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## EFFECTS OF CARBON SUBSTRATE LABILITY ON TROPICAL PEAT MINERALIZATION UNDER AEROBIC AND ANAEROBIC CONDITIONS

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### SUMMARY

Extensive draining at tropical ombrotrophic peatlands in Southeast Asia has made them global ‘hot spots’ for greenhouse gas emissions. Here, we present the first data on how management practises affect carbon (C) mineralization processes at these soils. We compared the peat carbon mineralization potentials of pristine forest to those of drained fire affected soils, with and without additional labile substrates (glucose, glutamate and NO<sub>3</sub>- N) and in oxic and anoxic conditions by dedicated *ex situ* experiments. Carbon mineralization (CO<sub>2</sub> and CH<sub>4</sub> production) rates were higher in the forest peat, which contains more labile C due to higher input via vegetation. Production rates decreased with depth in peat profile together with decreasing availability of labile carbon. Consequently, the increase in C mineralization rates after labile substrate addition was relatively modest from forest site as compared to the reclaimed site and from the top layers as compared to deeper layers. Methanogenesis had little importance in total carbon mineralization. Surprisingly, oxygen availability was not an ultimate requirement for substantial CO<sub>2</sub> production rates. Flooding of these sites will therefore reduce, but not completely cease, peat carbon loss. Reintroduced substantial vegetation and fertilization in degraded peatlands can enrich recalcitrant peat with simple C and N compounds and thus increase microbiological activity. This outcome reinforces the importance of decomposition-resistant litter types and sufficient litter allocation in the maintenance of ombrotrophic tropical peat carbon store regardless of the land management type.

**Keywords:** *anoxia, decomposition resistance, land use, labile carbon*

### INTRODUCTION

The fate of dead organic matter in tropical peatlands, like in any ecosystem, depends on the amount and characteristics of deposited litter and on the microbial community decomposing the substrate. Temperature, moisture and oxygen availability are recognized as important decomposition process controls in tropical peat (Adjie *et al.*, 2014; Jauhainen *et al.*, 2014), but the position of the groundwater table (GWT) is a simplified environmental factor mostly applied to explain gaseous emissions from peat decomposition (IPCC 2014).

Litter at the peat swamp forest is largely composed of woody debris, coarse and fine roots, and leaf litter. It is rich both in cellulosic and more complex ligneous substrates (Miyajima *et al.*, 1997). Close to the peat surface, where oxic conditions are most likely present, peat-forming organic polymers (litter) are largely decomposed in aerobic processes by bacteria and fungi. Lignin is more resistant to decomposition than cellulose (Harmon *et al.*, 2009). Over time, the proportion of decomposition-resistant organic substrates in the peat increases and these substrates are located for progressively longer periods in the water-saturated (anoxic) conditions further away from the surface (Harmon *et al.*, 2009). Deforested, drained and abandoned land is a common reclaimed tropical peatland (use) type, in which recurrent wildfires typically keep the vegetation biomass low and add on peat loss by progressively consuming topmost peat. Litter input rate is low in such degraded lands, and aerobic and anaerobic decomposition processes continue consuming aged (recalcitrant) peat materials resurfaced by fires. Litter in these replacement vegetation types (such as ferns) is typically formed from less decomposition-resistant substrates (e.g. Miyajima *et al.*, 1997; Yule and Gomez 2009).

There is demand for converting abandoned and degraded peat areas into active use. Substantial vegetation cover formed in successful reforestation in degraded peat will increase labile C input rates from the root systems, and a start of N fertilization increases markedly labile N availability in cropping lands and plantations. Increase in control over peat water tables will likely alter unsaturated peat profile O<sub>2</sub> conditions compared to peatlands in abandoned conditions.

We established *ex situ* microcosm experiments to provide the first data on tropical peat decomposition rates

under controlled oxic and anoxic conditions with differing labile C and N availability. Peat from undrained peat swamp forests represents the original land use and peat from clear-felled, drained, burned landforms the opposing extreme in converted land use types. Samples were taken from close to the peat surface (often facing oxic conditions), from variably water-saturated conditions, and from deeper layers that is typically water-saturated, anoxic environment.

## METHODS

Our study sites were in the upper catchment of Sabangau River, 20 km southeast of Palangka Raya city in Central Kalimantan, Indonesia. Sampling sites included undrained peat swamp forest (PF) and clear-felled, drained, fire affected degraded land (DL). We chose three vegetation-free subplots at the sampling sites from typical low surfaces along microtopography at about 20-m distances for the study. Possible recently deposited leaf litter on the top of surface was removed and peat samples were collected from 0–10 cm, 20–30 cm and 100–130 cm depths.

In the laboratory, all visible live root materials were removed from peat. Peat heterotrophic gas production and closed headspace gas composition were monitored in microcosm environments. A setup of microcosms and gas chromatograph (GC) was prepared for conducting the experiments. A robotized GC facilitated the high-frequency analyses of CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, NO, N<sub>2</sub> and O<sub>2</sub> of each sample headspace. Gas concentration analytics was conducted using the GC (Model 7890A, Agilent), equipped with 20-m wide-bore Poraplot Q column, 30-m 5Å mole sieve, 2 HayeSep columns for backflushing water, a thermal conductivity detector (TCD), an electron capture detector (ECD), a flame injection analyzer (FID) and a NO chemiluminescence analyzer. Gas samples (2 ml) were taken with an autosampler, and fed with a peristaltic pump to sampling loops further proving the GC (0.25 ml loop) and the NO-analyser (0.5 ml). For further details of the incubation system, please see Molstad *et al.* (2007). During laboratory incubation and analysis, the vials were held at laboratory temperature at ~ 22 °C or standing in a water bath at 25 °C. For the gas production rate calculations, CO<sub>2</sub> and CH<sub>4</sub> data was divided into condition sequences found in the headspace, e.g., during and after O<sub>2</sub> or NO<sub>x</sub> reduction.

Experiment A – C mineralization in sudden anoxic conditions. Peats in this experiment describe the soil microbiological functions without added C or nutrients. The experiment was conducted in sudden anoxic conditions in order to simulate conditions where O<sub>2</sub> depleted from peat. Approximately 8 g of field-moist peat was added into a 120-ml vial, which was filled with water to 50 ml, and sealed by butyl-rubber stopper with an aluminium seal. O<sub>2</sub> was removed from the vials by repeated evacuation and helium-flushing, and a replicate set was also amended with 10% C<sub>2</sub>H<sub>2</sub> for separately reported denitrification dynamics and N<sub>2</sub> production (*report in prep.*). The data obtained from the replicate C<sub>2</sub>H<sub>2</sub>-amended samples was used in this study to determine the accurate point where CO<sub>2</sub> production by denitrification ceased. Incubation lasted 145 hours, and gas concentrations were monitored at 5-hour time intervals.

Experiment B – Impact of nitrate addition on C mineralization. We determined the peat respiration dynamics in optimal NO<sub>3</sub><sup>-</sup> concentrations over time in peat slurries where oxic conditions develop into anoxic conditions. Approximately 8 g of field-moist peat was set into a 120-ml glass vial and KNO<sub>3</sub> was added to reach a 0.1 mM NO<sub>3</sub><sup>-</sup> concentration. The applied concentration of 0.1 mM NO<sub>3</sub><sup>-</sup> (given as KNO<sub>3</sub>) was based on the optimal level for achieving maximum denitrification rates in anoxic conditions in surface and deeper peat samples at both sites (*report in prep.*). The vials were filled to 40 ml with water and sealed. Each vial was evacuated and washed thoroughly with helium to remove O<sub>2</sub> and N<sub>2</sub> from the peat and the vials were supplemented to 0.25% O<sub>2</sub> in the headspace, and a set of replicate samples was also amended with 10% C<sub>2</sub>H<sub>2</sub>. Incubation lasted 44 hours and gas concentrations were monitored in 3-hour time intervals.

Experiment C – Impact of labile C and NO<sub>3</sub><sup>-</sup>-N addition on C mineralization. This experiment studied how heterotrophic CO<sub>2</sub> production benefits from C addition in the presence of added NO<sub>3</sub><sup>-</sup>-N in oxic and anoxic conditions. The slurry experiment was conducted with added glucose or glutamic acid, such that the amount of added C on sample DW basis was equal in both treatments. This experiment included peats from the top and deepest sampling depths in both sites. Approximately 8 g of field-moist peat was set into a 40-ml glass vial. Glucose or glutamate (as sodium glutamate) was added to reach an added 20% C concentration on g g<sup>-1</sup> DW basis in each vial. All vials were supplemented with 0.1 mM NO<sub>3</sub><sup>-</sup> on g g<sup>-1</sup> DW basis, filled to 40 ml with water, and sealed. Two sets of vials were prepared, half of which were supplemented with 0.25% O<sub>2</sub> and used for studying gaseous C dynamics, and the other half with 10% C<sub>2</sub>H<sub>2</sub> in addition to O<sub>2</sub>. Incubation lasted 67 hours and gas concentrations were monitored at 3.5-hour time intervals.

## RESULTS

Anaerobic CO<sub>2</sub> production rates from peat decomposition in anoxic conditions (Experiment A) were fastest in the upper peat layers, and the forest peat CO<sub>2</sub> production rates from all three depths were higher in comparison to the

rates of degraded land peat (Table 1). CO<sub>2</sub> accumulated linearly in the degraded land peat slurries, whereas an increase in peat CO<sub>2</sub> production after the reduction of NO<sub>x</sub> at 20 hours (N dynamics *in prep.*) was very pronounced in the forest top peat. Peat samples from both sites showed clearly lower peat anaerobic respiration rates at the deepest sampling depth than in the peat layers above. After the reduction of nitrogen oxides, CO<sub>2</sub> production rates were fastest in the two upper forest peat layers and the slowest in the two deepest degraded land peat layers. The lowest forest peat layer produced CO<sub>2</sub> approximately as fast as the top layer of the degraded land. The CO<sub>2</sub> production in the top forest peat was 6.5 × higher than that in the degraded land top peat. Peat CH<sub>4</sub> production was generally smaller than CO<sub>2</sub> production, also in the sudden anoxic conditions (Table 1). Methane production in the slurries without added substrates showed a very clear vertical distribution as the CH<sub>4</sub> production was highest in the top peat and decreased with sampling depth in the peat profiles. The average CH<sub>4</sub> production rate in the top forest peat was *ca.* 400 × faster in comparison to the rate in the degraded land top peat layer, whereas the slow CH<sub>4</sub> production rates in the two deepest forest peat layers were relatively close to values in all peat layers of degraded land.

Table 1: Forest (PF) and degraded land (DL) peat CO<sub>2</sub> and CH<sub>4</sub> production rates (Ave±SE, N = 3) during the main gas sphere conditions for respective depths between the sites, and numbers for various phases in gas space conditions) within the experiment.

Experiment	Site and depth	CO <sub>2</sub> production rate ( $\mu\text{g g}^{-1}\text{DW h}^{-1}$ )		CH <sub>4</sub> production rate ( $\mu\text{g g}^{-1}\text{DW h}^{-1}$ )	
		During reduction of	During reduction of	After reduction of NO <sub>x</sub>	After reduction of O <sub>2</sub>
No amendments	PF (0–10 cm)	--	1.583±0.304	5.885±1.217	1.93 <sup>2</sup> ±0.78 <sup>2</sup>
(Experiment A)	(20–30 cm) PF	--	0.876±0.078	1.730±0.433	5.92 <sup>4</sup> ±3.83 <sup>4</sup>
Optimal NO <sub>3</sub> <sup>-</sup>	(100–130 cm)	--	0.464±0.035	0.888±0.043	7.91 <sup>6</sup> ±3.54 <sup>6</sup>
(Experiment B)	DL (0–10 cm)		0.786±0.120	0.898±0.146	4.59 <sup>5</sup> ±0.83 <sup>5</sup>
Optimal NO <sub>3</sub> <sup>-</sup> and glucose	DL (20–30 cm)		0.398±0.181	0.327±0.138	2.11 <sup>5</sup> ±1.09 <sup>5</sup>
(Experiment C)	DL (100–130)		0.215±0.069	0.224±0.077	1.54 <sup>5</sup> ±0.40 <sup>5</sup>
Optimal NO <sub>3</sub> <sup>-</sup> and glutamate	PF (0–10 cm)	9.345±0.593	2.368±0.227	—	1.15 <sup>3</sup> ±0.15 <sup>3</sup> —
(Experiment C)	DL (0–10 cm)	1.664±0.248	0.413±0.067	—	(*)
	PF (0–10 cm) PF	7.725±0.122 (**)	2.638±0.001	59.498±3.197	1.05·2±2.30·4 (*)
	(100–130 cm)	5.488±0.573	2.595±0.464	2.944±0.898	7.33 <sup>5</sup> ±1.05 <sup>5</sup>
	DL (0–10 cm)	4.206±1.293 (**)	1.373±0.324 (**)	1.042±0.606 (**)	5.45 <sup>5</sup> ±2.47 <sup>7</sup>
	DL (100–130)	5.355±0.413	2.341±0.840	0.870±0.052	2.24 <sup>4</sup> ±1.26 <sup>4</sup>
	PF (0–10 cm) PF	9.821±0.874 (**)	2.922±0.319	3.499±0.312	3.10 <sup>2</sup> ±0.07 <sup>2</sup>
	(100–130 cm)	3.044±0.271	0.744±0.047	—	3.75 <sup>5</sup> ±2.05 <sup>5</sup>
	DL (0–10 cm)	3.520±0.061	1.746 (10 (**))	1.082±0.332	6.62 <sup>5</sup>
	DL (100–130)	6.572±0.359	2.890±1.306	0.470±0.030	—(*)

(\* Non-detectable amount of CH<sub>4</sub> produced, (\*\* Only 2 samples, (\*\*\*O<sub>2</sub> and NO<sub>x</sub> were exhausted simultaneously in 2 sample series.

Nitrate addition on C mineralization resulted in relatively small differences in the top peat layer CO<sub>2</sub> production rates supplemented with 0.1 mM NO<sub>3</sub><sup>-</sup> and set to developing anoxic conditions (Experiment B) when compared with the rates in respective peats without added substrates set in sudden anoxic conditions (Experiment A) (Table 1). The CO<sub>2</sub> production rate in the top forest peat with added NO<sub>3</sub><sup>-</sup> was nearly 2 × faster after O<sub>2</sub> reduction than the rate in sudden anoxic conditions, but the production rate in the degraded land peat with added NO<sub>3</sub><sup>-</sup> and developed anoxic conditions was only approximately half of the rate detected in sudden anoxic conditions. CH<sub>4</sub> production in degraded land peat remained practically non-existent in samples supplied with NO<sub>3</sub><sup>-</sup>. Labile C (glucose and glutamate) combined with the NO<sub>3</sub><sup>-</sup>-N addition (Experiment C) resulted in higher peat CO<sub>2</sub> production rates in most samples compared to rates in the peat without added substrates (Experiment A) (Table 1). Proportionally the highest difference in peat CO<sub>2</sub> production rates between the peats with and without added substrates occurred in the deepest sampling depth, where the CO<sub>2</sub> production rates were from 2.1 to 13.4 × faster in degraded land peat and 1.6 to 5.6 × faster in forest peat during and after the NO<sub>x</sub> reduction stages. Glucose and NO<sub>3</sub><sup>-</sup> addition to forest top peat resulted in the maximum CO<sub>2</sub> production rate found in the present study (59.5 ± 3.2  $\mu\text{g g}^{-1}\text{h}^{-1}$  in the ‘post-NO<sub>x</sub> reduction stage’) and this rate was 10 × faster than the respective rate in peat without added substrates. Both forest land top peat CO<sub>2</sub> production rates in labile C and N-supplemented samples were otherwise quite close, i.e., with a maximum of 1.7 × faster, to the CO<sub>2</sub> production rates detected in peat without added substrates. CO<sub>2</sub> production rates in degraded land top peat supplemented with glutamate was 2.1 × faster than the rate in peat without added substrates. The highest impacts of glucose and glutamate additions on CH<sub>4</sub> production were apparent in the two deepest peat layers. Glucose addition to the deepest layer resulted in a 9.2 × faster CH<sub>4</sub> production rate in forest peat and a 14.6 × faster rate in degraded land peat in comparison to rates detected in peat slurries without added substrates (Table 1). Comparatively, the glutamate addition yielded a 4.7 × faster CH<sub>4</sub> production rate in the forest deepest peat. CH<sub>4</sub>

production rates in top peat layers for both sites remained similar both without added substrates and with added labile C and N.

## DISCUSSION

Forest top peat (without added substrates) expressed the highest CO<sub>2</sub> production potential in both oxic and anoxic conditions and the highest CH<sub>4</sub> production potential in anoxic conditions. In peat swamp forests, tree dominated vegetation continuously deposits senesced leaves, and coarse and fine woody debris onto the peat surface and into the rooting zone. This recently deposited litter is rich in both cellulosic and complex lignous structural substrates (Miyajima *et al.*, 1997), but decomposition-resistant lignin-rich substrates increase proportionally downwards in the peat profile due to faster depletion of more simple cellulosic compounds (Harmon *et al.*, 2009). In peats from this forest site, holocellulose content on DW basis decreased from 10% in the topmost peat to 2% at 80 cm depth and Klason lignin content increased from 68% to 72%, respectively (see Könönen *et al.* this volume). Our results from the forest site support these findings in substrate composition as peat samples already from a depth of 20–30 cm below the forest floor surface resulted in clearly lower CO<sub>2</sub> and CH<sub>4</sub> production potentials, and even more so at the deepest peat sampling depth.

In clear-felled burned peatland, the lack of notable recent carbon inputs, recurrent fires and mineralization have created conditions where the content of relatively easily decomposable carbon substrates is low in the surface peat, and this was largely supported by the GHG production rate results. Therefore, the fastest CO<sub>2</sub> and CH<sub>4</sub> production rates in degraded land peat (without added substrates) in all three sampling depths were comparable with the values for the two lowest peat layers of the forest site. Klason lignin content of 76–82% in degraded land peat is higher than the highest content in forest peat (max. 72%) in peat profile down to the permanently water-saturated peat, and the topmost peat holocellulose content of 1% on DW basis in degraded land is only a fraction of the content (10%) in topmost forest peat (see Könönen *et al.* this volume). It is striking that the anaerobic CO<sub>2</sub> production (and CH<sub>4</sub> production) decreases rather than increases with depth in degraded land. This could be explained by microbial adaptation and differences in preferred carbon donor, where denitrifiers, Fe<sup>3+</sup> & Mn<sup>4+</sup> & SO<sub>4</sub><sup>2-</sup> reducers and methanogens may not be able to oxidize some C compounds that are easily decomposable by aerobic respiration. Alternatively, anabolic and catabolic metabolism could be limited by other nutrients besides carbon or by the electron acceptor rather than the donor.

Both of the abovementioned assumptions are supported by the results from the slurry Experiment C where the addition of nitrate together with glucose and glutamate increased anaerobic CO<sub>2</sub> production slightly in the top peat but by several times in the deepest peat layer samples from both sites. Labile C addition in anoxic conditions in degraded land peat enhanced CO<sub>2</sub> production practically only in the deepest peat layer, which suggests that the microbial community in the degraded land surface peat is able to process labile C in anoxic conditions and produce CO<sub>2</sub> when such substrates become available. Experiment C showed that deeper peat layers lack labile C and N substrates and thus CO<sub>2</sub> (and CH<sub>4</sub>) production can increase due to increase in available substrates. In Experiment C, where CO<sub>2</sub> (and CH<sub>4</sub>) production rates of deepest layer peats in both sites (representing the aged materials protected from oxic conditions) were enhanced in the presence of labile C and N sources compared to the respective rates in peat without added substrates. Varying GHG production responses in more heterogenic forest top peat may be a result of proportionally modest experimental labile substrate addition (in experiment C) in comparison to concentrations of comparable substrates readily contained in the samples. Labile C (glucose and/or glutamate) together with nitrate addition increased CH<sub>4</sub> production only in the deepest peat layers at both sites. The modest CH<sub>4</sub> production difference between labile C-supplemented peat and peat without added substrates in the forest top peat layer implies that the forest surface peat has the highest potential for CH<sub>4</sub> production (among the studied peats) in anaerobic conditions, that is likely typical condition at both sites during wet season. Hardwood lignin compounds can partially degrade under anoxic conditions, and the decomposition potential in such substrate remains low (Arai *et al.*, 2014). High Klason lignin content in the studied peats (see Könönen *et al.* this volume) partly explains slow CH<sub>4</sub> production rates. In degraded land top peat, CH<sub>4</sub> production rates in anoxic conditions differed modestly which likely indicates a low capacity of the methanogenic population in the surface peat. In contrast, comparable CH<sub>4</sub> production rates of the deepest sampled peat in both sites with added labile C can be regarded a sign of preserved comparable methanogenic populations despite of the difference in land management type.

In developing anoxic conditions (Experiments B and C), CO<sub>2</sub> production rates in slurries were generally fastest in the presence of O<sub>2</sub> (during the O<sub>2</sub> depletion stage) and later the rates became proportionally smaller in anoxic conditions. Unexpectedly, CO<sub>2</sub> production rates remained at a notable level in anoxic conditions. The percent decrease (%-change) in the CO<sub>2</sub> rates from oxic to anoxic conditions was 46–76% in forest deep peat, 66–72% in forest top peat (excluding the even higher rate change in the case of glucose addition), 52–77% in degraded land top peat and 56–93% in degraded land deep peat, respectively. A large disproportion between the CO<sub>2</sub> and CH<sub>4</sub> emission rates in anoxic conditions in the present study peats (with and without added substrates) suggest that CH<sub>4</sub> production from acetate is probably not a notable contributor to CO<sub>2</sub> production in anaerobic conditions. CO<sub>2</sub> production in low O<sub>2</sub> availability could be explained by the accumulation of fermentative low-molecular-weight

alcohols and acids and subsequent oxidation coupled with the reduction of inorganic terminal electron acceptors, such as  $\text{NO}_3^-$ ,  $\text{Mn}^{4+}$ ,  $\text{Fe}^{3+}$ , and  $\text{SO}_4^{2-}$  (e.g., Lipson *et al.*, 2010; Corbet *et al.*, 2015), or humic substances in water could also form both a suitable energy source and an organic electron acceptor in anoxic conditions (Kane *et al.*, 2013).

## CONCLUSION

This study indicated that substantial organic matter decomposition occurs in both oxic and anoxic conditions in tropical peat. Although flooding the soil surface can potentially reduce peat C loss, it cannot completely inhibit it because decomposition-producing  $\text{CO}_2$  and  $\text{CH}_4$  can continue in anoxic conditions. This outcome strengthens the importance of vegetation in regulation of peat carbon storage as it forms the only peat matter adding source both in undrained and drained conditions. Decomposition potential in degraded peat substrate persists although continued reduction in deposited litter amount and recurrent fires can lead to decrease in GHG production from the surface peat. Both aerobic and anaerobic decomposition processes in such aged and decomposition-resistant peat can be induced by an increase in available labile C and N substrates. Change from open and degraded peatlands to forested areas in ecological restoration and to plantations will likely enhance the heterotrophic C emissions from peat due to increases in rhizosphere productivity and labile N availability. These peat deposits are likely best secured by favouring anoxic conditions, which slow heterotrophic GHG release, and by maintaining high GWT and growing flood-tolerant tree species that deposit high amounts and proportions of woody litter below the peat surface.

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