CrossMark

REGULAR ARTICLE

Root oxygen loss from *Raphia taedigera* palms mediates greenhouse gas emissions in lowland neotropical peatlands

Jorge Hoyos-Santillan · Jim Craigon ·
Barry H. Lomax · Omar R. Lopez ·
Benjamin L. Turner · Sofie Sjögersten

Abstract

Aims Little is known about the influence of vegetation on the timing and quantities of greenhouse gas fluxes from lowland Neotropical peatlands to the atmosphere. To address this knowledge gap, we investigated if palm forests moderate greenhouse gas fluxes from tropical peatlands due to radial oxygen loss from roots into the peat matrix.

Methods We compared the diurnal pattern of greenhouse gas fluxes from peat monoliths with and without seedlings of *Raphia taedigera* palm, and monitored the effect of land use change on greenhouse gas fluxes from *R. taedigera* palm swamps in Bocas del Toro, Panama.

Results CH_4 fluxes from peat monoliths with *R. taedigera* seedlings varied diurnally, with the greatest emissions during daytime. Radial oxygen loss from the roots of *R. taedigera* seedlings partially supressed CH_4 emissions at midday; this suppression increased as seedlings grew. On a larger scale, removal of *R. taedigera* palms for agriculture increased CH_4 and N_2O fluxes, but decreased CO_2 fluxes when compared to nearby intact palm forest. The net impact of forest clearance was a doubling of the radiative forcing.

Conclusions *R. taedigera* palm forest influences the emission of greenhouse gases from lowland tropical peatlands through radial oxygen loss into the rhizosphere.

Keywords Tropical peatland · *Raphia taedigera* · Oxygen loss · Greenhouse gases · Methane · Nitrous oxide

J. Hoyos-Santillan (✉) · J. Craigon · B. H. Lomax ·
S. Sjögersten
School of Biosciences, The University of Nottingham, Sutton
Bonington, Leicestershire LE12 5RD, UK
e-mail: jhoyossantillan@hotmail.com

O. R. Lopez
Centro de Biodiversidad y Descubrimiento de Drogas, Instituto de
Investigaciones Científicas y Servicios de Alta Tecnología
(INDICASAT), Clayton, Republic of Panama

B. L. Turner
Smithsonian Tropical Research Institute, Apartado 0843-03092,
Balboa, Ancon, Republic of Panama

Introduction

Tropical peatlands are an important component of the global carbon cycle, playing a central role in global warming by exchanging greenhouse gases with the atmosphere (e.g., CO_2, CH_4, and N_2O) (Couwenberg et al. 2010; Lähteenoja et al. 2009; Page et al. 2011; Sjögersten et al. 2014). At the global scale, wetlands are estimated to be the most important natural source of CH_4 to the atmosphere (Ciais et al. 2013), emitting 0.1–0.23 Gt of CH_4 yr.$^{-1}$, equivalent to 17 to 40 % of the global CH_4 emissions (IPCC 2013; Laanbroek 2010). Two thirds of the global CH_4 emissions from wetlands are derived from undisturbed tropical wetlands

Springer

(Melton et al. 2013). With respect to CO_2, burning and anthropogenically induced peat decomposition (e.g., following drainage) releases between 0.22 and 0.35 Gt C yr.$^{-1}$ globally (Hooijer et al. 2010; van der Werf et al. 2010). Furthermore, land use change and drainage of tropical peatlands increase the emission of N_2O, which as a greenhouse gas is approximately 300 times more potent than CO_2 and contributes up to 9 % of the greenhouse gas emissions from tropical peatlands in terms of CO_2 equivalents (CO_{2-eq}) (Jauhiainen et al. 2012; Melling et al. 2007).

Vegetation plays a central role in the control of production, transport, and interchange of greenhouse gases with the atmosphere. For example, the photosynthetic activity of trees is correlated strongly with soil respiration in temperate savannah and temperate peatlands (Mikkelä et al. 1995; Tang et al. 2005; Thomas et al. 1996). The release of photosynthates through the rhizosphere provide labile substrate for decomposer organisms (Silvola et al. 1996; Ström et al. 2003; Wright et al. 2011), influencing the diurnal pattern of CO_2 and CH_4 emissions in both temperate and tropical ecosystems (Bahn et al. 2009; Wright et al. 2013b). Therefore, it is important to measure greenhouse gas fluxes on a diurnal basis, as this allows investigation of biotic and abiotic controls on the temporal variation of greenhouse gas emissions (Armstrong 1971; Ström et al. 2003; Wang and Han 2005). Importantly, it allows for the separation of long-term drivers which can strongly vary seasonally, e.g., temperature, humidity, and precipitation. In addition, quantifying diurnal patterns of greenhouse gas emissions reduces uncertainty of seasonal and annual emission estimates. This is because uncertainty is mainly derived from systematically measuring gas fluxes at times of the day when fluxes may be highest or lowest, producing significant over or underestimations when subsequently extrapolated to calculate seasonal and annual fluxes (Käki et al. 2001; Mikkelä et al. 1995; Weller et al. 2015).

The magnitude of the effect of vascular plants on the production and transport of greenhouse gas emissions varies among vegetation types. In the arctic tundra, CH_4 emissions decreased 11-fold after removal of vascular plants (Stephen et al. 1998; Torn and Chapin 1993). By contrast, in temperate peatlands, rhizosphere oxidation can reduce (Gerard and Chanton 1993; Holzapfel-Pschorn et al. 1986) or completely suppress CH_4 emissions (Fritz et al. 2011). The contrasting responses of CH_4 fluxes to vegetation in different geographical areas

highlight complex interactions between the vegetation type, climatic regions and CH_4 emissions. N_2O emissions are also strongly linked to substrate supply and concentrations of oxygen in the peat matrix, with high oxygen levels reducing emissions (Armstrong et al. 1991; De Bont et al. 1978; King and Wiebe 1978). These findings suggest that CO_2, CH_4, and N_2O emissions are controlled by competing processes linked to the type and activity of the vegetation. Despite the large contribution of tropical forested wetlands to greenhouse gas emissions, these controls remain poorly understood.

Greenhouse-gas related radiative forcing of peatlands can be estimated by using global warming potentials (GWP, expressed as CO_{2-eq}; Ström and Christensen 2007). Depending on the time horizon that is used for the estimation of the radiative forcing (e.g., 20, 100, or 500 yr.; GWP_{20}, GWP_{100}, GWP_{500}), peatlands can be defined as net sinks (negative radiative forcing) or sources (positive radiative forcing) of greenhouse gases to the atmosphere (Barthelmes et al. 2015). Considering the GWP_{100}, the radiative forcing derived from the combined effect of CO_2 and CH_4 emissions from pristine peatlands fluctuates from positive to negative, having no net effect on the climate (Barthelmes et al. 2015). However, using the same GWP_{100}, peatlands can turn into net sources if their CH_4 emissions are higher than the CO_2 uptake in terms of CO_{2-eq} (Rieley et al. 2008). In the long term, peatlands have had a net cooling effect on climate (Frolking et al. 2006; Wang et al. 2009; Yu et al. 2011). It is therefore important to define whether disturbances to the vegetation, such as land use change for agriculture, can shift the radiative forcing balance in Neotropical peatlands from net sink to net source of carbon to the atmosphere. This is particularly important in the tropics, since the biggest forest area loss in the world in recent years has occurred in these regions, specifically in Africa and South America (MacDicken et al. 2015).

Tropical peatlands support a range of vegetation types adapted to waterlogged conditions. Such adaptations included aerial roots, pneumatophores, and aerenchyma designed to transport oxygen to roots growing in anoxic conditions (Cronk and Fennessy 2001). The productivity of tropical peatland forests is variable, but can be high under favourable nutrient conditions (Sjögersten et al. 2014; Sjögersten et al. 2011). Large areas of Neotropical peatlands support productive palm forests that form extensive mixed and monodominant stands (Lähteenoja et al. 2009; Myers 1981; Phillips

et al. 1997; Roucoux et al. 2013). The peat swamp forests on the Caribbean coast of Panama and Costa Rica support either mono-dominant forests of the canopy forming evergreen palm *Raphia taedigera* (Mart.) (Myers 1981; Phillips et al. 1997), or mixed forest composed of *R. taedigera* and evergreen broadleaved hardwood trees (Phillips et al. 1997; Urquhart 1999). These forests emit both CO_2 and CH_4, with seasonal and spatial variability in emissions being related to both substrate availability and CH_4 oxidation processes (Wright et al. 2011; Wright et al. 2013b), indicating that the vegetation activity may moderate greenhouse gas emissions in these forests.

A fundamental knowledge gap is how rhizosphere processes, including radial oxygen loss (i.e. oxygen release from roots into the peat matrix), influence greenhouse gas emissions in tropical wetland forests (Sjögersten et al. 2014). To address this, we tested the following hypotheses: i) *R. taedigera* palm seedlings supress CH_4 emissions due to large radial oxygen loss from their root systems; ii) clearance of *R. taedigera* forest increases CH_4 and N_2O emissions as peat oxygen concentrations decline; iii) peat surface CO_2 emissions decrease as root respiration ceases following clearance; and iv) land use change affects the relative contribution to radiative forcing of greenhouse gas emissions from soil, increasing the relative importance of CH_4 emissions with respect to CO_2 and N_2O. To test these hypotheses we conducted in situ and ex situ experiments and measurements in peatlands on the Caribbean coast of western Panama.

located in the Bocas del Toro Province in the north-western Caribbean region of Panama. These sites included the Changuinola peat deposit (CPD, ≈ 80 km^2) in the San San Pond Sak wetland and peatlands along the Cricamola River shore (Table 1). Extensive palm forests are among the main forest types that can be found in the region (Hoyos-Santillan et al. 2015; Myers 1981; Phillips et al. 1997). The region is characterised by high precipitation averaging 3092 ± 181 mm yr.$^{-1}$ (2005 to 2011, Smithsonian Tropical Research Institute Physical Monitoring Program), with no pronounced seasonality (Hoyos-Santillan et al. 2015; Wright et al. 2011). The mean annual air temperature from 2003 to 2011 was 26.4 ± 0.1 °C (Smithsonian Tropical Research Institute Physical Monitoring Program).

Two separate palm swamp peatlands dominated by *R. taedigera* were selected (Table 1); the sites were freshwater, with conductivity below 200 μS cm^{-1}. The water table remains close to the peat surface throughout most of the year, fluctuating between $+0.15$ and -0.4 m relative to the peat surface. Peat pH was strongly acidic based upon the USDA-NRCS classification (5.05 to 5.52) (Schoeneberger et al. 2012), and bulk densities were around 0.1 g cm^{-3}, reflecting the high organic matter content (Table 2). The Cricamola sites had seasonal mineral inputs from flooding events from the nearby river. The surface of the palm forest sites were covered with a deep layer of leaf litter, with dense pneumatophores protruding from the surface, and a dense but shallow (ca. 1.1 m) fibrous root system (Wright et al. 2013b).

Materials and methods

Study sites

Field measurements and experiments were conducted on or using material from forested lowland peatlands

Experimental programme

Two approaches were used to determine if palm forests influence greenhouse gas emissions by radial oxygen loss from roots. Firstly, monitoring of ex situ diurnal CO_2 and CH_4 fluxes from *R. taedigera* seedlings

Table 1 Location and characteristics of study sites

Site	Coordinates	Distance to coast (m)	Dominant vegetation	% basal area (m^2 ha^{-1})[d]
Cricamola disturbed[a]	8°57′17.70″N, 81°54′41.35″W	1400	*R. taedigera*	Deforested
Cricamola control[b]	8°57′13.64″N 81°54′43.78″W	1500	*R. taedigera*	70.9
San San Pond Sak[c]	9°25′29.20″N, 82°24′05.60″W	500	*R. taedigera*	98.9

[a] Original plot set in December 2010 and turned into a rice field in March 2011

[b] Undisturbed palm swamp plot set in May 2011

[c, d] The San San Pond Sak site and its % of forest basal area correspond to site 1 from Sjögersten et al. 2011

Table 2 Physicochemical characteristics of surface peat

Site	pH	Conductivity	Bulk Density	Moisture	Loss on ignition	Total elements			
						C	N	S	P
		$\mu S\ cm^{-1}$	$g_{dw}\ cm^{-3}$	$g\ g_{fw}^{-1}$	$g\ g_{dw}^{-1}$	$mgC\ g_{dw}^{-1}$	$mgN\ g_{dw}^{-1}$	$mgS\ g_{dw}^{-1}$	$mgP\ g_{dw}^{-1}$
Cricamola[a]	5.52 ± 0.75	108 ± 15	0.13 ± na	0.83 ± 0.01	0.51 ± 0.12	458 ± 250	22.9 ± 18.2	4.7 ± 1.6	0.22 ± na
San San Pond Sak[b]	5.05 ± 0.23	64 ± 5	0.11 ± na	0.90 ± 0.02	0.92 ± 0.02	502 ± 200	12.1 ± 5.5	1.3 ± 0.7	0.27 ± na

Values presented correspond to mean ± SE, $n = 3$; excluding the bulk density and phosphorus, which were measured on a single sample

[a] Data from the palm plot prior to land use change

[b] The San San Pond Sak site is where the peat monolith and palm seedlings for the ex situ experiment were collected

growing on peat monoliths relative to controls without seedlings (addressing hypothesis (i)), and secondly monitoring of in situ CO_2, CH_4, and N_2O fluxes from the peat surface of an anthropogenically disturbed *R. taedigera* palm swamp compared to an undisturbed area (hypothesis (ii) to (iv)).

The ex situ seedlings experiment was conducted at the Smithsonian Tropical Research Institute station in Bocas del Toro (STRI-BDT). For this purpose, twelve peat monoliths and six *R. taedigera* seedlings were collected within the transect studied previously by Sjögersten et al. (2011) (9°25′34.90″N, 82°24′1.80″ W). Each monolith was collected and set up for the experiment in PVC pipes (diameter = 0.21 m, height = 0.5 m). Monoliths were collected by carefully cutting the peat with a blade around the PVC pipe, which was then manually inserted into the peat. Afterwards, the lower section of the peat was cut horizontally to retrieve the monolith. Peat monoliths were kept in their original upright positions and a PVC cap was fixed to the bottom of the pipe. The peat monoliths were carefully transported to the research station and positioned in the open on a hard surface. *R. taedigera* seedlings showing their first *eophyll* (leaf), with a height of 0.15 to 0.2 m, were planted into six of the twelve peat monoliths. The remaining six peat monoliths were used as unplanted controls. The water table was kept 50 mm above peat level to simulate flooded conditions in the field. The monoliths were subjected to natural variation in light and temperature. Experimental units were randomly divided in two blocks, each having three controls and three *R. taedigera* peat monoliths. Greenhouse gas fluxes were monitored across diurnal cycles on three occasions, from the time seedlings were transplanted into the peat monoliths (10 May 2011), until the end of the experiment on November 2011 (Monitoring dates: 7–8 July; 26–27 September; 5–6

November). Diurnal monitoring of CO_2 and CH_4 was carried out in 4 h intervals across 24 h. Each block was sampled within a single 24 h period. At the end of the experiment, *R. taedigera* plants were harvested and separated into leaves, stems and roots for determination of biomass.

The in situ monitoring of greenhouse gas fluxes was conducted in a palm swamp forests dominated by *R. taedigera* located close to the shore of the Cricamola River (Table 1). The first 0.1 ha (20 × 50 m) plot was set up in December 2010. A sampling well was installed in the plot to measure the water table, in situ dissolved O_2, temperature, and conductivity of the pore-water. Each well consisted of a 50 mm diameter PVC pipe with 10 mm diameter perforations at 50 mm intervals. During March 2011, the plot was anthropogenically disturbed, allowing us to monitor the effect of slash and burn agriculture on greenhouse gas fluxes. For this purpose, three additional 0.1 ha plots were established in May 2011. Two of these plots were located in an adjacent undisturbed palm forest and an extra plot was established in the disturbed area. The two plots corresponding to each treatment were ca. 50 m apart. This resulted in four experimental units, which were subsampled and used for comparisons between the disturbed and undisturbed areas. The undisturbed forest area was located 100 m SW from the anthropogenically disturbed site; in this undisturbed area a sampling well for monitoring the water table, conductivity, temperature, and dissolved O_2 concentrations of the pore-water was also installed. The forest clearance entailed cutting and burning of the palms, followed by rice seeding of the area (Online Resource 1). The peat in the disturbed site was not drained and the position of the water table was comparable to the water table in nearby undisturbed forest sites.

To characterise the forest a vegetation inventory was conducted in one of the undisturbed plots; all stems >0.1 m in diameter at breast height (1.30 m DBH) were measured, marked, tagged, and mapped. The basal area of the tree species found in the plots was calculated from the DBH data. However, given the multi-stem colonial growth of *R. taedigera*, it is plausible that basal area for this species was overestimated.

Greenhouse gas fluxes were measured in the first plot before it was anthropogenically disturbed (12 December 2010: Day 0) and when the vegetation was cleared (19 March 2011: Day 99). Subsequently, measurements were made in both the disturbed and the undisturbed-control plots five days after the site was burned (28 May 2011: Day 169) and on three consecutive occasions during rice growth (14 July, 10 of August, and 14 September 2011; corresponding to days 216, 243, and 278 respectively) (Online Resource 1). Greenhouse gas flux measurements were conducted in three randomly chosen locations in triplicate within each plot during the monitoring events. Thus, nine chambers were installed for the collection of gases at each plot. Once rice emerged, gas sampling chambers were placed on top of the peat in between the rice plants.

Gas flux measurements

Ex situ fluxes

Gas collection for flux determination on the peat monolith-seedlings experiment was performed using the closed chamber technique (Sjögersten et al. 2011). For this purpose, transparent polycarbonate chambers ($\approx$15.7 L; diameter = 0.2 m, height = 0.5 m) with a sampling port equipped with a Suba-Seal® rubber septa were used. During each monitoring event the chamber was placed on top of the peat monoliths, achieving air tight seal against the water surface. The air within the chambers was gently mixed during the chamber closure using a battery powered fan (50 × 50 mm) attached to the side of the chamber. Gas samples (20 mL) were taken through Suba-Seal® sampling ports using hypodermic needles (25 Gx1", TERUMO, UK) and plastic syringes at 0, 10, 20 and 40 min after the chamber was placed on top of the monoliths. Gas samples were injected into pre-vacuumed 12 mL borosilicate glass vials sealed with a screw cap-septum (Exetainer; LABCO, UK), leaving each vial with overpressure. All samples were shipped to the University of

Nottingham for gas chromatography analyses. Vials were discarded for chromatographic analyses if over-pressure was absent (< 5 %). CO_2 and CH_4 concentrations were determined using a single injection system with a 1 mL sample loop that passed the gas sample using N_2 as carrier through a non-polar methyl silicone capillary column (CBP1-W12-100, 0.53 mm I.D., 12 m, 5 mm; Shimadzu UK LTD, Milton Keynes, UK) and porous polymer packed column (HayeSep Q 80/100). Thermal conductivity (TCD) and flame ionization (FID) detectors were used to measure CO_2 and CH_4, respectively. Flux calculations were based on the linear accumulation of gases within the closed chamber, and gas samples that did not follow a linear accumulation trend were discarded for the calculation of gas fluxes.

In situ fluxes

The closed chamber technique was also used to conduct the in situ gas flux measurements. The chambers were made of opaque plastic, covering a 0.075 m^2 area, with a 0.1 m height, and 7 L volume. Each chamber had a sampling port equipped with a Suba-Seal® rubber septa. Although the forest floor was mostly unvegetated, trailing understory vegetation and fallen branches were removed, before the installation of the chamber. Peat disturbance was avoided as much as possible during the installation of the chambers, but slight pressure was applied to ensure an air-tight seal. Once installed and prior to the collection of gas samples, the chamber headspace was homogenised by repeatedly pumping the air within the chamber with a 20 mL syringe equipped with a hypodermic needle (see section 2.3.1 for details). Afterwards, gas samples were collected from each chamber after 0, 2, 10 and 20 min and stored in Exetainers. Gas samples were analysed for CO_2 and CH_4 as described above (see section 2.3.1), and N_2O was determined on the same GC using an electron capture detector (ECD).

Physicochemical parameters

For the ex situ experiment, dissolved O_2 in the peat matrix was measured using a micro dissolved-O_2 electrode (DO-166, Lazar Research Laboratories Inc., USA; 0.1 mg L^{-1} resolution). Dissolved O_2 (mg L^{-1}) was measured in three occasions between October and November 2011, when palm seedlings were fully grown. Measurements were conducted 10–20 mm beneath the

peat's surface (depending on the primary roots position), which was covered by a 50 mm water layer to simulate the in situ flooded conditions. For the purposes of this study, primary roots comprise, in addition to the tap root, the first–order branch roots that grow out from the tap root (also called lateral roots) (Barlow 2001). Primary roots were visually identified as they grew at the peat surface and were only partially covered by peat. In each peat monolith with *R. taedigera*, dissolved O_2 measurements were performed 0, 20, and 40 mm away from three primary roots (6 cores; $n = 162$); for this purpose, the micro electrode was carefully collocated in the desired position and gently stirred until the reading was stable. Dissolved O_2 measurements were also conducted on the control peat monoliths (6 cores; $n = 54$), following a cross-section transect. Temperature was recorded in the peat monoliths using portable thermocouples with data logging capabilities (Tinytag Talk 2, Tinytag, UK).

For the in situ monitoring, simultaneously to the collection of in situ gas samples, dissolved O_2 (DO; mg L^{-1}) and temperature (°C) in the top 0.5 m of the peat profile were measured at the sampling wells installed within each plot using a portable multiparametric probe (YSI 556 MPS, USA).

Peat sampling and characterization

Three soil samples from the peat 0.1 m top layer (0.1 × 0.1 × 0.1 m) were collected from disturbed and control plots. Samples were wrapped in aluminium foil and placed in plastic boxes for later transportation (< 3 h) to STRI laboratory in Bocas del Toro. All samples were refrigerated (2 °C) until transport to the University of Nottingham, UK.

Moisture content was determined by gravimetric analysis of the water mass loss of 10 g fresh peat samples after oven drying peat samples at 70 °C for 70 h (Wright et al. 2011). Loss on ignition (LOI), as an indirect measurement of soil organic matter content (SOM), was measured by gravimetric analysis of mass loss from dry peat samples placed in the muffle furnace for 7 h at 550 °C. Peat pH and conductivity were determined in a 1:2.5 peat fresh weight (fw)-deionized water solution. Total carbon (C), nitrogen (N), and sulphur (S) were measured from 0.5 g homogenised peat samples (homogenization was carried out in a Planetary Ball Mill, Retsch-PM400, Castleford, UK) using a total element analyzer (Thermo Flash EA 1112, CE

Instruments, Wigan, UK). Peat ash from loss on ignition analysis was dissolved in 6 M HNO_3 to estimate the peat phosphorus content by molybdate colorimetry (Andersen 1976).

Global warming potential calculations

Radiative forcing of greenhouse gas fluxes from peat was calculated by multiplying an estimation of the total annual fluxes of the non-CO_2 gases from peat (*i.e.*, CH_4 and N_2O) by their global warming potential index (GWP), thus obtaining the corresponding CO_2 equivalents (CO_2-eq) (Rieley et al. 2008). GWP indices used in this study include the estimation of climate-carbon feedbacks for both 20 and 100 yr. horizons. (GWP_{20} and GWP_{100}); GWP_{20}: $CH_4 = 86$, $N_2O = 268$ and GWP_{100}: $CH_4 = 34$, $N_2O = 298$ (IPCC 2013). The annual CO_2-eq estimations presented in this study do not include the whole-forest carbon exchange with the atmosphere; for example, net primary productivity and the land use change-fire related component of the radiative forcing were not measured. Thus, the CO_2-eq figures correspond exclusively to the CO_2, CH_4, and N_2O emissions from the surface peat without plant mediation.

Statistical analyses

Linear mixed models were used to compare the gas production rates and were fitted by using Residual Maximum Likelihood (REML). Gas fluxes were transformed (log_{10}) to fulfil the homogeneity of variance requirements of the linear models. Level of significance of the differences between the fixed effects was estimated by Wald tests using an F distribution. For the *ex situ* experiment, the presence of *R. taedigera* was used as fixed factor while the specific peat monolith and the sampling date block were included as random factors; the fluxes included in these analyses comprise the three monitoring events. For the analysis of the variation of CH_4 fluxes parallel to seedlings growth, only the daylight fluxes were included (9:00 to 17:00 h). The number of days since the seedlings were transplanted into the peat monoliths was used as a fixed factor, whereas the specific monolith was used as random factor. The variation of dissolved oxygen with the distance from the roots was analysed using a one-way blocked ANOVA, with the peat monoliths being the blocking factor. Tukey's HSD was performed as multiple comparison test ($P < 0.05$). For the analysis of the effect of land use

change on greenhouse gas fluxes, the anthropogenic disturbance and the monitoring dates were used as fixed factors, whereas the plots were used as random factors. Significance was attributed at $P < 0.05$. Relationships between gas fluxes and environmental factors (water table, temperature, and dissolved oxygen) were explored using regression analyses. The % of variance accounted (adjusted R^2) by regression statistical models is referred to as r^2 in text and figures. Results through text and graphs are presented as mean ± SE. All statistical analyses were performed in GenStat (VSN International 2011).

Results

Ex situ diurnal CO_2 and CH_4 fluxes

The CO_2 fluxes from the control peat monoliths did not follow a diurnal pattern, by contrast the CO_2 fluxes from monoliths with *R. taedigera* seedlings displayed a convex dial pattern with negative fluxes during daylight (*i.e.* photosynthetic assimilation) (Fig. 1a). *Ex situ* CH_4 fluxes in both control and *R. taedigera* peat monoliths were highest during daylight. However, the difference between CH_4 emissions from control and *R. taedigera* monoliths was highest during daylight (9:00 to 17:00 h), being 1.7 times lower in the *R. taedigera* seedling treatment (Fig. 1b). Furthermore, as *R. taedigera* seedlings grew, the daylight CH_4 fluxes in the *R. taedigera*

monoliths declined (Fig. 1c). Indeed, the presence of plant roots significantly increased the dissolved O_2 levels in the pore-water of peat monoliths. During daylight, the dissolved O_2 concentration in the pore-water of unplanted control peat monoliths was close to zero. However, in the peat monoliths with *R. taedigera* seedlings, the dissolved O_2 concentration in the pore-water was high close to the primary roots, but declined, reaching values close to zero, as the distance from the primary roots increased (Fig. 2).

By the end of the assay, 150 days after seedlings were transplanted to the peat monoliths, *R. taedigera* the biomass was distributed 80 ± 6 % aboveground (leaves and stems, 25.7 ± 2.8 g) while 19 ± 3 % was allocated below ground (roots, 6.2 ± 0.8 g) ($F_{2,14} = 7.85$, $P < 0.01$). Live roots of the *R. taedigera* seedlings occupied in average a volume of 95 ± 9 mL within each peat monolith at the end of the experiment, equivalent to ≈ 0.6 % of the total volume. The majority of the roots were located near the surface (upper 20 cm), but some thicker roots were distributed throughout the peat monolith; the root tissue was aerenchymatous.

Land use change effect on CO_2 and CH_4 fluxes

The palm forest at the Cricamola site was dominated by *R. taedigera* palm (Table 1) growing on acidic peat, with relatively low N and P concentrations (Table 2). Following land use change (*i.e.* slash and burn), dissolved O_2 (top 0.5 m) decreased 5-fold in the peat matrix of the
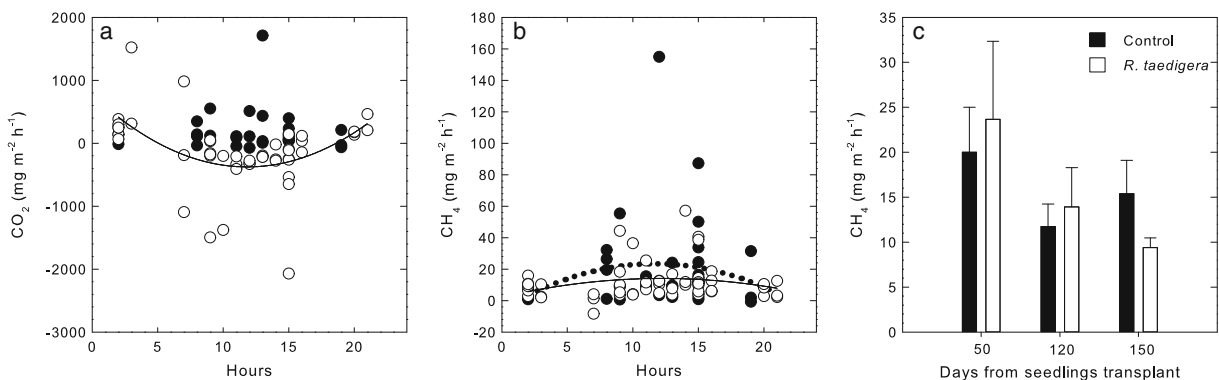

Fig. 1 Diurnal CO_2 (**a**) and CH_4 (**b**) fluxes from the *R. taedigera* seedling experiment. Closed symbols correspond to diurnal flux from control peat monoliths (●), while open symbols correspond to peat monoliths with *R. taedigera* (○). Dotted (···) and solid (—) lines represent the quadratic models describing the fluxes from control and *R. taedigera* peat monoliths respectively. The quadratic relationship in (a) was CO_2 (mg m^{-2} h^{-1}) = 8.18 × Hr of Day$_{0-24}^2$ − 193.7 × Hr of Day$_{0-24}$ + 770; $F_{2,44} = 7.96$, $P < 0.001$, adjusted

$r^2 = 23$ % for monoliths with seedlings; and in (b) there was a significant treatment effect between the two curved lines (Treatment: $F_{1,15} = 5.5$, $P < 0.05$; Quadratic term (x^2): $F_{1,41} = 4.5$, $P < 0.05$) when temperature was fitted added as a covariate. (**c**) Shows mean ± SE of CH_4 fluxes during daylight hours (9:00 to 17:00) throughout the experiment (Variation through time; CH_4: $F_{2,26} = 7.82$, $P < 0.001$)
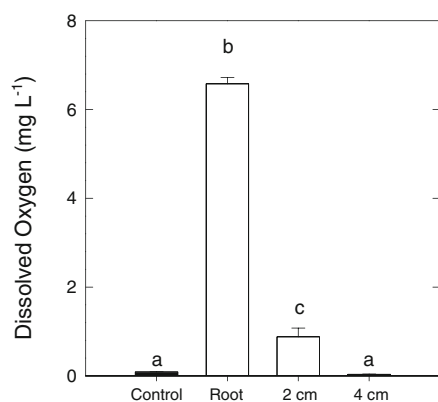
Fig. 2 Dissolved oxygen concentration in peat pore-water as function of the distance from *R. taedigera* seedling root (mean ± SE). *Black bar* correspond to peat monoliths without *R. taedigera* seedlings, whilst white bars correspond to peat monoliths with *R. taedigera* seedlings. Tukey's HSD multiple comparison test is indicated by letters ($P < 0.05$); different letters indicate a significant difference. One-way ANOVA output is: Dissolved oxygen (mg L^{-1}), Distance from root: $F_{3,199} = 664$, $P < 0.001$

disturbed site and remained significantly lower than the undisturbed site throughout the monitoring period (Fig. 3a). In addition, temperature in the surface peat increased following the anthropogenic disturbance (Fig. 3b). Once rice was seeded, its height was recorded at each monitoring event (Fig. 3c). The CO_2 fluxes were consistently higher in the undisturbed site and varied significantly through time (Fig. 3d). The CH_4 fluxes were significantly lower at the undisturbed site through time. However, CH_4 flux values from the disturbed site declined at the end of the study when the rice was fully grown (Fig. 3e). Parallel to CH_4 emissions, the undisturbed site had significantly lower N_2O emissions (Fig. 3f).

The strongest environmental control of the CH_4 and N_2O emissions was the dissolved O_2 concentration in the upper 0.5 m of the peat profile, with lower emissions when oxygen levels were high (Fig. 4 a-c: $\log_{10} CH_4 = -0.64 \times DO +1.16$, $F_{1,42} = 28.93$, $P < 0.001$, $r^2 = 40$ %; $\log_{10} N_2O = -0.57 \times DO -0.61$, $F_{1,25} = 7.33$, $P < 0.05$, $r^2 = 20$ %). The position of the water table was related to CO_2 ($\log_{10} CO_2 = -0.012 \times WT + 2.61$, $F_{1,120} = 20.49$, $P < 0.001$, $r^2 = 14$ %) and CH_4 ($\log_{10} CH_4 = 0.005 \times WT^2 + 0.056 \times WT + 0.14$, $F_{2,53} = 5.75$, $P < 0.01$, $r^2 = 15$ %), but not to N_2O (Fig. 4 d-f). Generally, low CO_2 emissions corresponded to a high water table (Fig. 4d). The highest CH_4 fluxes occurred when the water table was close to the peat surface and emissions decreased as water table dropped

just below the peat surface, but fluxes were highly variable and tended to increase when water table dropped further (0.15 m below the peat surface). Only the CH_4 fluxes were correlated to the peat surface temperature (Fig. 4 g-i), ($\log_{10} CH_4 = -0.043 \times T^2 + 2.42 \times T - 33.3$, $F_{2,37} = 11.14$, $P < 0.001$, $r^2 = 35$ %).

Effect of land use change on the combined radiative forcing of greenhouse gas fluxes

The magnitude of the difference between the combined radiative forcing of a single year of greenhouse gas fluxes (pulse) from surface peat of the control and disturbed *R. taedigera* sites was strongly dependent on the time period used to perform the calculations. Considering a 20 yr. horizon, the combine radiative forcing (combined GWP index) from the peat at the disturbed site was approximately three times higher than the control *R. taedigera* site in terms of CO_2-eq. In contrast, over a 100 yr. horizon the net radiative forcing was double at the disturbed site (Table 3). Using both time horizons, CO_2 was the main contributor to greenhouse gas emissions from the surface peat in the undisturbed *R. taedigera* site, comprising more than half of the total emissions (Table 3); CO_2 was followed by CH_4 and a small contribution by N_2O. However, in the disturbed site CH_4 was the main contributor to greenhouse gas emissions from the surface peat, followed by CO_2 and N_2O (Table 3).

Discussion

We have shown that fluxes of CO_2 and CH_4 varied with the activity of the vegetation both in situ and *ex situ*. *Ex situ* CO_2 fluxes followed a diurnal pattern that reflected the photosynthetic activity of *R. taedigera* seedlings, with the palm mesocosms acting as CO_2 sinks. By contrast, in the unvegetated monoliths, CO_2 fluxes were either close to zero or positive. This suggests that even relatively small palm seedlings can mitigate CO_2 release during peat decomposition, highlighting the critical role of NPP for the C balance of tropical peatlands (Sjögersten et al. 2014). In parallel, *ex situ* CH_4 fluxes were lower during daylight in monoliths with *R. taedigera* seedlings than in the control monoliths (Fig. 1b). Measurements of dissolved oxygen in the rhizosphere confirmed a significant radial oxygen loss from *R. taedigera* roots into the peat matrix (Fig. 2).
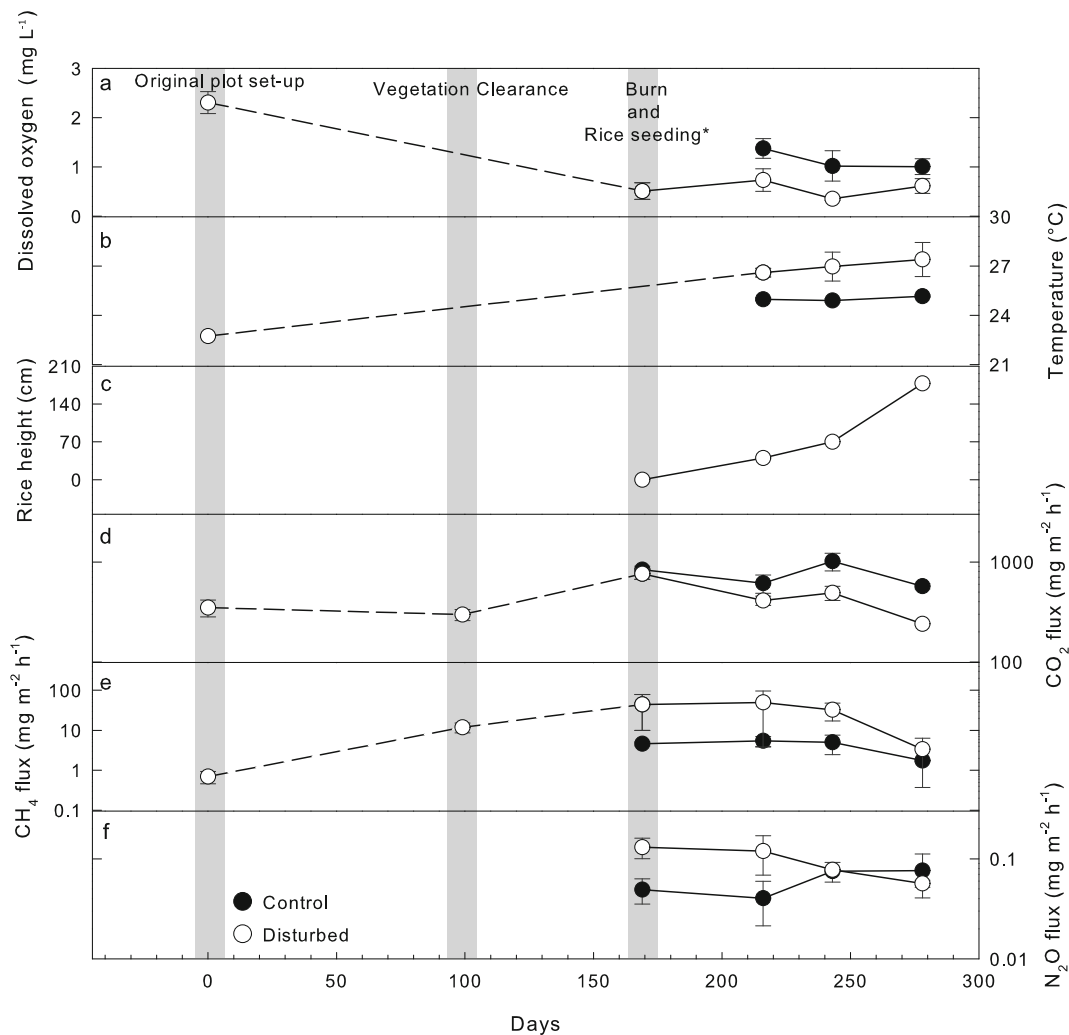
Fig. 3 In situ **a** dissolved oxygen (top 50 cm), **b** surface temperature, **c** rice height, **d** CO_2 fluxes, **e** CH_4 fluxes, and **f** N_2O fluxes. Symbols represent mean ± SE. Undisturbed and anthropogenically disturbed sites are presented as closed (●) and open (○) symbols respectively. Dashed lines connect the samplings before the original plot was subjected to disturbance. Statistical analyses only include post disturbance samplings as to compare both undisturbed and anthropogenically disturbed sites. REML outputs are: **a** Dissolved oxygen (mg L^{-1}) Anthropogenic disturbance: $F_{1,17} = 12.15$, $P < 0.01$, Time: $F_{2,17} = 1.74$, $P < 0.05$, Anthropogenic disturbance.Time: $F_{2,17} = 0.26$, $P > 0.05$; **b** Surface temperature (°C), Anthropogenic disturbance: $F_{1,17} = 16.59$, $P < 0.001$, Time: $F_{2,17} = 0.37$, $P > 0.05$, Anthropogenic disturbance.Time: $F_{2,17} = 0.14$, $P > 0.05$; **d** Log_{10} CO_2, Anthropogenic disturbance: $F_{1,90} = 23.05$, $P < 0.001$, Time: $F_{3,86} = 4.58$, $P < 0.01$, Anthropogenic disturbance.Time: $F_{3,90} = 1.45$, $P > 0.05$; **e** Log_{10} CH_4, Anthropogenic disturbance: $F_{1,29} = 0.85$, $P > 0.05$, Time: $F_{3,29} = 5.22$, $P < 0.01$, Anthropogenic disturbance.Time: $F_{3,29} = 2.34$, $P > 0.05$; **f** Log_{10} N_2O, Anthropogenic disturbance: $F_{1,22} = 4.99$, $P < 0.05$, Time: $F_{3,22} = 0.74$, $P > 0.05$, Anthropogenic disturbance.Time: $F_{3,22} = 0.62$, $P > 0.05$. *Control plot set-up

This suggests that oxygen input by *R. taedigera* into the peat enhanced CH_4 oxidation (De Bont et al. 1978; Calhoun and King 1997; Gerard and Chanton 1993; King 1996), and/or partially inhibited methanogenesis (Grosse et al. 1996; Holzapfel-Pschorn et al. 1986), reducing CH_4 fluxes by *ca.* 40 % compared to controls. In fact, the suppression of CH_4 fluxes increased as *R. taedigera* seedlings grew (Fig. 1c), indicating that

as the root aerenchymatous tissue spread through the peat monoliths, the release of O_2 into the peat matrix increased. This supports hypothesis (i), predicting a reduction of CH_4 emissions due to radial oxygen loss of *R. taedigera* into the peat matrix.

The in situ greenhouse gas fluxes from the undisturbed palms forest are in the range previously reported from peatlands in the area (Couwenberg et al. 2010;
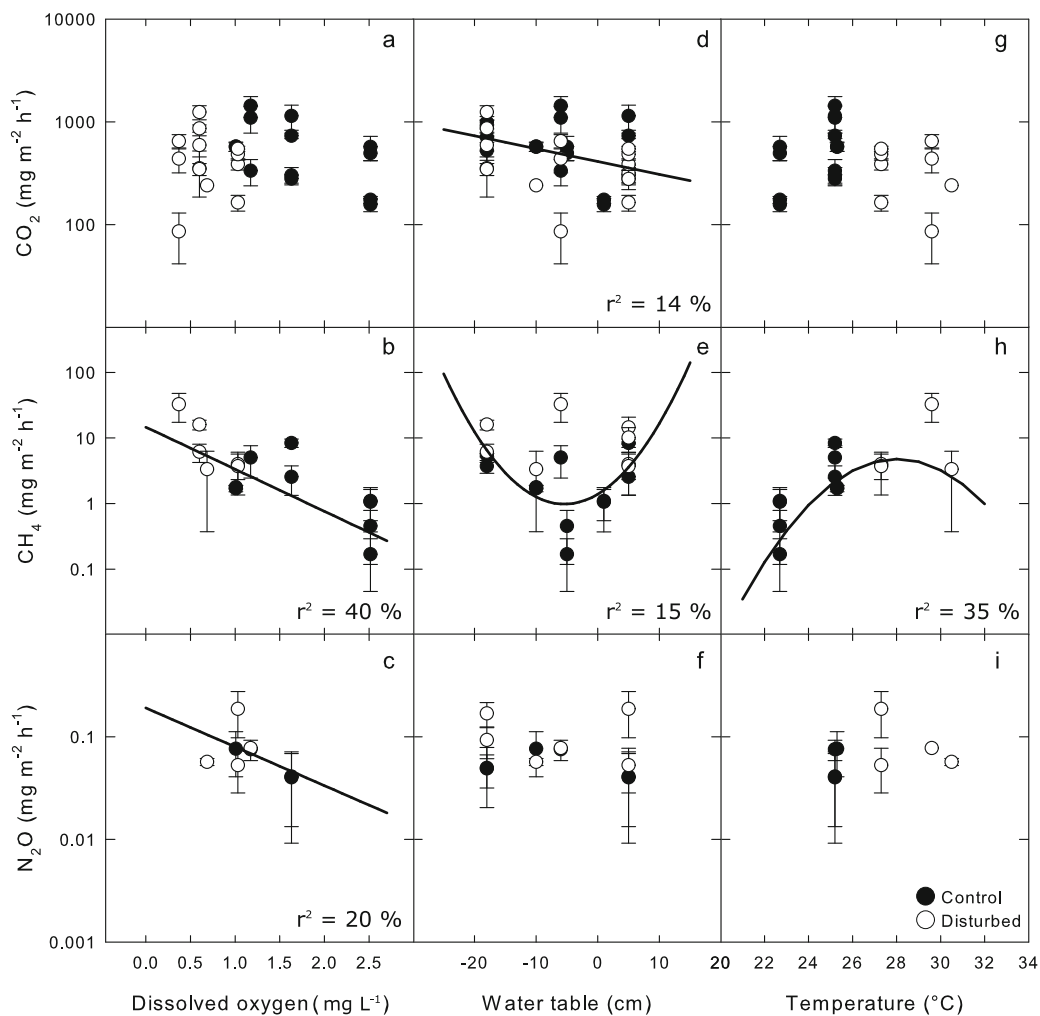
Fig. 4 Regression analyses between greenhouse gas fluxes (CO_2, CH_4, and N_2O) in the control (●) and disturbed (○) sites, and in situ parameters (dissolved oxygen in top 0.5 m peat, water table, and temperature in top 0.1 m peat). Symbols represent mean ± SE for each monitoring event, $n = 3$. Variance accounted by the models is reported as the adjusted r^2 when regression relationship was significant. Relevant statistics are shown in text

Jauhiainen et al. 2012; Sjögersten et al. 2014; Wright et al. 2013b). Land use change strongly increased CH_4 and N_2O emissions; with CH_4 fluxes being 17-fold higher than pre-disturbance fluxes and N_2O fluxes doubling after vegetation removal (Fig. 3 e, f). The strong increase in CH_4 emissions with palm removal contrasts dramatically with the substantial decline in emissions reported when land use change is associated to peat drainage and lower water tables (Couwenberg et al. 2010), highlighting the critical role of the water table for the CH_4 emissions in this context. The increase in N_2O emissions following land use change supports findings from peatlands in Southeast Asia, although

the magnitude of the increase is highly variable, possibly due to different levels of fertilizer application and drainage (Couwenberg et al. 2011; Dommain et al. 2010; Jauhiainen et al. 2011). The higher CH_4 and N_2O fluxes following land use change supported our second hypothesis, predicting that the clearance of *R. taedigera* would increase the CH_4 and N_2O fluxes.

Several mechanisms could account for the increase in CH_4 and N_2O fluxes following land use change. For example, once vegetation was cleared, temperature increased at the peat surface (Fig. 3b), which is likely to stimulate microbial activity (Abdalla et al. 2009; Blagodatskaya et al. 2014; Dunfield et al. 1993;

Table 3 Contribution of CO_2 and non-CO_2 greenhouse gas fluxes from surface peat[a] to radiative forcing of *R. taedigera* forest under the 20 (GWP_{20}) and 100 (GWP_{100}) years horizons

	Control	Disturbed
Total CO_2-eq (g m^{-2} y^{-1}) - GWP_{20}[b]	9959 ± 1338	$28{,}890 \pm 8518$
	% of contribution to Total CO_2-eq	
CO_2	67 ± 8.7	21 ± 15.8
CH_4	31 ± 9.3	78 ± 16.8
N_2O	1.5 ± 0.8	1.2 ± 1.0
Total CO_2-eq (g m^{-2} y^{-1}) - GWP_{100}[b]	8059 ± 1056	$14{,}104 \pm 3835$
	% of contribution to Total CO_2-eq	
CO_2	82 ± 5.0	37 ± 19.5
CH_4	15 ± 5.7	61 ± 20.9
N_2O	2 ± 0.9	2 ± 1.5

Data is presented as mean $\pm$ SE; $n = 4$

[a] The estimation of the total CO_2-eq does not comprise the assessment of the whole-forests carbon exchange with the atmosphere, it exclusively addresses the CO_2, CH_4, and N_2O emissions from the surface peat without plant mediation

[b] GWP consider the inclusion of climate-carbon feedbacks. $GWP_{20:}$ $CH_4 = 86$, $N_2O = 268$; GWP_{100}: $CH_4 = 34$, $N_2O = 298$

Turetsky et al. 2014b). Furthermore, the lower solubility of oxygen as temperature increased (Wilhelm et al. 1977) and cessation of radial oxygen loss from the roots following the clearing of the *R. taedigera* forest exacerbated anaerobic conditions (Fig. 3a). This is likely to promote CH_4 and N_2O production (Blagodatskaya et al. 2014; Inglett et al. 2012). In addition, the cessation of rhizosphere CH_4 oxidation, as observed ex situ (Fig. 1b), would further enhance CH_4 emissions (Gerard and Chanton 1993; Holzapfel-Pschorn et al. 1986). Indeed, the decline in CH_4 emissions at the later stages of rice growth (Fig. 3e) might be attributed to the gradual increase of CH_4 oxidation and inhibition of methanogenesis due to radial oxygen loss by rice root system (De Bont et al. 1978; Gerard and Chanton 1993; King 1996); or by the increasing contribution of plant mediated CH_4 emissions through rice aerenchyma, which we could not account for with our methodological approach (Butterbach-Bahl et al. 1997). Overall, the dissolved O_2 concentration in the pore-water of the surface peat was a strong driver of both CH_4 and N_2O emissions in situ, accounting for 40 and 20 % of the variance in fluxes for the two gases, respectively (Fig. 4 b, c), lending additional support to hypothesis (i). The clearance of the *R. taedigera* forest presumably caused a pulse of labile C and N from decaying leaf and root material, which is likely to contribute, in conjunction with the lower dissolved O_2 concentration in the surface peat, to the greater CH_4 and N_2O emissions from the deforested agricultural site (Blagodatskaya et al. 2014; Inglett et al. 2012; Ullah et al. 2008). The magnitude of this effect is difficult to assess, as forest clearance would also dramatically reduce root exudation, which would limit substrate supply (Bhullar et al. 2014; Ding et al. 2005). In addition, litter and roots decay slowly under waterlogged conditions (Hoyos-Santillan et al. 2015; Wright et al. 2013a), suggesting that the strong immediate effect on CH_4 and N_2O emissions following the palm forest clearance is linked to the lower oxygen levels in the peat matrix in the deforested area.

The higher soil respiration in the undisturbed palm forest, compared to the area affected by slash and burn agriculture (Fig. 3d), showed that the undisturbed *R. taedigera* forest maintained higher heterotrophic and rhizo-microbial respiration from the surface peat. This supported our third hypothesis, which predicted a decrease in the CO_2 fluxes from the peat surface following the clearance of *R. taedigera*. Root respiration and elevated respiration rates due to labile C inputs from roots contribute to net soil CO_2 emissions (Davidson and Janssens 2006). For example, root respiration contributed between 40 and 60 % from net soil emissions in forests in the Eastern Amazon during the dry season (Metcalfe et al. 2007). Therefore, we attribute the decline in CO_2 emissions to loss of respiration from *R. taedigera* roots, and to the suppression of root exudates, which are to some extent consumed and converted into CO_2 by rhizosphere microorganisms. The

observation of CO_2 emissions declining with agricultural land use change contrasts with previous research showing increasing CO_2 emissions in areas were land use change is associated with a lowering of the water table (Furukawa et al. 2005; Hatala et al. 2012; Hirano et al. 2012). This highlights the critical role of the water table regulating CO_2 emissions from tropical peatlands in the context of land use change.

The radiative forcing corresponding to surface peat emissions (expressed as CO_{2-eq}) was substantially increased by land use change (Table 3), related mainly to an increase in CH_4 fluxes from the disturbed area. Therefore, *R. taedigera* forests have a potential role in the mitigation of greenhouse gases emissions to the atmosphere in addition to the CO_2 uptake inherent to photosynthetic activity. Furthermore, land use change shifted the relative contribution of greenhouse gases to overall emissions, from CO_2 being the main contributor in the control site to CH_4 becoming the main contributor at the disturbed site. This suggests that *R. taedigera* controls not just the magnitude of the greenhouse gas emissions, but also influences the biochemical pathways responsible for such carbon emissions. It has been estimated that between 2010 and 2015 the land area under tropical forest declined at a rate of 5.5 M ha y^{-1} (Keenan et al. 2015). Evaluating how land use change alters the radiative forcing of tropical peat swamps emissions requires consideration of plant mediated release of greenhouse gases, which may constitute a substantial component of emissions both for rice (Neue et al. 1997) and trees in tropical wetlands (*e.g.* 21 % of CH_4 fluxes in tropical peat swamps in SE Asia) (Pangala et al. 2013). Furthermore, to fully determine how land use change impact the radiative forcing, both the C losses due to fire in the initial phase of land clearance and the photosynthetic activity of the vegetation need to be considered (Malhi et al. 2011; Sjögersten et al. 2014; Turetsky et al. 2014a).

Our study has shown that palm forest supress potential CH_4 and N_2O emissions from tropical peatlands and therefore provides an important ecosystem service in relation to climate change mitigation. Moreover, if radial oxygen loss from roots to the peat moderates CH_4 and N_2O emissions from tropical swamps more widely, then an important consequence of the current rapid deforestation of tropical peatlands may be greater CH_4 and N_2O emissions. To assess the net impact of the vegetation on greenhouse gas emissions from lowland tropical peatlands further research is required to: i) establish the mechanisms through which tropical peatland vegetation, such as *R. taedigera* and *C. panamensis*, mediate the gas transport from the peat matrix to the atmosphere; ii) quantify the relative importance of the radial O_2 loss and the labile carbon inputs as drivers for CH_4 emissions; and iii) how these drivers vary among plant species with different traits.

References

Abdalla M, Jones M, Smith P, Williams M (2009) Nitrous oxide fluxes and denitrification sensitivity to temperature in Irish pasture soils. Soil Use Manag 25:376–388. doi:10.1111/j.1475-2743.2009.00237.x

Andersen J (1976) An ignition method for determination of total phosphorus in lake sediments. Water Res 10:329–331. doi:10.1016/0043-1354(76)90175-5

Armstrong W (1971) Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. Physiol Plant 25:192–197. doi:10.1111/j.1399-3054.1971.tb01427.x

Armstrong W, Justin SHFW, Beckett PM, Lythe S (1991) Root adaptation to soil waterlogging. Aquat Bot 39:57–73. doi:10.1016/0304-3770(91)90022-W

Bahn M, Schmitt M, Siegwolf R, et al. (2009) Does photosynthesis affect grassland soil-respired CO2 and its carbon isotope composition on a diurnal timescale? New Phytol 182:451–460. doi:10.1111/j.1469-8137.2008.02755.x

Barlow PW (2001) Primary root. Encycl Life Sci. doi:10.1038/npg.els.0002059

Barthelmes A, Couwenberg J, Risager M, et al. (2015) Peatlands and climate in a Ramsar context: a Nordic-Baltic perspective. doi:10.6027/TN2015-544

Bhullar GS, Edwards PJ, Olde Venterink H (2014) Influence of different plant species on methane emissions from soil in a restored swiss wetland. PLoS One 9:e89588. doi:10.1371/journal.pone.0089588

Blagodatskaya E, Zheng X, Blagodatsky S, et al. (2014) Oxygen and substrate availability interactively control the temperature sensitivity of CO2 and N2O emission from soil. Biol Fertil Soils 50:775–783. doi:10.1007/s00374-014-0899-6

De Bont JAM, Lee KK, Bouldin DF (1978) Bacterial oxidation of methane in a rice paddy. Ecol Bull 91–96

Butterbach-Bahl K, Papen H, Rennenberg H (1997) Impact of gas transport through rice cultivars on methane emission from rice paddy fields. Plant Cell Environ 20:1175–1183. doi:10.1046/j.1365-3040.1997.d01-142.x

Calhoun A, King GM (1997) Regulation of root-associated methanotrophy by oxygen availability in the rhizosphere of two aquatic macrophytes. Appl Environ Microbiol 63:3051–3058

Ciais P, Sabine C, Bala G, et al. (2013) Carbon and other biogeochemical cycles. In: Stocker TF, Qin D, Plattner G-K, et al. (eds) Clim. Chang. 2013 Phys. Sci. Basis. Contrib. Work. Gr. I to Fifth Assess. Rep. Intergov. Panel Clim. Chang. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 465–570

Couwenberg J, Dommain R, Joosten H (2010) Greenhouse gas fluxes from tropical peatlands in south-East Asia. Glob Chang Biol 16:1715–1732. doi:10.1111/j.1365-2486.2009.02016.x

Couwenberg J, Thiele A, Tanneberger F, et al. (2011) Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. Hydrobiologia 674:67–89. doi:10.1007/s10750-011-0729-x

Cronk JK, Fennessy MS (2001) Wetland plants: biology and ecology.

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173. doi:10.1038/nature04514

Ding W, Cai Z, Tsuruta H (2005) Plant species effects on methane emissions from freshwater marshes. Atmos Environ 39:3199–3207. doi:10.1016/j.atmosenv.2005.02.022

Dommain R, Couwenberg J, Joosten H (2010) Hydrological self-regulation of domed peatlands in south-East Asia and consequences for conservation and restoration. Mires Peat 6:1–17

Dunfield P, Knowles R, Dumont R, Moore T (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol Biochem 25:321–326. doi:10.1016/0038-0717(93)90130-4

Fritz C, Pancotto VA, Elzenga JTM, et al. (2011) Zero methane emission bogs: extreme rhizosphere oxygenation by cushion plants in Patagonia. New Phytol 190:398–408. doi:10.1111/j.1469-8137.2010.03604.x

Frolking S, Roulet N, Fuglestvedt J (2006) How northern peatlands influence the Earth's radiative budget: sustained methane emission versus sustained carbon sequestration. J Geophys Res 111:G01008. doi:10.1029/2005JG000091

Furukawa Y, Inubushi K, Ali M, et al. (2005) Effect of changing groundwater levels caused by land-use changes on greenhouse gas fluxes from tropical peat lands. Nutr Cycl Agroecosyst 71:81–91. doi:10.1007/s10705-004-5286-5

Gerard G, Chanton J (1993) Quantification of methane oxidation in the rhizosphere of emergent aquatic macrophytes: defining upper limits. Biogeochemistry 23:79–97. doi:10.1007/BF00000444

Grosse W, Jovy K, Tiebel H (1996) Influence of plants on redox potential and methane production in water-saturated soil. Hydrobiologia 340:93–99. doi:10.1007/BF00012739

Hatala JA, Detto M, Sonnentag O, et al. (2012) Greenhouse gas (CO2, CH4, H2O) fluxes from drained and flooded agricultural peatlands in the Sacramento-San Joaquin Delta. Agric Ecosyst Environ 150:1–18. doi:10.1016/j.agee.2012.01.009

Hirano T, Segah H, Kusin K, et al. (2012) Effects of disturbances on the carbon balance of tropical peat swamp forests. Glob Chang Biol 18:3410–3422. doi:10.1111/j.1365-2486.2012.02793.x

Holzapfel-Pschorn A, Conrad R, Seiler W (1986) Effects of vegetation on the emission of methane from submerged paddy soil. Plant Soil 92:223–233. doi:10.1007/BF02372636

Hooijer A, Page S, Canadell JG, et al. (2010) Current and future CO2 emissions from drained peatlands in Southeast Asia. Biogeosciences 7:1505–1514. doi:10.5194/bg-7-1505-2010

Hoyos-Santillan J, Lomax BH, Large D, et al. (2015) Getting to the root of the problem: litter decomposition and peat formation in lowland neotropical peatlands. Biogeochemistry. doi:10.1007/s10533-015-0147-7

Inglett KS, Inglett PW, Reddy KR, Osborne TZ (2012) Temperature sensitivity of greenhouse gas production in wetland soils of different vegetation. Biogeochemistry 108:77–90. doi:10.1007/s10533-011-9573-3

IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change doi:10.1017/CBO9781107415324

Jauhiainen J, Hooijer a, SE P (2011) Carbon dioxide emissions from an Acacia plantation on peatland in Sumatra, Indonesia. Biogeosci Discuss 8:617–630. doi:10.5194/bgd-8-8269-2011

Jauhiainen J, Silvennoinen H, Hämäläinen R, et al. (2012) Nitrous oxide fluxes from tropical peat with different disturbance history and management. Biogeosciences 9:1337–1350. doi:10.5194/bg-9-1337-2012

Käki T, Ojala A, Kankaala P (2001) Diel variation in methane emissions from stands of Phragmites australis (cav.) trin. ex steud. and Typha latifolia L. in a boreal lake. Aquat Bot 71:259–271. doi:10.1016/S0304-3770(01)00186-3

Keenan RJ, Reams GA, Achard F, et al. (2015) Dynamics of global forest area: results from the FAO Global Forest resources assessment 2015. For Ecol Manag 352:9–20. doi:10.1016/j.foreco.2015.06.014

King GM (1996) In situ analyses of methane oxidation associated with the roots and rhizomes of a bur Reed, Sparganium eurycarpum, in a Maine wetland. Appl Environ Microbiol 62:4548–4555

King GM, Wiebe WJ (1978) Methane release from soils of a Georgia salt marsh. Geochim Cosmochim Acta 42:343–348. doi:10.1016/0016-7037(78)90264-8

Laanbroek HJ (2010) Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. Ann Bot 105:141–153. doi:10.1093/aob/mcp201

Lähteenoja O, Ruokolainen K, Schulman L, Oinonen M (2009) Amazonian peatlands: an ignored C sink and potential source. Glob Chang Biol 15:2311–2320. doi:10.1111/j.1365-2486.2009.01920.x

MacDicken K, Jonsson Ö, Piña L, et al. (2015) Global forest resources assessment 2015: How are the world's forests changing? Food and Agriculture Organization of the United Nations (FAO), Rome

Malhi Y, Doughty C, Galbraith D (2011) The allocation of ecosystem net primary productivity in tropical forests. Philos Trans R Soc Lond Ser B Biol Sci 366:3225–3245. doi:10.1098/rstb.2011.0062

Melling L, Hatano R, Goh KJ (2007) Nitrous oxide emissions from three ecosystems in tropical peatland of Sarawak, Malaysia. Soil Sci Plant Nutr 53:792–805. doi:10.1111/j.1747-0765.2007.00196.x

Melton JR, Wania R, Hodson EL, et al. (2013) Present state of global wetland extent and wetland methane modelling: conclusions from a model intercomparison project (WETCHIMP). Biogeosci Discuss 10:753–788. doi:10.5194/bg-10-753-2013

Metcalfe DB, Meir P, Aragão LEOC, et al. (2007) Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the Eastern Amazon. J Geophys Res 112: G04001. doi:10.1029/2007JG000443

Mikkelä C, Sundh I, Svensson BH, Nilsson M (1995) Diurnal variation in methane emission in relation to the water table, soil temperature, climate and vegetation cover in a Swedish acid mire. Biogeochemistry 28:93–114. doi:10.1007/BF02180679

Myers RL (1981) The ecology of low diversity palm swamps near tortuguero. University of Florida, Costa Rica

Neue HU, Wassmann R, Kludze HK, et al. (1997) Factors and processes controlling methane emissions from rice fields. Nutr Cycl Agroecosyst 49:111–117. doi:10.1023/A:1009714526204

Page SE, Rieley JO, Banks CJ (2011) Global and regional importance of the tropical peatland carbon pool. Glob Chang Biol 17:798–818. doi:10.1111/j.1365-2486.2010.02279.x

Pangala S, Moore S, Hornibrook ERC, Gauci V (2013) Trees are major conduits for methane egress from tropical forested wetlands. New Phytol 197:524–531. doi:10.1111/nph.12031

Phillips S, Rouse GEG, Bustin RM (1997) Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panamá. Palaeogeogr Palaeoclimatol Palaeoecol 128:301–338. doi:10.1016/S0031-0182(97)81129-7

Rieley JO, Wüst RAJ, Jauhiainen J, et al. (2008) Tropical peatlands: carbon stores, carbon gas emissions and contribution to climate change processes. In: Strack M (ed) Peatlands clim. Chang. International Peat Society, Jyväskylä, pp. 148–182

Roucoux KH, Lawson IT, Jones TD, et al. (2013) Vegetation development in an Amazonian peatland. Palaeogeogr Palaeoclimatol Palaeoecol 374:242–255. doi:10.1016/j.palaeo.2013.01.023

Schoeneberger PJ, Wysocki DA, Benham EC, Soil Survey Staff (2012) Field Book for Describing and Sampling Soils, Version 3.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE

Silvola J, Alm J, Ahlholm U, et al. (1996) The contribution of plant roots to CO2 fluxes from organic soils. Biol Fertil Soils 23:126–131. doi:10.1007/BF00336052

Sjögersten S, Black CR, Evers S, et al. (2014) Tropical wetlands: A missing link in the global carbon cycle? Global Biogeochem Cycles N/A–N/a. doi:10.1002/2014GB004844

Sjögersten S, Cheesman AW, Lopez O, Turner BL (2011) Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland. Biogeochemistry 104:147–163. doi:10.1007/s10533-010-9493-7

Stephen KD, Arah JRM, Daulat W, Clymo RS (1998) Root-mediated gas transport in peat determined by argon diffusion. Soil Biol Biochem 30:501–508. doi:10.1016/S0038-0717(97)00142-9

Ström L, Christensen TR (2007) Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. Soil Biol Biochem 39:1689–1698. doi:10.1016/j.soilbio.2007.01.019

Ström L, Ekberg A, Mastepanov M, Rojle Christensen T (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Glob Chang Biol 9:1185–1192. doi:10.1046/j.1365-2486.2003.00655.x

Tang J, Baldocchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. Glob Chang Biol 11:1298–1304. doi:10.1111/j.1365-2486.2005.00978.x

Thomas KL, Benstead J, Davies KL, Lloyd D (1996) Role of wetland plants in the diurnal control of CH4 and CO2 fluxes in peat. Soil Biol Biochem 28:17–23. doi:10.1016/0038-0717(95)00103-4

Torn MS, Chapin FS (1993) Environmental and biotic controls over methane flux from Arctic tundra. Chemosphere 26:357–368. doi:10.1016/0045-6535(93)90431-4

Turetsky MR, Benscoter B, Page S, et al. (2014a) Global vulnerability of peatlands to fire and carbon loss. Nat Geosci 8:11–14. doi:10.1038/ngeo2325

Turetsky MR, Kotowska A, Bubier J, et al. (2014b) A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. Glob Chang Biol 20:2183–2197. doi:10.1111/gcb.12580

Ullah S, Frasier R, King L, et al. (2008) Potential fluxes of N2O and CH4 from soils of three forest types in Eastern Canada. Soil Biol Biochem 40:986–994. doi:10.1016/j.soilbio.2007.11.019

Urquhart GR (1999) Long-term persistence of Raphia taedigera Mart. swamps in Nicaragua. Biotropica 31:565–569. doi:10.1111/j.1744-7429.1999.tb00403.x

VSN International (2011) GenStat for Windows 14th Edition.

Wang Y, Roulet NT, Frolking S, Mysak LA (2009) The importance of northern peatlands in global carbon systems during the Holocene. Clim Past Discuss 5:1231–1258. doi:10.5194/cpd-5-1231-2009

Wang Z-P, Han X-G (2005) Diurnal variation in methane emissions in relation to plants and environmental variables in the inner Mongolia marshes. Atmos Environ 39:6295–6305. doi:10.1016/j.atmosenv.2005.07.010

Weller S, Kraus D, Butterbach-Bahl K, et al. (2015) Diurnal patterns of methane emissions from paddy rice fields in the Philippines. J Plant Nutr Soil Sci 178:755–767. doi:10.1002/jpln.201500092

van der Werf GR, Randerson JT, Giglio L, et al. (2010) Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009). Atmos Chem Phys 10:11707–11735. doi:10.5194/acp-10-11707-2010

Wilhelm E, Battino R, Wilcock RJ (1977) Low-pressure solubility of gases in liquid water. Chem Rev 77:219–262. doi:10.1021/cr60306a003

Wright E, Black CR, Cheesman AW, et al. (2013a) Impact of simulated changes in water table depth on ex situ decomposition of leaf litter from a neotropical peatland. Wetlands 33:217–226. doi:10.1007/s13157-012-0369-6

Wright E, Black CR, Cheesman AW, et al. (2011) Contribution of subsurface peat to CO2 and CH4 fluxes in a neotropical peatland. Glob Chang Biol 17:2867–2881. doi:10.1111/j.1365-2486.2011.02448.x

Wright EL, Black CR, Turner BL, Sjögersten S (2013b) Environmental controls of temporal and spatial variability in CO2 and CH4 fluxes in a neotropical peatland. Glob Chang Biol 19:3775–3789. doi:10.1111/gcb.12330

Yu Z, Beilman DW, Frolking S, et al. (2011) Peatlands and their role in the global carbon cycle. EOS Trans Am Geophys Union 92:97. doi:10.1029/2011EO120001