Will CO2 Emissions from Drained Tropical Peatlands Decline Over Time? Links Between Soil Organic Matter Quality, Nutrients, and C Mineralization Rates

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Will CO₂ emissions from drained tropical peatlands decline over time? Links between soil organic matter quality, nutrients, and C mineralization rates

Shortened version: CO₂ production from tropical peat decomposition

Swails, E¹, Jaye, D¹, Verchot, L², Hergoualc’h, K³, Schirrmann, M⁴, Borchard, N³ ⁵, Wahyuni, N³, Lawrence, D¹

¹Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903,
²International Center for Tropical Agriculture, Km 17 Recta Cali-Palmira, Apartado Aereo 6713, Cali 763537, Colombia, ³Center for International Forestry Research, Jalan CIFOR, Situ Gede, Sindang Barang, Bogor 16115, Indonesia, ⁴Leibniz Institute for Agricultural Engineering and Bioeconomy, Max-Eyth-Allee 100, 14469 Potsdam, Germany, ⁵Ruhr-University Bochum, Institute of Geography, Soil Science/Soil Ecology, Universitätsstrasse 150, 44801 Bochum, Germany

Correspondence: Erin Swails, tel. +1 434 924 7761, e-mail: ees8rg@virginia.edu

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Abstract

Conversion, drainage, and cultivation of tropical peatlands can change soil conditions, shifting the C balance of these systems, which is important for the global C cycle. We examined the effect of soil organic matter (SOM) quality and nutrients on CO₂ production from peat
decomposition using laboratory incubations of Indonesian peat soils from undrained forest in Kalimantan and drained oil palm plantations in Kalimantan and Sumatra. **We found that oil palm soils had higher C:N and lower SOM quality than forest soils.** Higher substrate quality and nutrient availability, particularly lower ratios of aromatic:aliphatic carbon and C:N, rather than total soil organic matter or carbon, explained the higher rate of CO₂ production by forest soils (10.80 ± 0.23 µg CO₂-C g C hr⁻¹) compared to oil palm soils (5.34 ± 0.26 µg CO₂-C g C hr⁻¹) from Kalimantan. These factors also explained lower rates in Sumatran oil palm (3.90 ± 0.25 µg CO₂-C g C hr⁻¹). We amended peat with nitrogen (N), phosphorus (P), and glucose to further investigate observed substrate and nutrient constraints across the range of observed peat quality. Available N limited CO₂ production, in unamended and amended soils. **P addition raised CO₂ production when substrate quality was high and initial P state was low.** Glucose addition raised CO₂ production in the presence of added N and P. Our results suggest that decline in SOM quality and nutrients associated with conversion may decrease substrate driven rates of CO₂ production from peat decomposition over time.

**Introduction**

With estimated C stocks of 88.6 Pg C (Page et al., 2011), tropical peat soils comprise 19% of global tropical forest C stocks in an area that is roughly 1% of total tropical forest extent (Pan et al., 2011a). Indonesian peatlands hold an estimated one third of tropical peat soil carbon stocks (Gumbricht et al., 2017), but are a major and growing source of greenhouse gas emissions due to increasing pressure from agricultural uses, particularly the expansion of oil palm plantations (Hooijer et al., 2010; Koh et al., 2011; Miettinen et al., 2012). Conversion of tropical peat swamp forests to oil palm plantations usually entails emissions of CO₂, CH₄, and N₂O from
clearing and burning, while peat drainage generates additional and sustained CO$_2$ emissions from the decomposition of soil organic matter (SOM). By one estimate, development of existing government leases for oil palm in Kalimantan peatlands alone may contribute 18% (0.44-0.55 Gt CO$_2$-equivalent yr$^{-1}$) of Indonesia’s 2020 projected greenhouse gas emissions (Carlson et al., 2012).

Enhanced understanding of controls on peat decomposition is needed to reduce uncertainty in estimates of CO$_2$ emissions from tropical peat. Though CO$_2$ fluxes from peat soils are highly heterogeneous over space and time (Jauhiainen et al., 2005; Hirano et al., 2009, 2012), existing regional analyses rely on extrapolation of point-based flux measurements using land cover as a proxy for CO$_2$ emissions, applying for example IPCC emission factors (Drösler et al., 2014). These analyses do not directly consider the biogeophysical parameters influencing temporal and spatial variation in carbon emissions from peat. Among biogeophysical factors, water table depth is considered the dominant control on decomposition of tropical peat soils (Couwenberg et al., 2009). However, empirical evidence indicates that soil temperature and moisture influence mineralization of SOM in tropical peatlands (Hirano et al., 2007, 2009, 2012; Jauhiainen et al., 2008, 2014). The influence of SOM quality on decomposition as well as nutrients, specifically N and P, has been well documented in mineral soils (e.g. Haynes 1986; Hobbie and Vitousek 2000; Prescott 1995). These factors also affect spatial and temporal variability in decomposition of peat soils in boreal regions (Turetsky et al., 2000; Minkkinen et al., 2007; Sjögersten et al., 2016), temperate regions (Scanlon 2000; Schrier-Uijl et al., 2011; Juszczak et al., 2013), and tropical regions (Wright et al., 2011; Hoyos-Santillan et al., 2016), including Southeast Asia (Jauhiainen et al., 2016; Comeau et al., 2016).
In undrained mature tropical forests, peat SOM quality and nutrient content are determined by original bedrock material, climate, hydrological regime, and peat forming vegetation (Page et al., 1999; Wust & Bustin 2004; Dommain et al., 2011). Conversion of peat swamp forest to agricultural use alters peat SOM quality and nutrient content as a consequence of drainage, burning, and changes in litter and nutrient inputs in temperate (Heller et al., 2015) and tropical peatlands (Hirano et al., 2012; Jauhiainen et al., 2014; Könönen et al., 2015) (Figure 1). Increasing levels of disturbance in peatlands result in the loss of labile carbon and an increasing proportion of recalcitrant compounds in peat surface layers as well as depletion of N, P, and K (Könönen et al., 2016). Thus conversion of tropical peatlands to oil palm plantations may influence in situ rates of CO₂ production from microbial decomposition of peat by altering the quality of peat substrate available for decomposition.

Field based studies (e.g. Comeau et al., 2016) cannot easily separate physical drivers from chemical and biological controls on peat decomposition. To date, ex situ studies of CO₂ production by tropical peats have largely focused on forested peatlands (e.g. Wright et al., 2011; Jauhiainen et al., 2016; Hoyos-Santillan et al., 2016) and disregarded oil palm plantations. This ex situ study addresses gaps in knowledge of controls on microbial decomposition in undrained and drained tropical peat soils. Specifically, we investigated the influence of variation in SOM quality and nutrient availability on CO₂ production in peat from forests and oil palm plantations. Our study included soils from undrained peat forest and drained smallholder oil palm plantations on shallow peat (< 3 m) in Kalimantan and industrial oil palm plantations on deep peat (> 7 m) in Sumatra. Smallholder plantations are an important and growing source of palm oil production in Indonesia, accounting for 40% of total oil palm area (BPS 2015), and roughly a third of national production (Obidzinski et al., 2012). The geographic range and management variability in our
study allowed us to investigate a wide range of peat quality comparable to that observed in forested peatlands and oil palm plantations across Indonesia (Table 1).

We designed our experiments to test the hypothesis that CO$_2$ production from microbial decomposition of peat decreases with decreasing substrate quality (as measured by SOM quality and C:N ratio) and nutrient availability. In the course of the study, we asked three questions: (1) How do peat substrate quality and nutrient availability vary among our sites? (2) Does variation in substrate quality and nutrient availability explain variation in CO$_2$ production? And (3) does CO$_2$ production respond to the addition of labile carbon and nutrients?

To investigate the influence of variation in substrate quality and nutrients on CO$_2$ production, we conducted laboratory incubations. Observing significant relationships in unamended soils, we also conducted incubations of peat treated with N, P, and glucose to further explore relationships among SOM quality, nutrient availability, and CO$_2$ production. Given the stoichiometry of microbial biomass, N and P addition should increase C mineralization over the short term, though increased N availability may decrease mineralization of recalcitrant C over the long term (Moorehead and Sinsabaugh 2006; Craine et al., 2007). With short incubations, we address effects on the more labile C pool in soil samples.

**Materials and methods**

**Site description**

We collected peat samples at two sites in Kalimantan (S 02° 49.410’, E 111° 48.785’) and one site in Jambi, Sumatra (S 01°38.456’, E 103°54.335’, Figure 2). We sampled undrained peat forest and smallholder oil palm plantations in Central Kalimantan Province, approximately 10 km from the city of Pangkalan Bun, in and around Tanjung Puting National Park. Sumatra peat samples were collected from an industrial oil palm plantation near Berbak National Park,
approximately 20 km from the city of Jambi. The climate of the region is humid tropical, with little variation in temperature throughout the year and high annual rainfall. We used monthly mean weather observations from Iskandar airport in Pangkalan Bun and Sultan Thaha airport in Jambi during 2005-2014 to describe climate at the sampling sites. Mean annual temperature in Pangkalan Bun is 27.4°C. Mean annual rainfall is 1808 mm and September is typically the driest month (85 mm). In Jambi, mean annual temperature is 27.1°C. Mean annual rainfall is 1846 mm with the driest month (115 mm) typically occurring in June.

At each site, we collected samples from three plots that were 1-10 km apart. The plots represent a range of land use history and peat depth, as summarized in Table 2. Oil palm plantation age ranged from four to eight years at the Kalimantan site and from five to ten years at the Sumatra site. Kalimantan forest plots were situated at varying distances from the edge of the main stem of the river surrounding the peat dome and thus differed in peat depth (Table 2).

Information on land use history at the Kalimantan sites was based on interviews with smallholder plantation owners. The plot closest to the river (K-FOR-1) was a 30 year old secondary forest, likely formerly used as an agroforestry garden at the time Tanjung Puting National Park was established (Novita 2016), whereas the other two forest plots (K-FOR-2, K-FOR-3) were mature forest. Vegetation height and basal area was similar among the three sites, but K-FOR-1 had lower species diversity and evenness than K-FOR-2 and K-FOR-3, indicative of forest succession at K-FOR-1 (Novita 2016).

Smallholders began planting oil palm on their lands in the late 2000s, following the establishment of an industrial oil palm plantation adjacent to smallholder properties in the late 1990s. Part of the smallholder properties had been deforested, burned, and drained in 1989, undergoing several cycles of burning, cropping with rice and vegetables, and fallow before the
establishment of oil palm. To maintain drained conditions smallholders excavated small canals in the cultivated area of peat. In this area cleared in 1989, we installed one plot in a plantation established in 2011 (K-OP-2011). Another area was cleared in 2005 and also underwent cropping with rice and vegetables, likely experiencing multiple fires prior to the establishment of oil palm. We installed a second plot in this area where palm was planted in 2009 (K-OP-2009) and a third plot where palm had been established in 2007 (K-OP-2007). Information on land use history at the Sumatra sampling site was obtained from company authorities. The area included in our study was cleared in 2004 by the company and planted with oil palm in 2005 (S-OP-2005), 2007 (S-OP-2007), and 2010 (S-OP-2010).

Kalimantan smallholders implemented plantation management practices comparable to those implemented in the Sumatran industrial plantations. Smallholders worked at the nearby oil palm company and followed the company’s management practices. At both Kalimantan and Sumatra sites, palms were planted in a triangular design with inter-palm distance of 7-9 m (averaged 8m) for a density of 150 palms ha\(^{-1}\). Smallholders concentrated fertilizer application within a 200 cm radius of palms, applying controlled release fertilizer at a rate of 150 kg ha\(^{-1}\) yr\(^{-1}\) of N, 84 kg ha\(^{-1}\) yr\(^{-1}\) P, and 124 kg ha\(^{-1}\) yr\(^{-1}\) K in the youngest plantation (K-OP-2011) decreasing to 120 kg ha\(^{-1}\) yr\(^{-1}\) of N, 67 kg ha\(^{-1}\) yr\(^{-1}\) P, and 100 kg ha\(^{-1}\) yr\(^{-1}\) K in the oldest plantation (K-OP-2007). Fertilization rates for K-OP-2009 were not provided by smallholders. Fertilizer was usually applied four times per year in smallholder plantations, but the actual frequency of fertilization depended on available funds. In Sumatran industrial plantation with older vegetation straight fertilizers were applied two times per year (urea, muriate of potash, rock phosphate, CuSO\(_4\), ZnSO\(_4\), CaCO\(_3\), borate) which is standard practice for mature plantations Southeast Asia (Lim et al., 2012). Average drainage depth at the Sumatra site (-60 cm, Oktarita et al., 2017) was
Oil palm plots underwent single or multiple fires at both sites (Table 2).

**Soil sample collection**

We sampled the peat surface layer to assess the region of the soil column with maximum rates of C mineralization. Active carbon cycling in undisturbed tropical peat swamp forests is largely confined to the upper layer of peat soils. Sporadic aerobic conditions occur there and litterfall and roots transfer fresh organic material to the soil (Moore et al., 2013). Though drainage for oil palm is typically around 40 cm or deeper (Lim et al., 2012), root density and microbial activity is usually highest closer to the soil surface (Khalid et al., 1999, Goodrick et al., 2016).

In June of 2015, we collected the samples for incubations and chemical analysis from the peat surface layer (0-5 cm) using stainless steel bulk density rings (8 cm in diameter). Samples from each plot were taken at three within plot locations separated by 10-20 m. In oil palm plots, samples for incubation were collected along four transects emanating from one oil palm per location (Figure 2c). The transects ran in randomly determined directions between 0° – 90°, 90° – 180°, 180° – 270°, and 270° – 360°. Four samples were collected from each transect at randomly determined distances 1 – 2 m, 2 – 3 m, 3 – 4 m, and 4 – 5 m from the base of the palm. Total transect length covered roughly half the distance between the palm and its nearest neighbors. Similarly, in forest plots, transects originated from one tree per location at three within plot locations. Due to lower bulk density and higher water content of forest soil, two soil samples were drawn from each distance interval to yield an adequate dry mass of soil. Soil sampled along the four transects at each location were composited to yield one soil sample per location (n = 3 per plot). The samples were transported in plastic bags to the laboratory then air dried for 72 hours followed by manual root removal and storage at 4°C. A subsample of each composite was
These subsamples were air dried for an additional 4 days, followed by sieving to < 2 mm, manual removal of remaining small roots, and storage in sealed plastic bags. Finally, bulk density was determined from replicate samples taken alongside samples for incubation and soil chemistry. Samples were weighed in the field, transported in plastic bags, and oven dried to constant mass at 60°C (Warren et al., 2012). Soil collection was completed within three weeks, under dry climatic conditions.

Analysis of soil chemical properties

Analysis of total C and N content was conducted at the University of Virginia by dry combustion using a Thermo Scientific Flash 2000 CHNS/O analyzer. We also measured SOM content by loss on ignition at 500°C for 180 minutes. Analysis of available N (NO$_3^-$ and NH$_4^+$) (1 N KCl cadmium reduction) and available P (Bray II) was carried out by Brookside Laboratories, New Bremen, Ohio. Brookside also conducted measurement of pH (1:1 in H$_2$O) on samples collected from plots in July of 2014 (Swails et al., unpublished data). All analysis was conducted on air-dry soils except for total C and N determination for which soils were oven dried at 60°C to constant weight. All results are presented on an oven-dry basis.

Collection of Vis-NIR spectra

Visible to near infrared (Vis-NIR) spectroscopy detects absorbance of incident radiation at wavelengths corresponding to specific functional groups present in SOM, enabling rapid and cost-effective analysis of SOM quality compared to conventional soil analysis (Stenberg et al., 2010; Gholizadeh et al., 2013). This approach has successfully been used to detect levels of aromatic and aliphatic carbon compounds in soils and litter material (Terhoeven-Urselmans et al., 2006). We collected Vis-NIR spectra within the wavelength range 350 – 2500 nm on air-dried peat samples spread on petri dishes with a FieldSpec FR post dispersive spectrometer at the
Center for International Forestry Research in Bogor, Indonesia. Samples were illuminated by a DC lamp adjusted to 24° beam angle (Rodionov et al., 2014). A fiber optic probe placed 5 cm above the surface gave an optical scanning field with 3.8 cm diameter (Rodionov et al., 2014). In order to increase signal to noise ratio, we averaged three repeated measurements on each peat sample to generate one spectrum per sample. Absorbance spectra were obtained for all peat samples (three locations for each of three plots at three sites, n = 27). We removed baselines from the 27 absorbance spectra with the asymmetric least squares method implemented in the R package ‘baseline’ (Eilers & Boelens, 2005). Using the baseline corrected spectra, we quantified peak height at wavelengths associated with specific functional groups of interest. To facilitate visual inspection of the spectra absorption peaks that were indicative of soil matter composition and chemical structure, the spectra of the three plot locations were averaged to yield one representative baseline corrected spectra per plot (n=9). To distinguish specific wavelengths associated with functional groups of interest, we computed 1st derivatives of the spectra using the Savitsky-Golay filter (Savitsky & Golay, 1964).

While humic acids (600 nm), phenols (990 nm), lignin (2270 nm), cellulose (2270, 2330 nm), starches and sugars (2100nm), and clays (2200 nm) can be detected from Vis-NIR spectra (Shenk et al., 1992, Workman & Weyer 2008, Wight et al., 2016), we focused on aromatic and aliphatic hydrocarbons. The ratio of the two is indicative of the state of decomposition of the soil organic matter. A higher aromatic:aliphatic ratio is indicative of a higher proportion of recalcitrant SOM, which Haberhauer et al. (1998) and Ernakovich (2014) related to a more advanced state of decomposition in boreal peats. The absorption peak around 1730 nm is indicative of aromatic functional groups, while the adjacent peak around 1760 nm is associated with aliphatic carbohydrates as is the peak around 1200 nm (Workman & Weyer 2008). We
derived indices by dividing peak height at 1730 nm by peak height at 1760 nm (aromatic:aliphatic I) and 1200 (aromatic:aliphatic II). We expected higher ratios in more highly decomposed soils, and we expected lower rates of CO$_2$ production from those soils.

**Incubation without amendment**

The purpose of the first incubation was to determine the effect of differences in peat properties on CO$_2$ production across the range of land history and management conditions represented by oil palm and forest plots at the three sites. Both soil moisture and temperature were uniform across treatments, however, soil moisture was fixed while air temperature was allowed to vary with ambient temperature in the laboratory. Prior to incubation, the moisture content of air dried compositied soil samples was determined by weighing subsamples before and after oven drying at 60$^\circ$C for 48 hours (constant mass). Soils were brought to the target moisture level by adding deionized (DI) H$_2$O and maintained at that level with further additions throughout the experiment. The target gravimetric soil moisture level was 2 g DI H$_2$O / g oven dry soil. This value falls within the typical range of soil moisture measured from Jan 2014 to Jun 2015 in the oil palm plantations in Kalimantan (1.5 - 3.8 g DI H$_2$O g oven dry soil$^{-1}$, Swails *et al.*, in preparation).

Following initial soil moisture adjustment, we placed subsamples of approximately 20 g oven dry equivalent mass in 500 ml jars fitted with two one-way stopcock valves. Jars (3 sites * 3 plots * 3 locations * 3 reps = 81) were capped and soils allowed to equilibrate for 24 hours prior to the first measurement. The concentration of CO$_2$ and atmospheric pressure in each jar was measured with a PP Systems brand Infrared Gas Analyzer (IRGA) at 0, 1, 2, and 3 hours after capping. We followed this 4-hour sampling procedure again after 8, 24, 48, 96 and 168 hours (day 7). Jars were uncapped at the beginning of each measurement period to allow mixing.
of headspace with ambient air to draw down headspace CO$_2$ concentration. Jars remained closed between measurement periods.

Air temperature was recorded with a Weatherhawk mini-station placed in the same room with the incubation jars; it varied from 27.5 to 31.7$^\circ$C when measurements were being taken. Soil moisture was monitored by measuring the combined weight of each jar and subsample at the beginning of the incubation and at each measurement period. Mean moisture over the experiment (1.90 ± 0.12 g H$_2$O g d.m.$^{-1}$) remained close to the target of 2 g H$_2$O g d.m.$^{-1}$ with small but significant differences among jars from different locations within plots. After the last CO$_2$ measurement period, the final weights of jars and subsamples were recorded. Subsamples were oven dried to determine final soil moisture content and jar headspace volume was measured.

**Incubation with N, P and glucose amendment**

To further explore constraints on CO$_2$ production observed in the incubation of native soils, we next amended soils with N and P (NP experiment) and with glucose with and without N and P (NPG experiment). Physical limitations of our measurement approach prevented us from including all nine plots in the experiments with nutrient and labile carbon additions. The number of samples would have been too large to complete the first and second set of measurements in a timely manner so as to capture transient effects of amendment on CO$_2$ production. Therefore we used a subset of plots which included the 8-year old plantations in Sumatra and Kalimantan (S-OP-2007 and K-OP-2007) and one of the mature peat swamp forest plots in Kalimantan (K-FOR-3). By using one plot from each site, we were able to include the range of variation in soil substrate quality and nutrient availability represented by our three sites. We followed the same protocol used previously with some modifications. We incubated an equivalent of 15 g oven dry mass in the NP experiment and 20 g oven dry mass in the NPG experiment. Samples were
allowed to equilibrate for 48 hours prior to treatment. Treatments were added in 1 ml solution in the NP experiment and 3 ml solution in the NPG experiment. Controls received a volume of DI H₂O equal to treatments in both experiments. Target gravimetric soil moisture for both experiments was 2 g DI H₂O g d.m.⁻¹.

For the NP experiment, two subsamples from each location in each plot were randomly assigned as replicates to one of five treatments (3 plots * 3 locations * 5 treatments * 2 replicates = 90 samples): high N, low N, high P, low P, and control (DI H₂O). Low N treatment received 0.5 mg ammonium nitrate (NH₄NO₃) per g d.m. peat, a level equivalent to a single dose of 50 kg N ha⁻¹ to the top 10 cm of soil within a 2 m radius of a palm. This level is representative of N fertilization in Sarawak for adult oil palms growing on peat applied twice a year at a rate of 100 kg N ha⁻¹ year⁻¹ (Melling et al. 2007). N fertilizer application rates are comparable in Indonesia (102 – 170 kg N ha⁻¹ year⁻¹, Darmosarkoro et al., 2003) though lower rates of N application of 60 – 70 kg ha⁻¹ yr⁻¹ have also been reported (Marwanto & Agus, 2014; Comeau et al., 2016). In mature industrial plantations, the fertilization rates are typically based on leaf analysis (Lim et al., 2012). Low P treatment received 0.7 mg disodium phosphate (Na₂HPO₄) per g d.m. peat, equivalent to a single application of 75 kg rock phosphate ha⁻¹ to the top 10 cm of soil (or 0.5 kg rock phosphate per palm considering a palm density of 150 palms ha⁻¹). This dose is representative of P fertilization for plantations in Southeast Asia (Lim et al., 2012). High N and high P treatments received rates 10 times higher than low N and P treatments.

In the NPG experiment, glucose was added with and without N and P. Two subsamples from each location in each plot were randomly assigned as replicates in one of four treatments (3 plots * 3 locations * 4 treatments * 2 replicates = 72 samples): N + P, glucose, N + P + glucose, and control (DI H₂O). Application rates of N and P were the same as low N and P treatments in
the NP experiment. Glucose was applied at a rate of 0.5 mg per g d.m. (0.2 mg of C per g d.m.), approximately 0.04% of the total carbon pool in each jar. Glucose addition as low as 0.05 mg per g d.m. has been shown to satisfy labile C requirements for microbial respiration in soil incubations (Blagodaskaya et al., 2007). We selected a higher rate of glucose addition to ensure detection of enhanced CO$_2$ production with our measurement approach.

CO$_2$ measurements were taken (as described above) at 0, 8, 24, 48, 144 and 240 hours (day 10). An additional measurement was collected at 96 hr (day 4) in the NPG experiment. During measurements for the NP experiment, air temperature ranged between 25.9°C and 32.9°C and during the NPG experiment, it varied between 27.5°C and 32.6°C. Daily air temperature increased steadily over the course of the NP experiment (p < 0.001), but did not vary systematically during the NPG experiment. Mean soil moisture was 1.93 ± 0.01 g H$_2$O g d.m.$^{-1}$ and 2.13 ± 0.02 g H$_2$O g d.m.$^{-1}$ in the NP and NPG experiments, respectively.

Calculations and statistical analysis

All statistical analyses were completed using R (v 3.2.5) except for repeated measures ANOVA, conducted with SPSS (v 23). We used Bartlett’s test of equal variance and then Student’s t-test or Welch’s t-test as appropriate to detect differences in soil properties between forest and oil palm soils from Kalimantan and between Kalimantan and Sumatran oil palm soils.

The rate of CO$_2$ production (μg CO$_2$-C over time) was determined by linear regression of the concentration measured at each hour of the measurement period. We derived cumulative CO$_2$-C production over the experiment, assuming the rate between adjacent time points was the average of the rate at the two time points. We report on per g dry mass (d.m.) and per g C basis.

We assessed treatment effects on cumulative CO$_2$ production with one-way and two-way ANOVAs. To assess the effect of time on treatment response, we used one-way and two-way
repeated measures ANOVA. Despite efforts to keep soil moisture constant across treatments, it varied somewhat, as determined by one-way ANOVA with Tukey’s method for multiple pairwise comparisons. Therefore we treated soil moisture as a covariate in our ANOVA models to control for variation due to small differences in soil moisture. Though temperature in the laboratory varied with time, all jars were incubated under the same temperature conditions, and thus we did not treat temperature as a covariate. We used probability plots to assess normality of residuals and a Brown-Forsythe test for homogeneity of variance in CO$_2$ production among treatment groups.

For the incubation of unamended soils, we used one-way ANOVA with planned comparisons to compare total cumulative CO$_2$ production between sites. In the repeated measures ANOVA of rates through time, the data violated the assumption of sphericity (Mauchly’s $W = 0.080$, $p < 0.001$). Therefore, we applied the Greenhouse-Geyser correction for tests of within-subjects effects. We also used this experiment to assess relationships among measured soil parameters and indices of SOM quality and cumulative evolved CO$_2$-C. We used simple univariate regression and backwards stepwise multiple linear regression using Aikake’s Information Criterion (AIC) for model selection. Only soil chemical properties significantly related to CO$_2$ production in univariate regression were included in model selection.

In NP and NPG experiments, we used two-way ANOVA with planned comparisons to compare rates of CO$_2$ production among treatments. As in the incubation on unamended soils, data violated the assumption of sphericity for repeated measures ANOVA in NP (Mauchly’s $W = 0.035$, $p < 0.001$) and NPG (Mauchly’s $W = 0.007$, $p < 0.001$) experiments. Therefore, we again applied the Greenhouse-Geyser correction for test of within-subjects effects.
Results

Soil chemical properties

Peat substrate quality and nutrient content varied substantially among land uses and geographic location (Table 3). C:N ratio, at 27.4 ± 0.7, was 15% higher in Kalimantan oil palm than in Kalimantan forest soil (p = 0.004). Available P concentration was three times higher in oil palm soils (12.9 ± 3.2 mg kg\(^{-1}\)) than forest soils (3.9 ± 2.0 mg kg\(^{-1}\), p = 0.029). Available N concentration (sum of NO\(_3^–\) and NH\(_4^+\)) was 84.0 ± 6.6 mg kg\(^{-1}\) in oil palm and 114.9 ± 23.8 mg kg\(^{-1}\) for forest soils. NO\(_3^–\) was three times higher in oil palm soils (p = 0.010) despite NH\(_4^+\) being over two times higher in forest soils (p = 0.004). NH\(_4^+\) was also quite variable among forest plots, therefore total available N did not differ significantly between forest and oil palm in Kalimantan. Other properties, including the concentration of C and OM, did not differ significantly between the oil palm and forest soils in Kalimantan.

Sumatran oil palm soils were 39% higher than Kalimantan oil palm soils in total organic matter (p < 0.001), 25% higher in total C (p = 0.003) and 20% higher in total N (p = 0.009). Available N was more than two times higher in Kalimantan oil palm soils than in Sumatran oil palm soils. Significantly higher NO\(_3^–\) concentration in Kalimantan soils than Sumatran oil palm soils (p = 0.001) contributed substantially to the difference in available N, while NH\(_4^+\) concentration at the two sites was similar.

Baseline corrected Vis-NIR spectra displayed peaks in absorbance typical of soils with high organic matter content (Shenk et al., 1992, Figure 3). For the Kalimantan forest soils, the aliphatic peak at 1762 nm was higher than the aromatic peak at 1736 nm, with the exception of shallow peat soils from K-FOR-1 that had experienced fire 30 or more years ago. In contrast, for Sumatran oil palm soils the aliphatic peak was lower than the aromatic peak. The aliphatic and
aromatic peaks were roughly the same height for the Kalimantan oil palm soils, with the exception of soils from the six year old plantation (K-OP-2009), where the aromatic peak was higher than the aliphatic peak. Absorbance by aliphatics at 1200 nm was similar for Kalimantan and Sumatran oil palm soils, and K-FOR-1. K-FOR-2 and K-FOR-3 spectra displayed much higher absorbance at 1200 nm than other plots. The aromatic:aliphatic I ratio was higher in Sumatran oil palm than in Kalimantan oil palm, based on absorbance by aliphatics at 1760 nm (p = 0.002, Table 3). The opposite was true for the aromatic:aliphatic II ratio based on aliphatic compounds at 1200 nm (p = 0.0001). Aromatic:aliphatic II was higher in Kalimantan oil palm than Kalimantan forest peat (p = 0.005), but aromatic:aliphatic I was not significantly different.

Variability in basal respiration without amendment

Cumulative CO2 production by Kalimantan forest soils (1636.1 ± 37.6 µg CO2-C g C⁻¹, 663.3 ± 16.4 µg CO2-C g d.m.⁻¹) was roughly two times higher than production by Kalimantan oil palm soils (871.0 ± 46.1 µg CO2-C g C⁻¹, 339.0 ± 16.4 µg CO2-C g d.m.⁻¹) during the 7-day incubation (p < 0.001, Figure 4). Cumulative CO2 production by Kalimantan oil palm soils was significantly higher than that of Sumatran oil palm soils (600.1 ± 23.7 µg CO2-C g C⁻¹) on a per g C (p < 0.0001) but not per g d.m. basis (320.7 ± 16.4 µg CO2-C g d.m.⁻¹).

Throughout the experiment, on a per g C basis, the hourly rate of CO2 production by Kalimantan forest soils (10.80 ± 0.23 µg CO2-C g C hr⁻¹) was higher than that of Kalimantan oil palm soils (5.34 ± 0.26 µg CO2-C g C hr⁻¹), and the rate of Kalimantan oil palm soils was higher than that of Sumatran oil palm soils (3.90 ± 0.25 µg CO2-C g C hr⁻¹) (for both p < 0.001, Figure 5a). CO2 production was higher at the beginning of experiment (p = 0.004), declining about 20% to a fairly steady state after 24 hours.
Cumulative CO$_2$ production increased significantly with available N (Figure 6f). It declined significantly with increasing C:N ratio, available P, and aromatic:aliphatic ratios (Figure 6d, 6e, 6g, 6h). Aromatic:aliphatic ratio II and available N individually explained the most variation in cumulative CO$_2$ production. Other significant relationships were weaker ($R^2 < 0.50$). CO$_2$ production was not significantly related to total C or OM concentration, on a per g d.m or per g C basis. Considered together, C:N and aromatic:aliphatic ratios, available N and available P accounted for 69% of variance (multiple linear regression, $p < 0.0001$). However, only C:N ratio and aromatic:aliphatic ratio II were significant parameters in the model. The more parsimonious model generated with backwards stepwise selection also accounted for 69% of variance ($p < 0.0001$), and included C:N ratio, aromatic:aliphatic ratio II and available N. Aromatic:aliphatic ratio II was the most important parameter in the model (standard partial regression coefficient (sprc) = -0.42), followed by available N (sprc = 0.37) and C:N (sprc = -0.33).

Respiration in response to nutrient and labile carbon amendment

In the NP experiment, only the high N and high P treatments - those ten times the typical application rate in the field - significantly increased cumulative CO$_2$ production (Figure 7a). CO$_2$ production by high N treated soils (2196.3 ± 58.2 µg CO$_2$-C g C$^{-1}$) was 28% higher than controls (1722.1 ± 58.2 µg CO$_2$-C g C$^{-1}$) ($p < 0.001$), while CO$_2$ production by high P treated soils (1911.2 ± 58.2 µg CO$_2$-C g C$^{-1}$) was only 12% higher ($p = 0.001$). The N effect was driven by strong responses in Kalimantan forest and oil palm soils (Figure 7a). The effect of added P on cumulative CO$_2$ production was driven by a strong response in Kalimantan forest soils (Figure 7a). The temporal patterns of CO$_2$ production among treatments differed ($p < 0.001$, Figure 5b). Rates in the high N treatment were higher than controls through day 6, with differences peaking
at 8 hours. Rates were significantly enhanced under high P at 8 hours and 24 hours; differences peaked at 24 hours and rates were similar to controls again after 48 hours.

Glucose increased cumulative CO$_2$ production compared to controls, but significantly so only when N and P were also added (p < 0.001, Figure 7b). Cumulative CO$_2$ production in glucose plus NP treated (NPG) soils (1998.5 ± 55.0 µg CO$_2$-C g C$^{-1}$) was 21% higher than controls (1654.0 ± 54.7 µg CO$_2$-C g C$^{-1}$). Rates varied significantly with time (p = 0.004, Figure 5c), and temporal patterns differed among treatments (p < 0.001). During the first 24 hours, glucose alone and glucose with NP significantly enhanced CO$_2$ production rate compared to controls. Differences peaked at 8 hours, when glucose treated soils (17.4 ± 0.5 µg CO$_2$-C g C$^{-1}$ hr$^{-1}$) and NPG soils (18.0 ± 0.8 µg CO$_2$-C g C$^{-1}$ hr$^{-1}$) both had rates two times higher than controls (7.4 ± 0.5 µg CO$_2$-C g C$^{-1}$ hr$^{-1}$). Glucose treated soils returned to control levels after the first 24 hours, while rates in GNP soils remained higher than controls through day 4.

Discussion

Soil chemical properties influenced by geography and land use

At the plot level (within site), the organic matter, total C and N, available N and C:N ratio of our soils were representative of the range observed to date in Indonesian peatlands (Table 1). The high available N content we observed is characteristic of tropical peat swamp forest soils in Southeast Asia (van Lent et al., 2015). The peats are high in organic matter content prior to conversion, and oil palm is typically fertilized with 60 - 100 kg N ha$^{-1}$ yr$^{-1}$ (Melling et al., 2007; Marwanto & Agus, 2014; Comeau et al., 2016). Oil palm soils had higher C:N and lower SOM quality, and lower N availability than forest soils, despite application of N fertilizers.

A higher ratio of aromatic to aliphatic carbon compounds in oil palm than forest soils indicates that oil palm soils are more highly decomposed, reflecting the influence of drainage.
When the water table drops, soil organic matter is no longer protected by physical mechanisms
(von Lützow et al., 2006; Schmidt et al., 2011), and it can be mineralized or chemically
transformed. Fires may also have played a role in oil palm plots and K-FOR-1. Fire creates
recalcitrant “black carbon” at the soil surface (Gonzalez-Perez et al., 2004, Singh et al., 2012). In
addition, peat fires result in mass loss from surface layers (Rein et al., 2008) which exposes
subsurface peat layers with a relatively higher proportion of recalcitrant organic matter (Wright
et al., 2011). The shift to higher aromatic:aliphatic ratio may also reflect decreased quantity and
quality of litter inputs in oil palm. Palm fronds decompose more slowly than deciduous tree
leaves due to their higher lignin content and different nutrient balance (Arnason et al., 1984; de
Neiff et al., 2006). Lower input rates from root mortality and litterfall (Hergoualc’h & Verchot
2014) may also increase peat aromatic:aliphatic ratio post conversion.

Higher C:N ratio in oil palm soils compared to forest soils in Kalimantan is in agreement
with some observations of an increase in peat C:N ratio resulting from agricultural uses on peat
(Jauhiainen et al., 2014). However, change in C:N ratio following conversion shows no
consistent trend in the literature. Leaching associated with peat drainage and agricultural use can
drive decreases in the soil N pool (Humphrey & Pluth 1996) and increases in the C:N ratio over
time, while mineral fertilization may result in the opposite effect (e.g. Krüger et al., 2015). Soil
N is readily volatilized during peat fires, and ash remaining on site contains P, K, and other base
cations that may promote N mineralization and microbial immobilization (Certini 2005, Santín &
Doerr 2016). Ash also raises the pH which could increase microbial activity for peat soils with a
pH ~4, accelerating N losses (Certini 2005). Pyromineralization and increased hydrophobicity of
soil organic matter resulting from fire can lead to additional nutrient losses due to erosion,
leaching, exchange with the atmosphere, or uptake by plants (Certini 2005, Santín and Doerr
2016). Significant N export may also occur during harvest of palm oil bunches. While deposition of ash from regional fires could be a source of nutrient inputs (Ponette-Gonzalez et al., 2016), on-site fires are the more likely driver of nutrient availability in our plots. Our oil palm sites underwent single or multiple fires following conversion, resulting in apparent N loss compared to the forest site.

While available N was 30% lower in Kalimantan oil palm than forest, due to high variability in Kalimantan forest sites, the difference was not significant. Kimura et al. (2012) also observed a trend towards lower available N associated with conversion of peat swamp forest to oil palm in Sarawak, though Melling et al. (2007) observed the opposite. Significantly higher levels of NO$_3^-$ contribute to higher available N in Kalimantan oil palm and likely reflects application of nitrogen fertilizer the week prior to soil sample collection. Lower levels of available N in oil palm than in forest soils despite fertilizer application suggests a relatively high rate of N loss from the soil system, most likely through leaching, gaseous N emissions, and export of N in harvest.

Chemical drivers of microbial decomposition in peat soils

CO$_2$ production was related to substrate quality, as measured by aromatic:aliphatic and C:N ratios, not substrate quantity (organic matter and total C). We explored the importance of C quality as a driver of microbial respiration over C quantity, as well as the importance and potential drivers of N limitation. Higher aromatic:aliphatic ratio is consistent with exposure of soil organic matter to decomposition in peat soils (Haberhauer et al., 1998; Ernakovich 2014). Aliphatic C is preferentially mineralized, increasing the proportion of aromatic compounds as a component of SOM. The decomposition of aromatic compounds yields less net energy to microbes than aliphatic compounds, thus SOM becomes increasingly recalcitrant to
decomposition as aromatic:aliphatic ratio increases. As expected, microbial respiration in unamended soils decreased with increasing aromatic:aliphatic ratio.

$\text{CO}_2$ production also declined significantly with increasing C:N ratio (Figure 6d) and increased with available N (Figure 6f), suggesting that nitrogen availability was limiting to $\text{CO}_2$ production. Higher $\text{CO}_2$ production by N-treated soils confirmed the observations from unamended soils. Nitrogen can directly limit SOM decomposition primarily when labile carbon substrates are available to support microbial growth and activity (e.g. MacLean & Wein, 1978; Haynes 1986; Berg & Matzner 1997; Schimel & Weintraub, 2003; Moorhead & Sinsabaugh, 2006, Hopkins et al., 2006). A lower aromatic:aliphatic ratio in Kalimantan forest as compared to Kalimantan and Sumatran oil palm indicates that indeed higher quality C substrate was available in Kalimantan forest soils (Figure 6).

Like N, P can directly limit decomposition when labile carbon substrates are available (Cleveland et al., 2002). The weak negative relationship between $\text{CO}_2$ production and available P in untreated soils suggests that substrate quality and available N were more strongly limiting to $\text{CO}_2$ production than available P. High P treatments increased $\text{CO}_2$ production by Kalimantan forest soils, with relatively higher substrate quality and lower initial P, and did not increase $\text{CO}_2$ production by Kalimantan or Sumatran oil palm soils with relatively lower substrate quality.

We observed a trend towards higher $\text{CO}_2$ production, especially in the forest peat, in the low N and P treatments that were comparable to actual fertilization rates in the field, but the effect was too small to be significant. Similarly, increased rates of heterotrophic respiration in response to nitrogen fertilizer in the field, at application rates typical in Indonesia, are small and transient (Comeau et al., 2016). Microbial respiration in our soils likely remained limited by N, since our low N treatment was not sufficient to bring C:N to the level generally required to meet
microbial requirements. Assuming a microbial C:N ratio of 8:1 (Cleveland & Liptzin 2007; Chapin et al., 2011) and growth efficiency of 33% (Kroer 1993), a C:N ratio of 24:1 represents the threshold between C limitation and N limitation for microbial growth. Soil C:N ratio was above this threshold at both oil palm sites, and was marginal at the forest site (23.2 ± 1.1).

Our high N treatment was sufficient to alleviate N constraints on microbes, but limitation then may have shifted to SOM quality: Sumatran oil palm did not respond but Kalimantan oil palm and forest did. Our study suggests the magnitude of increase will be influenced by both application rate and peat substrate quality and nutrient availability. Conversion of forest to oil palm plantations may drive progressive N limitation and limitation by SOM quality. Fertilization at typical field rates may not increase CO$_2$ production from peat decomposition in situ. Ultimately, fire effects and time since drainage, through impacts on peat substrate quality and nutrient availability, may have a more profound influence than fertilization on CO$_2$ emissions from peat soils.

Glucose addition raised CO$_2$ production, however, in this study, the response was only significant in the presence of added N and P. Addition of glucose with N and P temporarily removed both N and SOM quality constraints. This was true even for the Sumatran oil palm soils with low SOM quality which did not respond to high N and P treatments in the absence of glucose. Amendment with glucose temporarily alleviated labile C constraints in Sumatran oil palm soils, allowing N and P to directly limit microbial respiration; the effect quickly disappeared if glucose were not also accompanied by added nutrients (Figure 5, 7). CO$_2$ evolved from glucose could not be distinguished from peat-evolved CO$_2$ in our NPG experiment, and the difference between glucose treated soils and controls was not greater than the amount of C added
Comparing CO₂ production across geographies and land use

Substrate quality played a strong role in determining rates of CO₂ production by peats from different islands and under different land uses. Sumatran oil palm soils had more C available for microbial decomposition than Kalimantan oil palm soils (Table 3), however, CO₂ production was similar on per g d.m. basis and significantly lower on per g C basis (Figure 4). Lower CO₂ production reflected the lower quality of the substrate: higher ratios of aromatic:aliphatic (I) and C:N (Table 3, Figures 3 and 6). Likewise, Kalimantan forest and oil palm soils had similar quantity of C available for microbial decomposition. Nevertheless, CO₂ production was significantly higher, on per g d.m. and per g C basis, in Kalimantan forest soils with higher quality SOM and lower C:N ratio.

CO₂ production by Kalimantan forest soils was two orders of magnitude lower than that of Panamanian peat swamp forest soils (Hoyos-Santillan et al., 2016), most likely due to lower SOM quality in Kalimantan peats. CO₂ production by oil palm soils in both Kalimantan and Sumatra was ca. 50% lower than ex situ CO₂ production from a deforested, drained, and abandoned peat (with no oil palm) in Central Kalimantan (Jauhiainen et al., 2016). Rates for our forest soil were five times lower than ex situ rates for an undrained forest adjacent to the abandoned peat in Jauhiainen et al. (2016). However, comparing results is difficult because the incubation methods were quite different (a slurry versus field moist soil).

Land use change and future CO₂ emissions from tropical peatlands

In addition to management practices that enhance peat decomposition over the short term, e.g. drainage, land use change may influence peat CO₂ emissions over the long term through effects
on peat soil properties. Our *ex situ* results are consistent with observed or inferred decreases in
CO$_2$ fluxes from drained peat soils under agricultural use over time (Wösten *et al.*, 1997; Hooijer
*et al.*, 2012). As suggested by comparing forest to oil palm in Kalimantan, recently drained
peatlands, high in labile carbon compounds, may emit CO$_2$ at higher rates in years immediately
following conversion compared to later years. In addition, changes in vegetation will alter inputs
of organic matter over time, with quality (Pardon *et al.*, 2017) and quantity (Hergoualc’h &
Verchot 2014) varying as the agro-ecosystem ages and the microbial community changes
(Tripathi *et al.*, 2016).

In Kalimantan, peat quality varied dramatically between undrained forest and oil palm
plantations cleared 10 to 26 years prior and managed for oil palm production for another four to
eight years. Both aromatic:aliphatic and C:N ratios were roughly 15% lower in forest than in oil
palm. Our incubation results indicate a substantial (50%) potential decline in substrate driven
rates of peat decomposition a decade or more after initial conversion to oil palm. Comparisons
between oil palm soils from Kalimantan and Sumatra, and within sites at both locations indicate
that variation in substrate quality across space will also influence CO$_2$ emissions from peatlands
under the same land use. Assessments of carbon emissions from land use change should consider
the dynamic nature of the soil substrate available for decomposition. Rates are likely to be higher
in the early period following conversion and in places where substrate quality is higher. Time
since disturbance has been assessed in temperate forests with remote sensing approaches that
have potential application in the tropics (e.g. Pan *et al.*, 2011b). If substrate quality is related to
canopy foliar nutrients, it could also be sensed remotely (Asner *et al.*, 2008; Balzotti *et al.*,
2016). The elements for an improved method of estimating region-wide CO$_2$ production may be
within reach. Given the importance of peat emissions for Indonesia and the global carbon cycle, a more refined approach to scaling up emissions from land use change is needed.

References


Kimura, S, Melling, L, Goh, KJ. 2012. Influence of soil aggregate size on greenhouse gas emission and uptake rate from tropical peat soil in forest and different oil palm development years. Geoderma 185: 1-5.


Marwanto, S, Agus, F. 2014. Is CO₂ flux from oil palm plantations on peatland controlled by soil moisture and/or soil and air temperatures?. Mitigation and adaptation strategies for global change 19: 809-819.


Table 1. Soil chemical properties measured on Southeast Asian peats.

<table>
<thead>
<tr>
<th>Property</th>
<th>This study</th>
<th>Previous studies</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>pH</td>
<td>3.9</td>
<td>3.7 – 4.1</td>
<td>3.8</td>
</tr>
<tr>
<td>OM (g 100 g⁻¹)</td>
<td>77</td>
<td>47 – 93</td>
<td>96.0</td>
</tr>
<tr>
<td>C (g 100 g⁻¹)</td>
<td>45</td>
<td>28 – 55</td>
<td>53.7</td>
</tr>
<tr>
<td>N (g 100 g⁻¹)</td>
<td>1.7</td>
<td>1.3 – 2.3</td>
<td>1.7</td>
</tr>
<tr>
<td>C:N</td>
<td>26.3</td>
<td>20.3 – 30.0</td>
<td>36.4</td>
</tr>
<tr>
<td>NH₄⁺ + NO₃⁻ (mg kg⁻¹)</td>
<td>79.7</td>
<td>29.4 – 184.2</td>
<td>169.1</td>
</tr>
</tbody>
</table>

Reference:
- a) Shimada et al. 2001,
- b) Takakai et al. 2006,
- c) Reiley and Page 2008,
- d) Ismawi et al. 2012,
- e) Kimura et al. 2012,
- f) Warren et al. 2012,
- h) Gandois et al. 2013,
- i) Melling et al. 2013,
- j) Inubushi et al. 2003,
- k) Melling et al. 2005

Table 3. Chemical properties of peat samples collected from the top 0-5 cm (n=18 for BD, n = 9 for other) and top 0-10 cm (pH only, n = 3) in the Kalimantan forest site (KAL FOR) and oil palm site (KAL OP) and the Sumatra oil palm site (SUM OP). Mean values are presented with standard errors.

<table>
<thead>
<tr>
<th>Property</th>
<th>Depth (cm)</th>
<th>KAL FOR</th>
<th>KAL OP</th>
<th>SUM OP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BD (g cm⁻³)</td>
<td>0-5</td>
<td>0.16 ± 0.06</td>
<td>0.24 ± 0.06</td>
<td>0.19 ± 0.02</td>
</tr>
<tr>
<td>pH</td>
<td>0-10</td>
<td>3.97 ± 0.07</td>
<td>3.70 ± 0.20</td>
<td>3.97 ± 0.18</td>
</tr>
<tr>
<td>OM (g 100 g⁻¹)</td>
<td>0-5</td>
<td>72.5 ± 6.3</td>
<td>66.1 ± 3.1^A</td>
<td>91.8 ± 0.6^B</td>
</tr>
<tr>
<td>C (g 100 g⁻¹)</td>
<td>0-5</td>
<td>40.8 ± 3.2</td>
<td>41.2 ± 2.8^A</td>
<td>53.8 ± 0.8^B</td>
</tr>
<tr>
<td>N (g 100 g⁻¹)</td>
<td>0-5</td>
<td>1.8 ± 0.2</td>
<td>1.5 ± 0.1^A</td>
<td>1.9 ± 0.1^B</td>
</tr>
<tr>
<td>C:N</td>
<td>0-5</td>
<td>23.2 ± 1.1^a</td>
<td>27.4 ± 0.7^b</td>
<td>28.6 ± 1.0</td>
</tr>
<tr>
<td>NH₄⁺ (mg kg⁻¹)</td>
<td>0-5</td>
<td>100.3 ± 21.5^a</td>
<td>38.7 ± 9.4^b</td>
<td>37.7 ± 5.7</td>
</tr>
<tr>
<td>NO₃⁻ (mg kg⁻¹)</td>
<td>0-5</td>
<td>14.6 ± 5.8^a</td>
<td>45.3 ± 8.8^b,A</td>
<td>2.6 ± 0.8^B</td>
</tr>
<tr>
<td>NH₄⁺ + NO₃⁻ (mg kg⁻¹)</td>
<td>0-5</td>
<td>114.9 ± 23.8</td>
<td>84.0 ± 6.6^A</td>
<td>40.3 ± 5.5^B</td>
</tr>
<tr>
<td>Bray II P (mg kg⁻¹)</td>
<td>0-5</td>
<td>3.9 ± 2.0^a</td>
<td>12.9 ± 3.2^b</td>
<td>32.2 ± 8.6</td>
</tr>
</tbody>
</table>

Significant differences in mean values between KAL FOR and KAL OP are indicated by superscripts a, b. Significant differences in mean values between KAL OP and SUM OP are indicated by superscripts A, B. Abbreviations are BD: bulk density, OM: organic matter.
Table 2. Characteristics of the sampling plots at the three study sites.

<table>
<thead>
<tr>
<th>Code</th>
<th>Island</th>
<th>Location</th>
<th>Landuse</th>
<th>Plantation</th>
<th>Clearance</th>
<th>Fires</th>
<th>Distance to River</th>
<th>Peat Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>K-FOR-1</td>
<td>Kalimantan</td>
<td>S 02° 49.4’ E 111° 48.8’</td>
<td>Forest</td>
<td>-</td>
<td>pre 1982</td>
<td>Multiple</td>
<td>0.5 km</td>
<td>27 cm</td>
</tr>
<tr>
<td>K-FOR-2</td>
<td>Kalimantan</td>
<td>S 02° 49.3’ E 111° 50.4’</td>
<td>Forest</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1 km</td>
<td>155 cm</td>
</tr>
<tr>
<td>K-FOR-3</td>
<td>Kalimantan</td>
<td>S 02° 50.9’ E 111° 48.1’</td>
<td>Forest</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2 km</td>
<td>290 cm</td>
</tr>
<tr>
<td>K-OP-2011</td>
<td>Kalimantan</td>
<td>S 02° 47.3’ E 111° 48.6’</td>
<td>Smallholder oil palm</td>
<td>4 Year</td>
<td>1989</td>
<td>Multiple</td>
<td>3.5 km</td>
<td>20 cm</td>
</tr>
<tr>
<td>K-OP-2009</td>
<td>Kalimantan</td>
<td>S 02° 47.3’ E 111° 48.1’</td>
<td>Smallholder oil palm</td>
<td>6 Year</td>
<td>2005</td>
<td>Multiple</td>
<td>3.5 km</td>
<td>47 cm</td>
</tr>
<tr>
<td>K-OP-2007</td>
<td>Kalimantan</td>
<td>S 02° 47.2’ E 111° 48.1’</td>
<td>Smallholder oil palm</td>
<td>8 Year</td>
<td>2005</td>
<td>Multiple</td>
<td>3.5 km</td>
<td>47 cm</td>
</tr>
<tr>
<td>S-OP-2010</td>
<td>Sumatra</td>
<td>S 01° 38.4’ E 103° 54.3’</td>
<td>Industrial oil palm</td>
<td>5 Year</td>
<td>2004</td>
<td>Multiple</td>
<td>20 km</td>
<td>850 cm</td>
</tr>
<tr>
<td>S-OP-2007</td>
<td>Sumatra</td>
<td>S 01° 38.2’ E 103° 52.3’</td>
<td>Industrial oil palm</td>
<td>8 Year</td>
<td>2004</td>
<td>Multiple</td>
<td>20 km</td>
<td>665 cm</td>
</tr>
<tr>
<td>S-OP-2005</td>
<td>Sumatra</td>
<td>S 01° 38.5’ E 103° 50.0’</td>
<td>Industrial oil palm</td>
<td>10 Year</td>
<td>2004</td>
<td>Single</td>
<td>20 km</td>
<td>575 cm</td>
</tr>
</tbody>
</table>
Figure 1. Conceptual model of changes in peat soil organic matter quality (SOM) and nutrient availability associated with conversion of tropical peat swamp forest to oil palm plantation. Burning results in removal of surface peat layers (a) and enhances drainage-facilitated leaching of N and P (b). Microbial activity is enhanced by increased oxygen availability in drained peat layers (c). This drives decomposition of labile C compounds resulting in increasing SOM recalcitrance over time, and gaseous N losses. Decreased quantity and quality of litter inputs in drained peat layers (a) may also enhance the accumulation of recalcitrant C in soil organic matter. N and P inputs are received from fertilization in oil palm plantations (d) leading to additional C and N losses to the atmosphere and drainage waters. Refer to text for citations.

Figure 2. Research sites and soil sampling design. Peat soils were collected at sites on the islands of Kalimantan and Sumatra (inset, lower left) from three plots in undrained forest and three plots in nearby smallholder oil palm plantations in Kalimantan (a) and from three plots in an industrial oil palm plantation in Sumatra (b). At each plot, soil samples were collected from three locations determined using a systematic random approach. At each location soils were collected along 5 m transects arrayed in a stratified random design, centered on an individual palm or tree (c). Each circle in (c) represents one soil sample collected from the top 0-5 cm with a bulk density ring. Maps are hand digitized images from GoogleEarth. Source: DigitalGlobe 2016
Figure 3. Vis-NIR baseline corrected absorbance spectra of soil from plots in Kalimantan undrained forest (K-FOR-1, K-FOR-2, K-FOR-3), Kalimantan smallholder oil palm plantations (K-OP-2011, K-OP-2009, K-OP-2007) and Sumatran industrial oil palm plantations (S-OP-2010, S-OP-2007, S-OP-2005) on peat. Noticeable peaks around 1400 nm and 1900 nm are associated with H-O-H and O-H absorption bands (Shenk et al., 1992), and indicate that some water remained in soils after air drying. A strong absorption around 2200 nm by soils from K-FOR-1 was likely due to high mineral content. The waveband 1000-2000 nm is magnified in the inset. Each spectra represents the average of measurements collected on soil samples from three within plot locations (n=3).
Figure 4. Mean cumulative CO₂ production by peat soils from Kalimantan forest (KAL FOR, green) and oil palm (KAL OP, orange) sites and Sumatran oil palm (SUM OP, blue) sites during incubation without amendment. Production is expressed on per g C basis in (a) and per g d.m. basis in (b). Significant differences in mean total cumulative CO₂ production over the 7 day incubation values are indicated by different letters in inset (a) and inset (b). Error bars represent standard error of the mean (n = 27).

Figure 5. Mean CO₂ production rate by peat soils (a) from Kalimantan forest (KAL FOR) and oil palm (KAL OP) sites and Sumatran oil palm (SUM OP) sites during incubation without amendment; (b) with three levels of nitrogen (N) and phosphorus (P) amendment (no amendment: C; high level: hi; low level: lo); and (c) with glucose in the presence (NPG) or absence (G) of N and P amendment, with N and P amendment without glucose (NP) and in controls (C). Error bars represent standard error of the mean. In (a) n = 27, (b) n = 18, and (c) n = 18.
Figure 6. Mean cumulative CO$_2$ production over seven days by soils incubated without amendment as a function of soil properties (n = 27). Each data point represents the average of three replicates of soil from each of the three trees within plot locations. Green circle: peat forest in Kalimantan, gold triangle: oil palm in Kalimantan, orange triangle: oil palm in Sumatra.

Figure 7. Mean cumulative CO$_2$ production by peat soils from Kalimantan forest (KAL FOR) and oil palm (KAL OP) and Sumatran oil palm (SUM OP) sites in (a) each treatment group incubated with nitrogen (N) and phosphorous (P) amendment and in (b) each treatment group incubated with glucose (G) amendment in the presence or absence of N and P amendment. Significant difference compared to control is indicated with *. Error bars represent standard error of the mean (n=6).