

Root-derived CO₂ flux from a tropical peatland

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Abstract Tropical peatlands release significant quantities of greenhouse gases to the atmosphere, yet the relative contributions of heterotrophic and autotrophic respiration to net CO₂ fluxes remains sparsely quantified. We used a combination of in situ trenching and vegetation removal in ex situ pots to quantify root-derived CO₂ under two plant functional types within a mixed species forest. Trenching significantly reduced surface CO₂ flux, indicating that approximately two-thirds of the released CO₂ was derived from roots. In contrast, ex situ vegetation removal in pots indicated that root-derived CO₂ accounted for 27% of the total CO₂ flux for *Camposperma panamensis*, a broad-leaved evergreen tree, and 49% for *Raphia taedigera*, a canopy palm. The results show that root-derived CO₂ is a major contribution to net CO₂ emissions in tropical peatlands, and that the magnitude of the emissions is affected by plant species composition. This is

important in the context of land use change driving alterations in vegetation cover.

Keywords Tropical peat · Carbon dioxide · Soil respiration · Root respiration · Trenching

Introduction

Tropical peatlands are a globally important carbon store containing 69.6–129.8 Pg of carbon (Page et al. 2011; Dargie et al. 2017) and are a significant source of CH₄ and CO₂ (Sjögersten et al. 2014). However, significant uncertainty remains around the relative contributions of autotrophic and heterotrophic respiration to net CO₂ fluxes.

CO₂ fluxes from peats comprise several components: root-derived CO₂, microbial heterotrophic degradation of organic matter, and the oxidation of CH₄ (Rustad et al. 2000; Crow 2005). A variety of approaches have previously been used to separate the relative contribution of roots to net CO₂ fluxes, including tree girdling to reduce the transfer of recent photosynthate to roots (Hogberg et al. 2001), stable isotope probing (Andrews et al. 1999; Kuzya-kov and Cheng 2001), trenching (Li et al. 2004; Bond-Lamberty et al. 2011) and surface vegetation removal, termed “clipping” in grassland ecosystems (Wan and Luo 2003; Wang et al. 2011).

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Root contributions to CO₂ fluxes are also driven by several sources. Autotrophic root respiration is a measure of the respiration by roots for maintaining cell metabolism (Kuzyakov and Larionova 2005). In addition, plants release root exudates comprising species-specific combinations of sugars, organic acids and amino acids, which represent an additional significant substrate for heterotrophic microbial respiration (Smith 1976; Hanson et al. 2000; Girkin et al. 2018). A third significant source of CO₂ from anoxic wetlands is the oxidation of CH₄ driven by radial oxygen loss from root systems (Hoyos-Santillan et al. 2016a) and aerobic surface peat (Jauhiainen 2005; Wright et al. 2013a). Terms applied to describe this combination of processes include “root-rhizosphere respiration” (Sayer and Tanner 2010), “root respiration” (Andrews et al. 1999), “rhizosphere respiration”, and “root-derived CO₂” (Kuzyakov and Larionova 2005). We adopt the latter term because it most accurately describes the combination of processes associated with CO₂ production from roots and the methods by which it is calculated.

Studies of root-derived CO₂ have previously been conducted across a range of tropical environments with a range of estimates reflecting diversity in environmental, biogeochemical and species differences. The high rates of net primary productivity in tropical ecosystems mean that root-derived CO₂ can make a large contribution to these net fluxes (Malhi et al. 2011), although relatively few studies have been conducted in tropical peatlands. Estimates from Sago, oil palm and forest covered peatlands in Malaysia were 52, 60, and 62% respectively (Melling et al. 2013), but only 9–26% when measured in an *Acacia* plantation on peat in Indonesia (Jauhiainen et al. 2012), and 14–29% in an Indonesian oil palm plantation. In tropical forests generally, measurements are equally variable. A study of root-derived CO₂ in *Tabebuia heterophylla* dominated secondary forest in Puerto Rico estimated 70% compared to 56% in a nearby *Pinus caribaea* plantation (Li et al. 2004). Lower values of root-derived CO₂ include 39% and 58–77% in mature secondary lowland tropical forest in Panama (Nottingham et al. 2010; Sayer and Tanner 2010), and 16–24% measured in two *Eucalyptus* plantations in Brazil over a 3 month period (Binkley et al. 2006). No studies could be found that had estimated root-derived CO₂ in Panamanian peatlands,

despite the critical role of plant inputs in regulating net efflux.

We quantified the combined contribution from root-derived CO₂ to net surface CO₂ fluxes using a combination of in situ and ex situ experiments in a tropical peatland in Panama. First, we quantified root-derived CO₂ by trenching in a mixed-forest stand adapting the methods of Sayer et al. (2010). Second, we assessed root-derived CO₂ flux in an ex situ plant-removal experiment to assess relative differences between *Camposperma panamensis* (Standl.), a broadleaved evergreen tree, and *Raphia taedigera* (Mart.), a canopy palm, which represent distinct plant functional types and form mix species and monodominant stands. We hypothesised that i) trenching and vegetation removal would result in a significant decline in net CO₂ efflux, and ii) the surface root mat formed by *R. taedigera* would result in a more significant contribution of root-derived CO₂ to net fluxes compared to *C. panamensis*.

Methods

Site description

The experiment was carried out in the 80 km² ombrotrophic peatland at Changuinola, in Bocas del Toro province, Panama, in February 2015. This peatland began to form 4000–5000 years ago and is estimated to be > 8 m deep at the centre of the peat dome. Vegetation is grouped into seven plant successional stages, with mangrove swamp at the coastal edge succeeded by monodominant and mixed forest stands of *R. taedigera* palms and *C. panamensis* broadleaved evergreen trees (Phillips et al. 1997). Accompanying the vegetation gradient is a strong declining trend in available nutrients to the centre of the wetland (Sjögersten et al. 2011). Mean annual air temperature is 26 °C with mean annual rainfall of 3207 mm. Peat temperature is approximately 25 °C with limited seasonal variation. During the study period, the mean temperature was 25.6 °C, with total rainfall of 239.5 mm. The water table height varies by approximately 20 cm from just above to just below the peat surface (Wright et al. 2013a).

In situ trenching

In situ respiration was measured using a paired plot design across four sites within a mixed forest stand. Trenches were cut to a depth of 50 cm using a machete and a hand saw in 0.25 m² plots. Paired plots were no more than 1 m apart and were within 0.5 m of the nearest tree. Sampling points were selected for areas with no understory vegetation to prevent roots of other species from contributing to estimates of root-derived CO₂. Fluxes were measured in the centre of plots using a closed static chamber technique (Wright et al. 2013b). Chambers had a total volume of 0.19 dm³ and were fitted with Suba seal[®] rubber septa (Fisherbrand, Loughborough, UK) to allow headspace sampling. Chambers were lightly pushed into the peat surface to minimise peat and root disturbance. Headspace gases were mixed using a 20 ml syringe and needle and injected into pre-evacuated 12 ml glass exetainers (LABCO, UK) sealed with a screw cap septum, resulting in slight over-pressure. Samples were collected between 10 am and 4 pm over 4 days during a 7 day period, beginning immediately following initial trenching. Three gas samples were collected over 10 min following installation of chambers. One sample exetainer was subsequently discarded prior to analysis due to loss of pressure.

Generally studies estimating root-derived CO₂ are conducted over several months to account for decomposition of root material. However, in tropical peatlands, root material represents one of the dominant peat components (Hoyos-Santillan et al. 2015), and the highly acidic and anoxic conditions will prevent the immediate decomposition of recent root necromass (Hoyos-Santillan et al. 2016b). These unique conditions allow for the measurement of CO₂ efflux during a relatively short window immediately following trenching. The use of a shorter period for sampling has also been applied in other tropical systems, with results closely matching those collected over a year following trenching (Sayer and Tanner 2010).

In this experiment, the data from the final time point (7 days following trenching) was excluded from subsequent analysis due to decomposition of decaying roots increasing fluxes significantly from trenched plots. Prior to this, fluxes remained consistent over time within both trenched and untrenched plots.

Ex situ vegetation removal

Six *C. panamensis* and six *R. taedigera* saplings all with similar diameter-at-breast-height (DBH) and height were transplanted from a mixed species stand in the San San Pond Sak peatland to pots at the Smithsonian Tropical Research Station on Isla Colón. Plants were excavated carefully to ensure root systems remained intact and retained peat from their original growing location. Water table height was maintained at 1 cm above the peat surface to match in situ conditions. One month following transplantation, three plants from each species were cut just above the soil surface leaving the root system in place. Gases were collected using the closed static chamber technique (Wright et al. 2013b). Chambers (0.19 dm³) were pushed gently into the peat and turned to ensure a tight seal. Peat CO₂ fluxes were measured immediately after vegetation removal and over 6 subsequent days. Three gas samples were collected over 10 min following installation of chambers between 10 am and 4 pm each day. Fluxes were only analysed from the initial 3 days of sampling due to the subsequent increase in fluxes most likely driven by root decomposition. Prior to this time point, fluxes remained consistent in both harvested and unharvested pots. Mean fluxes were calculated for the presence and absence of surface vegetation. At the conclusion of the experiment, the remaining plants were harvested and oven dried at 65 °C for 3 days prior to weighing to estimate aboveground and belowground biomass. Peat samples were collected for further characterisation (see below).

CO₂ flux measurement

CO₂ concentrations were measured using a single injection system with a 1 ml sample loop using He₂ as a carrier gas through a non-polar methyl silicone capillary column using a thermal conductivity detector (GC-2014; Shimadzu, Milton Keynes, UK). Calculations of CO₂ flux were made using the ideal gas law and assuming the linear accumulation of gas in the chambers (Hogg et al. 1992). Root-derived CO₂ was calculated by subtracting CO₂ fluxes from trenched plots/vegetation removal pots from CO₂ fluxes from untrenched/control pots. Root-derived CO₂ was not calculated in the vegetation removal experiment by comparing fluxes before and after cutting due to the

lack of time points collected from before treatment, and known temporal variability in fluxes. This time point was used to confirm that fluxes decreased following cutting.

Plant and peat properties

Height and DBH were measured 22 trees and palms in situ. For *R. taedigera*, DBH was measured at the maximum possible height prior to the stem separating into individual fronds. Palm height was measured at the highest point on an individual frond. Aboveground and belowground biomass were not estimated due to a lack of available information of wood specific densities and the difficulty of estimating in situ root biomass. Peat subsamples were analysed for pH, conductivity and redox from 24 points across the mixed forest stand. Bulk density was measured by oven-drying 100 cm³ section of peat. Gravimetric moisture content was estimated from oven drying 10 g wet weight peat for 24 h at 105 °C. Organic matter content was estimated by loss on ignition. Total C and N were measured using a total element analyser (Flash EA 1112, CE Instruments, Wigan, UK).

Statistical analysis

CO₂ fluxes from both in situ and ex situ experiments were log transformed to give normal distribution of residuals. Differences in respiration rates were assessed in situ by one-way ANOVA. Differences in fluxes between ex situ harvested and unharvested pots were assessed using a linear mixed effects model using species and treatment as fixed effects. Measures of plant size (total aboveground and belowground biomass, stem diameter and height) were investigated to confirm no difference in vegetation properties between harvested and unharvested pots, as fluxes can be dependent on plant biomass and carbon inputs. All statistical analyses were carried out using Genstat v17.0. Figures were produced in GraphPad Prism v7.

Results

Forest and peat properties

The mixed forest stand predominantly comprised *C. panamensis* trees and *R. taedigera* palms with a mean

height of 27.2 m and a DBH of 17.7 cm (Table 1). pH was extremely acid with a mean of 4.0. Electrical conductivity was low (95.8 µS), and redox potential was slightly reducing (306.6 mV). Bulk density was consistently low (0.1 g cm⁻³), and gravimetric moisture content was high (89.5%). Organic matter content (93.1%), total carbon (41.8%), total nitrogen (2.5%), and C:N (17.1) measurements all supported characterisation as a highly organic peat.

Mean heights of transplanted *C. panamensis* and *R. taedigera* saplings were 0.20 and 0.24 cm, respectively, with DBH of less than 1 cm. Aboveground biomass ranged from 0.4 to 5.7 g for *C. panamensis*, and 0.4–4.7 g for *R. taedigera*. Belowground biomass had a smaller range of between 0.3 and 1.8 g for *C. panamensis*, and 0.3–3.3 g for *R. taedigera*.

In situ root-derived CO₂

Mean CO₂ fluxes decreased significantly on trenching from 751.1 mg CO₂ m⁻² h⁻¹ to 240.1 mg CO₂ m⁻² h⁻¹ in mixed forest plots ($F_{1,8} = 19.53$, $p = 0.002$) (Fig. 1). In situ root-derived CO₂ was 511.0 ± 186.2 mg CO₂ m⁻² h⁻¹, accounting for $63.2 \pm 7.4\%$ of total surface CO₂ efflux.

Ex situ root-derived CO₂

For *C. panamensis*, CO₂ fluxes were lower from harvested pots, with a mean of 174.2 mg CO₂ m⁻² h⁻¹ compared to 246.3 mg CO₂ m⁻² h⁻¹ in the

Table 1 In situ peat properties. Means \pm one SE

Variable	Mean
Stand height (m)	27.2 \pm 1.8
DBH (cm)	17.7 \pm 2.5
pH	4.0 \pm 0.1
Electrical conductivity (µS)	95.8 \pm 10.8
Redox potential (mV)	306.6 \pm 2.9
Bulk density (g cm ⁻³)	0.1 \pm 0.01
Gravimetric moisture content (%)	89.5 \pm 0.4
Organic matter content (%)	93.2 \pm 1.0
Total carbon (%)	41.8 \pm 2.2
Total nitrogen (%)	2.5 \pm 0.2
C:N	17.1 \pm 0.4

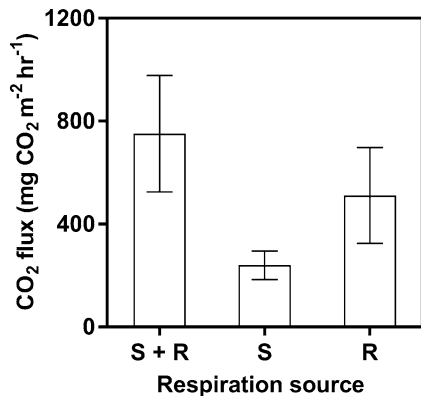


Fig. 1 In situ soil and root (S + R), soil (S), and root-derived CO₂ (R) in a mixed forest stand (n = 4). Means ± one SE

control pots (Fig. 2). For *R. taedigera* fluxes were 87.8 mg CO₂ m⁻² h⁻¹ from the harvested pots and 178.6 mg CO₂ m⁻² h⁻¹ from the control pots. However, this decrease was not found to be significant ($F_{1,30} = 2.55$, $p = 0.121$). Net fluxes were significantly higher under *C. panamensis* compared to *R. taedigera* ($F_{1,30} = 6.16$, $p = 0.019$). There was no significant interaction between treatment and species ($F_{1,30} = 0$, $p = 0.95$). Root-derived CO₂ fluxes accounted for 27.4% (72.1 mg CO₂ m⁻² h⁻¹) of the total CO₂ flux under *C. panamensis* and 49.3% (90.8 mg CO₂ m⁻² h⁻¹) under *R. taedigera*.

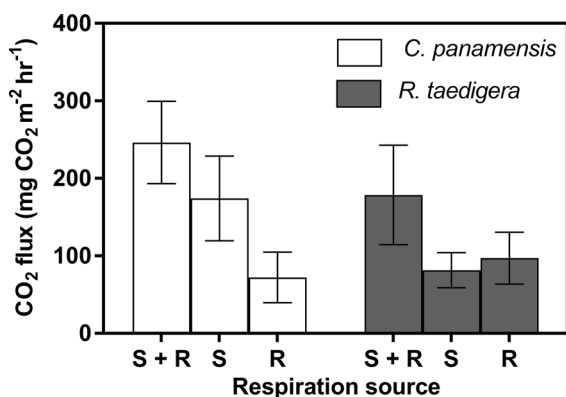


Fig. 2 Ex situ soil and root (S + R), soil (S), and root-derived CO₂ (R) from *C. panamensis* and *R. taedigera* (n = 3). Means ± one SE

Discussion

Mean contributions of root-derived CO₂ to total surface CO₂ fluxes measured in situ matched previously reported values in the literature for other tropical peatlands as well as upper estimates for other biomes. For example, root-derived respiration was estimated as 62% of the total CO₂ flux from a forested peatland in Malaysia (Melling et al. 2013), 38% from a lowland tropical forest in Panama (Sayer and Tanner 2010), 24–61% in Amazon forests (Silver et al. 2005; Metcalfe et al. 2007).

Rates of root respiration in forest ecosystems have previously been found to be dependent on biotic variables including root size, age and morphology and N content, as well as environmental variables including soil temperature and moisture content, which can be influenced by surface vegetation (Zogg et al. 1996; Burton et al. 2002; Volder et al. 2005). Root-derived CO₂ may be further influenced by differences in root exudate composition between species (Girkin et al. 2018) and with plant age and developmental stage, which will affect microbial substrate availability (Smith 1976; Aulakh et al. 2001), and rates of root oxygen loss which can enhance CH₄ oxidation (Hoyos-Santillan et al. 2016a). Differences in *C. panamensis* and *R. taedigera* rooting structures have previously been noted with large surface root mats and pneumatophores under *R. taedigera*, and large buttress roots and a microtopography dominated by knee-roots under *C. panamensis*, which may account for the observed differences in fluxes (Wright et al. 2013b). Similarly, differences in plant litter inputs can substantially alter peat chemical properties and thereby influence soil respiration rates (Upton et al. 2018).

Contributions from root-derived CO₂ in situ were greater than most ex situ measurement, and as expected total in situ fluxes were also greater than ex situ fluxes. As in situ plots feature fully grown trees and palms with entire root systems it is highly plausible that there is greater root biomass, resulting in a larger contribution to net CO₂ fluxes (Wright et al. 2011).

Increases in CO₂ fluxes have previously been reported following trenching due to root decomposition, although the extent of the effect can vary depending on soil type and environmental conditions (Silver et al. 2005; Subke et al. 2006; Sayer and Tanner 2010). Taking immediate measurements also avoided

the need to maintain trenches due to root regrowth into trenched plots or apply a decay constant to account for root decomposition over time (Subke et al. 2006). However, roots can retain significant carbohydrate reserves that may sustain root metabolism for a short period of time following treatment, which might lead to an over-estimation of root-derived CO₂ fluxes (Subke et al. 2006).

Measurements in both experiments were made during the dry season and therefore do not address the possible impact of seasonality on CO₂ fluxes. A seasonal effect was reported for root-derived CO₂ at another tropical site, with a decline from 61% during the dry season to 42% in the wet season at sites in the eastern Amazon (Metcalf et al. 2007). In temperate biomes, root respiration is generally higher during the growing seasons (Hanson et al. 2000). However, the limited intra-annual variation of environmental variables, including soil and air temperatures and water table height which have previously been shown to regulate rates of root respiration (Subke et al. 2006), mean that seasonal effects are likely to be less important in our study. In the ex situ pot experiment, environmental conditions were maintained to match field conditions, with consistent water table height (1 cm above the peat surface) and stable temperature (Wright et al. 2013a).

Conclusion

Our estimate of 63.2% in situ root-derived CO₂ for the San San Pond Sak wetland site indicates that roots make a major contribution the total CO₂ flux from this wetland. The significant difference in CO₂ flux between species highlights the important role of vegetation in regulating greenhouse gas production. Together, the findings of this study are important in demonstrating how changes in vegetation cover may alter root-derived CO₂ through changes in root morphology, biomass and labile carbon inputs. These results are particularly relevant in the context of changing land use in tropical peatlands globally. Future studies should assess differences in respiration rates between plant functional types in situ and attempt to quantify the specific contributions of root and rhizomicrobial respiration to net fluxes.

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