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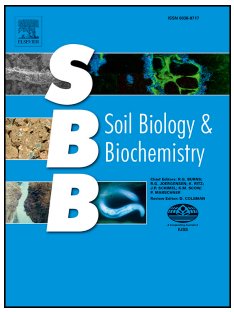

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Composition and concentration of root exudate analogues regulate greenhouse gas fluxes from tropical peat

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Abstract

Tropical peatlands are a significant carbon store and source of carbon dioxide (CO_2) and methane (CH_4) 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 CO_2 and CH_4 production from tropical peats under anoxic conditions. For CO_2 production, substrate concentration was the more important driver, with increased CO_2 fluxes following higher addition rates of four out of the six exudate analogues. In contrast, exudate type was the more important driver of CH_4 production, with acetate addition associated with the greatest production, and inverse correlations between exudate concentration and CH_4 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 CO_2 and warming.

1. Introduction

Globally, peatlands are a significant source of methane (CH_4) emissions, contributing between 20 – 39% of annual CH_4 production, as well as making a significant contribution to atmospheric carbon dioxide (CO_2) 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 means 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 CO_2 and CH_4 (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, including in tropical forested peatlands (Badri and Vivanco, 2009).

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 CO_2 and CH_4 production; ii) the extent of increases in CO_2 and CH_4 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 km^2 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 C*ampnosperma 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).

Six 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, Basiliko 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 two minutes 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 two minutes, 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). 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 H_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). Thermal conductivity (TCD) and flame ionization (FID) detectors were used to measure CO_2 and CH_4, 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 $\mu g\ CO_2\ g^{-1}\ hr^{-1}$ or $\mu g\ CH_4\ g^{-1}\ hr^{-1}$, was calculated assuming a linear accumulation rate of gases in the headspace (Hogg et al., 1992).

2.4. Peat characterization

Three composite sub-samples from each plot were used to characterize peat physiochemical properties prior to beginning the 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 hours. Organic matter content was determined as the mass lost after ignition for 7 hours 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 hours. 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 CO_2 and CH_4 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 CO_2 and CH_4 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. CO_2 and CH_4 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.

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 CO_2 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 CO_2 flux was from the 0.2 mg C g^{-1} oxalate addition (8.92 µg CO_2 g^{-1} hr^{-1}). In general, increased exudate concentration yielded greater CO_2 fluxes. The exception was formate, for which the highest mean CO_2 flux occurred under the lowest exudate

143 concentrations, suggesting inhibition at higher concentrations. The most rapid increases in fluxes occurred with
144 0.3 mg sugar additions, but this effect was transitory, observable only for the duration of exudate addition. By
145 day 52 there were only limited differences in fluxes between concentrations. With organic acid additions, there
146 were fewer discernible differences in response among different concentrations. In general, the greatest increase
147 in fluxes occurred during the 14 day treatment period. Cumulative CO_2 production also differed significantly
148 between treatments ($F_{18,90}$ = 12.00, $p < 0.001$, Fig. 3a). A post-hoc Bonferroni test indicated that oxalic
149 treatments were associated with the greatest cumulative fluxes.
150 With the exception of the 0.3 mg formate addition, all treatments significantly increased CH_4 fluxes compared
151 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
152 < 0.001). In addition, there was a significant interaction between treatment and time ($F_{108,570} = 6.68$, $p < 0.001$).
153 Lower concentrations were generally associated with greater increases in CH_4 fluxes, an observation consistent
154 for all sugar treatments and formate addition (Fig. 3b). The 0.2 mg C g^{-1} formate addition had a mild inhibitory
155 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
156 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}
157 formate resulted in fluxes up to 190% higher than the control by day 52. Greatest CH_4 production was
158 consistently associated with acetate addition, with up to 426% increase in production relative to the control for
159 the 0.1 mg C g^{-1} addition, 411% for 0.2 mg C g^{-1}, and 377% for 0.3 mg. Cumulative CH_4 fluxes were more
160 sensitive to the concentration of the REC addition than CO_2 fluxes, with reduced fluxes at higher concentrations
161 for all treatments, with the exception of acetate ($F_{18,90} = 4.52$, $p < 0.001$, Fig. 3b).
162

163 **3.3. Exudate effects on peat properties**

164 REC addition significantly altered peat pH, with the effect dependent on both concentration and the compound
165 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.
166 High concentration additions (0.3 mg) caused a greater reduction in pH to 3.6. In contrast, organic acid additions
167 increased pH, with no significant effect of increased concentration on pH.
168 REC addition significantly affected redox potential, with extent of the response affected by both the type of
169 REC addition and concentration ($F_{18,88.3} = 152.84$, $p < 0.001$, Fig. 4b). All sugar additions increased redox
170 potential compared to the control, with more pronounced increases at higher concentrations. In contrast, all
171 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 CO_2 and CH_4 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 disproportionally important effect on GHG emissions, as higher REC concentrations were not necessarily associated with the greatest CO_2 and CH_4 production.

All sugar solution additions and oxalate additions increased CO_2 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 & Murphy, 2007) and increased activity of hydrolytic enzymes (Shi et al. 2011). Acetate, the most important substrate for methanogenesis, was associated with the greatest CH_4 efflux, with increases in production occurring more rapidly than other additions. Acetate has been estimated to contribute to up to two-thirds of net CH_4 production, with formate recognised as the second most important substrate (Ferry, 1992, Fox & Comerford, 1990).

For all REC additions, CO_2 production increased more rapidly than CH_4 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 CO_2 production. CH_4 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 ^{13}C and ^{14}C 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 treatments may therefore be due to different rates of 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 & Schaefer, 2012). Over time, changes in microbial community composition may explain the increase in CH_4 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 CH_4 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 & Rother, 2009). However, this process is unlikely to fully account for the observed results, as CO toxicity would also have inhibited CO_2 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 CH_4 production pathway), which have resulted in reduced cumulative CH_4 production (Guyot, 1986, Guyot & Brauman, 1986). Subsequently, the gradual consumption of formate may have resulted in a reduction in inhibition and account for the increased CH_4 production for the 0.1 mg C g^{-1} treatment between 45 and 52 days (Figure 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 CO_2 (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 CO_2 (Yan et al., 1996) and CH_4 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 CH_4 production, methanotrophs and CH_4 oxidation, and heterotrophic respiration (Tokarz & Urban, 2015).

In situ, root inputs of exudates contribute significantly to net GHG fluxes. For example, approximately two-thirds of CO_2 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 CO_2 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 & Vicanco 2009).

Our results demonstrate that the type and concentration of root exudates influence CO_2 and CH_4 production. For CO_2 production, substrate concentration was the most important driver of fluxes over the short term, whereas for CH_4 production the most critical driver is exudate type, with peat CH_4 fluxes most sensitive to acetate addition.

Moreover, there is an inverse relationship between REC addition concentration and CH_4 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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References

AVERY, G. B., SHANNON, R. D., WHITE, J. R., MARTENS, C. S. & ALPERIN, M. J. 2003. Controls on methane production in a tidal freshwater estuary and a peatland: methane production via acetate fermentation and CO2 reduction. *Biogeochemistry,* 62**,** 19-37.

BADRI, D. V. & VIVANCO, J. M. 2009. Regulation and function of root exudates. *Plant Cell and Environment,* 32**,** 666-681.

BASILIKO, N., STEWART, H., ROULET, N. T. & MOORE, T. R. 2012. Do Root Exudates Enhance Peat Decomposition? *Geomicrobiology Journal,* 29**,** 374-378.

BAUDOIN, E., BENIZRI, E. & GUCKERT, A. 2003. Impact of artificial root exudates on the bacterial community structure in bulk soil and maize rhizosphere. *Soil Biology & Biochemistry,* 35**,** 1183-1192.

CASIDA, L. E. 1977. Microbial Metabolic-Activity in Soil as Measured by Dehydrogenase Determinations. *Applied and Environmental Microbiology,* 34**,** 630-636.

CHANDER, K., GOYAL, S., MUNDRA, M. C. & KAPOOR, K. K. 1997. Organic matter, microbial biomass and enzyme activity of soils under different crop rotations in the tropics. *Biology and Fertility of Soils,* 24**,** 306-310.

CHEESMAN, A. W., TURNER, B. L. & REDDY, K. R. 2012. Soil Phosphorus Forms along a Strong Nutrient Gradient in a Tropical Ombrotrophic Wetland. *Soil Science Society of America Journal,* 76**,** 1496-1506.

DAKORA, F. D. & PHILLIPS, D. A. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant and Soil,* 245**,** 35-47.

DARGIE, G.C., LEWIS, S.L., LAWSON, I.T., MITCHARD, E.T.A., PAGE, S.E., BOCKO, & Y.E., IFO, S.A., 2017. Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature*, 542, 86–90. doi:10.1038/nature21048

DEANGELIS, K. M., BRODIE, E. L., ANDERSON, G. L., LINDOW, S. E., FIRESTONE, M. K. 2009. Selective progressive response of soil microbial community to wild oat roots. *ISME Journal*, 3, 168-178

DUNFIELD, P., KNOWLES, R., DUMONT, R. & MOORE, T. R. 1993. Methane Production and Consumption in Temperate and Sub-Arctic Peat Soils - Response to Temperature and Ph. *Soil Biology & Biochemistry,* 25**,** 321-326.

FERRY, J.G., 1992. Methane from acetate. Journal of Bacteriology 174, 5489–5495.

FAO, 2016. FAOSTAT Gateway 2014. URL http://faostat3.fao.org/faostat-gateway/go/to/home (accessed 08.04.18.).

FLESSA, H. & BEESE, F. 1995. Effects of Sugar-Beet Residues on Soil Redox Potential and Nitrous-Oxide Emission. *Soil Science Society of America Journal,* 59**,** 1044-1051.

GUYOT, J. P. 1986. Role of formate in methanogenesis from xylan by *Cellulomonas* sp. associated with methanogens and *Desulfovibrio vulgaris*: Inhibition of the aceticlastic reaction, *FEMS Microbiology Letters.* 34, 149-153.

GUYOT, J. P. & BRAUMAN, A. 1986. Methane Production from Formate by Syntrophic Association of *Methanobacterium bryantii* and *Desulfovibrio vulgaris* JJ. Applied and Environmental Microbiology, 52, 1436-1437

HAMER, U. & MARSCHNER B. 2002. Priming effects of sugars, amino acids, organic acids and catechol on the mineralization of lignin and peat. J*ournal of Plant Nutrition and Soil Science*. 165. 261-268.

JONES, D.L., DENNIS, P.G., OWEN, A.G., VAN HEES, P.A.W., 2003. Organic acid behavior in soils - misconceptions and knowledge gaps. *Plant and Soil.* 248, 31–41.

JONES, D.L., MURPHY, D.V., 2007. Microbial response time to sugar and amino acid additions to soil. *Soil Biology & Biochemistry*. 39, 2178–2182.

FOX, T.R., COMERFORD, N.B., 1990. Low-molecular-weight organic-acids in selected forest soils of the southeastern USA. *Soil Science Society of America Journal* 54, 1139–1144.

GALAND, P. E., FRITZE, H., CONRAD, R. & YRJALA, K. 2005. Pathways for methanogenesis and diversity of methanogenic archaea in three boreal peatland ecosystems. *Applied and Environmental Microbiology,* 71**,** 2195-2198.

GIRKIN, N. T., TURNER, B. L., OSTLE, N., CRAIGON, J. & SJOGERSTEN, S. 2018a. Root exudate analogues accelerate CO_2 and CH_4 production in tropical peat. *Soil Biology & Biochemistry,* 117**,** 48-55.

GIRKIN, N. T., TURNER, B. L., OSTLE, N. & SJOGERSTEN, S. 2018b. Root-derived CO_2 flux from a tropical peatland. *Wetlands Ecology and Management,* 1, 1-7.

GRAMSS, G., VOIGT, K. D., BUBLITZ, F. & BERGMANN, H. 2003. Increased solubility of (heavy) metals in soil during microbial transformations of sucrose and casein amendments. *Journal of Basic Microbiology,* 43**,** 483-498.

GRAYSTON, S. J. & CAMPBELL, C. D. 1996. Functional biodiversity of microbial communities in the rhizospheres of hybrid larch (Larix eurolepis) and Sitka spruce (Picea sitchensis). *Tree Physiology,* 16**,** 1031-1038.

HAMER, U. & MARSCHNER, B. 2002. Priming effects of sugars, amino acids, organic acids and catechol on the mineralization of lignin and peat. *Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde,* 165**,** 261-268.

HOGG, E. H., LIEFFERS, V. J. & WEIN, R. W. 1992. Potential Carbon Losses from Peat Profiles - Effects of Temperature, Drought Cycles, and Fire. *Ecological Applications,* 2**,** 298-306.

HOYOS-SANTILLAN, J., LOMAX, B. H., TURNER, B. L., SJÖGERSTEN, S. 2018. Nutrient limitation or home field advantage: Does microbial community adaptation overcome nutrient limitation of litter decomposition in a tropical peatland? *Journal of Ecology*.

HUSSON, O. 2013. Redox potential (Eh) and pH as drivers of soil/plant/microorganism systems: a transdisciplinary overview pointing to integrative opportunities for agronomy. *Plant and Soil,* 362**,** 389-417.

JONES, D. L., DENNIS, P. G., OWEN, A. G. & VAN HEES, P. A. W. 2003. Organic acid behavior in soils - misconceptions and knowledge gaps. *Plant and Soil,* 248**,** 31-41.

KUZYAKOV, Y. & DOMANSKI, G., 2000. Carbon input by plants into the soil. Review. J*ournal of Plant Nutrition and Soil Science* 163, 421–431.

LAANBROEK, H. J. 2010. Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. *Annals of Botany*, 105**,** 141-153.

LIPSON, D. A., JHA, M., RAAB, T. K. & OECHEL, W. C. 2010. Reduction of iron (III) and humic substances plays a major role in anaerobic respiration in an Arctic peat soil. *Journal of Geophysical Research-Biogeosciences*, 115.

LOPEZ-HERNANDEZ, D., SIEGERT, G. & RODRIGUEZ, J. V. 1986. Competitive Adsorption of Phosphate with Malate and Oxalate by Tropical Soils. *Soil Science Society of America Journal,* 50**,** 1460-1462.

LOVLEY, D. R., COATES, J. D., BLUNTHARRIS, E. L., PHILLIPS, E. J. P. & WOODWARD, J. C. 1996. Humic substances as electron acceptors for microbial respiration. *Nature*, 382**,** 445-448.

MANGALASSERY, S., MOONEY, S. J., SPARKES, D. L., FRASER, W. T. & SJÖGERSTEN, S. 2015. Impacts of zero tillage on soil enzyme activities, microbial characteristics and organic matter functional chemistry in temperate soils. *European Journal of Soil Biology*, 68**,** 9-17.

OELGESCHLAGER, E., ROTHER, M. 2009. Influence of carbon monoxide on metabolite formation in Methanosarcina acetivorans. *FEMS Microbiology Letters*, 292, 254–260.

OHLINGER, R. 1995. Dehydrogenase activity with the substrate TTC. *In:* SCHINNER, F., OHLINGER, R., KANDELER, E. & MARGESIN, R. (eds.) *Methods in Soil Biology*. Springer.

PAGE, S. E., RIELEY, J. O. & BANKS, C. J. 2011. Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, 17**,** 798-818.

PHILLIPS, S., ROUSE, G. E. & BUSTIN, R. M. 1997. Vegetation zones and diagnostic pollen profiles of a coastal peat swamp, Bocas del Toro, Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 128**,** 301-338.

PICCOLO, A., NARDI, S., CONCHERI, G., 1996. Macromolecular changes of humic substances induced by interaction with organic acids, *European Journal of Soil Science*, 47, 319-328

PIRKER, J., MOSNIER, A., KRAXNER, F., HAVLIK, P., OBERSTEINER, M. 2016. What are the limits to oil palm expansion? *Global Environmental Change*, 40, 73-81

RENELLA, G., EGAMBERDIYEVA, D., LANDI, L., MENCH, M. & NANNIPIERI, P. 2006. Microbial activity and hydrolase activities during decomposition of root exudates released by an artificial root surface in Cd-contaminated soils. *Soil Biology & Biochemistry*, 38**,** 702-708.

RUSSELL, J. B. 1992. Another explanation for the toxicity of fermentation acids at low pH: anion accumulation versus uncoupling. *Journal of Applied Bacteriology*, 73, 363-370.

SANCHEZ-CARRILLO, S., ALVAREZ-COBELAS, M., ANGELER, D. G., SERRNO-GRIJALVA, L., SANCHEZ-ANDRES, R., CIRUJANO, S. & SCHMID, T. 2018. Elevated Atmospheric CO2 Increases Root Exudation of Carbon in Wetlands: Results from the First Free-Air CO_2 Enrichment Facility (FACE) in a Marshland. *Ecosystems, 21 852–867*

SCHIMEL, J.P & SCHAEFFER, S. M. 2012. Microbial control over carbon cycling in soil. *Frontiers in Microbiology*. 3, 1-11.

SHI, S. J., RICHARDSON, A. E., O'CALLAGHAN, M., DEANGELIS, K. M., JONES, E. E., STEWART, A., FIRESTONE, M. K. & CONDRON, L. M. 2011. Effects of selected root exudate components on soil bacterial communities. *Fems Microbiology Ecology*, 77**,** 600-610.

SJÖGERSTEN, S., CHEESMAN, A. W., LOPEZ, O. & TURNER, B., L. 2011. Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland. *Biogeochemistry*, 104**,** 147-163.

SRINIVASAN, K. & MAHADEVAN, R. 2010. Characterization of proton production and consumption associated with microbial metabolism. *Bmc Biotechnology*, 10.

STROM, L., OWEN, A. G., GODBOLD, D. L. & JONES, D. L. 2002. Organic acid mediated P mobilization in the rhizosphere and uptake by maize roots. *Soil Biology & Biochemistry*, 34**,** 703-710.

TREVORS, J. T. 1984. Effect of Substrate Concentration, Inorganic Nitrogen, O_2 Concentration, Temperature and pH on Dehydrogenase-Activity in Soil. *Plant and Soil*, 77**,** 285-293.

TROXLER, T. G., IKENAGA, M., SCINTO, L., BOYER, J. N., CONDIT, R., PEREZ, R., GANN, G. D. & CHILDERS, D. L. 2012. Patterns of Soil Bacteria and Canopy Community Structure Related to Tropical Peatland Development. *Wetlands*, 32**,** 769-782.

TOKARZ, E. & URBAN, D. 2015. Soil redox potential and its impact on microorganisms and plants of wetlands. *Journal of Ecological Engineering*. 16, 20-30.

TONKS, A. J., APLIN, P., BERIRO, D. J., COOPER, H., EVERS, S., VANE, C. H. &, S. 2017. Impacts of conversion of tropical peat swamp forest to oil palm plantation on peat organic chemistry, physical properties and carbon stocks. *Geoderma*, 289, 36-45.

UPTON, A., VANE, C. H., GIRKIN, N., TURNER, B. L., & SJOGERSTEN, S. 2018. Does litter input determine carbon storage and peat organic chemistry in tropical peatlands?. *Geoderma*, 326, 76-87.

USELMAN, S. M., QUALLS, R. G. & THOMAS, R. B. 2000. Effects of increased atmospheric CO□, temperature, and soil N availability on root exudation of dissolved organic carbon by a N-fixing tree (*Robinia pseudoacacia* L.). *Plant and Soil*, 222, 191-202

VANČURA, V. 1968. Root exudates of plants III. Effect of temperature and 'cold shock' on the exudation of various compounds from seeds and seedlings of maize and cucumber. *Plant and Soil*, 27, 319–328.

VAN HEES, P.A.W., JONES, D.L., JENTSCHKE, G., GODBOLD, D.L. 2005. Organic acid concentrations in soil solution: effects of young coniferous trees and ectomycorrhizal fungi. *Soil Biology & Biochemistry*, 37, 771–776.

VAN HEES, P. A. W., VINOGRADOFF, S. I., EDWARDS, A. C., GODBOLD, D. L. & JONES, D. L. 2003. Low molecular weight organic acid adsorption in forest soils: effects on soil solution concentrations and biodegradation rates. *Soil Biology & Biochemistry*, 35**,** 1015-1026.

VELMOUROUGANE, K., VENUGOPALAN, M. V., BHATTACHARYYA, T., SARKAR, D., PAL, D. K., SAHU, A., RAY, S. K., NAIR, K. M., PRASAD, J. & SINGH, R. S. 2013. Soil dehydrogenase activity in agro-ecological sub regions of black soil regions in India. *Geoderma*, 197**,** 186-192.

VERMA, L., J. P. MARTIN, J. P., & HAIDER, K. 1975. Decomposition of Carbon-14-labeled proteins, peptides, and amino acids; free and complexed withhumic polymers. Soil Science Society of America Journal. 39, 279-284.

WANG, Z. P., DELAUNE, R. D., MASSCHELEYN, P. H. & PATRICK, W. H. 1993. Soil Redox and Ph Effects on Methane Production in a Flooded Rice Soil. *Soil Science Society of America Journal*, 57**,** 382-385.

WIECZOREK, A. S., DRAKE, H. L., KOLB, S. 2011. Organic acids and ethanol inhibit the oxidation of methane by mire methanotrophs. *FEMS Microbiology Ecology*, 77, 28-39

WRIGHT, E. L., BLACK, C. R., TURNER, B. L. & SJÖGERSTEN, S. 2013. Environmental controls of temporal and spatial variability in CO_2 and CH_4 fluxes in a neotropical peatland. *Global Change Biology*, 19**,** 3775-89.

YAN, F., SCHUBERT, S. & MENGEL, K. 1996. Soil pH increase due to biological decarboxylation of organic anions. *Soil Biology & Biochemistry*, 28**,** 617-624.

YE, R. Z., JIN, Q. S., BOHANNAN, B., KELLER, J. K., MCALLISTER, S. A. & BRIDGHAM, S. D. 2012. pH controls over anaerobic carbon mineralization, the efficiency of methane production, and

methanogenic pathways in peatlands across an ombrotrophic-minerotrophic gradient. *Soil Biology & Biochemistry*, 54**,** 36-47.

Tables and figures

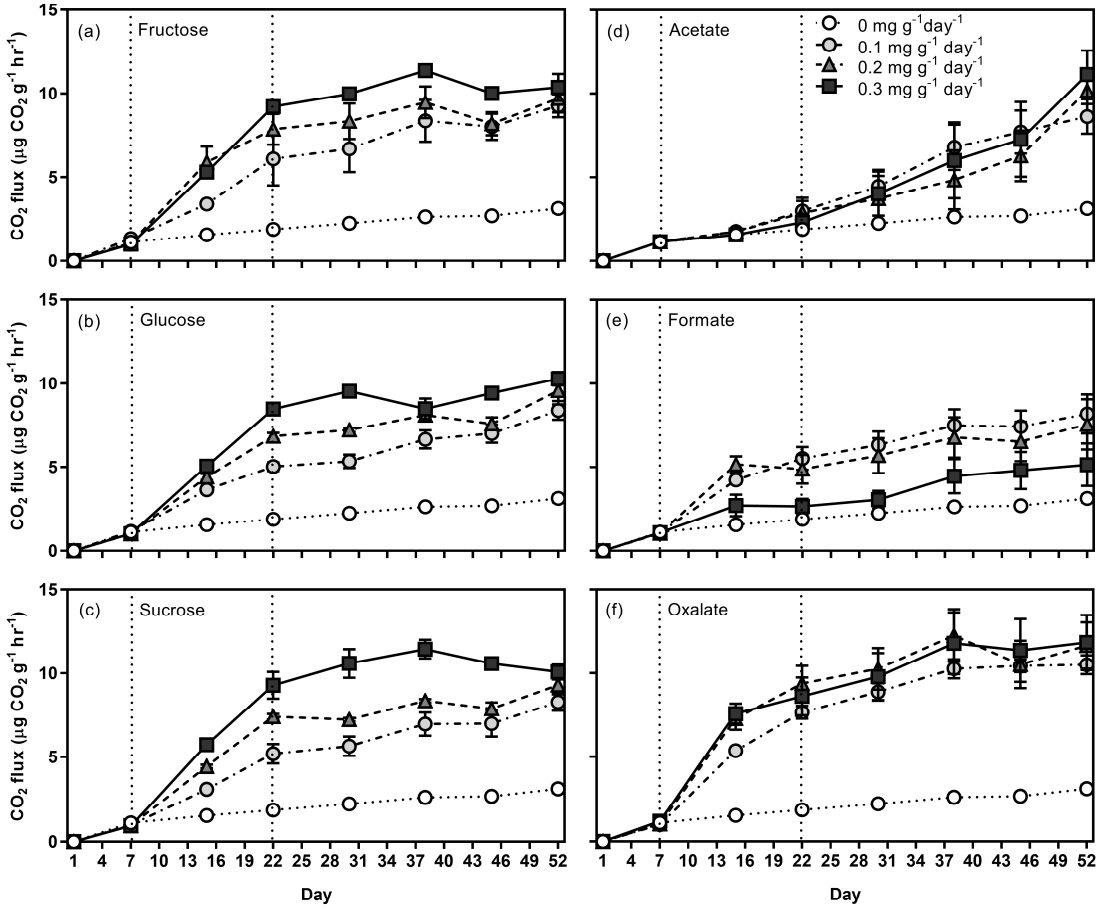
Table 1: *In situ* site properties of the mixed forest stand on the Changuinola peat deposit. Means ± 1 SEM.

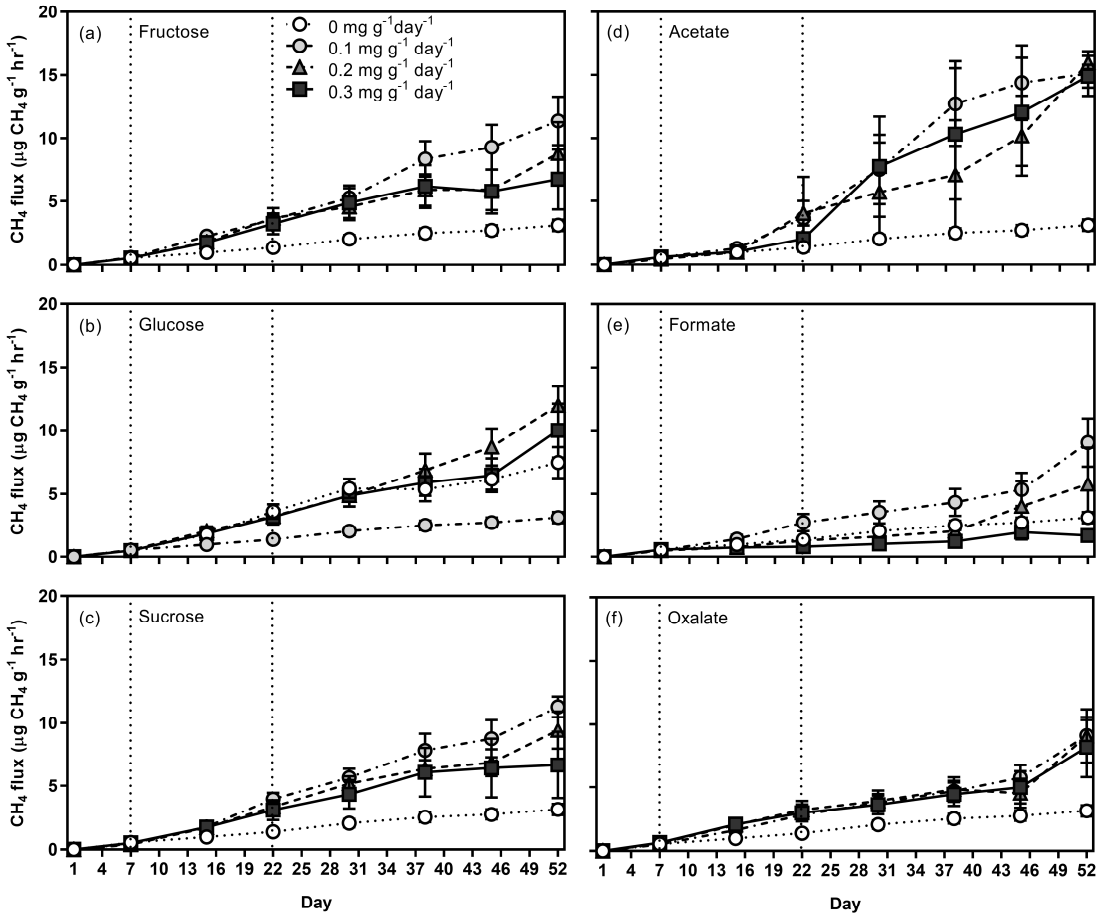
Fig. 1: CO_2 flux derived from (a) fructose, (b) glucose and (c) sucrose, (d) acetate, (e) formate and (f) oxalate addition at 0.1 – 0.3 mg g^{-1} day^{-1}. Means ± 1 SEM (n = 6). SEM not shown if smaller than symbol.

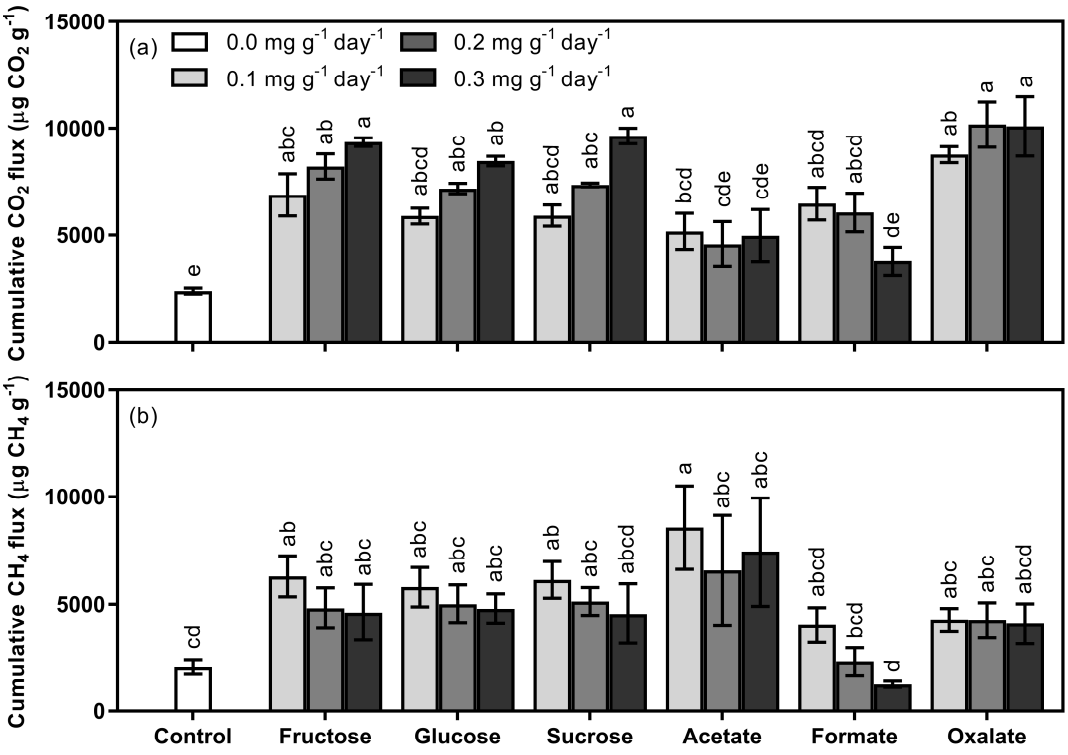
Fig. 2: CH_4 flux derived from (a) fructose, (b) glucose and (c) sucrose, (d) acetate, (e) formate and (f) oxalate addition at 0.1 – 0.3 mg g^{-1} day^{-1}. Means ± 1 SEM (n = 6). SEM not shown if smaller than symbol.

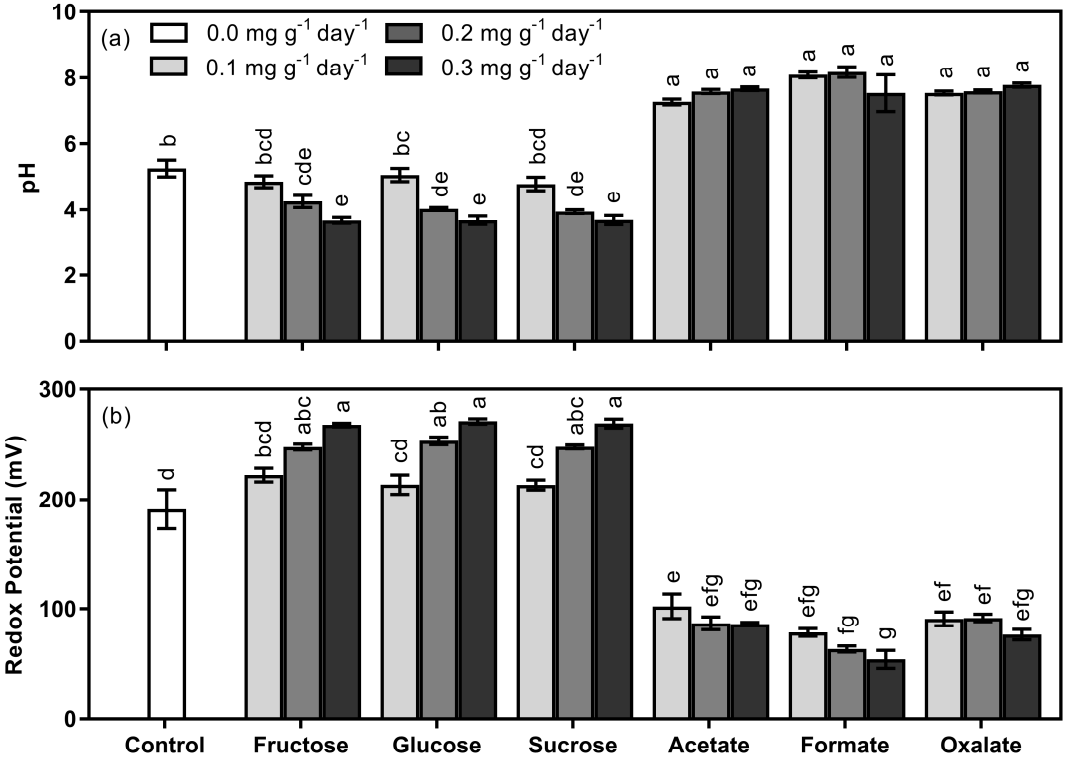
Fig. 3: Cumulative (a) CO_2 flux, (b) CH_4 flux derived from REC compound at addition rates of 0.1 – 0.3 mg g^{-1} day^{-1}. Means ± 1 SEM (n = 6). Letters indicate significant differences from a post-hoc Bonferroni test ($p < 0.05$) for all compositions and concentrations.

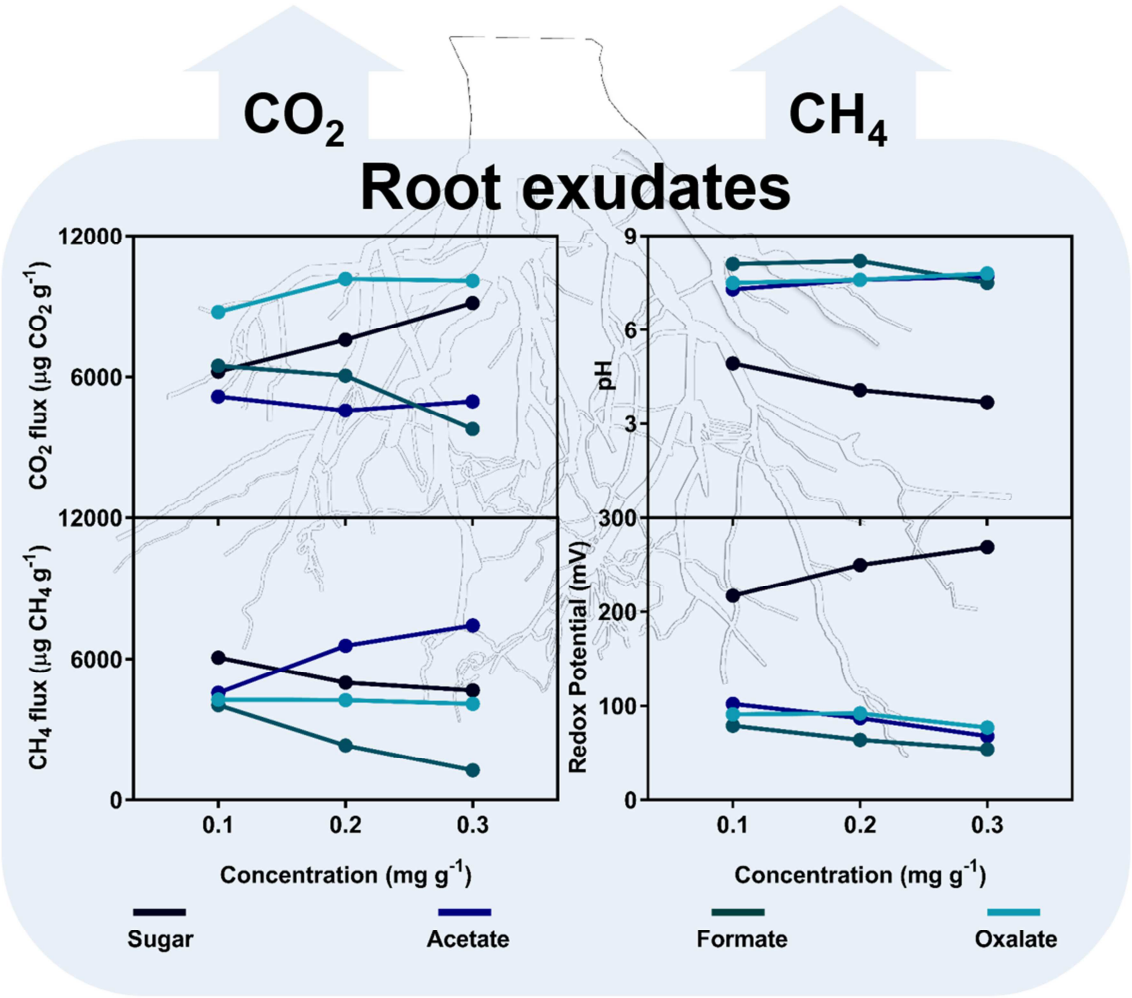
Fig. 4: Root exudate component influence on (a) pH, and (b) redox potential from addition rates of 0.1 – 0.3 mg g^{-1} day^{-1}. Means ± 1 SEM (n = 6). Letters indicate significant differences from a post-hoc Bonferroni test ($p < 0.05$) for all compositions and concentrations.


(a) Fructose
(b) Glucose
(c) Sucrose
(d) Acetate
(e) Formate
(f) Oxalate
0 mg g-1day-1
0.1 mg g-1 day-1
0.2 mg g-1 day-1
0.3 mg g-1 day-1
CO2 flux (µg CO2 g-1 hr-1)
Day









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

- CO_2 production increased at higher C input rates.
- CH_4 production was generally inhibited at higher C input rates.
- Acetate additions were associated with highest CH_4 production.
- Redox potential and pH showed concentration and composition dependent responses.