likely influences the carbon cycle in two distinct ways—by regulating carbon inputs through its influence on plant community composition and litter quality, and by influencing decomposition rates by below-ground organisms.

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