



Composition and concentration of root exudate analogues regulate greenhouse gas fluxes from tropical peat

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ABSTRACT

Tropical peatlands are a significant carbon store and source of carbon dioxide (CO₂) and methane (CH₄) to the atmosphere. Plants can contribute to these gas emissions through the release of root exudates, including sugars and organic acids amongst other biomolecules, but the roles of concentration and composition of exudates in regulating emissions remains poorly understood. We conducted a laboratory incubation to assess how the type and concentration of root exudate analogues regulate CO₂ and CH₄ production from tropical peats under anoxic conditions. For CO₂ production, substrate concentration was the more important driver, with increased CO₂ fluxes following higher addition rates of four out of the six exudate analogues. In contrast, exudate type was the more important driver of CH₄ production, with acetate addition associated with the greatest production, and inverse correlations between exudate concentration and CH₄ emission for the remaining five treatments. Root exudate analogues also altered pH and redox potential, dependent on the type of addition (organic acid or sugar) and the concentration. Overall, these findings demonstrate the contrasting roles of composition and concentration of root exudate inputs in regulating greenhouse gas emissions from tropical peatlands. In turn this highlights how changes in plant communities will influence emissions through species specific inputs, and the possible impacts of increased root exudation driven by rising atmospheric CO₂ and warming.

1. Introduction

Globally, peatlands are a significant source of methane (CH₄) emissions, contributing between 20 and 39% of annual CH₄ production, as well as making a significant contribution to atmospheric carbon dioxide (CO₂) emissions (Laanbroek, 2010). Tropical peatlands in particular are a significant carbon (C) store, accounting for only 11% of total peatland area but containing approximately 104.7 Gt C (Page et al., 2011; Dargie et al., 2017).

Vegetation exerts a strong influence on tropical peatland greenhouse gas (GHG) emissions through inputs of leaf, root and shoot litter, which can determine key peat properties (Wright et al., 2013). Plants also release root exudates, which represent a significant source of labile C released at depth. This addition can impact peat properties, but the precise effect on net GHG emissions is unclear (Kuzyakov and Domanski, 2000). Root exudates have been ascribed a variety of functions, including as a mechanism of chelating limiting minerals and nutrients and as a chemoattractant (Dakora and Phillips, 2002; Strom

et al., 2002), and have been shown to directly affect properties such as pH (Dunfield et al., 1993; Yan et al., 1996). In turn, changes in nutrient availability and pH, amongst other peat properties, can regulate GHG emissions, through processes mediated by microbial communities (Sjögersten et al., 2011; Troxler et al., 2012). This represents an important process in the context of land use change in tropical peatlands, as any process that alters plant communities may affect the concentration and composition of exudate inputs, as well as alter peat properties (Tonks et al., 2017).

We previously showed that root exudate analogues significantly increase peat microbial community activity and enhance the production of both CO₂ and CH₄ (Girkin et al., 2018a). However, the precise role of exudate concentration in regulating net fluxes remains to be clarified. This is an important knowledge gap as rates of root exudation are linked to rates of C fixation during photosynthesis, and therefore plant C inputs have a strong regulatory role in ecosystems with high rates of net primary productivity, which includes tropical forested peatlands (Badri and Vivanco, 2009).

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This study assesses how six different root exudate components, added at three different concentrations, regulate GHG production from tropical peat. We hypothesised that: i) increased concentration of labile C addition significantly increases net CO₂ and CH₄ production; ii) the extent of increases in CO₂ and CH₄ production will vary between exudate types (i.e. sugars compared to organic acids); and iii) labile C additions alter soil pH and redox, with responses depending on the concentration and type of substrate.

2. Methods

2.1. Study site

Peat samples were collected in February 2015 from the 80 km² ombrotrophic peatland at Changuinola, part of the San San Pond Sak freshwater and marine wetland located in Bocas del Toro province, Panama. The central peat dome is approximately 8 m deep and was initiated approximately 4000–5000 years ago (Phillips et al., 1997). The site features seven distinct plant phasic communities beginning with a *Rhizophora mangle* mangrove swamp on the coastal margins, which is succeeded by palm swamp dominated by *Raphia taedigera*, a mixed forest stand, a monodominant *Campnosperma panamensis* forest stand, and a *Myrica-Cyrilla* bog-plain (Phillips et al., 1997). This vegetation gradient follows a pronounced decrease in nutrient availability from the margins to the centre of the wetland (Sjögersten et al., 2011; Cheesman et al., 2012), and trends in microbial community structure (Troxler et al., 2012).

Peat samples were collected from six plots in the mixed forest stand (09° 18' 13.00"N, 82° 21' 13.80"W) located approximately 600 m from the coast. Samples were collected from two points within each plot, located no more than 1 m apart, under both *R. taedigera* and *C. panamensis* plants, from a depth of 10–20 cm using a hand trowel to reduce the effect of inputs from recent litterfall and sample from a depth likely to receive regular inputs of exudates. Previously, variation in peat properties between the same set of samples, including pH, conductivity, redox potential, organic matter and gravimetric water content, was found to be low, with no statistically significant differences (Girkin et al., 2018a). Samples were sealed in zip-lock bags and transported to the Smithsonian Tropical Research Institute station in Bocas del Toro and refrigerated for four weeks 4 °C prior to transportation to the University of Nottingham, UK. Samples from the two points were homogenised to create a composite. Samples were not sieved but larger roots were removed by hand.

2.2. Experimental design

2.2.1. Root exudate compound selection

Root exudate compounds (RECs) were selected using data from a previously reported literature survey of common sugars and organic acids from 33 tree species (Girkin et al., 2018a). The selected additions were glucose, sucrose and fructose sugars, and acetate, formate and oxalate organic acids. Compounds were added at three addition rates: of 0.1, 0.2 and 0.3 mg C g⁻¹ day⁻¹ (calculated using peat dry weight equivalent). These rates were selected to match previously reported root exudate input rates and represent low, medium and high plant photosynthetic activities in forest ecosystems, although no reported data was available specifically for tropical forested peatlands (Grayston and Campbell, 1996; Baudoin et al., 2003; Shi et al., 2011; Basiliiko et al., 2012). All REC solutions were prepared by dissolving the sugar or organic acid in DI water and adjusting the pH to 5.5 using NaOH and HCl, to match *in situ* measurements, and prevent a reduction in pH on treatment addition (Renella et al., 2006). Following preparation, REC solutions were sterilised by autoclaving and stored at 4 °C.

2.3. Incubation

Peat samples (7.5 g dry weight equivalent) were placed in 120 ml glass serum bottles (Kinesis, St. Neots, UK), and saturated with DI water to give a total occupied volume of 40 ml, leaving 80 ml headspace. This approach was adopted to simulate the water-saturated and anoxic conditions found at the site. Serum bottles were flushed for 2 min with nitrogen to displace headspace gases, before sealing with a rubber septa (13 × 19 × 12 mm; Rubber B.V., Hilversum, NL), and an aluminium crimp. Each of the 18 treatments and the control were replicated six times, resulting in 114 replicates. Serum bottles were placed in a 28 °C temperature control room for two weeks for acclimation prior to beginning the experiment. Serum bottles were subsequently opened, flushed with nitrogen for 2 min, and then re-sealed. Headspace gas samples were collected after seven days incubation, prior to the addition of REC solutions. REC solutions were added at a rate of 1 ml per day, over 14 days, with 1 ml autoclaved de-ionised water as a control, between days 8 and 22. Headspace gas samples were collected on days 15 and 22 (during exudate addition) and on days 30, 38, 45 and 52. At the conclusion of the experiment bottles were opened to characterise peat properties.

During headspace sampling, gas samples (5 ml) were extracted by syringe and analysed by gas chromatography (GC-2014, Shimadzu UK LTD, Milton Keynes, UK). CO₂ and CH₄ concentrations were determined using a single injection system, with a 1 ml sample loop that passed the gas sample using H₂ 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). Thermal conductivity (TCD) and flame ionization (FID) detectors were used to measure CO₂ and CH₄, respectively (Wright et al., 2011). Gas concentrations were adjusted for incubation temperature (28 °C) and changes in pressure and headspace volume within the serum bottles, according to the ideal gas law. The rate of potential gas production, expressed as μg CO₂ g⁻¹ hr⁻¹ or μg CH₄ g⁻¹ hr⁻¹, was calculated assuming a linear accumulation rate of gases in the headspace (Hogg et al., 1992).

2.4. Peat characterization

Three sub-samples of composite peat from each plot were used to characterise peat physiochemical properties prior to incubation. Gravimetric water content was determined by analysis of the mass of water lost from 10 g wet weight peat oven dried at 105 °C for 24 h. Organic matter content was determined as the mass lost after ignition for 7 h at 550 °C. Bulk density was measured by collecting 10 cm × 10 cm × 20 cm sections from the peat surface, and oven drying at 105 °C for 24 h. Total peat carbon (C) and total nitrogen (N) were determined from 0.2 g dry, homogenised peat combusted using a total element analyser (Thermo Flash EA 1112, CE Instruments, Wigan, UK). Solution pH and redox potential were measured using a Hanna 209 meter coupled with pH and redox probes at the conclusion of the experiment.

2.5. Statistical analysis

A repeated measurements ANOVA was used to assess differences in CO₂ and CH₄ fluxes between treatments, using a combined variable comprising REC compound and concentration of addition as a fixed effect. This approach prevented aliasing from the control treatment. Subsequently, a one-way ANOVA was used to assess differences in cumulative CO₂ and CH₄ production, with a post-hoc Bonferroni test used to assess differences between treatments. Differences in redox potential and pH were assessed using a one-way ANOVA. CO₂ and CH₄ fluxes were log-transformed to meet test assumptions. Significance was assessed at $p < 0.05$. All statistical analyses were carried out in Genstat v17.1, and figures were produced using Graphpad Prism v7.01.

Table 1
In situ site properties of the mixed forest stand on the Changuinola peat deposit. Means ± 1 SEM.

Peat property	
Gravimetric water content (%)	81.7 ± 4.7
Organic matter content (%)	92.2 ± 1.7
Bulk density (g cm ⁻³)	0.1 ± 0.0
pH	5.3 ± 0.1
C (%)	44.1 ± 1.2
N (%)	2.6 ± 0.1
C:N	16.9 ± 0.0

3. Results

3.1. Peat properties

The peat was strongly acidic (pH 5.3) and waterlogged, with high gravimetric moisture (81.7%) and low bulk density (0.1 g cm⁻³) (Table 1). Organic matter content was high (92.2%), as was total carbon and nitrogen, with a C:N of 16.9. In general, peats showed limited variability in properties between replicates.

3.2. Exudate influence on greenhouse gas fluxes

All REC additions were associated with a significant increase in CO₂ fluxes (F_{18,90} = 12.72, p < 0.001, Fig. 1a–f), with a significant increase in fluxes over time (F_{6,570} = 1498.4, p < 0.001). In addition, there was a significant interaction between treatment and time (F_{108,570} = 8.97, p < 0.001). The greatest mean CO₂ flux was from the 0.2 mg C g⁻¹ oxalate addition (8.92 μg CO₂ g⁻¹ hr⁻¹). In general, increased exudate concentration yielded greater CO₂ fluxes. The exception was formate, for which the highest mean CO₂ flux occurred under the lowest exudate concentrations, suggesting inhibition at higher concentrations. The most rapid increases in fluxes occurred with 0.3 mg sugar additions, but this effect was transitory, observable only for the duration of exudate addition. By day 52 there were only limited differences in fluxes between concentrations. With organic acid additions, there were fewer discernible differences in response among different concentrations. In general, the greatest increase in fluxes occurred during the 14 day treatment period. Cumulative CO₂ production also differed significantly between treatments (F_{18,90} = 12.00, p < 0.001,

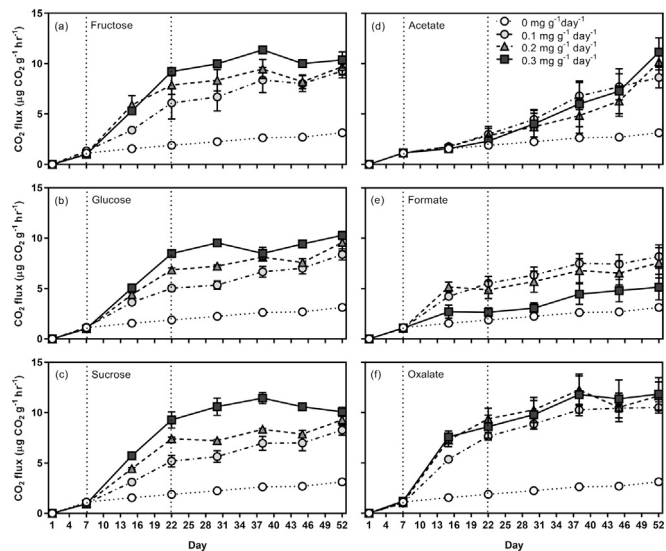


Fig. 1. CO₂ flux derived from (a) fructose, (b) glucose and (c) sucrose, (d) acetate, (e) formate and (f) oxalate addition at 0.1–0.3 mg g⁻¹ day⁻¹. Means ± 1 SEM (n = 6). SEM not shown if smaller than symbol.

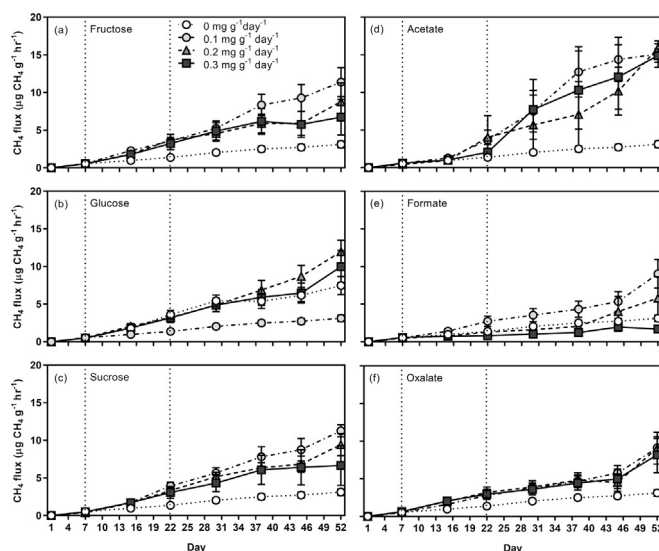


Fig. 2. CH₄ flux derived from (a) fructose, (b) glucose and (c) sucrose, (d) acetate, (e) formate and (f) oxalate addition at 0.1–0.3 mg g⁻¹ day⁻¹. Means ± 1 SEM (n = 6). SEM not shown if smaller than symbol.

Fig. 3a). A post-hoc Bonferroni test indicated that oxalic treatments were associated with the greatest cumulative fluxes.

With the exception of the 0.3 mg formate addition, all treatments significantly increased CH₄ fluxes compared to the control (F_{18,90} = 3.86, p < 0.001, Fig. 2a–f), with a significant increase in fluxes over time (F_{6,570} = 491.8, p < 0.001). In addition, there was a significant interaction between treatment and time (F_{108,570} = 6.68, p < 0.001). Lower concentrations were generally associated with greater increases in CH₄ fluxes, an observation consistent for all sugar treatments and formate addition (Fig. 3b). The 0.2 mg C g⁻¹ formate addition had a mild inhibitory effect up to day 38 compared to the 0.1 mg C g⁻¹ addition, with a reduction of fluxes compared to the control of up to 22% but by day 52, fluxes were 85% higher than the control. By comparison, the addition of 0.1 mg C g⁻¹ formate resulted in fluxes up to 190% higher than the control by day 52. Greatest CH₄ production was consistently associated with acetate addition, with up to 426% increase in production relative to the control for the 0.1 mg C g⁻¹ addition, 411% for 0.2 mg C g⁻¹, and 377% for 0.3 mg. Cumulative CH₄ fluxes were more sensitive to the concentration of the REC addition than CO₂ fluxes, with reduced fluxes at higher concentrations for all

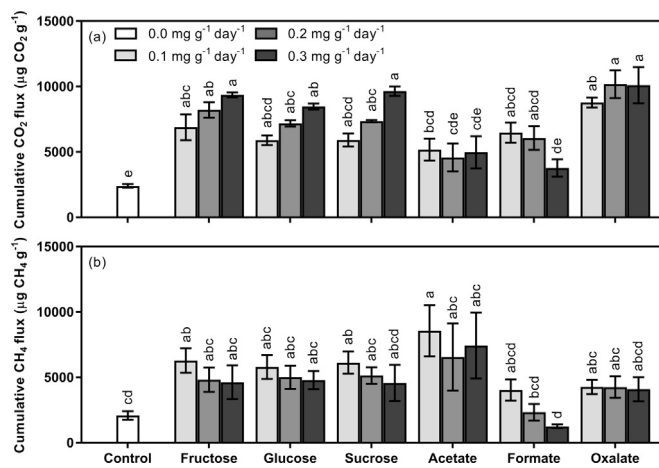


Fig. 3. Cumulative (a) CO₂ flux, (b) CH₄ flux derived from REC compound at addition rates of 0.1–0.3 mg g⁻¹ day⁻¹. Means ± 1 SEM (n = 6). Letters indicate significant differences from a post-hoc Bonferroni test (p < 0.05) for all compositions and concentrations.

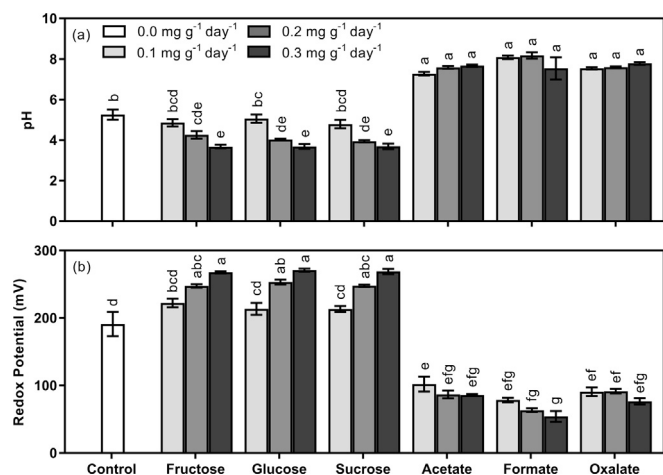


Fig. 4. Root exudate component influence on (a) pH, and (b) redox potential from addition rates of 0.1–0.3 mg g⁻¹ day⁻¹. Means ± 1 SEM (n = 6). Letters indicate significant differences from a post-hoc Bonferroni test (p < 0.05) for all compositions and concentrations.

treatments, with the exception of acetate ($F_{18,90} = 4.52$, $p < 0.001$, Fig. 3b).

3.3. Exudate effects on peat properties

REC addition significantly altered peat pH, with the effect dependent on both concentration and the compound added ($F_{18,87.5} = 92.1$, $p < 0.001$, Fig. 4a). Low concentration sugar additions (0.1 mg) reduced pH to 4.8–5.1. High concentration additions (0.3 mg) caused a greater reduction in pH to 3.6. In contrast, organic acid additions increased pH, with no significant effect of increased concentration on pH.

REC addition significantly affected redox potential, with extent of the response affected by both the type of REC addition and concentration ($F_{18,88.3} = 152.84$, $p < 0.001$, Fig. 4b). All sugar additions increased redox potential compared to the control, with more pronounced increases at higher concentrations. In contrast, all organic acid additions significantly decreased redox potential, with the greatest decreases generally found at the highest REC concentrations. The exception to this pattern was 0.2 mg C g⁻¹ addition of oxalate which resulted in a slightly higher redox potential than 0.1 and 0.3 mg C g⁻¹ additions.

4. Discussion

We previously showed that the addition of RECs in combination increased net CO₂ and CH₄ fluxes more than higher concentration additions comprising fewer individual components (Girkin et al., 2018a). For example, the addition of 0.3 mg C g⁻¹ comprising three sugars and one organic acid added to an anoxic peat soil resulted in lower cumulative fluxes than a 0.2 mg C g⁻¹ addition comprising four organic acids. In this study, we demonstrate that low concentrations of specific RECs may have a disproportionately important effect on GHG emissions, as higher REC concentrations were not necessarily associated with the greatest CO₂ and CH₄ production.

All sugar solution additions and oxalate additions increased CO₂ fluxes more rapidly than acetate and formate additions, and were associated with greater cumulative production. Previous incubation experiments demonstrated the rapid use of sugars by peat microbial communities (Jones and Murphy, 2007) and increased activity of hydrolytic enzymes (Shi et al., 2011). Acetate, the most important substrate for methanogenesis, was associated with the greatest CH₄ efflux, with increases in production occurring more rapidly than other additions. Acetate has been estimated to contribute to up to two-thirds of

net CH₄ production, with formate recognised as the second most important substrate (Ferry, 1992; Fox and Comerford, 1990).

For all REC additions, CO₂ production increased more rapidly than CH₄ production, in keeping with previous incubation studies of tropical peats (Avery et al., 2003; Galand et al., 2005), an effect driven by the preferential depletion of a series of terminal electron acceptors during C mineralisation (Lipson et al., 2010). In four of six additions, higher concentration additions yielded greater CO₂ production. CH₄ production was more dependent on the type of addition than the concentration, but with some inhibition of fluxes at higher concentrations for four of six treatments. In both cases, the extent of decomposition and net fluxes of both gases arising from labile C additions may be constrained in part by nutrient availability (Hoyos-Santillan et al., 2018), and differences in inherent organic matter properties (Upton et al., 2018).

Studies using ¹³C and ¹⁴C isotope methodology have demonstrated that labile C additions can significantly enhance the decomposition of older, more recalcitrant organic matter in a process termed priming, and that the effect is frequently determined by the chemical composition of the additions (Verma et al., 1995; Hamer and Marschner, 2002). This has been speculated as being driven by a combination of the activation of specific microbial groups and the behaviour of the individual organic molecules added. Conversely, it has been reported that some additions, for example oxalate, can bind to lignin structures, reducing availability for enzyme activity (Piccolo et al., 1996). Part of the difference in fluxes between organic acid adsorption, which can reduce C mineralisation, rates of decomposition and overall microbial growth (Lopez-Hernandez et al., 1986). Monovalent organic acids, including acetate and formate, are more weakly adsorbed by soils compared to divalent organic acids such as oxalate (Jones et al., 2003), although these processes can be very slow, occurring at the rate of hours to months (Van Hees et al., 2005). Microbial uptake of low weight molecular compounds, including organic acids and sugars, is a much more rapid process which occurs over several minutes (Van Hees et al., 2005). A combination of differences in the relative adsorption of organic acids versus microbial uptake likely explains the resulting differences in GHG fluxes between REC addition types. It is also plausible that some parts of the microbial community may also be more dependent on the specific exudates released by the plant species and therefore some of the differences in response to contrasting REC additions may be because the community is not fully adapted for its decomposition (Deangelis et al., 2009; Schimel and Schaefer, 2012). Over time, changes in microbial community composition may explain the increase in CH₄ production in oxalate treatments by day 56.

Organic acid additions have been reported to inhibit methanotroph activity under aerobic conditions (Wieczorek et al., 2011), inhibit enzyme activities, and alter bacterial taxa diversity and abundance (Shi et al., 2011). High concentrations of acetate can have an inhibitory effect at pH < 4.5 due to the protonated forms disturbing microbial cell membranes (Russell, 1992). As higher concentrations of formate were only associated with reduced CH₄ fluxes, and these treatments were associated with an increase in pH, it is possible that the methanogenic community was particularly sensitive to this perturbation, although previous studies have indicated that methanogen activity increases at higher pH (Ye et al., 2012). Autoclaving may have resulted in the thermal decomposition of formate, resulting in carbon monoxide (CO) formation, which can inhibit methanogenesis (Oelgeschläger and Rother, 2009). However, this process is unlikely to fully account for the observed results, as CO toxicity would also have inhibited CO₂ production which did not differ significantly between the three formate concentrations, or compared to high concentration oxalate additions. High formate concentrations have been reported to inhibit acetoclastic methanogenesis (the dominant CH₄ production pathway), which have resulted in reduced cumulative CH₄ production (Guyot, 1986; Guyot and Brauman, 1986). Subsequently, the gradual consumption of formate may have resulted in a reduction in inhibition and account for the

increased CH₄ production for the 0.1 mg C g⁻¹ treatment between 45 and 52 days (Fig. 2e).

All organic acid additions increased pH significantly compared to the control, whereas sugar additions decreased pH. Microbial degradation of carboxylic acids consumes H⁺ liberating OH⁻ and CO₂ (Gramss et al., 2003), while the utilisation of sugars generates H⁺ (Srinivasan and Mahadevan, 2010). Increases in pH after organic acid additions are associated with significant shifts in microbial communities (Shi et al., 2011) and increases in CO₂ (Yan et al., 1996) and CH₄ production (Wang et al., 1993).

Redox potential increased with sugar addition, and decreased with organic acid addition. Addition of labile plant residues can also reduce redox potential as high respiration depletes oxygen (Fig. 4a) (Flessa and Beese, 1995). Changes in pH, redox potential and conductivity are closely coupled, because redox reactions frequently involve the transfer of H⁺ due to changes in the oxidative state of Fe, Mn or N (Husson, 2013). Combined, changes in pH and redox potential can affect microbial community structure and activity may account for the inhibition of GHG production at higher REC concentrations. Tropical peatland microbial communities are likely to be relatively well-adapted to changing redox potential due to frequent fluctuations in water table height, altering the balance between anoxic conditions favouring methanogens and CH₄ production, methanotrophs and CH₄ oxidation, and heterotrophic respiration (Tokarz and Urban, 2015).

In situ, root inputs of exudates contribute significantly to net GHG fluxes. For example, approximately two-thirds of CO₂ emissions from the Changuinola mixed forest stand are root-derived, an estimate which includes components from both root respiration and microbial use of exudates (Girkin et al., 2018b). This is particularly important in the context of land use change in tropical peatlands, for example the expansion of plantation agriculture in Southeast Asia. Malaysia alone has undergone a 150% increase in land area planted by oil palm, with significant expansion onto peatlands (Fao, 2016; Pirker et al., 2016). While this changes peat physical properties (Tonks et al., 2017), our results suggest that any changes in plant community composition that alter root exudate profiles may result in substantial changes to GHG emissions. However, due to the sparsity of studies assessing root exudate profiles of tropical plant species, particularly palms, the precise effect on GHG fluxes remains to be elucidated. Climate change may also significantly affect *in situ* root exudation. Elevated atmospheric CO₂ has been found to increase rates of root exudation in wetland ecosystems (Sanchez-Carrillo et al., 2018). Increases in temperature have also been reported to increase rates of exudation in some tree species (Uselman et al., 2000), and alter the composition of exudate profiles (Vančura, 1967; Badri and Vivanco, 2009).

Our results demonstrate that the type and concentration of root exudates influence CO₂ and CH₄ production. For CO₂ production, substrate concentration was the most important driver of fluxes over the short term, whereas for CH₄ production the most critical driver is exudate type, with peat CH₄ fluxes most sensitive to acetate addition. Moreover, there is an inverse relationship between REC addition concentration and CH₄ fluxes. These effects are most likely driven by differing levels of adsorption and shifts in peat properties following addition. These findings are particularly important in the context of understanding how plant inputs are able to regulate GHG emissions from tropical peatlands, because any process which alters plant community composition may alter root exudate profiles.

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