Determining the effects of land-use change and climate variability on greenhouse gas emissions from tropical peatlands

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CHAPTER ONE

Introduction

Background

Climate change is one of the most critical and pressing issues facing the present generation of decision makers. Actions taken now will have far reaching impacts on our ability to limit global warming to 1.5^{o}C above pre-industrial levels as called for in the 2015 Paris climate agreement. Land-use and land-use change play a large role in contributing to increased atmospheric concentrations of greenhouse gases (GHG), accounting for an estimated 24% of global anthropogenic GHG emissions (IPCC 2014). Decisions regarding land-use can thus have an important impact on global climate.

Indonesian peatlands are a major and growing globally important source of GHG emissions due to increasing pressure from the expansion of oil palm. Land-use change and forestry accounts for 68% of anthropogenic GHG emissions in Indonesia, the 8th largest emitter in the world (WRI 2014). A large proportion of these emissions are attributed to land-use conversion in peat swamp forests. Tropical peat swamp forests store tremendous amounts of organic carbon in vegetation and waterlogged soils, up to three times more on a per area basis than tropical, temperature, and boreal forests on mineral soils (Murdiyarso *et al.*, 2009). Conversion of tropical peat forest to oil palm plantations usually entails clearing and burning of forest vegetation followed by peat ditching and draining to lower water table levels, a requirement for oil palm cultivation. Clearing and burning results in immediate emissions of CO_2, CH_4, and N_2O. Peat drainage generates additional massive long-term CO_2 emissions from the decomposition of soil organic material over time.

Tropical peatlands in Southeast Asia occupy mostly low altitude coastal and sub-coastal environments. In Indonesia, they occur predominantly in Sumatra, Kalimantan and Papua (Figure 1a) covering 19.5 million ha in total (Gumbricht *et al.*, 2017). Between 2000 and 2010, 2.2 million ha of peat swamp forest were deforested (Miettinen *et al.*, 2011), primarily for conversion to oil palm and pulpwood plantations (Miettinen *et al.*, 2012). Annual conversion rates in Sumatra and Kalimantan between 2000 and 2010 were 5.2% and 1.7% respectively, with only 25% of original forested peatlands remaining in Sumatra by 2010 (Miettinen *et al.*, 2012). Deforestation rates across Indonesia accelerated between 2000 and 2012, with increased rates of clearing in wetlands (Margono *et al.*, 2014). Deforestation rates in Papua remain relatively low, but existing government plans to double 2010 palm oil production by 2020 could accelerate oil palm plantation development there, putting increasing pressure on Indonesia's remaining forested peatlands (Afriyanti *et al.*, 2016).

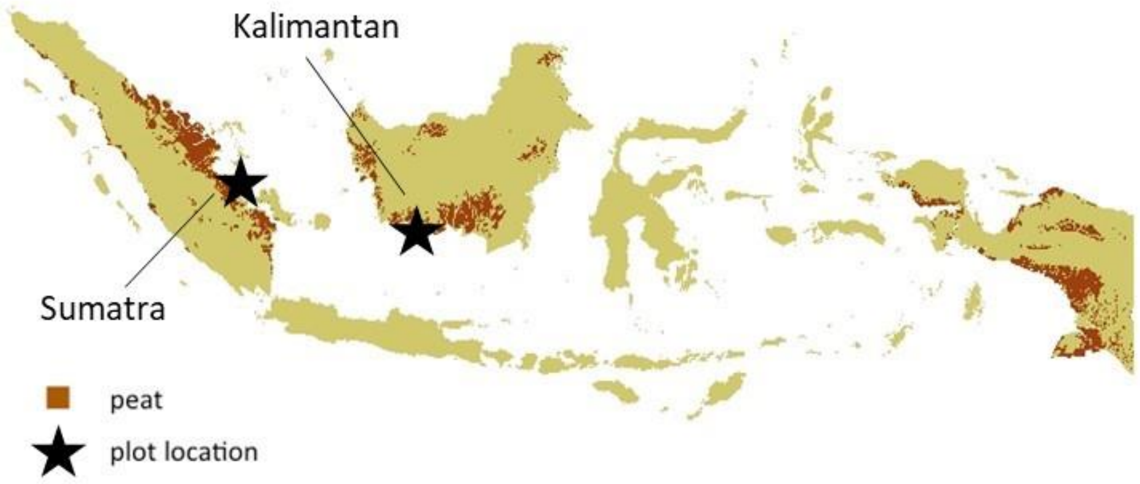

Figure 1. Peatland extent in Indonesia and study site locations in Sumatra and Kalimantan. Source peatland extent: Wetlands International.

Southeast Asian peatlands account for 38% of global tropical peatland area, with Indonesia contributing the deepest and most extensive peats in the tropics (Gumbricht *et al.*, 2017). By one estimate, converted peatlands in Southeast Asia could emit as much as 31.9 Gt CO_2 over the next 100 years under a moderate twenty-first century climate (Warren *et al.*, 2017). Kalimantan Province in Indonesia alone is projected to contribute 128.4 – 211.4 Mt CO_2 yr^{-1} from a business as usual scenario for oil palm expansion (Austin *et al.*, 2015), equivalent to 16 – 27% of CO_2 emissions from international aviation in 2015 (ATAG, 2016). Land-use change in tropical peatlands is a potentially significant source of anthropogenic carbon emissions for Indonesia, and for the world.

Though drainage depth has been suggested as the dominant factor controlling microbial decomposition of tropical peat soils (Couwenberg *et al.*, 2010), observations from the field are not consistent, indicating that other factors have an important influence on emissions from peatlands. For example, the relationship between water table level and soil respiration varies among land covers and land uses in tropical peatlands (Jauhinen *et al.*, 2008; Hirano *et al.*, 2009; Comeau, 2016). In a meta-analysis of soil respiration across typical land-uses in tropical peatlands, Hergoualc'h and Verchot (2011) found that soil respiration was not correlated with water table level. Given that oil palm plantations on peat are drained, alleviating oxygen limitations on aerobic respiration, other factors must explain variation in rates of CO_2 production from microbial decomposition of peat.

Variability in organic matter quality can influence carbon emissions from peat soils, and it is one of the factors I investigated in this dissertation. Active carbon cycling in undisturbed tropical peat swamp forests is largely confined to the upper layer of peat soils. In this layer, microbial decomposition is enhanced by sporadic aerobic conditions and inputs of fresh organic material from litterfall and roots (Jackson *et al.*, 2008, Hirano *et al.*, 2009). Drainage enhances soil CO_2 flux in peatland ecosystems presumably from accelerated microbial decomposition at the surface and in deeper peat layers (Juahianen *et al.*, 2008, Hirano *et al.*, 2007, 2009; Couwenberg *et al.*, 2010). However, the rate of soil carbon loss from disturbed peatlands appears to slow over a period of years; Hirano et al. (2012) suggest that slowing of carbon loss may result from depletion of relatively labile carbon compounds in subsurface peat layers. In addition, nutrient limitations constrain microbial decomposition in tropical mineral soils (e.g. Vitousek 1998; Hobbie and Vitousek, 2000; Cleveland *et al.*, 2002) and likely also constrain CO_2 production in peat soils.

Existing studies of GHG emissions from Indonesian peatlands have largely focused on the impact of land-use change, with less attention given to the influence of climate variability. Precipitation regime is an important factor determining soil carbon storage and loss in tropical peatland ecosystems. Peatlands develop when the rate of organic matter accumulation in soils exceeds the rate of decomposition. In cooler climates low temperatures and saturation both play a role in limiting the rate of soil organic matter decomposition. In tropical climates, where temperature does not limit decomposition, peatlands form in low-lying areas where high precipitation and poor drainage lead to permanent waterlogging of soils. In the areas where peatlands occur in Indonesia, rainfall varies from 1,800 to 3,800 mm per year, including a somewhat drier period of a few months. In undisturbed peat swamp forests, the amount and timing of rainfall is one of the dominant controls on hydrological conditions because rates of evapotranspiration and groundwater outflow are relatively constant (Takahashi *et al.*, 2002, 2003). During wet periods, groundwater rises to levels near or above the soil surface, decreasing oxygen available for aerobic decomposition and favoring peat accumulation and carbon storage, Though CH_4 emissions from anaerobic decomposition and leaching may be important avenues for soil carbon loss in saturated conditions, the magnitude of flux is small compared to losses from aerobic decomposition. During dry periods, groundwater levels fall, increasing the depth of the oxic soil profile and accelerating peat decomposition. A future climate regime characterized by more frequent and severe El Niño events could impact emissions in both drained and undrained tropical peatlands, though this effect may already be felt. Increased emissions from Southeast Asian peatlands could help explain massive emissions from the tropics during the 2015 El Niño that could negate the land sink for that year (Liu *et al.*, 2017). In this dissertation, I explore the interacting effects of land use change, soil substrate quality, and climate variability in driving GHG emissions from tropical peatlands.

Study Region

For this study, permanent plots for field data collection were located in undrained peat swamp forest and drained smallholder oil palm plantations in a Central Kalimantan peatland, on the southern coast of Indonesian Borneo, about 10 km from the city of Pangkalan Bun (Figure 1). I collected soil samples for incubation experiments from these two sites plus one additional oil palm site. To address the potential impact of different underlying geology, peat dynamics and history of land use, I also sampled soils from an industrial plantation on the island of Sumatra, approximately 20 km from the city of Jambi (Figure 1).

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). Industrial oil palm accounts for a disproportionately larger share of emissions from conversion of peat swamp forest for oil palm production, with smallholders clearing more forest on mineral soils than peat (Lee *et al.*, 2014). However, management practices for oil palm cultivation on peat are likely similar overall in smallholder and industrial plantations across Indonesia. Smallholder plantations are frequently managed in association with an oil palm company (Vermeulen & Goad, 2006), where farmers receive technical assistance and agricultural inputs for their plantations from the company, as they did in our study. In Indonesia smallholder plantations average 2 ha in size but can range up to 50 ha (Vermeulen & Goad, 2006). Industrial scale oil palm plantations can be as large as 20,000 to 40,000 ha in size (Caroko *et al.*, 2011).

The climate of the region is humid tropical, with high annual rainfall and little variation in temperature throughout the year. Mean annual temperature measured at Iskander airport in Pangkalan Bun during 2005-2014 was 27.4^{o}C and mean annual rainfall was 1808 mm. September was typically the driest month in Pangkalan Bun (85 mm). In Jambi, mean annual temperature measured at Sultan Thaha airport during the same time period was 27.1^{o}C and mean annual rainfall was 1846 mm. The driest month (115 mm) typically occured in June in Jambi.

The Kalimantan smallholder oil palm plantations were 2, 4, and 6 years old at the beginning of the monitoring period in January 2014. They were converted from degraded peat forest, approximately 3.5 km from the edge of Sekonyer river in the community of Bedaun (2^{o}47’16’’S, 111^{o}47’56’’E). Peat swamp forest plots were located in Tanjung Puting National Park on the opposite side of the Sekonyer river. The area was designated as a National Park in 1982, and communities living inside the park were eventually moved across the river. An industrial oil palm plantation was established on lands adjacent to smallholder properties in the late 1990s. Smallholders began plating oil palm on their own lands in the late 2000s. 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. 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. The Sumatran peatland included in the study was cleared in 2004 by a palm oil company and planted with oil palm by the same company thereafter.

In this dissertation, I began with a field experiment to test the impact of land use change and climatic variability on GHG emissions from tropical peat soils. Once per month from January 2014 through June 2015, and once again in September 2015, I measured fluxes of CO_2, CH_4, and N_2O from soils concomitantly with environmental parameters at the permanent plots in undrained forest and drained oil palm plantations in the Kalimantan peatland. The monitoring period covered one year with normal precipitation in 2014, and a severe El Niño event in 2015. I found that in a normal year, land-use change increased total soil respiration in oil palm plantations by 22%, roughly equivalent to a 60% increase in microbial decomposition of peat soils (Chapter 2). During the El Niño event in 2015, owing to greater sensitivity to extreme drying in peat swamp forest, total soil respiration in forest was briefly higher than oil palm, with associated microbial decomposition equaling rates in oil palm.

Peat forests vary geographically and that variation could affect the impact of land use change. Variation in inherent soil characteristics could even mitigate differences due to land use. To best address the role of peat forest conversion on Indonesia’s GHG emissions and feedbacks on the global carbon cycle, the effect of local and regional geographic variation in soil characteristics must be considered. In this study, I investigated the influence of soil organic matter quality and nutrients on rates of peat decomposition in forest and oil palm through laboratory incubations. I collected peat soil samples from the forest and smallholder oil palm sites in Central Kalimantan, and the industrial oil palm plantation on peat in Jambi, Sumatra. Higher organic matter quality and nutrient availability, particularly lower ratios of aromatic:aliphatic carbon and C:N, explained differences in rates of CO_2 production by soils from the three sites (Chapter 3). These results suggest that changes in peat substrate quality associated with conversion of peat swamp forests to oil palm plantations may result in declining CO_2 emissions from microbial decomposition of peat soils over time.

Land-use change and climate variability also impact rates of emissions of CH_4 and N_2O from tropical peat soils, which are respectively 25 and 298 times more powerful GHGs than CO_2. To characterize emissions of CH_4 and N_2O and assess their contribution to GHG budgets in forest and oil palm, I measured CH_4 and N_2O fluxes from soils concurrently with CO_2 fluxes and environmental parameters. While the global warming impact of increased N_2O emissions in oil palm outweighed decreased CH_4 emissions in the post-conversion land-use, the contribution of changes in both gases to GHG budgets was eclipsed by the impact of increased emissions of CO_2 associated with peat drainage (Chapter 4).

Additional measurements over space and time are needed to more accurately characterize how tropical peatlands are currently contributing to global anthropogenic emissions of GHG, and how their contribution may change under an altered climate regime in the future. Remote sensing is a powerful tool that is potentially useful for scaling up and constraining estimates of CO2 emissions from peat CO_2. I related monthly terrestrial water storage anomaly measurements from the Gravity Recovery and Climate Experiment (GRACE) to ground measurements of total soil respiration and environmental parameters collected from the permanent plots in Central Kalimantan. Monthly changes in soil water storage measured by GRACE explained almost half of the variation in total soil respiration measured on the ground at our research site (Chapter 5). By facilitating regular sampling across broad spatial scales that captures essential variation in a major driver of soil respiration that is influenced by El Niño, this novel approach could improve understanding of the role of tropical peat in the global carbon cycle under future climate change.

In this dissertation I used several different approaches to investigate controls on GHG emissions from forest and oil palm in an Indonesian peatland: a field experiment, laboratory incubations and analysis of soils, and remote sensing. I addressed several areas of uncertainty in drivers of emissions from tropical peatlands, investigating how anthropogenic and climate driven changes in water regime, vegetation, and soil affect GHG emissions in Indonesian peatlands, particularly CO_2 emissions. This dissertation was guided by the following questions: (1) What is the magnitude of change in CO_2, CH_4, and N_2O emissions from Indonesian peatlands associated with conversion of forested peatlands to oil palm? (2) How do primary climate driven biogeophysical controls of soil emissions vary in peat swamp forest and oil palm plantations on peat, and do they correlate with GHG fluxes? (3) How do peat properties influence the rate of carbon loss from peat decomposition? (4) Are ground measurements of soil CO_2 flux in tropical peatlands correlated with spaceborne observations of soil water status?

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CHAPTER TWO

Seasonal and interannual variation in total soil respiration from forest and oil palm in an Indonesian peatland

Abstract

To accurately quantify tropical peatlands' contribution to global greenhouse gas emissions and to understand how peat emissions may change in the future, long-term measurements over months, seasons, and years are needed. We collected monthly measurements of total soil respiration and environmental variables from forest and smallholder oil palm plantations on peat in Central Kalimantan, Indonesia from January 2014 through September 2015. Our study period covered wet - dry transitions during one year with relatively normal precipitation and one El Niño year. Oil palm plots, with lower water table, had 22% higher total soil respiration (0.71 ± 0.04 g CO_2 m^2 hr^{-1}) than forest plots (0.58 ± 0.04 g CO_2 m^2 hr^{-1}) over the entire monitoring period. However, during the El Niño event in September 2015, despite overall lower water table levels in oil palm plots, total soil respiration in forest was higher than in oil palm. Though land-use change continues to be an important driver of CO_2 emissions from these ecosystems, the stronger response of total soil respiration to extreme dry down in forest indicates the potential importance of climate regime in determining future net C emissions from Indonesian peatlands. Future warming and increased intensity of seasonal drying may increase C emissions from Indonesian peatlands regardless of land use.

Introduction

Indonesian peatlands store an estimated one third of tropical peat soil carbon (C) stocks (Gumbricht *et al.*, 2017), or roughly 5% of global tropical forest C (Pan *et al.*, 2011). However, due to increasing pressure to convert and drain peatland areas for agricultural uses, particularly oil palm plantations, Indonesian peatlands are a large and growing net source of C emissions to the atmosphere (Koh *et al.*, 2011; Miettinen *et al.*, 2012; Austin *et al.*, 2015). Aerobic decomposition of soil organic matter, accelerated by peat drainage for agricultural production, releases C to the atmosphere as CO_2. Even undrained peatlands may function as a net C source during periods of reduced precipitation and associated drying (Hirano et al. 2009). Existing efforts to understand the contribution of Indonesian peatlands to anthropogenic C emissions to the atmosphere have largely focused on the impact of land-use change on these ecosystems. The impact of a phenomenon such as El Niño Southern Oscillation (ENSO), potentially indicative of and influenced by future climate change, is unknown.

Precipitation regime is an important factor determining soil carbon storage and loss in tropical peatland ecosystems. Weaker seasonality in precipitation (wet – dry alternation) and weaker ENSO dynamics in coastal areas compared to inland areas may have promoted coastal peat accumulation even when inland peat domes were entering a phase of decline between 7000 and 4000 years ago in modern Indonesia (Hanebuth *et al.*, 2011; Dommain *et al.*, 2011). Data collected from the upper catchment of the Sebangau river suggest that some inland peat domes of Central Kalimantan continue to decline (Page *et al.*, 1999) while coastal areas continue to accumulate peat under the current climate regime (Dommain *et al.*, 2011). Clearly, the degree of seasonality affects the pace and direction of changes in peat carbon storage. El Niño, by intensifying the dry season in Indonesia (Kripalani & Kulkarni 1997), plays an important role in determining tropical peat carbon storage. Existing projections indicate that influential ENSO dynamics may be altered by global climate change. Coupled Model Intercomparison Project Phase 5 (CMIP5) outputs in the Intergovernmental Panel on Climate Change Assessment Report 5 did not signal a clear enhancement or dampening of ENSO by global warming as measured by changes in sea surface temperature variability (Collins et al. 2010). However, more recent climate projections, focusing on changes in precipitation patterns rather than sea surface temperatures, indicate increased ENSO frequency and severity in the future (Chadwick et al. 2013, Power et al. 2013, Cai et al. 2014). More frequent and severe periods of reduced precipitation could enhance decomposition of peat soils and associated CO_2 emissions at a regional scale, resulting in a positive feedback on global atmospheric CO_2 concentration and on global warming.

Long-term measurements are needed to accurately quantify the contribution of tropical peatlands to anthropogenic C emissions. In addition to understanding the impact of land-use change on peat carbon storage, we must assess how C emissions in tropical peatlands respond to changes in temperature, soil moisture, and water table associated with climate change. Water table depth has been suggested to be the dominant biogeophysical control on decomposition of tropical peat soils, but field observations are not consistent (Couwenberg *et al.*, 2010; Hirano *et al.*, 2009). Vegetation, soil moisture and temperature, as well as peat substrate quality and nutrient content may also influence CO_2 emissions from peat soils (Jauhiainen *et al.*, 2016; Swails *et al.*, 2017). These direct biogeophysical controls on trace gas fluxes from peat soils are themselves influenced by land management practices as well as climatic factors, notably precipitation, but also air temperature, and solar radiation.

In this study we focused on one of the main components of the peat carbon budget, soil respiration. Net CO_2 flux to/from soil in tropical peatlands is calculated as the balance between C inputs of litter from above- and below-ground and outputs via heterotrophic soil respiration and dissolved organic C export from tropical peatlands. Heterotrophic respiration accounts for 90% of this budget (Hergoualc’h and Verchot, 2014). However, in our study we measured total respiration, which consists of root (autotrophic) and microbial (heterotrophic) respiration, with only microbial respiration contributing actively to soil C changes. Heterotrophic respiration accounts for roughly 50% of total soil respiration in intact peat swamp forest (Ishida *et al.*, 2001; Hergoualc'h *et al.*, 2017) and 70% in oil palm plantations on peat (Melling *et al.*, 2007; Dariah *et al.*, 2013; Comeau *et al.*, 2016; Hergoualc'h *et al.*, 2017). We applied these percentages to the total soil respiration measurements in forest and oil palm to estimate heterotrophic respiration in the two land uses. By using these well-established ratios we can determine the portion of soil respiration that will result in a major shift in soil carbon storage following peat forest conversion.

We collected monthly measurements of total soil respiration and environmental parameters in smallholder oil palm plantations and undrained peat forest in Central Kalimantan, Indonesia from Jan 2014 to Sep 2015. Our study period covered wet – dry transitions during one year with relatively normal total precipitation and one year with an El Niño event that ranked among the most severe on record (Field *et al.*, 2016). We ask three questions about the influence of land use and climate on soil respiration in tropical peatlands: (1) How do soil respiration and climate drivers vary on seasonal and interannual timescales in oil palm and forest? (2) How do soil respiration and drivers differ between land uses and spatial position within a land use? (3) Does soil respiration respond differently to climate drivers in oil palm and forest?

Materials and methods

Site description

We carried out the research at permanent plots established in 2012 by the Center for International Forestry Research in the area of Tanjung Puting National Park on the southern coast of Indonesian Borneo in Central Kalimantan (S 02° 49,410', E 111° 48.785' Figure 2a).

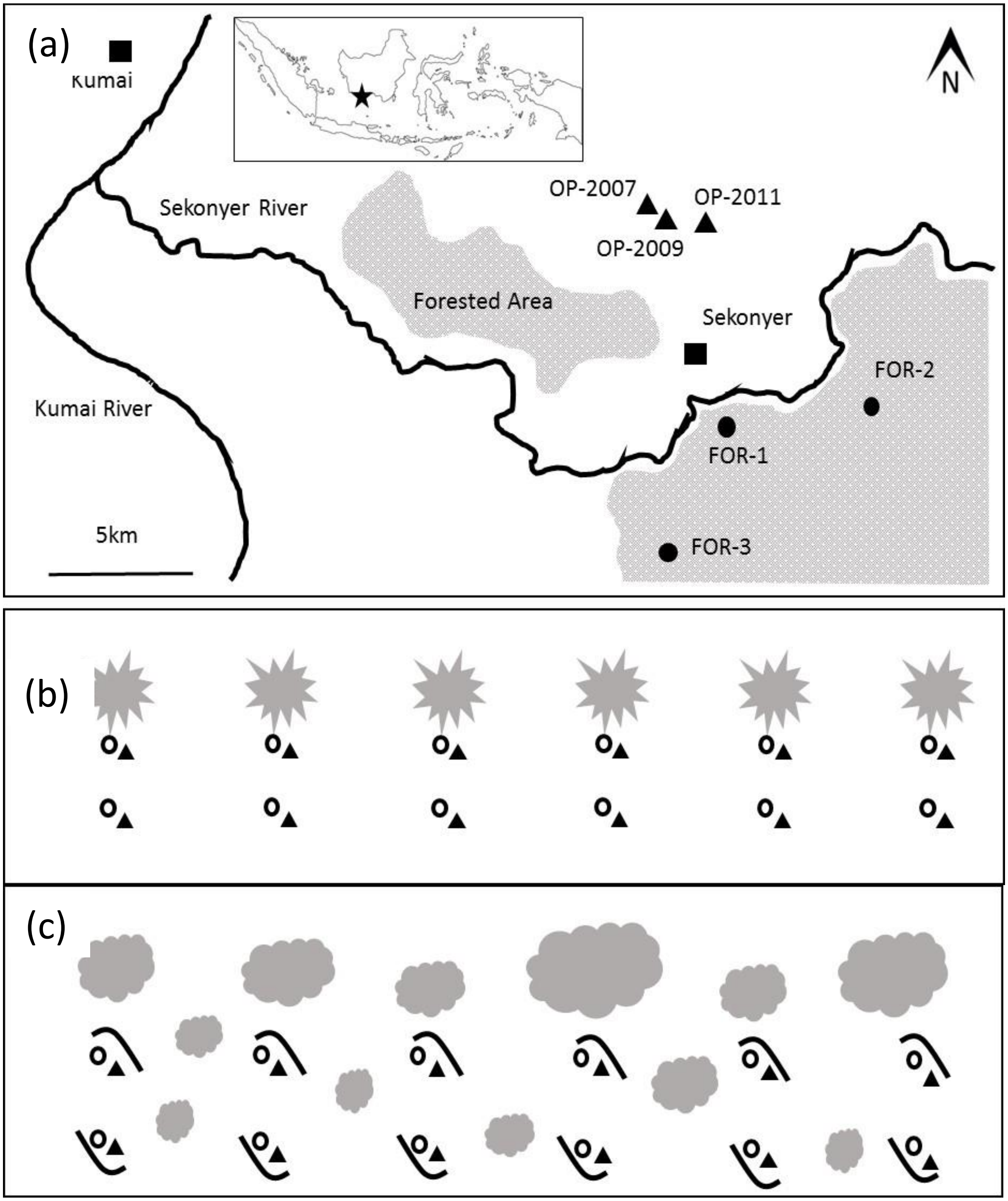


Figure 2. Research site and sampling design. Measurements were collected on the island of Kalimantan (inset) from three plots in undrained forest (FOR-1, FOR-2, FOR-3) and three plots in nearby smallholder oil palm plantations (OP-2007, OP-2009, OP-2011) (a). In each plot, CO_2 collars (circles) and dipwells (triangles) were installed at 6 subplot locations in oil palm (b) and forest (c). At each subplot, one collar and dipwell set was installed at the base of a palm and another at a distance of three meters from the palm in oil palm plots. In forest plots, we installed one set on a hummock and one set in the adjacent hollow. (after Swails et al., 2017)

Three plots were installed in smallholder oil palm plantations adjacent to the park and three in undrained peat forest inside the park boundaries for a total of six plots. The sampling site was located approximately 10 km outside the city of Pangkalan Bun. The climate of the region is humid tropical, characterized by high annual rainfall with average daily temperature remaining fairly constant during the year. To assess long term climate variables at the sampling location, we used daily weather observations at Iskandar airport in Pangkalan Bun obtained from the National Oceanic and Atmospheric Administration’s Climate Data Center. Mean annual temperature during 2004-2014 in Pangkalan Bun was 26.6^{o}C, with mean monthly temperature ranging from 26.1^{o}C in July to 27.2^{o}C in May. Mean annual rainfall over this period was 2058 mm and August was, on average, the driest month (105 mm).

The plots comprised a range of peat depths, land-use history and vegetation age (Table 1). The three forest plots were located at different distances from the edge of the main channel of the Sekonyer river. Peat depth varied in forest plots from less than 50 cm at the plot closest (0.5 km) to the river to over two meters at the plot located farthest from the river (2 km; Table 1).

Table 1. Characteristics of the sampling plots in Central Kalimantan, Indonesia. (After Swails et al., 2017)

Code	**Location**	**Landuse**	**Clearance Year**	**Plantation Age**	**Fires**	**Distance to River**	**Peat Depth**
FOR-1	S 02^{o} 49.410’ E 111^{o} 48.784’	Forest	pre 1982	-	Multiple	0.5 km	27 cm
FOR-2	S 02^{o} 49.341’ E 111^{o} 50.434’	Forest	-	-	-	1 km	155 cm
FOR-3	S 02^{o} 50.852’ E 111^{o} 48.155’	Forest	-	-	-	2 km	290 cm
OP-2011	S 02^{o} 47.379’ E 111^{o} 48.624’	Oil palm	1989	4 year	Multiple	3.5 km	20 cm
OP-2009	S 02^{o} 47.292’ E 111^{o} 48.190’	Oil palm	2005	6 year	Multiple	3.5 km	47 cm
OP-2007	S 02^{o} 47.230’ E 111^{o} 48.089’	Oil palm	2005	8 year	Multiple	3.5 km	47 cm

Two of the plots (FOR-2, FOR-3) were primary forests whereas the plot closest to the river was a 30 year old secondary forest (FOR-1), likely formerly used as an agroforestry garden (Novita 2016). Higher ash content in FOR-1 soils than FOR-2 and FOR-3 (Swails *et al.*, unpublished data) indicate the site was likely burned for agricultural purposes. The area was established as a National Park in 1982 and communities living inside it were moved to the other side of the Sekonyer river. 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 the area cleared in 1989, we installed one plot in a plantation established in 2011 (OP-2011). The palm trees were three years old at the beginning of our study. Another area cleared in 2005 also underwent cropping with rice and vegetables, likely experiencing multiple fires prior to the establishment of oil palm. We installed two other plots in this area, where palms were planted in 2009 (OP-2009) and 2007 (OP-2007). The palms in these plots were respectively five and seven years old at the beginning of the study. Our plots were nucleus estate smallholder plantations, an important and growing part of the palm oil industry in Indonesia. Smallholder plantations represent 40% of total oil palm area in Indonesia (BPS 2015), and accounted for roughly a third of national production in 2011 (Obidzinski *et al.,* 2012).

Palms were planted in a triangular design with inter-palm distance of 7-9 m (averaged 8 m) for a density of 150 palms ha^{-1}. Smallholders fertilized oil palm four times per year, most often in the months of March, June, September, and December. Fertilizer application was concentrated within a 200 cm radius of palms at a rate of 150 kg N ha^{-1} yr^{-1}, 84 kg P ha^{-1} yr^{-1}, and 124 kg K ha^{-1} yr^{-1} in the youngest plantation (OP-2011) decreasing to 120 kg N ha^{-1} yr^{-1}, 67 kg P ha^{-1} yr^{-1}, and 100 kg K ha^{-1} yr^{-1} in the oldest plantation (OP-2007). Fertilization rate in OP-2009 was not provided by the smallholder. Rates of fertilizer application reported by smallholders were comparable to observations elsewhere in Indonesia (e.g. 102 - 170 kg N ha^{-1} yr^{-1}, Darmosakoro *et al.*, 2003). 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} consistent with industry standards. Soil organic matter quality was higher and C:N ratio was lower in forest than oil palm (Swails *et al.*, 2017).

Monthly sampling regime

We collected measurements of total soil respiration and environmental parameters once each month from January 2014 through June 2015 and again in September 2015. Plots were sampled on consecutive days between the hours of 0800 and 1200. We took measurements of water table level, soil moisture and temperature at 5 cm depth, and air temperature concomitantly with CO_2 measurements. Bulk density samples were collected every two months at the same time as environmental parameter and CO_2 measurements. Daily precipitation, air temperature, and solar irradiance data for the area were obtained from Iskander Airport in Pangkalan Bun, 10 km away.

Our sampling approach was designed to capture spatial heterogeneity in soil respiration and environmental conditions (Figure 2b and 2c). Sixteen months before the beginning of this study, we installed sets of two PVC collars at six subplot locations for a total of 12 collars per plot. In oil palm plots, we installed at each subplot location one collar at the base of a palm (near) and one collar at mid-distance between two palms (far). In peat swamp forest, the microtopography is characterized by alternating raised mounds (hummocks) and depressions (hollows). In forest plots, at each subplot location we installed one collar on a hummock and one collar in the adjacent hollow. Total soil respiration was measured by the dynamic closed chamber method (Pumpanen *et al.*, 2009) with a portable infrared gas analyzer/EGM-4 (Environmental Gas Monitor) connected to a Soil Respiration Chamber (SRC-1) (PP System, Amesburry, USA). The chamber was placed on the permanent PVC collar (inner diameter 10.16 cm) inserted in the soil to 5 cm depth. CO_2 concentrations were recorded automatically at 4.5 seconds intervals for 80-124 seconds. At each collar, in addition to soil respiration, we measured water table level, soil temperature, and air temperature. Water table level was measured using dipwells permanently installed next to each CO_2 collar. Soil temperature was measured using a soil temperature probe, and air temperature using a pocket humidity/temperature pen (EXTECH 44550).

For soil moisture determination twelve samples were collected from the peat surface (0-5 cm) at randomly determined locations away from collars. Six sampling locations were representative of near/hummock conditions and six were representative of far/hollow conditions. Samples were collected using a metal scoop and wrapped in aluminum foil. Bimonthly bulk density samples were also collected away from collars. We took six samples per plot, three from near/hummock representative conditions and three from far/hollow representative conditions. Samples were collected from the peat surface using stainless steel rings (height 5 cm and diameter 8 cm). Soil moisture and bulk density samples were weighed in the field, stored in plastic bags for transport, and oven dried to constant mass at 60^{o}C in the laboratory (Warren *et al.*, 2012; Farmer *et al.*, 2014). Water-filled pore space (WFPS) values were calculated from bimonthly bulk density samples according to the method of Linn and Doran (1984) assuming a particle density of 1.3 g cm^{-3} (Firdhaus *et al.*, 2010).

For extrapolating variables at the plot scale, we determined the proportion that the near/far and hummock/hollow spatial positions represented. For this, in each forest plot we measured the length of hummocks and hollows along two perpendicular 50 m transects and divided the total length of hummocks by the total length of hollows to calculate the ratio of hummock to hollow area. In oil palm plots, we assume that measurements at collars near palms are representative of the area within a 2 m radius of the base of the palms. This is the zone where smallholders applied fertilizers and root density is usually highest (Comeau *et al*., 2016, Khalid *et al*., 1999). We calculated the area within a 2 m radius of the base of the palms using planting density and average palm diameter measured in each plot. Sensitivity analysis testing indicates this design adequately captures spatial variability in total soil respiration in mature oil palm plantations (Hergoualc'h et al., 2017). We obtained hummock to hollow ratios of 49:51 in FOR-1, 51:49 in FOR-2, and 57:43 in FOR-3. Near to far ratios in oil palm plantations were 25:75 in OP-2011, 27:73 in OP-2009, and 37:63 in OP-2007.

Soil sample collection for chemical analysis

Samples for chemical analysis of the soil profile were collected in September of 2014, using a systematic sampling regime. Within each plot, 6 cores were drawn from each of 3 locations using a Russian peat borer for a total of 18 samples per plot. At each location, 3 samples were located within 1 m of the palm or tree, and 3 samples were located at mid-distance between two palms or two trees. Peat cores were divided into depth interval segments of 0 – 10cm, 10 – 20cm, 20 – 30cm, 30 – 50cm, and 50 – 100cm. The 18 segments from each depth were composited to yield one composite sample per depth interval per plot. The samples were stored in plastic bags for transport from the field and air dried for 72 hours followed by sieving to < 2 mm and manual removal of remaining small roots. Three additional randomly located cores were drawn from each plot and divided into 0 – 10cm, 10 – 20cm, 20 – 30cm, 30 – 50cm, and 50 – 100cm segments for measurement of bulk density. Each bulk density sample segment was weighed in the field, wrapped in aluminum foil and stored in a plastic bag for transport and oven dried to constant mass at 60^{o}C in the laboratory.

Analysis of soil chemical properties

Analyses of total C and N content was carried out by Brookside Laboratories, New Bremen, Ohio on air-dried soil by dry combustion using a Thermo Scientific Flash 2000 CHNS/O analyzer. Brookside also conducted analysis of pH (1:1 in H_2O), mineral N (NO_3^- and NH_4^+) (1 N KCl cadmium reduction), and available P (Bray II), and total K, Ca, Mg, Al, Fe, Na, Cu, and S (Mehlich III extractable elements) on air-dried soil. We measured organic matter content at the University of Virginia by loss on ignition at 500°C for 180 minutes. All results are presented on an oven-dry (48 hours at 60°C) basis.

Calculations and statistical analysis

To compare total soil respiration and environmental parameters between land uses we calculated a weighted average of hummock/hollow and near/far measurements for each of the six subplot locations in each plot (six locations at three plots, n=18 per land use). Hummock/hollow and near/far conditions were compared using unweighted values measured at each collar in each plot (six hummocks in three plots (n=18) vs six hollows in three plots (n=18); six near in three plots (n=18) vs six far in three plots (n=18)). We used one-way repeated measures ANOVA with planned comparisons to assess differences in total soil respiration and environmental parameters between land uses and between spatial positions within each land use. We assessed values over the entire study period but also compared dry season months to wet season months. We considered months with total precipitation ≤ 100 mm “dry” months, and months with total precipitation > 100 mm “wet” months after Aini *et al.*, 2015. The dry season in Central Kalimantan has been defined as the period May-Oct and the wet season as Nov-Apr (Hirano *et al.*, 2007), based on a threshold monthly precipitation of 100 mm. Repeated measures ANOVA was computed using Statistical Analysis Software (SAS v 9.4). All other analyses were completed using R (v 3.2.5). We used Bartlett's test of equal variance and then Student's t-test or Welch's t-test with independent samples to compare values between land-uses and spatial conditions within plots month by month. We used paired t-tests to compare measurements collected within a land-use in Sep 2015 during the El Niño event to measurements collected a year earlier in Sep 2014, under typical climate conditions. Independent t-tests were used to detect differences in soil properties between forest and oil palm at each depth interval measured.

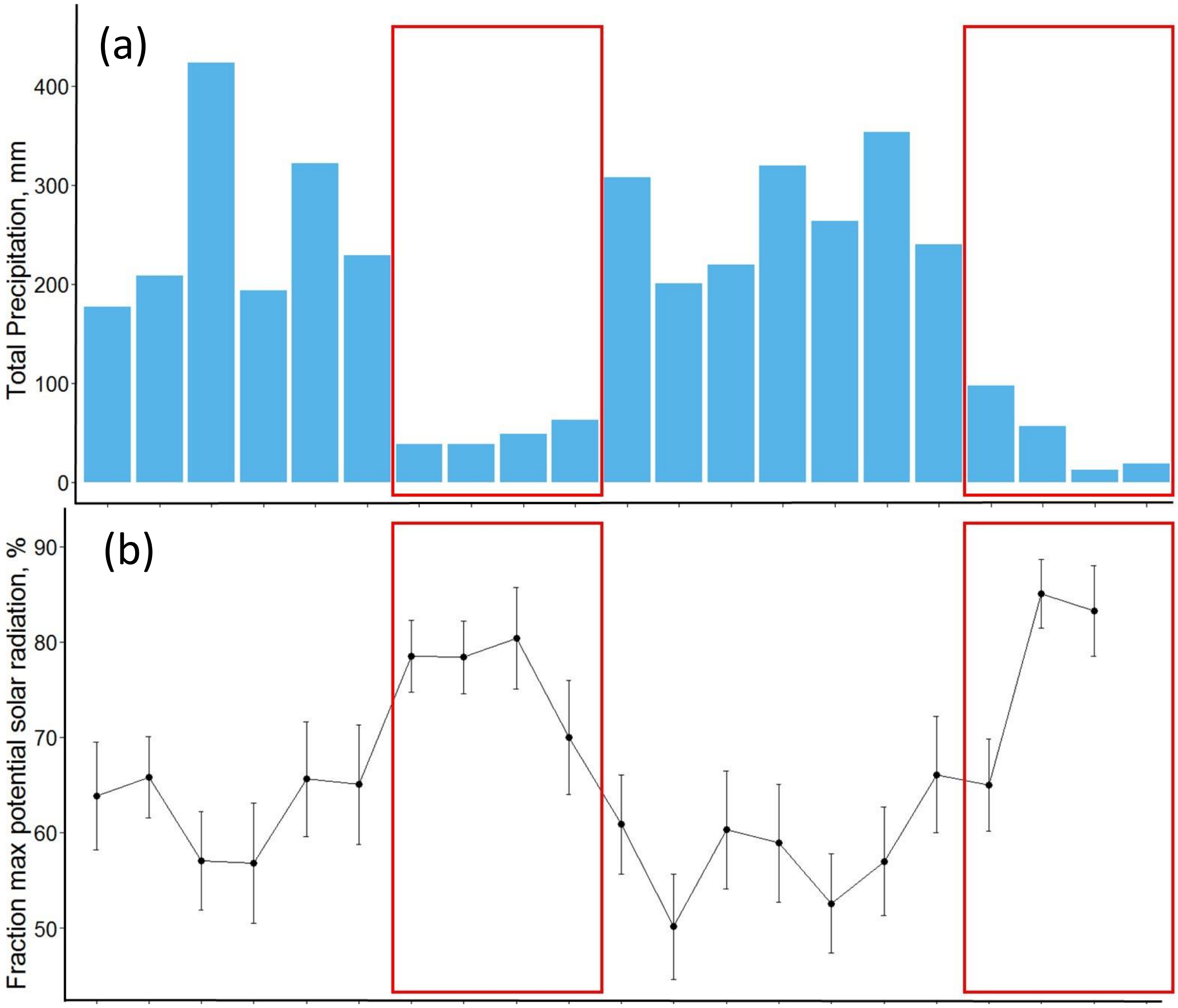
We calculated mean hourly rates of total soil respiration for each spatial position in each plot in oil palm and forest in each month during the monitoring period. Hergoualc'h et al. (2017) found no significant diurnal variation in total and heterotrophic soil respiration rates in oil palm or forest at our study site. Therefore, we multiplied hourly respiration rates by 24 to convert to daily respiration rates. To calculate a mean daily respiration rate between measurement points, we took the average of the two points. This value was extrapolated over the days intervening between the two measurements, and cumulative annual total soil respiration was calculated by annualizing the summed daily flux values over the entire monitoring period from January 2014 to September 2015. We used one-way ANOVA with Tukey HSD to test for differences in cumulative annual total respiration among plots in forest and oil palm, and independent t-tests to detect differences between land-uses and between spatial positions in each land use and each plot.

To test for relationships among total soil respiration and environmental parameters, we used univariate and backwards stepwise multiple linear regression with Aikake's Information Criterion (AIC) for model selection. For univariate regressions, we averaged measurements collected at hummock/near positions or hollow/far positions to yield two pooled values per month per plot for each measured parameter. For multiple regression, we combined weighted plot values to yield one value per month per land use for each measured parameter. We calculated variance inflation factors and used correlation analysis to check for relationships among environmental parameters in multiple regressions.

Results

Interannual and interseasonal variation in climate drivers

Annual precipitation during 2014 was 2250 mm, within the average variation for the previous 10 years of 2053 ± 217 mm. Monthly precipitation was ≤ 100 mm during the months of Jul-Oct 2014 and Jun-Oct 2015, and reached a high of 424 in the month of Mar 2014 (Figure 3a).



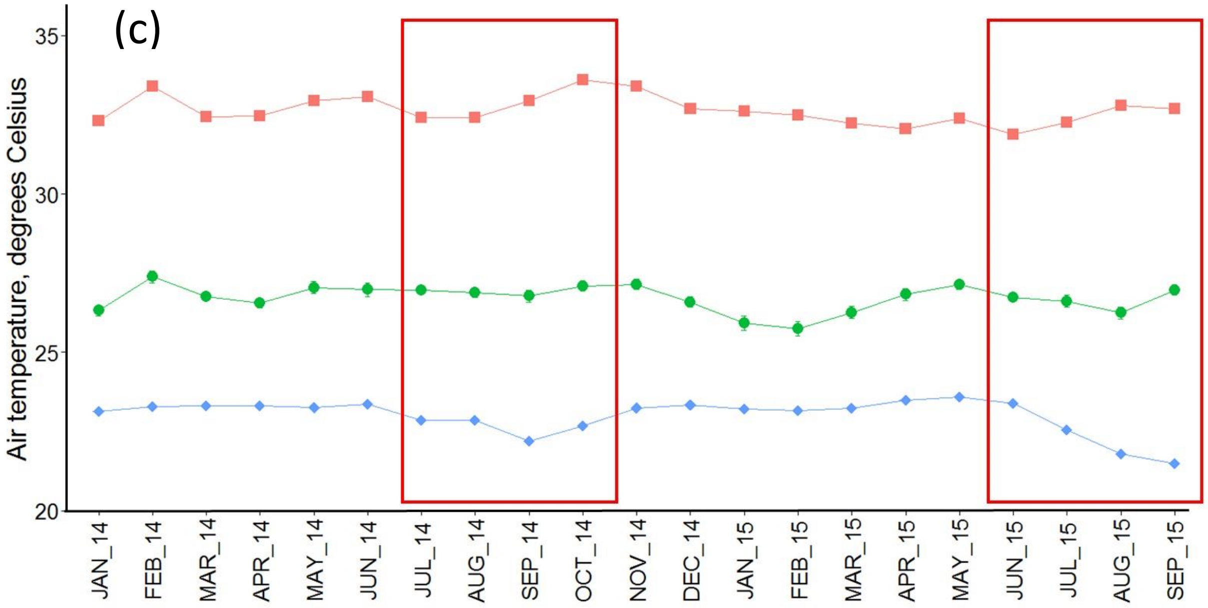


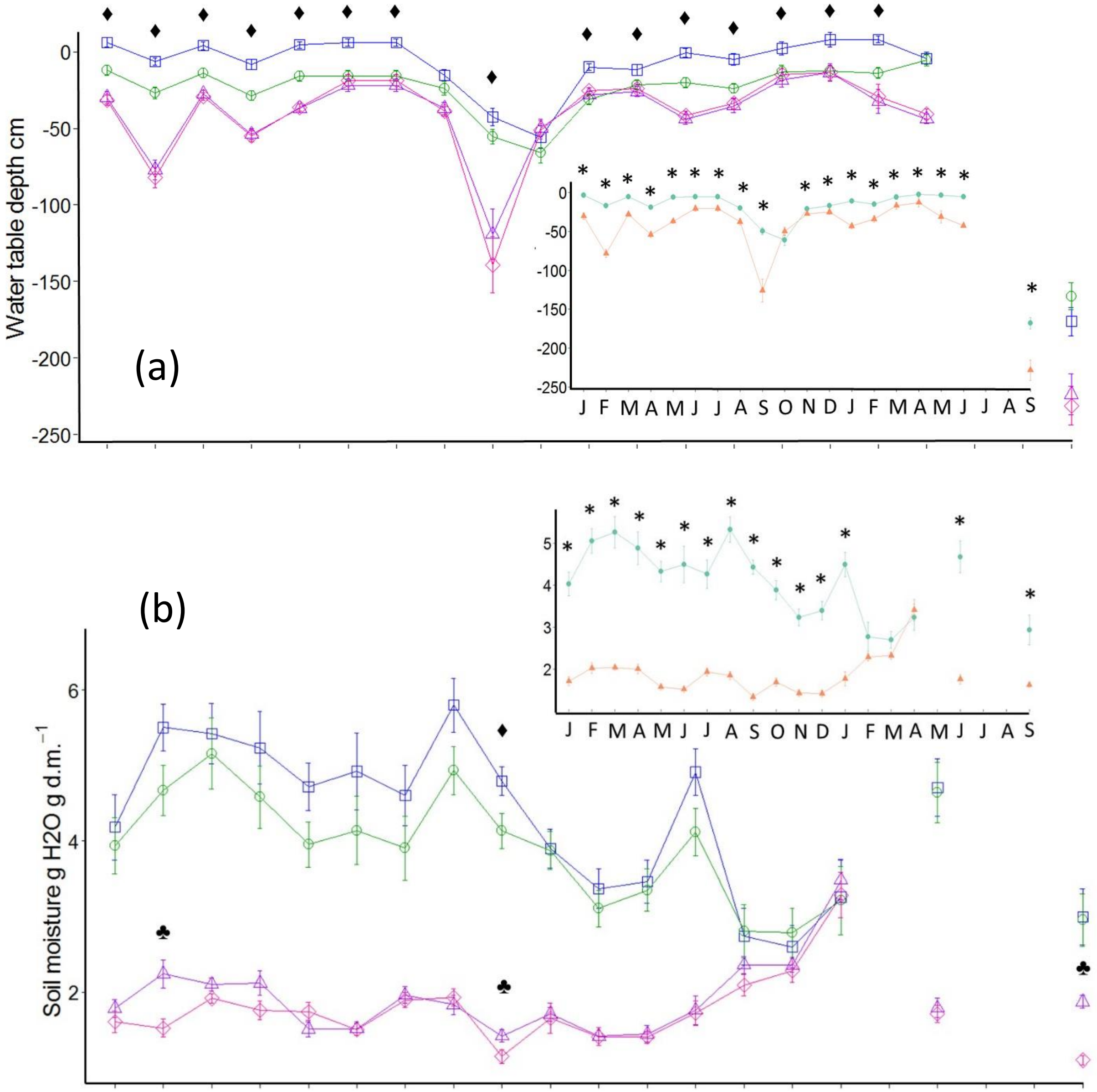
Figure 3. Total monthly precipitation (a), mean daily fraction maximum potential solar irradiance per month (b), and mean daily minimum (blue diamond), mean (green circle), and maximum (pink square) air temperature per month (c) measured at Iskandar airport in Pangkalan Bun, Indonesia. Error bars in (b) and (c) represent standard error of the mean. Months with total precipitation < 100 mm are indicated by red boxes.

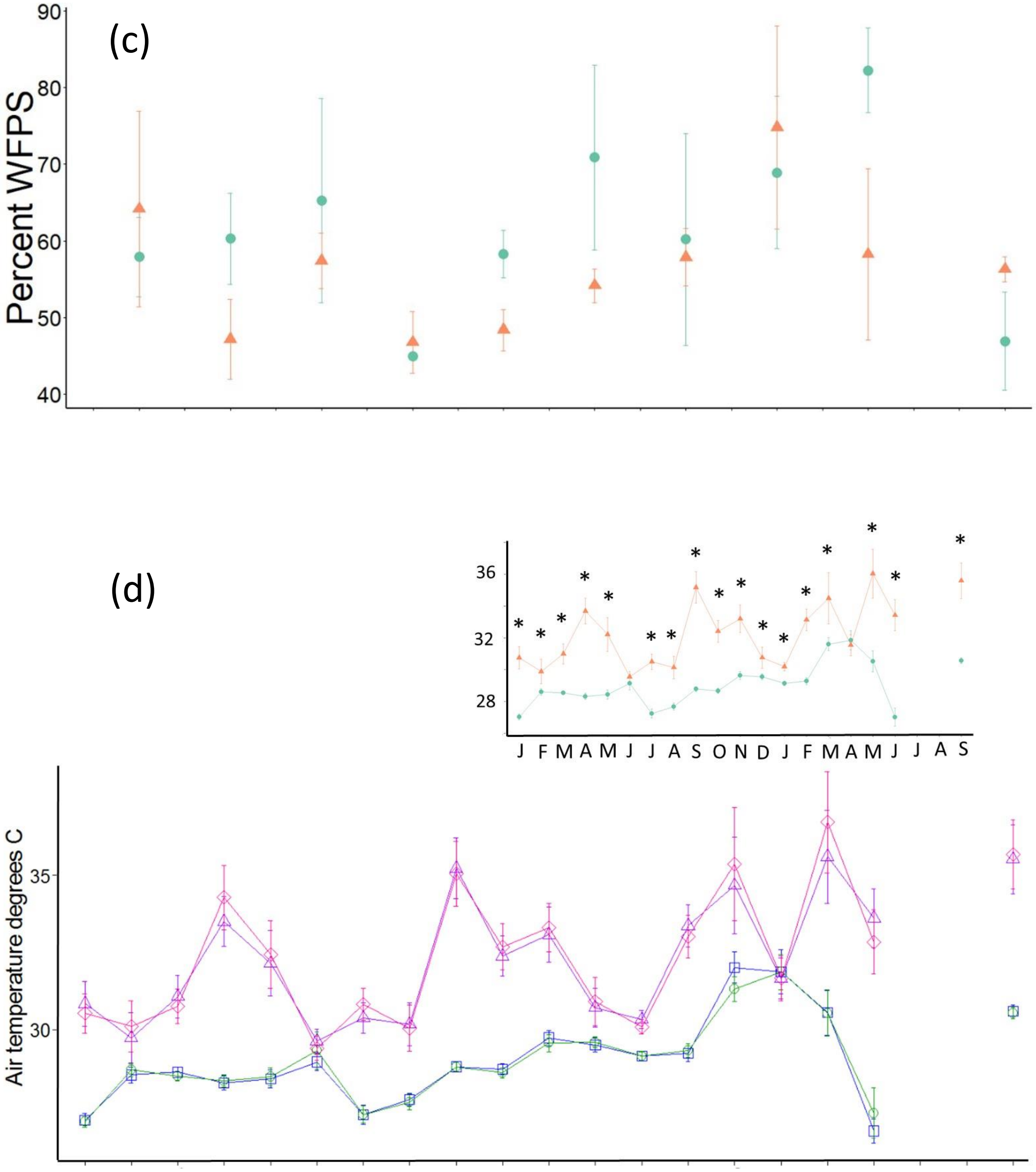
Monthly precipitation was lowest in Aug 2015 (13 mm). Total precipitation for the Nov-Apr wet seasons of 2013 – 2014 and 2014 – 2015, at 1531 and 1664 mm respectively, were higher than the wet season average of 1404 ± 108 mm for the preceding 10 years. Total precipitation for the May-Oct dry season in 2014 (740 mm) was similar to the previous 10 year dry-season average of 813 ± 123 mm while in 2015 dry season precipitation was lower (at 425 mm) than long-term averages. Mean daily percent maximum potential solar irradiance was highest (77%) during dry months and declined to 60% during wet months (Figure 3b). Mean monthly air temperature did not vary substantially month to month, fluctuating between 26.2 and 27.4 °C (Figure 3c), but mean daily temperature ranged from 23.7 to 29.2 °C. Temperature varied more on a diurnal basis, ranging from a mean low of 23.0 ± 0.12 °C to a mean high of 32.6 ± 0.10 °C. The temperature during which our measurements were taken (0800 to 1200 hours) ranged from 27.0 to 31.8 °C in forest and from 29.6 to 36.0 °C in oil palm.

Variation of environmental parameters

The water table was twice as deep in oil palm plots (-49.9 ± 6.3 cm) as in forest plots (-23.1 ± 6.3 cm, $p = 0.04$, Figure 4a) over the entire study period. Water table level was lower in dry months than in wet months in both land uses, decreasing from -34.1 ± 2.9 cm to -74.2 ± 3.1 cm in oil palm plots ($p < 0.0001$) and from -10.1 ± 2.9 cm to -51.5 ± 3.1 cm in forest plots ($p < 0.0001$). During El Niño in September 2015, the water table level was substantially lower than in September 2014 in both oil palm (109.6 cm lower, $p < 0.0001$) and forest plots (118.5 cm lower, $p < 0.001$, Figure 4a). In forest plots, water table level was twice as low in hummocks (-30.3 ± 1.0 cm) as in hollows (-15.4 ± 1.0 cm) over the entire period of the study ($p < 0.0001$), driven by a significant difference during wet months ($p < 0.0001$). During dry months, there was no significant difference in water table level between hummocks and hollows. Distance from palm did not affect water table level in oil palm plots.

Soil moisture was twice as high in forest plots (4.1 ± 0.3 g H_2O g^{-1} d.m.) than in oil palm plots (1.9 ± 0.3 g H_2O g^{-1} d.m., $p = 0.01$, Figure 4b) over the entire study period. Soil moisture was lower in dry than in wet months in both forest (4.0 ± 0.1 g H_2O g^{-1} d.m. versus 4.3 ± 0.2 g H_2O g^{-1} d.m., $p = 0.042$) and oil palm (1.7 ± 0.2 g H_2O g^{-1} d.m. versus 2.0 ± 0.1 g H_2O g^{-1} d.m., $p < 0.0001$). During El Niño, soil moisture was lower than in September the previous year in forest plots ($p < 0.0001$) but not oil palm plots. In forest plots, soil moisture was higher in hollows (4.2 ± 0.4 g H_2O g^{-1} d.m.) than hummocks during wet months (3.9 ± 0.4 g H_2O g^{-1} d.m., $p = 0.0039$), but not during dry months or overall. In oil palm plots, soil moisture was higher far from palms (1.9 ± 0.1 g H_2O g^{-1} d.m.) than near palms (1.8 ± 0.1 g H_2O g^{-1} d.m., $p = 0.02$) over the entire study period. Though soil moisture was higher in forest than oil palm, WFPS was not significantly different overall between the two land uses (61.6 ± 4.5% in forest and 56.5 ± 4.5% in oil palm, Fig 4c), owing to higher soil bulk density in oil palm (p = 0.0053, Table 3).

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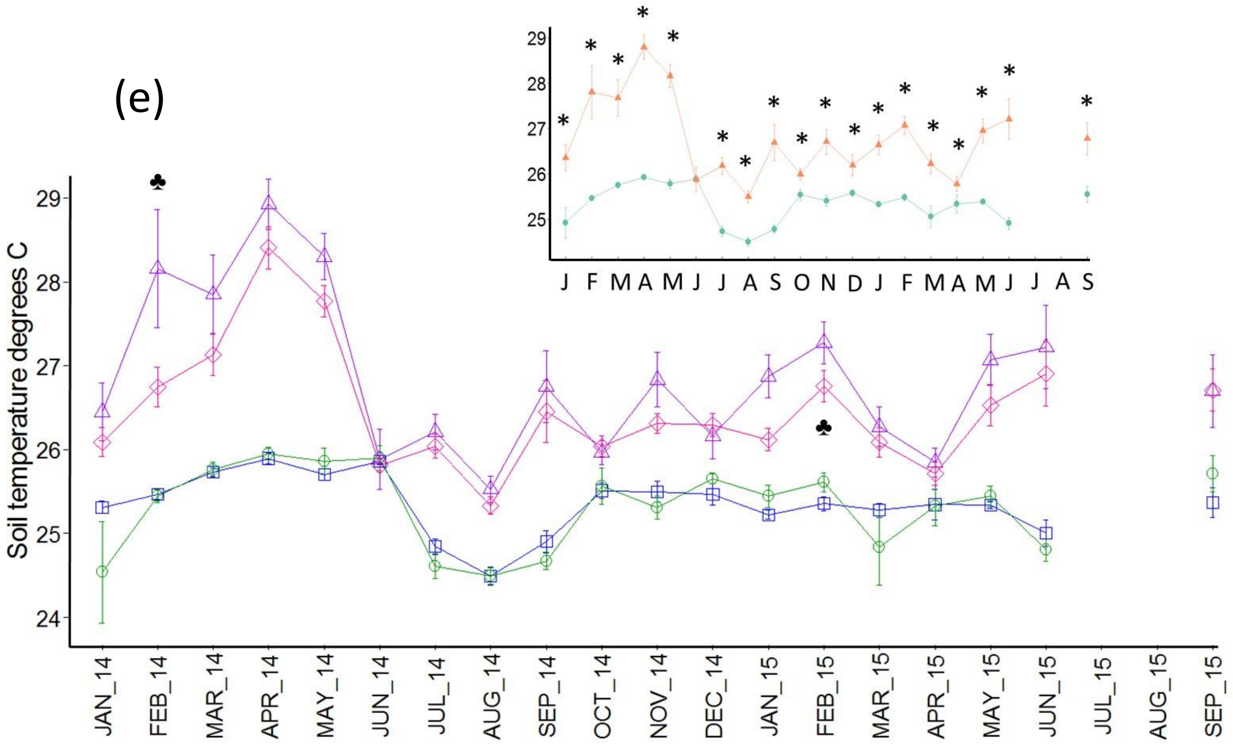

Figure 4. Mean water table depth (a), soil moisture (b), water filled pore space (c), air temperature (d), and soil temperature (e) in forest hummock (green open circle) and hollow (blue open square), and near (pink open diamond) and far from oil palms (purple open triangle) from January 2014 through September 2015. n=3 for (c) and n=18 for all other. Mean overall environmental parameter values are indicated with orange solid triangle for oil palm and green solid circle for forest (n=3). Error bars represent standard error of the mean. * indicates months with significant differences between land uses, ♦ significant difference between hollow/hummock in forest plots, ♣ significant differences between near/far in oil palm plots.

Air temperature and soil temperature were both higher in oil palm plots (32.3 ± 1.0 ^{o}C for air, 26.8 ± 1.0 ^{o}C for soil) than in forest plots (29.0 ± 1.0^{o}C and 25.3 ± 1.0 ^{o}C, respectively) over the entire study period ($p < 0.0001$ for both air and soil, Figure 4d and 4e). In forest plots, air temperature was higher in wet months than in dry months (+1.1 ^{o}C, $p < 0.0001$), but in oil palm air temperature was higher in dry months (+0.9 ^{o}C, p = 0.). Soil temperature was higher in wet than in dry months in both forest (+0.5 ^{o}C, $p < 0.0001$) and oil palm (+0.6 ^{o}C, $p < 0.0001$). During September of El Niño, both air and soil temperatures were higher than in September of the previous year in forest (+1.8 ^{o}C air, $p < 0.0001$; +0.77 ^{o}C soil, p = 0.0005), but not in oil palm. Soil temperature was 0.4°C and 0.3°C higher far from palms than near palms during, respectively, wet months ($p < 0.0001$) and overall ($p = 0.0013$) but similar at the two spatial positions during dry months. Air temperature did not differ near and far from palms. Hummocks and hollows had similar air and soil temperatures during the study period.

Total soil respiration

Total soil respiration was 22% higher in oil palm plots (0.71 ± 0.04 g CO_2 m^2 hr^{-1}) than in forest plots (0.58 ± 0.04 g CO_2 m^2 hr^{-1}, Figure 5) during the study period ($p = 0.0494$), driven by a significant difference during wet months ($p = 0.0020$). During dry months, soil respiration did not differ significantly between the two ecosystems. In oil palm plots, soil respiration was 19% higher in dry months (0.80 ± 0.06 g CO_2 m^2 hr^{-1}) than in wet months (0.67 ± 0.04 g CO_2 m^2 hr^{-1}, $p = 0.0003$), but the increase in total soil respiration during dry months was smaller than in forest. Soil respiration rate in forest plots during dry months (0.84 ± 0.06 g CO_2 m^2 hr^{-1}) was almost twice the rate in wet months (0.47 ± 0.04 g CO_2 m^2 hr^{-1}, $p < 0.0001$). During El Niño in September 2015, the increase was so great that total soil respiration was 38% higher in forest (1.24 ± 0.20 g CO_2 m^2 hr^{-1}) than in oil palm (0.90 ± 0.09 g CO_2 m^2 hr^{-1}, $p = 0.03$). In forest, soil respiration responded strongly to dry conditions in the normally wet hollows. Total soil respiration was higher in September 2015 than September 2014 in forest ($p=0.007$) but not oil palm.

Soil respiration was 17% higher in hummocks (0.62 ± 0.03 g CO_2 m^2 hr^{-1}) than in hollows (0.53 ± 0.03 g CO_2 m^2 hr^{-1}) overall and during wet months ($p < 0.001$), but not during dry months (Figure 5b). During extremely dry El Niño conditions, this effect was reversed: Soil respiration from hollows was almost three times higher than soil respiration from hummocks (2.37 ± 0.34 vs. 0.80 ± 0.18 g CO_2 m^2 hr^{-1}, $p = 0.0008$, Figure 6b). In oil palm plots, total soil respiration was higher near palms than far from palms (Figure 6c), during wet months (27% higher, $p < 0.0001$), dry months (64% higher, $p = 0.0004$) and during El Niño conditions (114% higher, $p = 0.0072$).

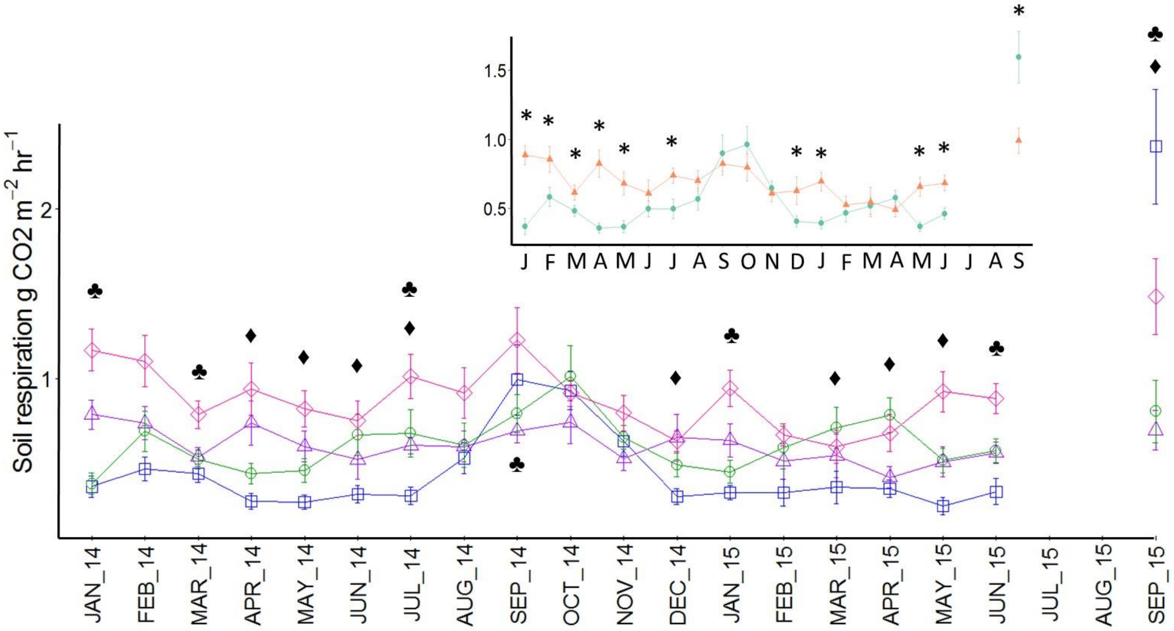

Figure 5. Mean total soil respiration in forest hummock (green open circle) and hollow (blue open square) (b), and near (pink open diamond) and far from oil palms (purple open triangle) from January 2014 to September 2015 (n=18). Mean overall total soil respiration values in oil palm (orange solid triangle) and forest (green solid circle) plots are shown in the inset (n=3). Error bars represent standard error of the mean. * indicates months with significant differences between land uses; ♦ significant difference between hollow/hummock in forest plots and ♣ significant differences between near/far in oil palm plots.

Cumulative annual soil respiration measured between January 2014 and September 2015 was higher in hummocks than hollows in forest plots ($p=0.0005$) and higher near palms than far from palms in oil palm plots ($p=0.002$, Table 2). Cumulative annual rates in forest and oil palm were only marginally different during the monitoring period ($p=0.055$).

Table 2. Total cumulative annualized soil respiration in each plot and spatial condition. Data are presented as mean ± standard error from January 2014 to September 2015. a and b indicate significant differences between spatial condtions within a landuse or individual plot. c and d indicate significant differences between plots within a land-use. No letters are displayed in the absence of a significant difference.

		CO_2 (t ha^{-1} yr^{-1})		
Landuse	Plot	Hummock/Near	Hollow/Far	Total
Forest		62.9 ±4.9 ^{a}	40.2 ±2.9 ^{b}	54.0 ±4.5
	FOR-1	68.6 ±9.6	53.2 ±5.5	60.8 ±2.5^{c}
	FOR-2	62.8 ±7.9 ^{a}	38.1 ±3.0 ^{b}	50.2 ±2.7^{d}
	FOR-3	60.5 ±9.6	38.3 ±6.3	51.0 ±2.9^{d}
Oil Palm		80.0 ±6.6 ^{a}	53.3 ±5.0 ^{b}	62.0 ±3.5
	OP-2007	87.5 ±12.4 ^{a}	39.4 ±1.5 ^{b}	57.2 ±1.9 ^{c}
	OP-2009	85.4 ±13.6	75.7 ±4.3	78.3 ±1.9 ^{d}
	OP-2011	67.0 ±4.7	44.8 ±9.0	50.4 ±2.3 ^{c}

Soil properties

Forest soils had higher total N than oil palm soils at 0-10cm and 10-20cm (p=0.03 and p=0.005 0.02 respectively, Table 3). As soil total C was similar in the two land-uses, CN ratio was accordingly lower in forest than in oil palm at both depths (0-10cm, p=0.03 and 10-20 cm, p=0.005). K content was also higher in forest soils (p<0.01). N and K content decreased and CN ratio increased with depth in both forest and oil palm plots. Soil mineral N and mineral P in the top 0-20cm of soil were highly variable among oil palm plots and not different between the two land-uses.

Table 3. Chemical properties of the peat soil profile in forest and oil palm (n=3 per depth interval). Mean values are presented with standard error. a and b indicate significant differences between forest and oil palm at the same depth. BD bulk density. OM organic matter. No letters are displayed in the absence of a significant difference.

Property	Depth (cm)	Forest	Oil Palm
BD (g cm^{-3})	0-5	0.20 ±0.02 ^{a}	0.34 ±0.01 ^{b}
	10-20	0.31 ±0.08	0.29 ±0.05
	20-30	0.46	0.37
	30-50	0.36	0.38
	50-100	0.33	
pH	0-10	3.97 ±0.07	3.70 ±0.20

	10-20	3.97	±0.12	3.67	±0.07
	20-30	4.05		3.60	
	30-50	4.10		3.50	
	50-100	4.25			
OM (%)	0-10	67.7	±7.2	73.0	±2.8
	10-20	63.9	±6.5	63.7	±9.8
	20-30	69.2		66.4	
	30-50	77.5		55.8	
	50-100	69.7			
C (%)	0-10	43.3	±4.9	43.2	±3.2
	10-20	43.4	±4.5	42.4	±5.4
	20-30	48.7		42.7	
	30-50	53.0		36.6	
	50-100	50.0			
N (%)	0-10	1.94	±0.28 ^{a}	1.35	±0.16 ^{b}
	10-20	1.76	±0.13 ^{a}	0.87	±0.18 ^{b}
	20-30	1.60		0.78	
	30-50	1.14		0.63	
	50-100	1.08			
CN	0-10	22.3	±1.5 ^{a}	32.2	±2.6 ^{b}
	10-20	24.7	±1.7 ^{a}	50.6	±4.4 ^{b}
	20-30	30.7		55.7	
	30-50	46.9		57.9	
	50-100	46.3			
$NH_4^+ + NO_3^-$ (mg kg^{-1})	0-10	18.92	±0.63	27.05	±3.95
	10-20	17.75	±0.42	19.32	±2.84
	20-30	14.88		18.99	
	30-50	12.31		12.73	
	50-100	10.71			
Bray II P (mg kg^{-1})	0-10	6.15	±0.51	11.01	±7.15
	10-20	6.64	±1.85	3.61	±0.92
	20-30	3.92		2.76	
	30-50	2.86		1.62	
	50-100	1.67			
K (mg kg^{-1})	0-10	71.9	±3.6 ^{a}	42.3	±3.7 ^{b}
	10-20	54.5	±3.3 ^{a}	22.5	±2.7 ^{b}
	20-30	36.4		17.7	
	30-50	18.9		10.8	
	50-100	10.6			

Linking total soil respiration and environmental drivers

Total soil respiration increased as water table level became lower in both forest and oil palm plots (Figure 6a). The response to water table level in forest plots was driven by a strong linear relationship in hollows. Total soil respiration quadrupled in hollows as water table level decreased from +20 to -200 cm. In hummocks, the relationship between soil respiration and water table depth was very weak and the rate of increase in soil respiration was greater when the water table was near the peat surface. In oil palm, the response of total soil respiration to water table level was weak but significant near palms.

Total soil respiration increased with decreasing soil moisture near palms in oil palm plots but not in forest plots (Figure 6b). Total soil respiration did not vary with air temperature or soil temperature in forest or oil palm ecosystems considered separately. However, across forest and oil palm plots, there was an extremely weak but significant positive relationship between total soil respiration and air temperature ($R^2 = 0.04$, $p = 0.001$) and soil temperature ($R^2 = 0.02$, $p = 0.03$).

The multiple regression analysis indicated that water table depth, soil moisture, air temperature, and soil temperature accounted for 91% of temporal variation in total soil respiration in forest ($p < 0.0001$) and 56% of temporal variance in oil palm ($p = 0.004$). In both models the only significant parameter was water table depth. Variance inflation factors (VIF) were < 2.25 for all parameters included in the models, though air temperature was correlated negatively with soil moisture in forest ($R = -0.65$, $p > 0.01$). VIF for solar radiation was >3 and insignificant in both oil palm and forest models and therefore excluded from the analysis. Models generated with backward stepwise multiple linear regression included water table depth, air temperature, and soil temperature for forest; water table depth and air temperature in oil palm.

The step-wise model explained 76% of temporal variation in total soil respiration in forest ($p < 0.0001$). Water table depth was the most important parameter in the forest model (standard partial regression coefficient (sprc) = -0.85), followed by air temperature (sprc = 0.25) and soil temperature (sprc = -0.24). The step-wise model explained 41% of temporal variance in total soil respiration in oil palm ($p = 0.01$). Water table depth was the most important parameter (sprc = -0.74), followed by air temperature (sprc = -0.34).

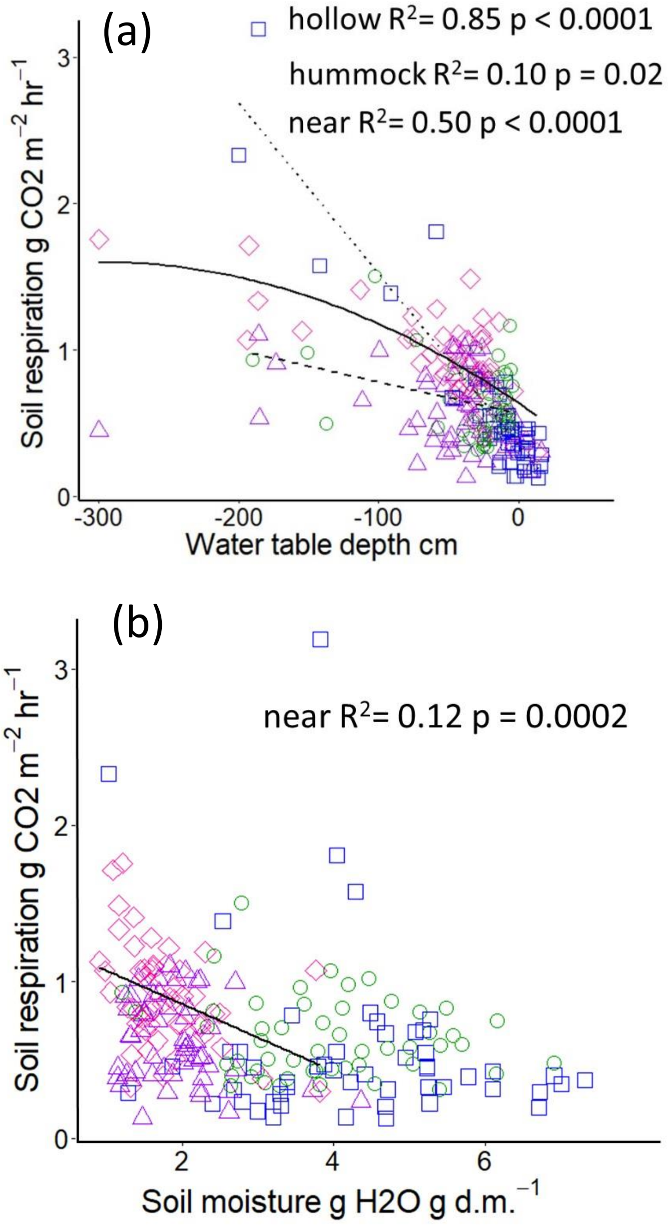

Figure 6. Total soil respiration as a function of water table depth (a) and soil moisture (b) in forest hollow (green circle and dotted line) and hummock (blue square and dashed line), and near (pink diamond and solid line) and far from oil palms (purple triangle). Each data point represents the average of all hummock/near or hollow/far collars in each plot in a month (n=57).

Discussion

Drivers of total soil respiration in forest and oil palm

Overall, moisture regime was a more important driver than air and soil temperature for explaining variation in total soil respiration in forest and oil palm plots. In forest plots total soil respiration was closely related to water table level in hollows. These results agree with other studies of total soil respiration in tropical peat forest which also found increased soil respiration rates as the water table falls further below the soil surface and the peat profile becomes increasingly oxygenated (e.g. Hirano *et al.*, 2007, 2009; Marwanto and Agus 2014; Hergoualc'h et al., 2017). The relationship between groundwater level and soil CO_2 emissions varies among land covers in tropical peatlands (Jauhianen *et al.*, 2008; Hirano *et al.*, 2012) and is not significant in some drained peatlands in Indonesia (Jauhianen *et al.*, 2012, Comeau *et al.*, 2013).

The relationship between water table level and soil respiration was weaker in our oil palm plantations. The weaker response in oil palm than in forest plots is in part due to the fact that by design, in oil palm plantations the water table level is maintained by drainage. Average drainage depth in the smallholder plantations (-50 cm) was between best management practices for oil palm cultivation on peat (-40 cm, Lim *et al.*, 2012) and standard practice in industrial plantations of -60 cm (Hergoualc'h and Verchot 2014).

Lowering of the water table and associated drying should enhance total soil respiration to a point, but excessive drying could result in desiccation of surface layers which can inhibit both microbial and root activity. Desiccation of surface layers could explain the declining response of total soil respiration to decreased water table level in our oil palm plots (Figure 6a). This response is also consistent with declining microbial activity as deeper soil layers become aerated: substrate quality declines with depth (higher C:N) in our plots (Table 3) and in other Indonesian peats (Wright *et al.*, 2011). As reported elsewhere, substrate quality also limits soil CO2 flux in our plots (Swails *et al.*, 2017).

Unlike water table depth, soil moisture in oil palm plantations varies more with time since the last rain event as well as plant water uptake. In our oil palm plots, total soil respiration increased as soil moisture decreased near palms. However, as discussed further below, increased root activity may have resulted in lower soil moisture near palms, instead of lower soil moisture driving increased respiration; respiration was not related to soil moisture far from palms where root density was lower (Hergoualc'h *et al.*, 2017). We did not detect a relationship between total soil respiration and soil moisture in forest plots. Peat swamp forest often has a shallow or positive water table and the peat remains wet, wetter than in plantations, for some time even when the water table drops. However, there was a correlation between soil moisture and air temperature in forest that may have masked the influence of soil moisture on total soil respiration in forest in combination with other factors.

As a single driving factor, air or soil temperature had only a very weak effect on soil respiration across land uses and no effect when the land uses were considered separately. However, in both forest and oil palm, temperature helped to explain variation in total soil respiration when combined with water table level. Marwanto and Agus (2014) also noted a lack of influence of air and soil temperature on total soil respiration in oil palm plantations on peat in the Indonesian province of Jambi, Sumatra. Total soil respiration has been found to increase with soil temperature in tropical peat forest; the influence of soil temperature at our plots may have been masked by other more influential variables. Both soil temperature and air temperature were overall higher in wet months in forest plots, when water table level was highest, than dry months.

Variation in soil respiration and drivers by subplot condition

We found higher total soil respiration near palms than far from palms, which is consistent with existing observations in oil palm plantations (Comeau *et al.*, 2016; Dariah *et al.*, 2014; Goodrick *et al.*, 2016). The reduced soil moisture near palms, as observed here, was attributed by Nelson et al. (2006) to root activity of the palms. Thus, lower soil moisture and higher total soil respiration near palms is evidence that roots may have increased total soil respiration directly near palms, through root respiration. Reduced soil moisture may have also enhanced microbial decomposition near palms. In addition, palms may have enhanced microbial decomposition through root exudation and senescence, with labile carbon inputs priming microbial decomposition or simply adding substrate (Goodrick *et al.*, 2016). A combination of these mechanisms - root uptake and peat drying, root exudation and priming or adding to decomposition, or root respiration - could explain higher soil respiration near palms.

In forests, where water table level was usually near or above the soil surface, hollows were wetter than hummocks. Total soil respiration was higher in hummocks than hollows, and soil respiration was more responsive to water table level in hollows. These results are consistent with previous observations of higher total soil respiration in hummocks at our site (Hergoualc'h *et al.*, 2017) and elsewhere in Central Kalimantan (Jauhianen *et al.*, 2005) and greater sensitivity to water table levels in hollows (Jauhianen *et al.*, 2005). Higher respiration from hollows than hummocks during extremely dry conditions, as we found in September 2015, has not been reported elsewhere.

ENSO and peat CO_2 emissions under climate change

We sampled total soil respiration and environmental parameters over temperature and moisture conditions representative of a potential future climate regime in Indonesia characterized by more severe El Niño events. ENSO reduced dry season precipitation one standard deviation below the ten year average in 2015. These observations reflect conditions in other parts of Indonesia in the second half of 2015. Almost no rain fell over Southern and Central Kalimantan in September 2015, as well as Southern Sumatra and the island of Java (Voiland, 2015). Recent climate projections indicate increased ENSO frequency and severity in the future (Chadwick et al. 2013, Power et al. 2013, Cai et al. 2014).

In this study, conversion of forest to oil palm increased total soil respiration by 22% in a normal year, but the sensitivity of soil respiration to extreme drying and warming was greater in forest than in oil palm. In Sep 2015, a dry year, compared to Sep 2014, a year with normal precipitation, soil respiration in forest increased by113%, and for a brief period total soil respiration was higher in forest than oil palm. Both autotrophic and heterotrophic respiration likely contribute to increased total soil respiration under increasingly dry conditions. Drainage aerates plant roots and enhances plant productivity, while also encouraging CO_2 production from microbial decomposition of peat. Only heterotrophic respiration contributes to net CO_2 emissions from the decomposition of peat soils. Heterotrophic respiration accounts for approximately 50% of total soil respiration in forest and 70% in oil palm under normal precipitation conditions (Hergoualc'h *et al.*, 2017). Assuming similar ratios during the extreme drying associated with El Niño, rates of heterotrophic respiration were roughly equal in our forest and oil palm plots in September 2015. However, Hergoualc'h et al., (2017) found that the contribution of heterotrophic respiration to total soil respiration increased with higher litterfall during the previous or concurrent month in our plots, and increased rates of litterfall have been observed in tropical peat swamp forests during El Niño in Central Kalimantan (Harrison *et al.*, 2007). Likewise, the contribution of heterotrophic respiration to total respiration increased as soil moisture declined in our oil palm plots (Hergoualc'h et al., 2017). The contribution of microbial decomposition to total respiration in both forest and oil palm on peat could increase during El Niño. Increased frequency and severity of El Niño events in the future could tip Indonesian peatlands to become a net source of C emissions to the atmosphere.

Though throughfall reduction experiments have found no effect of short-term or prolonged drought on soil CO_2 efflux in tropical forests on mineral soils (Davidson *et al.*, 2008, van Straaten et al. 2010; Ohashi et al., 2015), global scale modeling indicates increased heterotrophic soil respiration from tropical ecosystems during El Niño years (Zeng *et al.*, 2005). The El Niño response in our forest plots may have been driven in part by higher organic matter content in peat compared to mineral soil. Higher quality substrate can support increased rates of microbial activity. Additionally, in peatlands the water table level is closer to the soil surface than in upland forests, even in drained peat, and therefore more limiting to both heterotrophic and autotrophic soil respiration. Reduced precipitation during El Niño (Figure 3a) had such a severe effect on water table levels, soil moisture, air and soil temperature in forest plots, that forest plots surpassed oil palm plots in total soil respiration. This was true despite a lower water table, lower soil moisture and higher air and soil temperature in oil palm plots. The greater sensitivity of respiration to drying in our forest soils may be explained by higher nutrient content and peat organic matter quality than oil palm soils (Swails *et al.*, 2017).

For evaluating how climatic variation, specifically El Niño, could impact net peat C emissions, all components of the C budget need to be considered, including above and belowground C inputs, and C outputs through heterotrophic respiration, as well as dissolved organic and inorganic carbon losses. Nonetheless, microbial respiration represents an important part of this budget, accounting for at least half of the increase in total soil respiration due to conversion from forest to oil palm (Hergoualc'h & Verchot, 2011). Much more work is needed to understand how the heterotrophic component of soil respiration responds to El Niño, with wider sampling across the region. Increased frequency and severity of El Niño could push Indonesian peatlands past the tipping point where climate becomes a stronger driver of soil CO_2 emissions than land-use change.

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CHAPTER THREE

Will CO_2 emissions from drained tropical peatlands decline over time? Links between soil organic matter quality, nutrients, and C mineralization rates

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 CO_2 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 CO_2 production by forest soils (10.80 ± 0.23 µg CO_2-C g C hr^{-1}) compared to oil palm soils (5.34 ± 0.26 µg CO_2-C g C hr^{-1}) from Kalimantan. These factors also explained lower rates in Sumatran oil palm (3.90 ± 0.25 µg CO_2-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 CO_2 production, in unamended and amended soils. P addition raised CO_2 production when substrate quality was high and initial P state was low. Glucose addition raised CO_2 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 CO_2 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 CO_2, CH_4, and N_2O 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; Sjörgersten *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 7). 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 CO_2 production from microbial decomposition of peat by altering the quality of peat substrate available for decomposition.

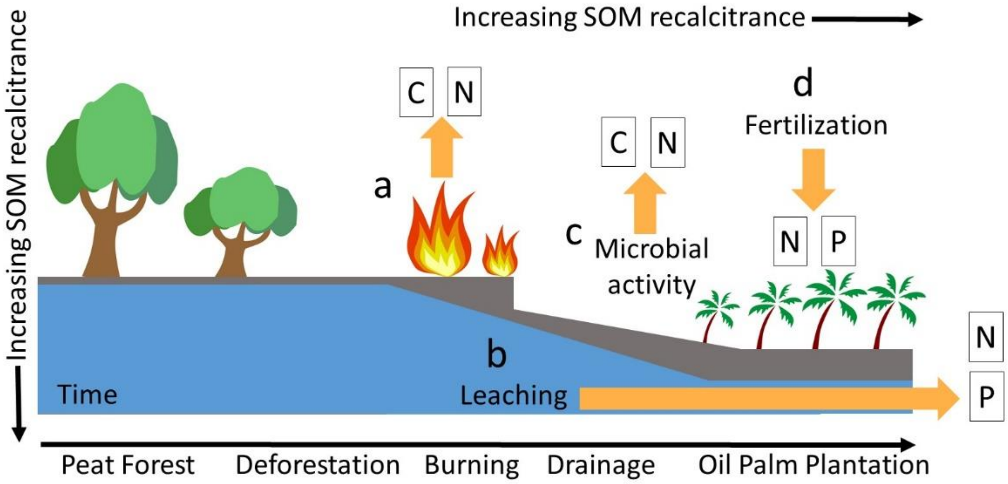

Figure 7. Conceptual model of changes in peat soil organic matter quality (SOM) and nutrient availability associated with conversion of tropical peat swamp forest to oil palm plantation. Burning results in removal of surface peat layers (a) and enhances drainage-facilitated leaching of N and P (b). Microbial 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 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.

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 CO_2 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 CO_2 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 4).

Table 4. Soil chemical properties measured on Southeast Asian peats.

	This study		**Previous studies**		
Property	**Mean**	**Range**	**Mean**	**Range**	**Reference**
pH	3.9	3.7 – 4.1	3.8	3.2 – 4.8	d), e), h), i)
OM (g 100 g^{-1})	77	47 – 93	96.0	45.0 – 99.8	c), d) ,h) , i)
C (g 100 g^{-1})	45	28 – 55	53.7	30.9 – 66.2	a), b), d), e), f), h), i)
N (g 100 g^{-1})	1.7	1.3 – 2.3	1.7	1.3 – 2.3	b), d), e), i)
C:N	26.3	20.3 – 30.0	36.4	24.6 – 47	b), d), e)
$NH_4^+ + NO_3^-$ (mg kg^{-1})	79.7	29.4 – 184.2	169.1	20.6 – 472.5	b), e), k)

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

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^{o} 49,410’, E 111^{o} 48.785’ Figure 8a) and one site in Jambi, Sumatra (S 01^{o}38.456’, E 103^{o}54.335’, Figure 8b). 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^{o}C. Mean annual rainfall is 1808 mm and September is typically the driest month (85 mm). In Jambi, mean annual temperature is 27.1^{o}C. Mean annual rainfall is 1846 mm with the driest month (115 mm) typically occurring in June.

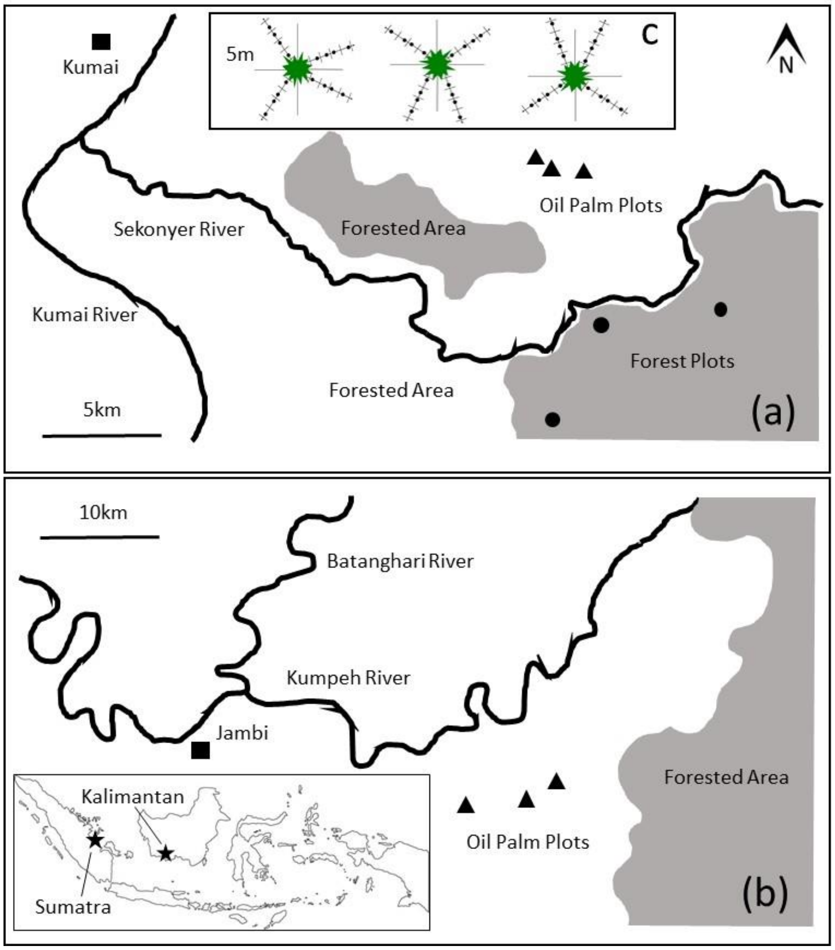

Figure 8. Research sites and soil sampling design. Peat soils were collected at sites on the islands of Kalimantan and Sumatra (inset, lower left) from three plots in undrained forest and three plots in nearby smallholder oil palm plantations in Kalimantan (a) and from three plots in an industrial oil 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 ample collected from the top 0-5 cm with a bulk density ring. Maps are hand digitized images from GoogleEarth. Source: DigitalGlobe 2016

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 5).

Table 5. Characteristics of the sampling plots in Sumatra and Central Kalimantan, Indonesia.

Code	**Island**	**Location**	**Landuse**	**Plantation Age**	**Clearance Date**	**Fires**	**Distance to River**	**Peat Depth**
K-FOR-1	Kalimantan	S 02° 49.4’ E 111° 48.8’	Forest	-	pre 1982	Multiple	0.5 km	27 cm
K-FOR-2	Kalimantan	S 02° 49.3’ E 111° 50.4’	Forest	-	-	-	1 km	155 cm
K-FOR-3	Kalimantan	S 02° 50.9’ E 111° 48.1’	Forest	-	-	-	2 km	290 cm
K-OP-2011	Kalimantan	S 02° 47.3’ E 111° 48.6’	Smallholder oil palm	4 Year	1989	Multiple	3.5 km	20 cm
K-OP-2009	Kalimantan	S 02° 47.3’ E 111° 48.1’	Smallholder oil palm	6 Year	2005	Multiple	3.5 km	47 cm
K-OP-2007	Kalimantan	S 02° 47.2’ E 111° 48.1’	Smallholder oil palm	8 Year	2005	Multiple	3.5 km	47 cm
S-OP-2010	Sumatra	S 01° 38.4’ E 103° 54.3’	Industrial oil palm	5 Year	2004	Multiple	20 km	850 cm
S-OP-2007	Sumatra	S 01° 38.2’ E 103° 52.3’	Industrial oil palm	8 Year	2004	Multiple	20 km	665 cm
S-OP-2005	Sumatra	S 01° 38.5’ E 103° 50.0’	Industrial oil palm	10 Year	2004	Single	20 km	575 cm

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 greater than at the Kalimantan site (-50 cm, Swails *et al.*, in preparation). Oil palm plots underwent single or multiple fires at both sites (Table 5).

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 8c). 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 retained for chemical analysis. 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_2O) 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^{o} 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 composited soil samples was determined by weighing subsamples before and after oven drying at 60°C for 48 hours (constant mass). Soils were brought to the target moisture level by adding deionized (DI) H_2O and maintained at that level with further additions throughout the experiment. The target gravimetric soil moisture level was 2 g DI H_2O / 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_2O 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^{o}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_2O g d.m.$^{-1}$) remained close to the target of 2 g H_2O 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 H_2O equal to treatments in both experiments. Target gravimetric soil moisture for both experiments was 2 g DI H_2O 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 H_2O). Low N treatment received 0.5 mg ammonium nitrate (NH_4NO_3) 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 (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 (Na_2HPO_4) 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 H_2O). 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_2O g d.m.$^{-1}$ and 2.13 ± 0.02 g H_2O 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 6). 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.

Table 6. 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.

Property	**Depth (cm)**	**KAL FOR**		**KAL OP**		**SUM OP**	
BD (g cm^{-3})	0-5	0.16	± 0.06	0.24	± 0.06	0.19	± 0.02
pH	0-10	3.97	± 0.07	3.70	± 0.20	3.97	± 0.18
OM (g 100 g^{-1})	0-5	72.5	± 6.3	66.1	± 3.1 ^{A}	91.8	± 0.6 ^{B}
C (g 100 g^{-1})	0-5	40.8	± 3.2	41.2	± 2.8 ^{A}	53.8	± 0.8 ^{B}
N (g 100 g^{-1})	0-5	1.8	± 0.2	1.5	± 0.1 ^{A}	1.9	± 0.1 ^{B}
C:N	0-5	23.2	± 1.1 ^{a}	27.4	± 0.7 ^{b}	28.6	± 1.0
NH_4^+ (mg kg^{-1})	0-5	100.3	± 21.5 ^{a}	38.7	± 9.4 ^{b}	37.7	± 5.7
NO_3^- (mg kg^{-1})	0-5	14.6	± 5.8 ^{a}	45.3	± 8.8 $^{b, A}$	2.6	± 0.8 ^{B}
$NH_4^+ + NO_3^-$ (mg kg^{-1})	0-5	114.9	± 23.8	84.0	± 6.6 ^{A}	40.3	± 5.5 ^{B}
Bray II P (mg kg^{-1})	0-5	3.9	± 2.0 ^{a}	12.9	± 3.2 ^{b}	32.2	± 8.6

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.

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 9). 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 ($p = 0.002$). 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.

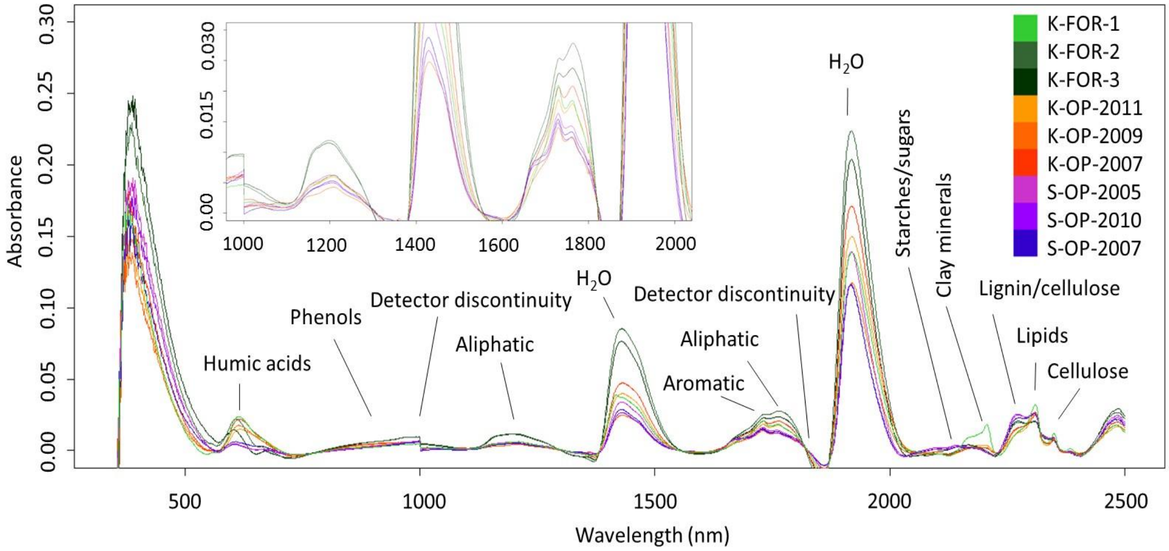

Figure 9. Vis-NIR baseline corrected absorbance spectra of soil from plots in Kalimantan undrained forest (K-FOR-1, K-FOR-2, K-FOR-3), Kalimantan smallholder oil palm plantations (K-OP-2011, K-OP-2009, K-OP-2007) and Sumatran industrial oil palm plantations (S-OP-2010, S-OP-2007, S-OP-2005) on peat. 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).

Variability in basal respiration without amendment

Cumulative CO_2 production by Kalimantan forest soils (1636.1 ± 37.6 µg CO_2-C g C^{-1}, 663.3 ± 16.4 µg CO_2-C g d.m.$^{-1}$) was roughly two times higher than production by Kalimantan oil palm soils (871.0 ± 46.1 µg CO_2-C g C^{-1}, 339.0 ± 16.4 µg CO_2-C g d.m.$^{-1}$) during the 7-day incubation ($p < 0.001$, Figure 10). Cumulative CO_2 production by Kalimantan oil palm soils was significantly higher than that of Sumatran oil palm soils (600.1 ± 23.7 µg CO_2-C g C^{-1}) on a per g C ($p < 0.0001$) but not per g d.m. basis (320.7 ± 16.4 µg CO_2-C g d.m.$^{-1}$).

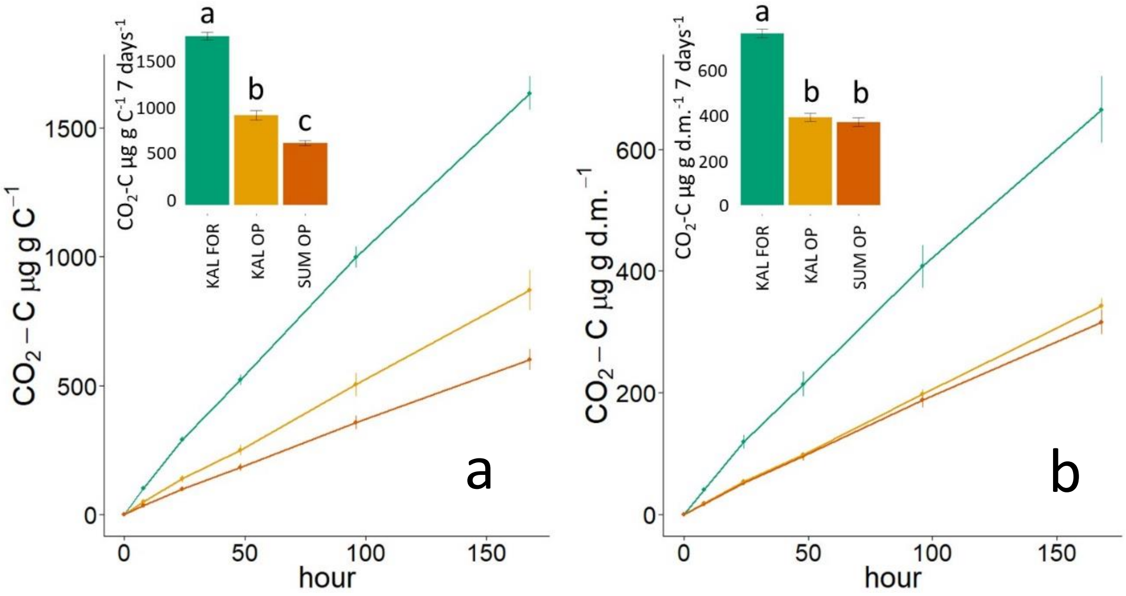

Figure 10. Mean cumulative CO_2 production by peat soils from Kalimantan forest (KAL FOR, green) and oil palm (KAL OP, orange) sites and Sumatran oil palm (SUM OP, blue) sites during incubation without amendment. Production is expressed on per g C basis in (a) and per g d.m. basis in (b). Significant differences in mean total cumulative CO_2 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).

Throughout the experiment, on a per g C basis, the hourly rate of CO_2 production by Kalimantan forest soils (10.80 ± 0.23 μg CO_2-C g C hr^{-1}) was higher than that of Kalimantan oil palm soils (5.34 ± 0.26 μg CO_2-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 CO_2-C g C hr^{-1}) (for both $p < 0.001$, Figure 11a). CO_2 production was higher at the beginning of experiment ($p = 0.004$), declining about 20% to a fairly steady state after 24 hours.

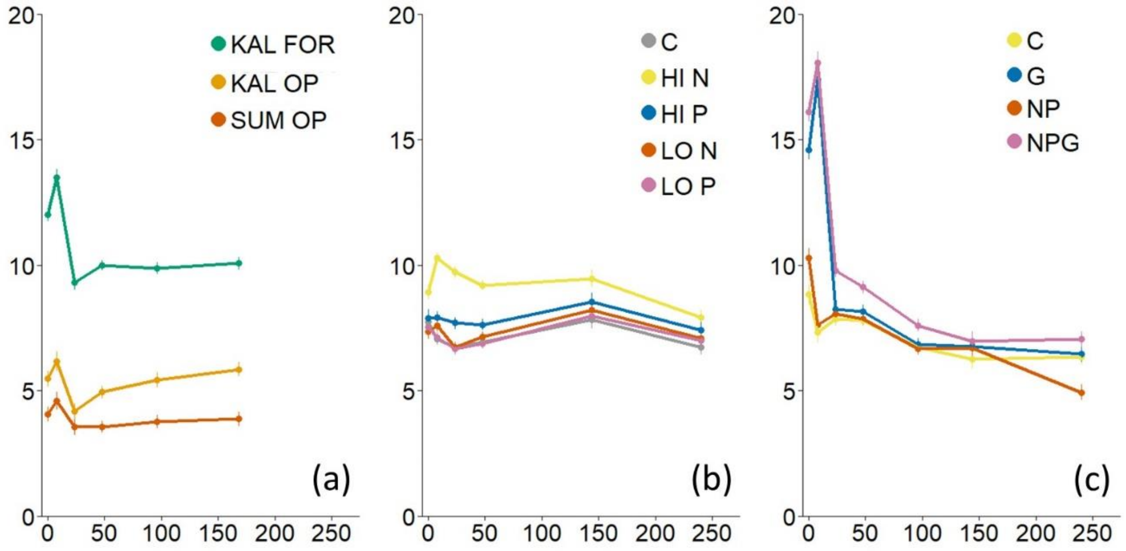

Figure 11. Mean CO_2 production rate by peat soils (a) from Kalimantan forest (KAL FOR) and oil palm (KAL OP) sites and Sumatran oil palm (SUM OP) sites during incubation without amendment; (b) with three levels of nitrogen (N) and phosphorus (P) amendment (no amendment: C; high level: hi; low level: 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.

Cumulative CO_2 production increased significantly with available N (Figure 12f). It declined significantly with increasing C:N ratio, available P, and aromatic:aliphatic ratios (Figure 12d, 12e, 12g, 12h). 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).

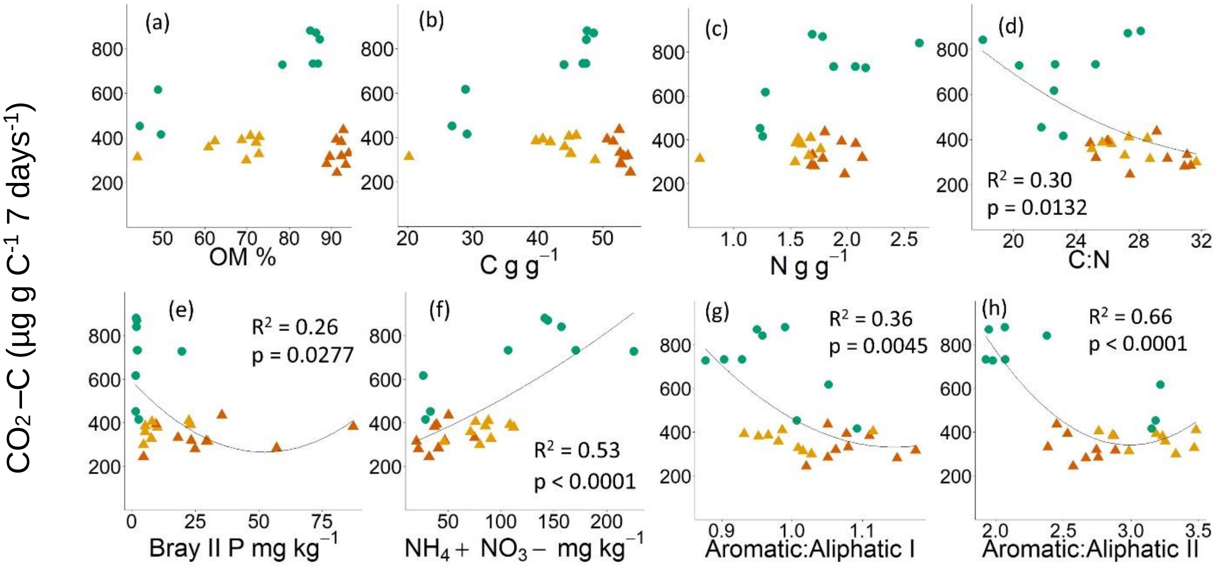

Figure 12. Mean cumulative CO_2 production over seven days by soils incubated without amendment as a function of soil properties (n = 27). Each data point represents the average of three replicates of soil from each of the tree three within plot locations. Green circle: peat forest in Kalimantan, gold triangle: oil palm in Kalimantan, orange triangle: oil palm in Sumatra.

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 13a). 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 13a). The effect of added P on cumulative CO_2 production was driven by a strong response in Kalimantan forest soils (Figure 13a). The temporal patterns of CO_2 production among treatments differed ($p < 0.001$, Figure 11b). 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.

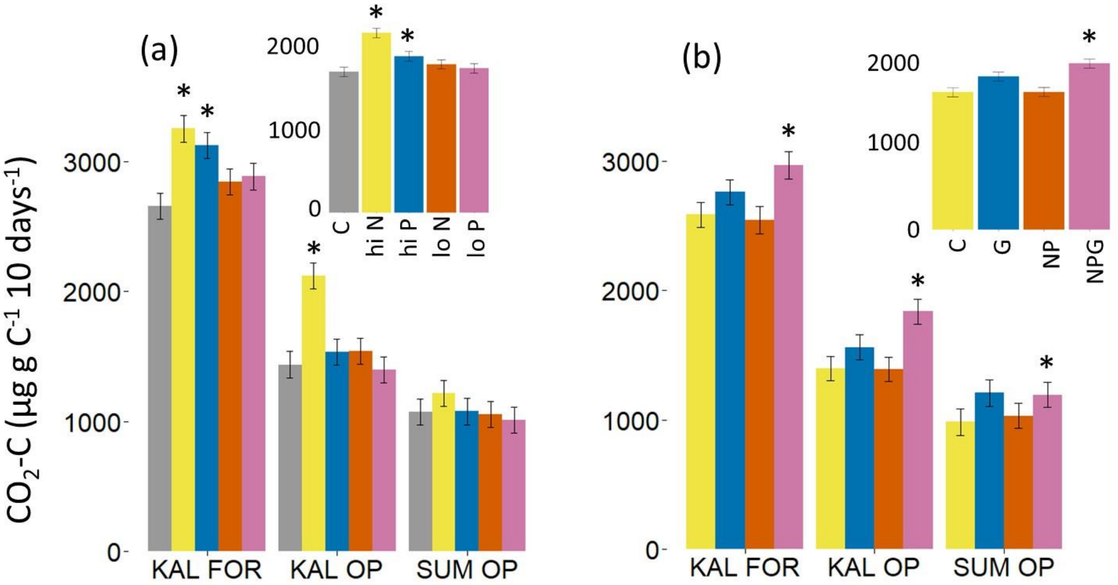

Figure 13. Mean cumulative CO_2 production by peat soils from Kalimantan forest (KAL FOR) and oil palm (KAL OP) and Sumatran oil palm (SUM OP) sites in (a) each treatment group incubated with nitrogen (N) and phosphorous (P) amendment and in (b) each treatment group incubated with glucose (G) amendment 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).

Glucose increased cumulative CO_2 production compared to controls, but significantly so only when N and P were also added ($p < 0.001$, Figure 13b). 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 11c), 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 ± .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.

CO_2 production also declined significantly with increasing C:N ratio (Figure 12d) and increased with available N (Figure 12f), suggesting that nitrogen availability was limiting to CO_2 production. Higher 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 12).

Like N, P can directly limit decomposition when labile carbon substrates are available (Cleveland *et al.*, 2002). The weak negative relationship between CO_2 production and available P in untreated soils suggests that substrate quality and available N were more strongly limiting to CO_2 production than available P. High P treatments increased CO_2 production by Kalimantan forest soils, with relatively higher substrate quality and lower initial P, and did not increase CO_2 production by Kalimantan or Sumatran oil palm soils with relatively lower substrate quality.

We observed a trend towards higher 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 11, 13). 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 in glucose treatments (4,000 µg C). Therefore, we cannot assess any enhancement effect on mineralization of recalcitrant C or “priming”.

Comparing CO_2 production across geographies and land use

Substrate quality played a strong role in determining rates of CO_2 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 6), however, CO_2 production was similar on per g d.m. basis and significantly lower on per g C basis (Figure 10). Lower CO_2 production reflected the lower quality of the substrate: higher ratios of aromatic:aliphatic (I) and C:N (Table 6, Figures 9 and 12). Likewise, Kalimantan forest and oil palm soils had similar quantity of C available for microbial decomposition. Nevertheless, CO_2 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.

CO_2 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. CO_2 production by oil palm soils in both Kalimantan and Sumatra was ca. 50% lower than *ex situ* CO_2 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 CO_2 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 CO_2 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.

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CHAPTER FOUR

Contribution of methane and nitrous oxide to GHG emissions from forest and oil palm in an Indonesian peatland

Abstract

Land-use change in tropical peatlands impacts emissions of GHGs CH_4 and N_2O in addition to emissions of CO_2. However, the contribution of CH_4 and N_2O to total GHG budgets in these ecosystems is uncertain. Concurrent measurements of CH_4, N_2O, and CO_2 are needed to improve understanding of how these GHGs respond to changes in water table level, vegetation, and litter and nutrient inputs associated with land-use change in tropical peatlands. We collected monthly measurements of CH_4 and N_2O concurrently with measurements of total soil respiration and environmental parameters from January 2014 to June 2015, and again in September 2015. CH_4 emissions were lower in oil palm than forest, while N_2O emissions were higher. The global warming impact of decreased CH_4 emissions in oil palm was more than offset by increased N_2O emissions. However, the contribution of both CH_4 and N_2O to GHG budgets in forest and oil palm were far outweighed by the increase in CO_2 emissions from microbial decomposition of peat in oil palm.

Introduction

Conversion of tropical peat swamp forest to oil palm is a large and growing source of greenhouse gas (GHG) emissions to the atmosphere. Efforts to characterize the impact of tropical peatland conversion to oil palm have largely focused on increased emissions of CO_2 and C storage loss associated with peat drainage. Changes in emissions of CH_4 and N_2O are also significant but less well characterized. Peat drainage decreases emissions of CH_4 stemming from anaerobic decomposition of soil organic matter (Inubushi *et al.*, 2003; Hergoualc'h & Verchot, 2012). However, the simultaneous large increase in CO_2 emissions has a greater global warming impact (Hergoualc'h & Verchot, 2012). Application of nitrogen (N) fertilizers increases emissions of N_2O (Oktarita *et al.*, 2017) and may increase CO_2 emissions by enhancing microbial decomposition (Comeau *et al.*, 2016; Swails *et al.*, 2017). N_2O is a much more potent GHG than CO_2, with almost 300 times the global warming potential (Forster *et al.*, 2007). However current understanding of the mechanisms and magnitude of soil N_2O emissions in tropical peatlands is limited (van Lent *et al.*, 2015). Concurrent measurements of CH_4 and N_2O fluxes from soils in addition to CO_2 will improve understanding of the relationships among fluxes of these different GHGs and their relative impacts on the atmosphere.

N_2O is an intermediate product of both nitrification and denitrification. The quantity of N_2O released during nitrification is correlated with the total flux through the nitrification pathway ("leaky pipe model", Firestone and Davidson 1989). NH_4+ is generated by microbial decomposition of soil organic matter and is converted to NO_3- by nitrifying bacteria under aerobic conditions. Denitrifying bacteria reduce NO_3- ultimately producing N_2 but also producing N_2O. Application of N fertilizers can increase N_2O production by increasing the supply of NO_3-. When NO_3- is relatively more abundant than labile organic carbon, N_2O production is favored. Although existing estimates from unfertilized converted tropical peatlands indicate that N_2O emissions stemming from peat decomposition are small (Hergoualc'h and Verchot 2014; van Lent *et al.*, 2015), intensive monitoring following fertilization indicates that N_2O emissions cannot be neglected in estimates of GHG emissions from converted peatlands (Oktarita *et al.*, 2017).

We collected monthly measurements of N_2O and CH_4 fluxes from soils and environmental variables in forest and smallholder oil palm plantations on peat in Central

Kalimantan, Indonesia from January 2014 through September 2015. We designed our field experiment to address three questions: (1) How do CH_4, and N_2O emissions from peat soils differ in oil palm plantations and forest? (2) How do emissions vary on seasonal and interannual timescales? (3) Do physical controls (moisture, temperature), peat substrate quality, and nutrients influence emissions of these trace gases from peat soils in forest and oil palm plantations? Ultimately, given observed variability in space and time, we compare the contributions of CH_4 and N_2O with CO_2 in terms of global warming potential.

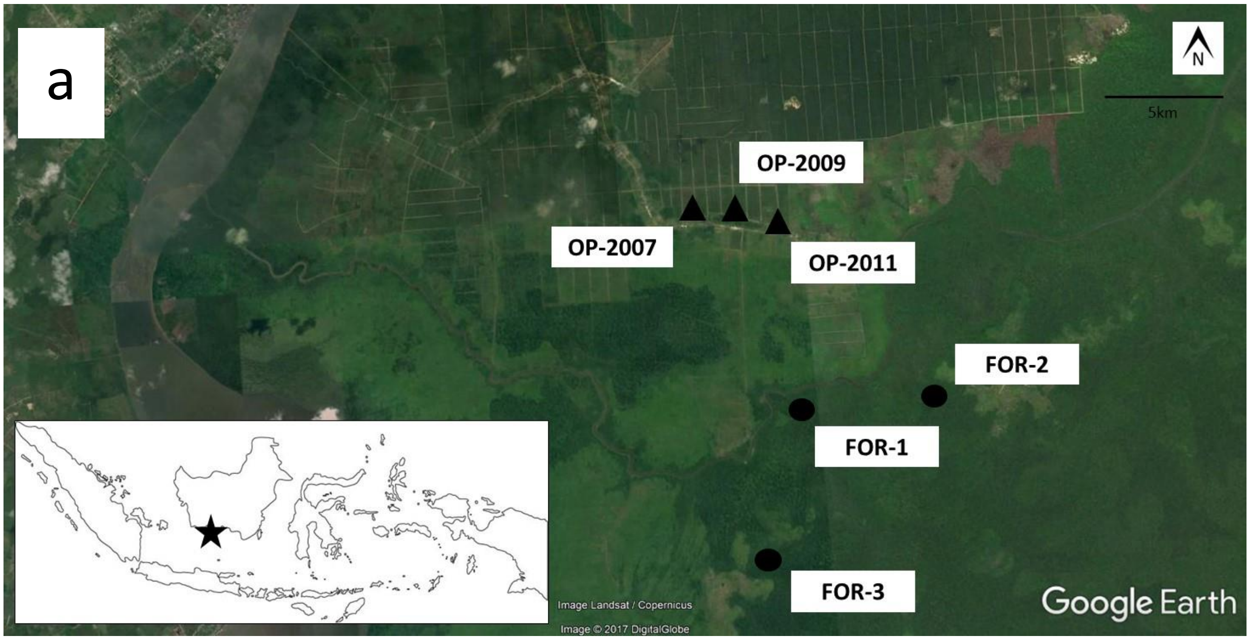
Materials and methods

Site description

We conducted the research at permanent plots in a peatland on the southern coast of Indonesian Borneo in Central Kalimantan, approximately 10 km outside the city of Pangkalan Bun (S 02° 49,410', E 111° 48.785' Figure 14, Table 7). The plots were established in 2012 by the Center for International Forestry Research at three locations in undrained forest inside Tanjung Puting National Park and at three locations in nearby drained smallholder oil palm plantations. The regional climate is humid tropical. Total annual precipitation is high and average daily temperature remains fairly constant during the year. We used daily weather observations from Iskander airport in Pangkalan Bun to assess climate at our study site. The weather observations were obtained from the National Oceanic and Atmospheric Administration's Climate Data Center. During 2004-2014 mean annual rainfall in Pangkalan Bun was 2058 mm and August was, on average, the driest month (105 mm). Mean annual temperature over this period was 26.6°C. Mean monthly temperature ranged from 26.1°C in July to 27.2°C in May.

The plots comprised a range of peat depths, land use history and vegetation age. The three forest plots were located at different distances from the edge of the main channel of the

Sekonyer river. Peat depth varied in forest plots from less than 50 cm at the plot closest (0.5 km) to the river to over two meters at the plot located farthest from the river (2 km). The plot closest to the river (K-FOR-1) was a 30 year old secondary forest, likely being managed as an agroforestry garden when Tanjung Puting National Park was established in 1982 and communities were moved across the Sekonyer river (Novita 2016). The other two forest plots (K-FOR-2, K-FOR-3) were not being managed for agricultural production when the park was created. Smallholders started planting their lands with oil palm in the late 2000s, after a company



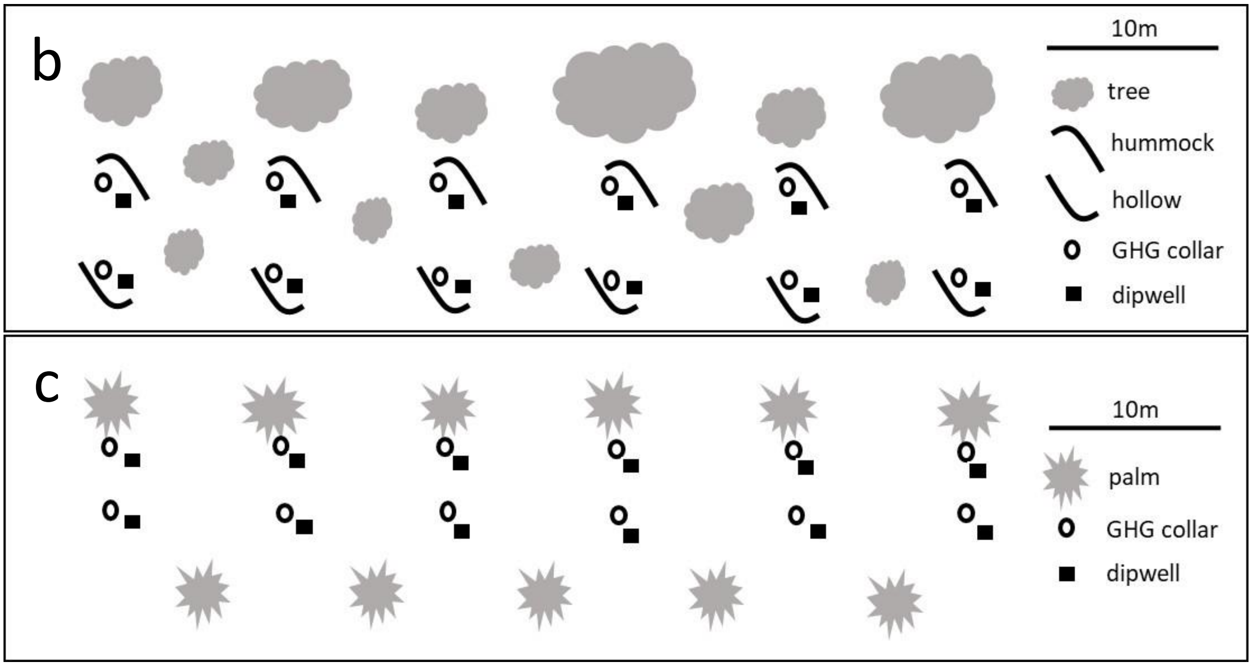


Figure 14. Research site and sampling design. Measurements were collected from a peatland on the island of Kalimantan (inset) in three plots in undrained forest (FOR-1, FOR-2, FOR-3) and three plots in nearby smallholder oil palm plantations (OP-2007, OP-2009, OP-2011) (a). In each plot, GHG collars (circles) and dipwells (squares) were installed at 6 subplot locations in oil palm (b) and forest (c). At each subplot, one collar and dipwell set was installed at the base of a palm and another at a distance of three meters from the palm in oil palm plots. In forest plots, we installed one set on a hummock and one set in the adjacent hollow. (after Swails et al., 2017)

Smallholders started planting oil palm on their lands after a large oil palm plantation was established adjacent to their properties in the late 1990s. Oil palm was planted in 2007 (OP-2007) and 2009 (OP-2009) on land cleared in 2005. Oil palm was planted in 2011 (OP-2011) on land previously cleared in 1989 and managed for rice and vegetable production. Land use history and land management practices in smallholder oil palm plantation plots are described in detail in Swails *et al.* (2017).

Table 7. Characteristics of the sampling plots in Central Kalimantan, Indonesia. (After Swails et al., 2017)

Code	**Location**	**Landuse**	**Fires**	**Distance to River**	**Peat Depth**
FOR-1	S 02^{o} 49.410’ E 111^{o} 48.784’	Forest	Multiple	0.5 km	27 cm
FOR-2	S 02^{o} 49.341’ E 111^{o} 50.434’	Forest	-	1 km	155 cm
FOR-3	S 02^{o} 50.852’ E 111^{o} 48.155’	Forest	-	2 km	290 cm
OP-2011	S 02^{o} 47.379’ E 111^{o} 48.624’	Oil palm	Multiple	3.5 km	20 cm
OP-2009	S 02^{o} 47.292’ E 111^{o} 48.190’	Oil palm	Multiple	3.5 km	47 cm
OP-2007	S 02^{o} 47.230’ E 111^{o} 48.089’	Oil palm	Multiple	3.5 km	47 cm

Monthly sampling regime

We collected measurements of trace gas fluxes once per month from January 2014 until June 2015 and once more in September 2015. Measurements of water table depth, soil moisture and temperature at 5 cm depth, and air temperature were collected concomitantly with trace gas flux measurements, as described in Swails *et al.* (in preparation). We sampled plots on consecutive days between the hours of 0800 and 1200.

We designed our sampling approach to capture spatial heterogeneity in environmental conditions and trace gas fluxes from soils (Figure 1). CH_4 and N_2O flux rates were determined by static chamber method (Hutchinson and Livingston, 1993; Verchot *et al.*, 1999). Chambers were permanently installed PVC collars (inner diameter 25 cm) equipped with portable PVC hoods. We installed collars sixteen months before the beginning of this study. In each plot, collars were installed at six subplot locations for a total of 12 collars per plot. At each subplot location in oil palm plots, we installed one collar at the base of a palm (near) and one collar at mid-distance between two palms (far). We installed one collar on a hummock and one collar in the adjacent hollow at each subplot location in forest plots. Each PVC collar was equipped with a portable PVC hood. Samples were collected at 0, 10, 20, and 30 minutes after placing the hood on the collar to create the closed chamber. We collected gas samples in 40 ml pre-evacuated glass using a syringe connected to the outlet of the chamber hood with silicone tubing and a polycarbonate three way stopcock. Vials were also fitted with stopcocks to prevent gas leakage during transportation from the field.

Gas chromatography

The gas samples were analyzed using a Shimadzu gas chromatograph (GC) fitted with an electron capture detector (ECD) for N_2O, and a flame ionization detector (FID) for CH_4. We used ultra high purity grade N_2 as our carrier gas with a flow rate of 25 mL min^{-1}. The N_2O channel of the GC was equipped with a Valco 10-port 2-way valve with a 2 mL sample loop and a standard back-flush system using a Porapak Q (80/100 mesh) column. We set the ECD temperature to 340°C for the analysis. The CH_4 channel of the GC was equipped with a Valco 6-port 2-way valve and a single Poropak Q (80/100 mesh) column directly connected to the FID. The GC oven was operated at 60°C.

Peak areas for each gas sample integrated automatically on the chromatograms by the Shimadzu chromatography software were compared to a curve produced from standard gases and adjusted as necessary. Regression analysis of peak area was used to predict N_2O and CH_4 concentrations of samples.

Calculations and statistical analysis

CH_4 and N_2O fluxes were calculated from the rate of change of the concentration of the analyte in the chamber headspace, determined by linear regression based on the four sequential samples (Verchot *et al.*, 1999, Verchot *et al.*, 2000). Curves were visually inspected, and in cases of departure from linearity, the flux was calculated with fewer samples (e.g. the final sample or even the final two samples were not included in the calculation). If any of the vials except T_0 had a CH_4 or N_2O concentration equal to ambient value, and the other points indicated a clear trend over time, we assumed that the vial with the ambient concentration leaked. We discarded the observation, unless there was no clear trend. This occurs when gas flux from the soil surface is zero or very low. In these cases we did not discard observations. The slope of the best linear fit to the data was converted to a flux using the ideal gas law.

To compare trace gas fluxes between land uses we calculated a weighted average for each of the six subplot locations in each plot (six locations at three plots, n=18 per land use) for each of 19 monthly observations. The weighting was based on the ratio of hummock/hollow and near/far subplot conditions in each plot. Determination of the proportion of subplot condition type in oil palm and forest plots is described in Swails et al. (in preparation). The hummock to hollow ratios in forest plots were 49:51 (FOR-1), 51:49 (FOR-2), and 57:43 (FOR-3). In oil palm plots, we based our weighting on the ratio of area within a 2 m radius of palms (near) to the area outside of this radius (far). The area within a 2 m radius of palms is where smallholders applied fertilizers and root density is usually highest (Comeau *et al.*, 2016, Khalid *et al.*, 1999). The near to far ratio in oil palm plots were 25:75 (OP-2011), 27:73 (OP-2009), and 37:63 (OP-2007). Hummock/hollow and near/far conditions were compared using unweighted values measured at each collar in each plot (six hummocks in three plots (n=18) vs six hollows in three plots (n=18); six near in three plots (n=18) vs six far in three plots (n=18)).

We used one-way repeated measures ANOVA with planned comparisons to detect differences in trace gas fluxes between land uses and spatial positions (hummock/hollow and near/far) within plots. We assessed overall fluxes during the entire study period and we compared dry months to wet months. We treated months with total precipitation ≤ 100 mm as “dry” months, and months with total precipitation > 100 mm were treated as “wet” months after Aini *et al.*, 2015 and Hirano *et al.*, 2007. Central Kalimantan experiences a dry season between May and October with a wet season between November and April (Hirano *et al.*, 2007). To compare monthly values we used Welch's t-test. ANOVA was computed using Statistical Analysis Software (SAS v 9.4). We used R (v 3.2.5) for all other analyses. To test for relationships among trace gas fluxes and environmental parameters, we used univariate regression. We averaged measurements collected at each subplot location to yield one pooled value per month per plot for each measured parameter. We also tested for relationships among trace gas fluxes and measurements of soil C:N and NO_3^- /NO_3^-+NH_4^+ ratios. Measurements of soil properties are described in Swails et al. (in preparation). C:N ratio is a measure of soil substrate quality, and van Lent *et al.* (2015) observed that soil N_2O flux increases with increasing NO_3^-/NO_3^-+NH_4^+ratio.

We calculated hourly flux rates for both CH_4 and N_2O at each chamber in each plot in oil palm and forest in each month during the monitoring period. We multiplied hourly respiration rates by 24 to convert to daily respiration rates after Hergoualc'h *et al.* (2017) and Swails *et al.* (2017). To calculate a mean daily flux rate between measurement points, we took the average of the two points. This value was extrapolated over the days intervening between the two measurements, and cumulative annual total soil respiration was calculated by annualizing the summed daily flux values over the entire monitoring period from January 2014 to September 2015. To test for differences in cumulative annual trace gas fluxes between land uses and spatial positions within a land use, we calculated a weighted cumulative average for each of the six sub-plot locations in each plot. We used one-way ANOVA with Tukey HSD to test for differences in cumulative annual total respiration among plots in forest and oil palm (n=6), and independent t-tests to detect differences between land-uses and between spatial positions in each land use (n=18). We used paired t-tests to detect differences between spatial positions in each plot. To convert trace gas fluxes to CO_2 equivalents (CO_2e) we used a 100 year time horizon global warming potential (GWP) of 25 for CH_4 and 298 for N_2O (IPCC 2007).

Results

CH_4 and N_2O flux rates

Over the 19 months of the study, CH_4 flux rate varied 13-fold in forests and four-fold in oil palm (Figure 15a). Mean CH_4 flux rate was over seven times higher in forest plots (4.39 ± 0.61 mg CH_4 m^2 d^{-1}) than oil palm plots (0.61 ± 0.61 mg CH_4 m^2 d^{-1}, $p = 0.001$, Figure 15a). Higher methane flux from forests overall was driven by a significant difference during wet months ($p = 0.0003$). During dry months, the difference in CH_4 flux from the two land uses was marginally significant ($p = 0.0525$). Under extremely dry conditions during the El Niño event in September 2015, forest became a weak CH_4 sink (-1.36 ± 0.70 mg CH_4 m^2 d^{-1}), while oil palm remained a weak CH_4 source (1.60 ± 0.51 mg CH_4 m^2 d^{-1}), and the difference in flux between the two land uses was significant ($p=0.004$). The mean rate of methane flux ranged from 1.67 ± 1.38 mg CH_4 m^2 d^{-1} in the forest plot furthest from the river to 5.5 ± 1.38 mg CH_4 m^2 d^{-1}in the plot nearest the river. Methane production in oil palm varied only 3-fold from plot to plot.

N_2O flux was not as variable over the course of the study as CH_4 flux. It was moderately more variable in oil palm than in forest (Figure 15b). N_2O flux was five times higher in oil palm plots (1.25 ± 0.26 ng N m^2 hr^{-1}) than forest plots (0.26 ± 0.0.26 ng N m^2 hr^{-1}, Figure 15b) during the study period overall ($p = 0.02$). The difference between forest and oil palm was not significant during dry months ($p = 0.3$), but was significant in wet months ($p = 0.04$). N_2O flux did not differ between forest and oil palm plots during the El Niño event in September 2015. The highest mean flux, 2.35 ± 0.31 ng N m^2 hr^{-1},was observed in OP-2011, and the lowest, 0.36 ± 0.31 ng N m^2 hr^{-1}, was observed in OP-2009. Forests varied from 0.86 ± 0.31 ng N m^2 hr^{-1} in

FOR-2 to flux not different from zero in FOR-1. Forest plots varied less from month to month than oil palm. CH_4 and N_2O flux were not different in hummocks and hollows or near and far from palms.

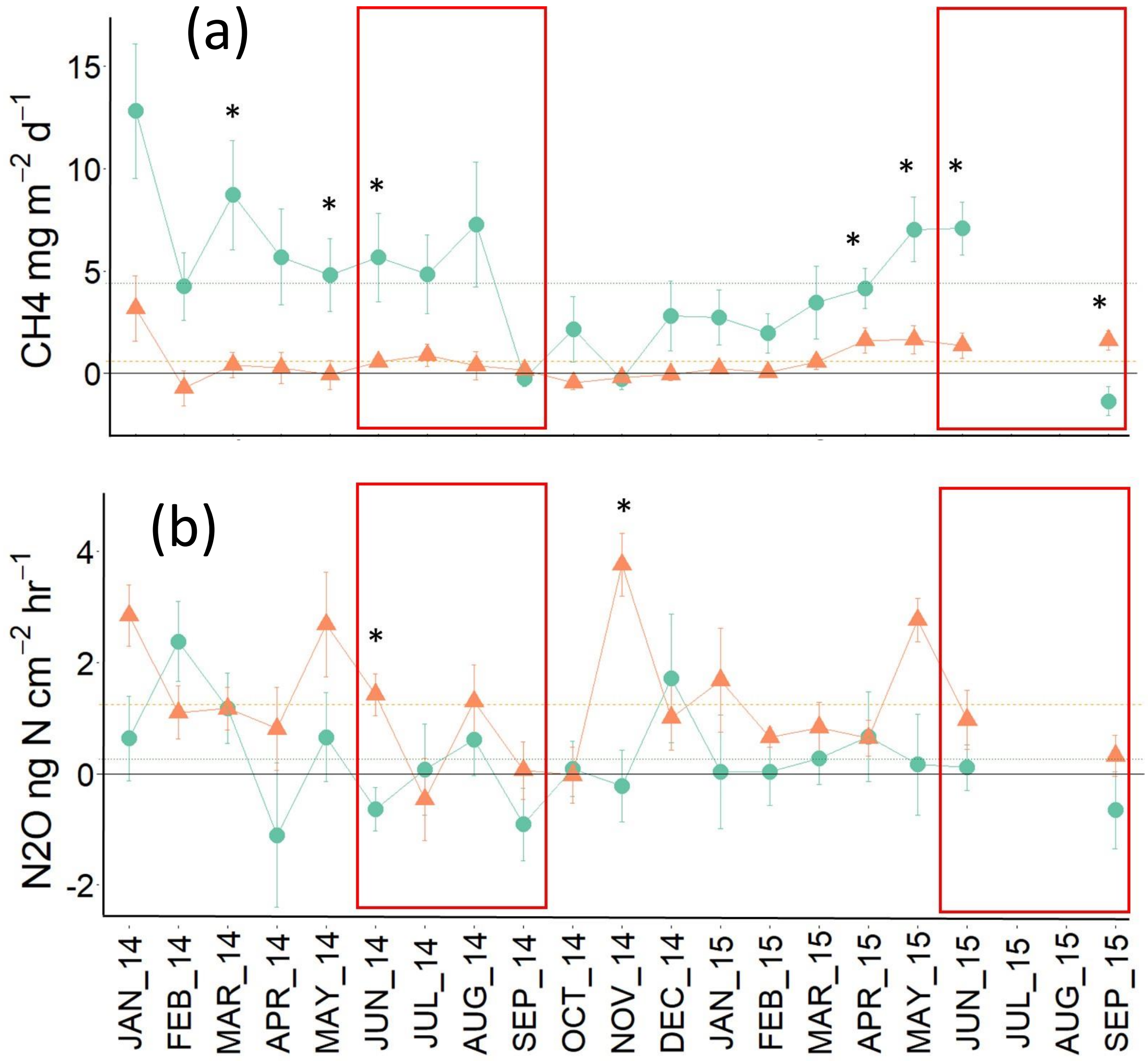


Figure 15. Mean soil CH_4 flux (a) and N_2O flux (b) in forest (circle, dotted line) and oil palm (triangle, dashed line) from January 2014 to September 2015 (n=18). Error bars represent standard error of the mean. * indicates months with significant differences between land uses. Months with total precipitation less than 100 mm are indicated by red box.

Linking soil trace gas flux rates to drivers

Soil CH_4 flux decreased as water table declined in forest plots ($p<0.001$, Figure 16a) but was not related to water table level in oil palm plots. In oil palm plots, soil N_2O flux increased as the water table rose closer to the soil surface, but the relationship was weak ($p=0.049$, $R^2 = 0.11$, Figure 16b). N_2O flux did not vary significantly with water table depth in forest. In both forest and oil palm, N_2O flux varied widely when water table level was near the soil surface with some N_2O consumption. Fluxes of CH_4 and N_2O were not related to C:N and $NO_3^-/NO_3^-+NH_4^+$ ratios , or soil and air temperature, or soil moisture in either land use.

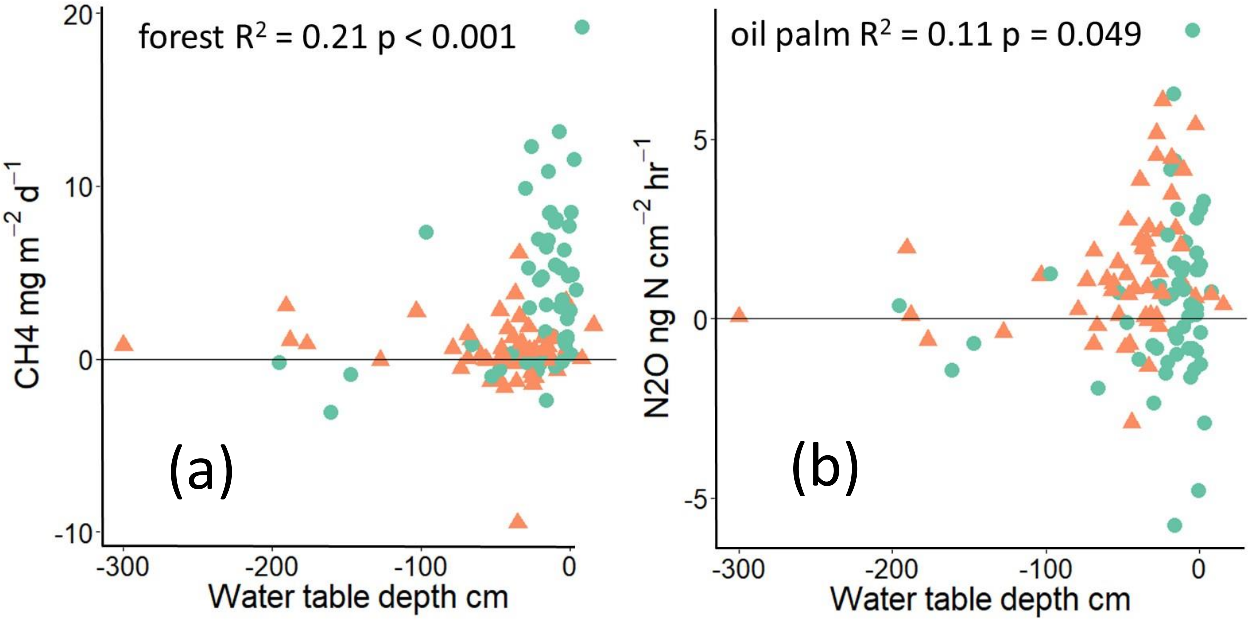
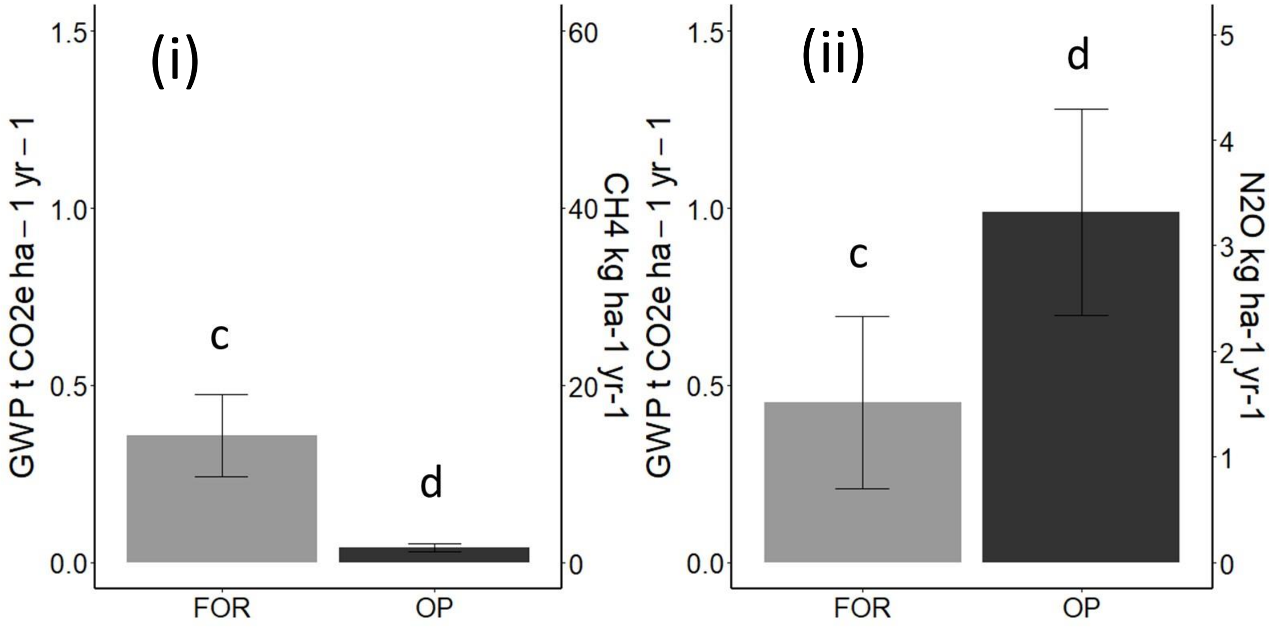


Figure 16. CH_4 flux (a) and N_2O flux (b) from soils as a function of water table depth in forest (green circle) and oil palm (orange triangle). Each data point represents combined weighted averages for each of the six subplot locations in a plot in a month (3 plots * 19 months, n=57).

Cumulative annual fluxes of CH_4 and N_2O in forest and oil palm

Cumulative annual CH_4 flux over the monitoring period was far higher in forest (14.35 ± 3.73 kg ha^{-1} yr^{-1}) than oil palm (1.68 ± 1.33 kg ha^{-1} yr^{-1}, $p<0.001$, Figure 17a). Cumulative annual N_2O flux was twice as high in oil palm (3.32 ± 0.82 kg ha^{-1} yr^{-1}) as in forest (1.52 ± 1.22 kg ha^{-1} yr^{-1}, $p=0.01$, Figure 17b). The difference in mean CH_4 flux in forest and oil palm was equal to 0.32 t

CO_2e ha^{-1} yr^{-1} whereas the difference in N_2O flux in forest and oil palm was equal to 0.54 t CO_2e ha^{-1} yr^{-1}. However, owing to high variability in fluxes of CH_4 and N_2O within plots, cumulative trace gas fluxes were not different among plots within a land-use, or between spatial conditions (hummock/near and hollow/far) within a land-use or plot. On an annual time scale, there was no effect on CH_4 or N_2O flux of plot or spatial conditions within a plot, only land-use.



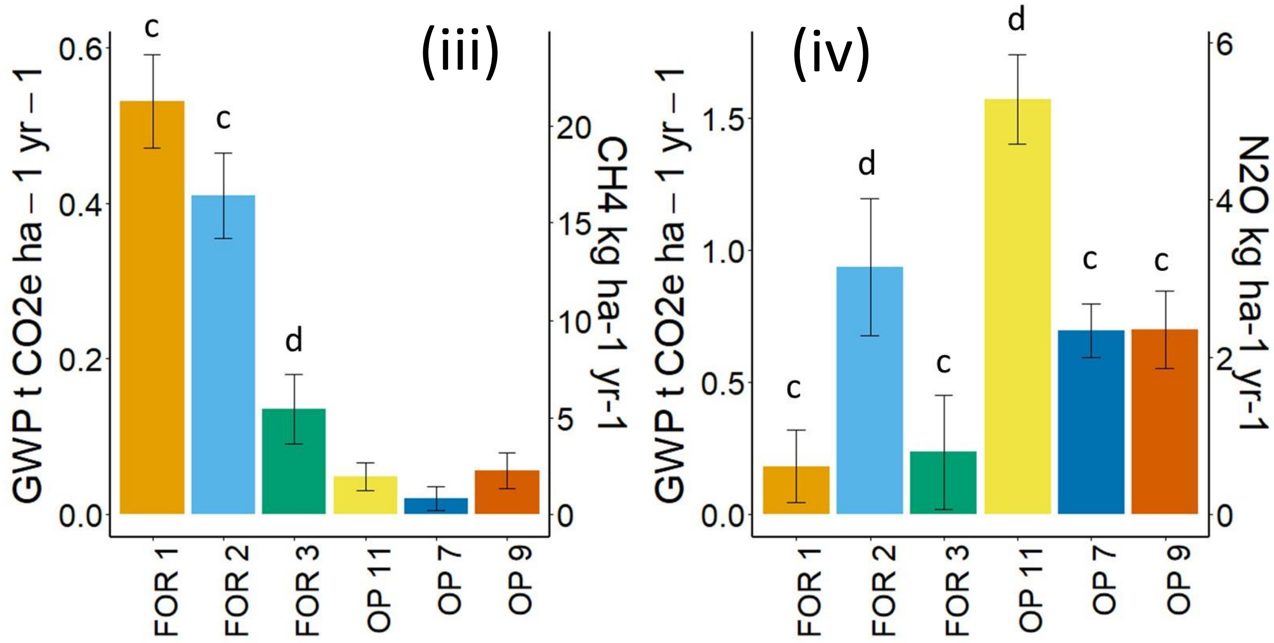


Figure 17. Cumulative annual CH_4 flux (i and iii) and N_2O flux (ii and iv) from soils in forest and oil palm. Error bars represent standard error of the mean (n=18 in i an 11; n=6 in iii and iv). Significant differences between land-uses and between plots within a land use are indicated by c, d.

Discussion

Drivers of methane and nitrous oxide emissions in forest and oil palm

At the landscape scale, water table depth was a driver of variation in CH_4 emissions at our study site. Oil palm plots, with lower water table level than forest plots due to drainage, had lower rates of CH_4 emissions than forest plots. Reduction of methane emissions from peat soils following drainage is consistent with observations across the tropics (Hergoualch'h and Verchot 2012). At 4.39 ± 0.61 mg CH_4 m^2 hr^{-1} and 0.61 ± 0.61 g CH_4 m^2 hr^{-1} respectively, rates of CH_4 emissions from our forest and oil palm plots were similar to rates measured elsewhere in Southeast Asia (Jauhiainen *et al.*, 2005; Hergoualc'h and Verchot 2012). Water table level was so low that CH_4 emissions did not respond to changes in water level in oil palm overall, as water table levels remained well below the soil surface during most months. In forest plots, methane emissions increased exponentially as water table level approached the soil surface and were higher in wet months than dry months. During wet months, increased rainfall results in water table levels at or above the soil surface in undrained peat forest. Waterlogging of surface layers creates anoxic conditions conducive to anaerobic respiration and methanogenesis. Nevertheless, water table depth only explained 21% of variation in methane production in forests over time. Other factors, such as facilitation of methane egress by vegetation (Pangala *et al.*, 2013) and ebullition are known to affect methane flux and may be playing a role here.

During dry months, our forest plots tended to flip from a CH_4 source to a weak CH_4 sink (Figure 15a). Oxygenation of soil surface layers in peat forest can promote methanotrophy over methanogenesis, resulting in net CH_4 consumption (Jauhiainen *et al.*, 2005). We did not observe a tendency towards CH_4 consumption in oil palm plots during dry months or overall, possibly due to a post-conversion shift in the microbial community (Nurulita *et al.*, 2014). N_2O consumption by soils is not uncommon across the tropics (Chapuis-Lardy *et al.*, 2007) and peat forest soils also appeared as an occasional sink for N_2O. Negative values were also observed in oil palm, but they were not significantly different from zero (Figure 15b).

In oil palm, N_2O emissions were higher than in forest, and responsive to water table depth. Observations from other Indonesian peatlands showed increased N_2O emissions post-conversion consistent with our observations (Furukawa *et al.*, 2005; Takakai *et al.*, 2006), but other studies showed no effect on N_2O emissions (Inubushi *et al.*, 2003; van Lent *et al.*, 2015) or decreased N_2O emissions (Hadi *et al.*, 2005). Application of N fertilizers in oil palm plantations likely contributed to higher N_2O emissions. Smallholders applied N fertilizer four times a year at annual rates exceeding 150 kg N ha^{-1} yr^{-1}, and soils collected from our oil palm plots within a week of fertilization had significantly higher NO_3^- concentrations than forest soils (Swails *et al.*, 2017). Application of N fertilizers may have promoted N_2O production during nitrification under conditions of low water table level by increasing the supply of NO_3-. Increased NO_3^- supply may have promoted N_2O production during denitrification under conditions of higher water table levels, especially since labile carbon supply was poor in our oil palm plots (Swails *et al.*, 2017). N_2O emissions from soils increase at higher water filled pore space values through greater losses from denitrification (Wolf & Russow, 2000). Timing and quantity of fertilizer application may have had considerable influence on the rate of N_2O production in oil palm soils, as water table depth only explained 11% of variation in N_2O production.

The global warming impact of changes in GHG emissions from Indonesian peatlands

In terms of global warming impact, the effect on the atmosphere of reduced CH_4 emissions in oil palm was less than the impact of increased N_2O emissions. In CO_2 equivalents, the global warming impact of N_2O (298 times CO_2) is higher than the global warming impact of CH_4 (25 times CO_2). Thus a small increase in N_2O more than offset the decrease in CH_4. However during the same time period (January 2014 to January 2015) estimated soil CO_2 emissions from heterotrophic respiration were 43 t CO_2 ha^{-1} yr^{-1} in oil palm and 27 t CO_2 ha^{-1} yr^{-1} in forest (Swails *et al.*, 2017) an increase of 16 t CO_2 ha^{-1} yr^{-1}, compared to 0.54 t CO_2e ha^{-1} yr^{-1} from N_2O, already offset somewhat by the reduction in CH4 flux (0.32 t CO_2e ha^{-1} yr^{-1}).

Indonesian peatlands are an important and growing source of GHG emissions to the atmosphere. Clearing and burning of forest vegetation on peatland generates immediate and massive emissions of CO_2, CH_4, and N_2O. Drainage of peat soils results in long term CO_2 emissions from accelerated soil organic matter decomposition and dissolved organic carbon (DOC) losses (Gandois *et al.*, 2016). Changes in litter and nutrient inputs also decrease soil C storage in peatlands converted to oil palm plantations. Reduced C storage in tropical peatlands has an important influence on global climate. Our results indicate that N_2O emissions represent an additional 3% of change in global warming potential of peat soil emissions following conversion from peat swamp forest to oil palm plantation. This is offset in part by the 2% decline in global warming potential due to a decline in methane production. While these trace gases should not be neglected in GHG budgets for tropical peatlands converted to oil palm, increased emissions of CO_2 make a much larger contribution to anthropogenic GHG emissions.

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CHAPTER FIVE

Linking soil respiration in tropical peatlands with remotely sensed observations of water storage from the Gravity Recovery and Climate Experiment

Abstract

Available estimates indicate that CO_2 emissions from peatlands in Southeast Asia are contributing substantially to anthropogenic emissions. Remote sensing is a powerful tool that is potentially useful for scaling up and constraining estimates of peat CO_2 emissions over space and time. We related remotely sensed measures of soil water status from the Gravity Recovery and Climate Experiment (GRACE) to ground measurements of precipitation, water table depth and total soil respiration, combining observations from undrained forest and drained smallholder oil palm plantations on peat in Central Kalimantan between January 2014 and September 2015. Monthly changes in soil water storage measured by GRACE explained 48% of variation in total soil respiration measured on the ground. By facilitating regular sampling across broad spatial scales that captures essential variation in a major driver of soil respiration, our novel approach could improve understanding of the role of tropical peat in the global carbon cycle.

Introduction

Over the past several decades the area of oil palm plantations has risen steeply, more and more at the expense of tropical forest and carbon (C) rich peat swamps. This is particularly true in Indonesia and Malaysia, where most of the world's palm oil is produced. Available estimates indicate that C emissions from peatlands in Southeast Asia are contributing substantially to global anthropogenic emissions (Hooijer et al. 2010; Carlson et al. 2012; Harris et al. 2012). To accurately quantify their contribution and to understand how peat C emissions may change in the future, long-term measurements over months, seasons, and years are needed. In addition to understanding future drivers of land use change, we must assess how C emissions in tropical peatlands respond to future climate change. Studying seasonal and interannual changes in temperature and moisture can provide insight. Remote sensing is a powerful tool for understanding spatial and temporal variation in environmental conditions influencing peat C storage and loss.

Water table depth and soil moisture are critical environmental conditions influencing soil C storage and loss in tropical peat ecosystems (Hirano et al. 2007). Water table depth, determined by rainfall and influencing soil moisture throughout the soil column, is related to soil respiration across tropical peatland sites (Hergoualc'h & Verchot 2014). NASA Gravity Recovery and Climate Experiment (GRACE) data enable spaceborne observations of changes in water storage by terrestrial ecosystems over time. Thus GRACE may provide a new tool for understanding peat C fluxes that are mainly driven by soil moisture. GRACE supplies measurements of the Earth's time variable gravity field. After oceanic and atmospheric effects are removed, monthly and interannual variations in Earth's gravity field are mostly accounted for by changes in terrestrial water storage. GRACE data have been used to estimate depletion of ground water in aquifers around the world (Rodell et al. 2009, Famiglietti et al. 2011, Voss et al. 2013). Application of GRACE to assess trace gas fluxes from soils have largely been limited to studies of methane (Bloom et al. 2010; Bloom et al. 2012). This study represents a new application of GRACE data: to assess changes in total respiration from peat soils associated with changes in soil water storage.

We related monthly satellite observations of GRACE Terrestrial Water Storage Anomaly (TWSA) to ground-based estimates of precipitation, water table depth and total soil respiration derived from measurements in undrained forest and drained smallholder oil palm plantations on peat in Central Kalimantan, Indonesia. Data were collected between January 2014 and September 2015. Our ultimate aim was to test for a relationship between a remotely sensed measure of changes in soil water storage and ground measurements of total soil respiration in a tropical peatland (Figure 18).

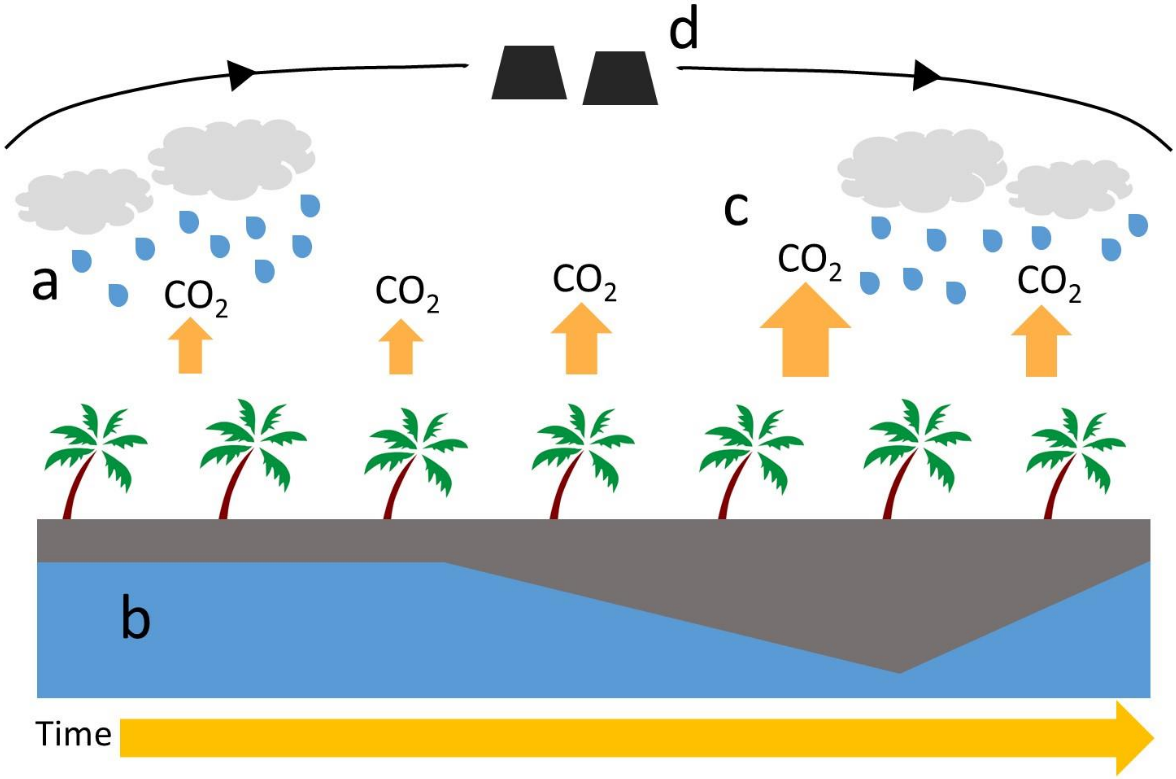


Figure 18. Conceptual model of links among precipitation, water table depth, total soil respiration, and GRACE observations of terrestrial water storage anomaly (TWSA) in an Indonesian peatland. Precipitation (a) influences water table depth (b). Water table depth increases under conditions of reduced precipitation during dry periods, and total soil respiration increases (c). GRACE TWSA indicates monthly changes in soil water storage ultimately driven by variation in precipitation (d).

If TWSA is related to rainfall and thereby water table depth, then TWSA could be used to predict total soil respiration in tropical peatlands. Since soil respiration is one of the main components of the peat C budget (Hergoualc’h & Verchot 2014), successful scaling up of our novel remote sensing approach could improve understanding of the influence of seasonal and interannual variation in water storage on the C cycle.

Materials and methods

Site description

We collected ground measurements at permanent plots in 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 (-2.82806, 111.813, Figure 19a). The climate of the region is humid tropical, with little variation in temperature throughout the year and high annual rainfall. We used weather observations from Iskandar airport in Pangkalan Bun during 2004-2013 to describe climate at the sampling site. Mean annual temperature in Pangkalan Bun is 27.4^{o}C. Mean annual rainfall is 2058 mm and September is typically the driest month (85 mm).

Three plots were established in forest, and three in oil palm plantations, for a total of six plots. The plots were located 1-10 km apart, comprising a range of peat depths, land use histories and vegetation ages (Table 8). All sites fell within one GRACE grid cell, 0.5° x 0.5° or 55 km x 55 km. Forest plots were situated at varying distances from river's edge and thus differed in peat depth. Two of the plots (K-FOR-2, K-FOR-3) were mature forest whereas the plot closest to the river (K-FOR-1) was a 30 year old secondary forest, likely formerly used as an agroforestry garden (Novita 2016). Oil palm plantations were planted in 2007 (K-OP-2007), 2009 (K-OP-2009), and 2011 (K-OP-2011). Oil palm plots underwent multiple fires.

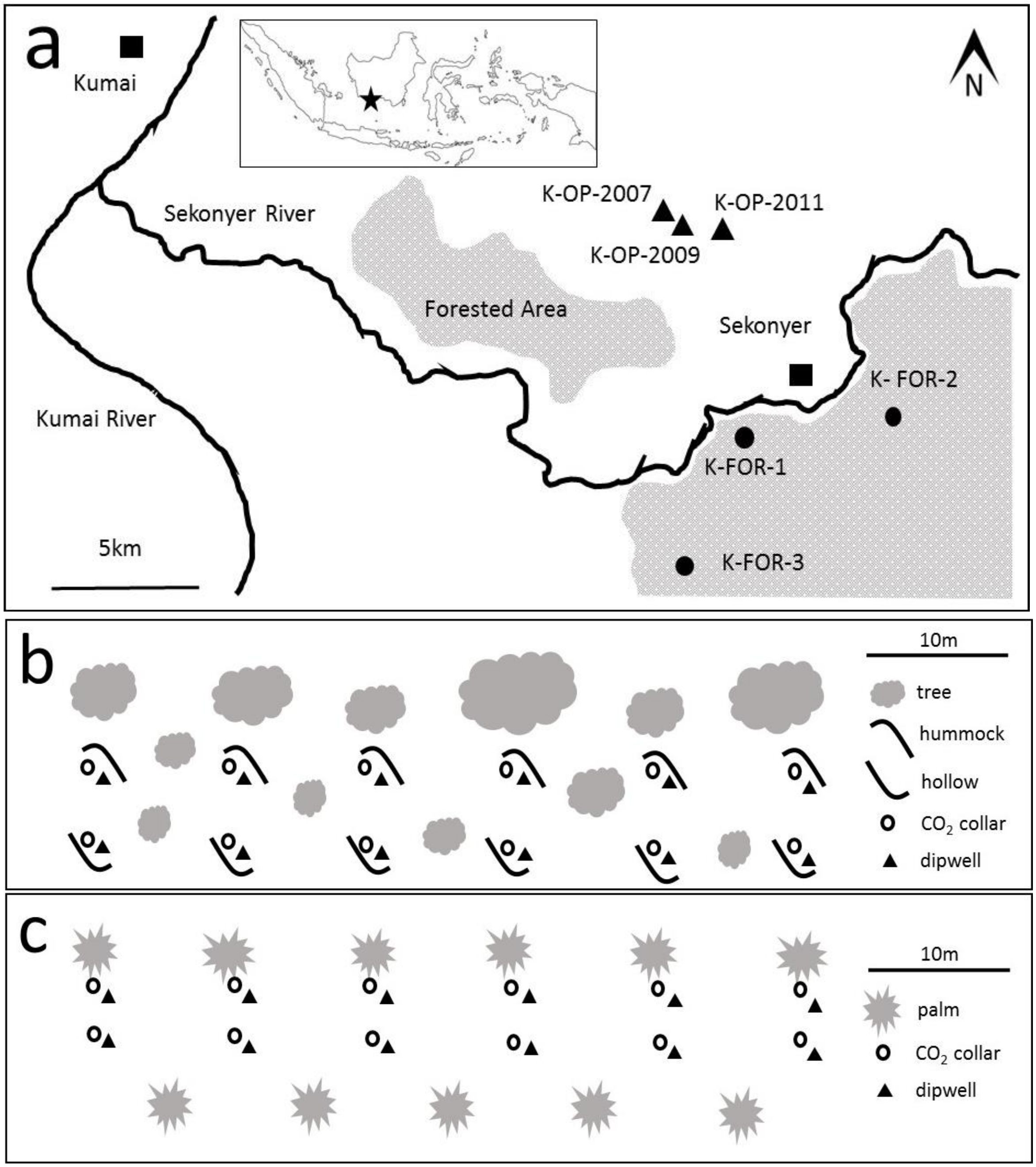


Figure 19. Research sites and sampling design. Location of the three plots in undrained forest and three plots in nearby drained smallholder oil palm plantations (a) in Central Kalimantan, Indonesia (inset, a). We used similar sampling designs to collect measurements from six locations in each plot in forest and oil palm. In forest plots, at each location we installed a CO_2 collar and a dipwell on a hummock, and a matched set in the adjacent hollow (b). In oil palm plots, at each location we installed one set at the base of a palm and one set at mid-distance between two adjacent rows of palms (c).

Table 8. Characteristics of the sampling plots in Central Kalimantan, Indonesia. (After Swails et al., in review)

Code	**Landuse**	**Location**		**Clearance Year**	**Plantation Age**	**Fires**	**Distance to River**	**Peat Depth**
K-FOR-1	Forest	-2.82360	111.813	pre 1982	-	Multiple	0.5 km	27 cm
K-FOR-2	Forest	-2.82220	111.807	-	-	-	1 km	155 cm
K-FOR-3	Forest	-2.83080	111.802	-	-	-	2 km	290 cm
K-OP-2011	Oil palm	-2.82310	111.810	1989	4 year	Multiple	3.5 km	20 cm
K-OP-2009	Oil palm	-2.82170	111.803	2005	6 year	Multiple	3.5 km	47 cm
K-OP-2007	Oil palm	-2.82060	111.801	2005	8 year	Multiple	3.5 km	47 cm

Monthly ground measurements

We collected measurements of total soil respiration and water table depth from plots once each month from January 2014 through June 2015 and again in September 2015. Plots were sampled on consecutive days between the hours of 0800 and 1200 usually during the last week of the month. We measured water table depth concomitantly with CO_2 measurements. Daily precipitation data for the area were obtained from Iskander Airport in Pangkalan Bun.

Our ground sampling approach was designed to account for spatial heterogeneity in soil respiration and environmental conditions while capturing temporal heterogeneity in both (Figure 19b and 19c). Sixteen months before the beginning of this study, we inserted sets of two PVC collars to 5 cm depth at six locations per plot. In forest plots, we installed one collar on a hummock and one collar in the adjacent hollow (Figure 19b). In oil palm plots, we installed one collar at the base of a palm (near) and one collar at mid-distance between two adjacent rows of palms (far, Figure 19c). Total soil respiration was measured by the dynamic closed chamber method (Pumpanen et al. 2009) with a portable infrared gas analyzer/EGM-4 (Environmental Gas Monitor) connected to a Soil Respiration Chamber (SRC-1) (PP System, Amesbury, USA) placed on the permanent PVC collar. Water table depth was measured in a dipwell permanently installed next to each CO_2 collar. The dipwells were perforated PVC pipe (2.5 cm diameter) inserted to 2 m depth below the peat surface.

With a goal of creating a single monthly number against which to compare remotely sensed data, we combined data in a way appropriate to the scale of the measurements. First, we calculated weighted averages of total soil respiration and water table depth measurements based on the spatial extent of conditions within the plot (hummock/hollow and near/far). In forest plots, we measured the length of hummocks and hollows along two perpendicular 50 m transects and divided the total length of hummocks by the total length of hollows to calculate the ratio of hummock to hollow area in each forest plot. In oil palm plots, we assume that measurements at collars near palms are representative of the area within a 2 m radius of the base of the palms. This is the zone where smallholders apply fertilizers and root density (Comeau et al. 2016; Khalid et al. 1999) and activity (Nelson et al. 2006) are usually highest. In forest plots, the ratios of hummock to hollow area were 48:52 (K-FOR-1), 52:48 (K-FOR-2), and 63:37 (K-FOR-3). In oil palm plots, the ratios of the area within a 2 m radius of palms (near) to the area outside of this radius (far) were 25:75 (OP-2011), 27:73 (OP-2009), and 37:63 (OP-2007). For each plot, we multiplied the mean value of hummock/near measurements by the hummock/near ratio, and the mean value hollow/far measurement by the hollow/far ratio. To calculate mean monthly values of total soil respiration and water table depth, we combined the weighted averages from each plot in each month to yield a single value for each land use (three plots, n=3 per land use). Detailed soil respiration rates for each plot are reported elsewhere (Swails et al. in preparation).

Finally, we combined data from the two land uses to derive a single value for comparison with GRACE TWSA. We multiplied the mean respiration rate by the proportional coverage of the two land uses in our 0.5° x 0.5° GRACE grid cell. We determined the proportional coverage of oil palm and forest by overlaying a 10 x 10 grid on the GRACE cell boundaries in Google Earth. The proportional coverage of forest (60%) and oil palm (30%) in each of the .05° x .05° cells was determined by visual inspection. We inspected each of the 100 cells individually, and tallied the coverage by land use in each cell. The actual factors used in weighting (forest, 2/3 and oil palm, 1/3) spread the residual effect of the area in water, urban areas, or other crops (10%) proportionally across the two land uses. We weighted data for water table depth in the same manner to generate a single landscape-scale value representative of the GRACE grid cell. We related these weighted average monthly values for the landscape—derived from measurements in oil palm and forest—to GRACE TWSA.

GRACE data acquisition

We extracted GRACE TWSA observations for our study site from one grid cell (-2.75000 111.750, star in Figure 2, inset) in JPL-RL05 GRACE monthly mass grids (Watkins et al. 2015; Wiese 2015). JPL-RL05 uses a-priori constraints in space and time to estimate global, monthly gravity fields in terms of equal area 3-degree spherical cap mass concentration functions. A Coastal Resolution Improvement (CRI) filter is applied in post-processing to separate land and ocean portions of mass. The mass grids, updated monthly, provide surface mass changes relative to a baseline average over January 2004 to December 2009 with a spatial sampling of 0.5° (approximately 55 km at the equator). Seasonal mass changes are caused by changes in water storage. The vertical extent of these changes can be thought of as a thin layer of water concentrated at the Earth’s surface, measured in units of centimeters equivalent water thickness. Scaled uncertainty estimates are also provided on a 0.5° global grid in the JPL-RL05 product.

About one month of satellite measurements are required to generate the GRACE monthly mass change data, although occasionally, values represent less than a month of observations.

Nevertheless, the temporal resolution of GRACE TWSA is fixed at one month. The mass changes reported for a given month were usually calculated as the average of measurements collected from day 16 of the previous month to day 16 of the present month. We matched these data with the measurements of soil respiration and water table depth closest in time, most often taken at the end of the month, within a week or two of the GRACE value determined by integrating over the last half of the previous month and the first half of the current month.

Rather than the Jan 2004 – Dec 2009 baseline, we used a January 2014 – September 2015 baseline to match the time of our study. To calculate TWSA relative to 2014 – 2015, we calculated an average of TWSA values over our study period relative to the Jan 2004 – Dec 2009 baseline, and subtracted that value from the TWSA value for each month. TWSA data were unavailable for the months of February, July, and December 2014, and June 2015 due to satellite battery management.

Calculations and statistical analysis

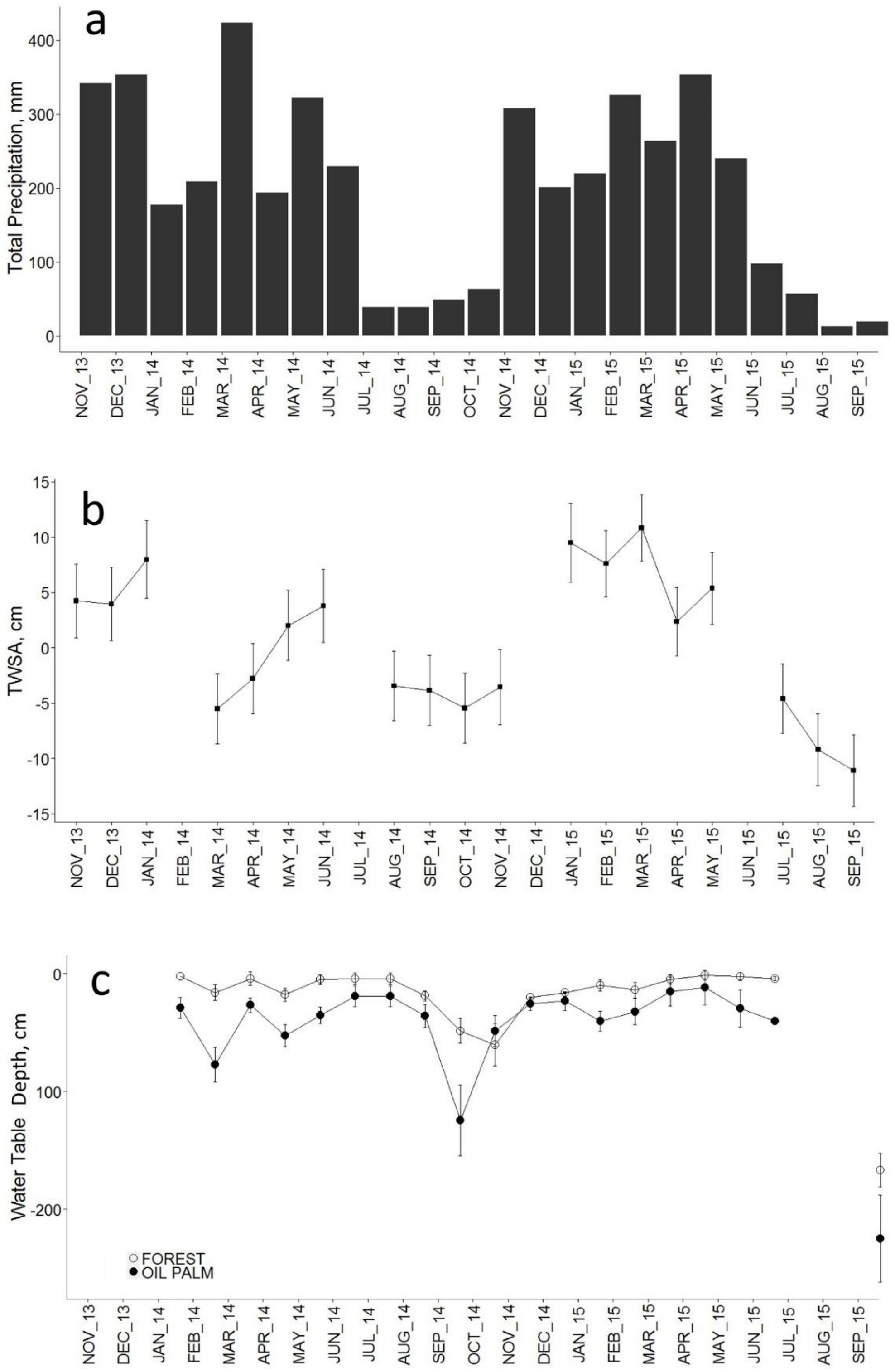
All statistical analyses were completed using R (v 3.2.5). We used ordinary least squares (OLS) linear regression to test for relationships among precipitation, GRACE TWSA, water table depth, and total soil respiration at our plots. Since the beginning and end of GRACE measurement periods did not correspond to the first and last day of calendar months, we related GRACE TWSA to rainfall that fell immediately before and during the GRACE measurement period. We used cumulative precipitation over the 60 and 30 days preceding the final day of the GRACE measurement period. We also related water table depth with cumulative precipitation over the 60 and 30 days preceding the last day of field measurements.

We used data transformation as necessary to adequately model the functional form of dependent variables, e.g. we used log transformed soil respiration data to model the relationship between GRACE TWSA and combined total soil respiration as a linear function. To assess the normality assumption of OLS regression we used normality probability plots with a 95% confidence envelope produced using a parametric bootstrap. Durbin-Watson test was used to test for autocorrelation. To test for heteroscedasticity we used a score test of the hypothesis of constant error variance against the alternative that the error variance changes with the level of the fitted values. We identified outliers for examination using Bonferroni adjusted p-value for the largest absolute studentized residual. Data points with high leverage were identified using the hat statistic p/n, where p is the number of parameters estimated and n is the sample size. We examined observations with hat values greater than 3 times the average hat value. We used Cook's D to identify influential observation.

Results

Variation in total soil respiration, drivers, and TWSA

Precipitation, TWSA, water table depth, and total soil respiration showed clear seasonal variation in both oil palm and forest sites. Monthly precipitation was ≤ 100 mm during the months of July – October 2014 and June – September 2015. Precipitation reached a high of 424 mm in the month of March 2014 (Figure 20a) and was lowest in August 2015 (13 mm). Monthly TWSA showed considerable variation between wet and dry seasons (Figure 21). Monthly TWSA ranged from 10.8 cm in March 2015 to -11.1 cm in September 2015 (Figure 20b). In both forest and oil palm, the water table was highest in April 2015 (-2.3 ± 3.5 cm and -13.7 ± 3.8 cm, respectively) and lowest in September 2015 (-167.9 ± 6.5 cm and -227.3 ± 9.0 cm, respectively). Total soil respiration was lowest in April 2014 in the forest (0.36 ± 0.04 g CO_2 m^{-2} hr^{-1}) and April 2015 in the plantations (0.54 ± 0.07 g CO_2 m^{-2} hr^{-1}) and highest in September 2015 in both forest (1.54 ± 0.23 g CO_2 m^{-2} hr^{-1}) and oil palm (1.07 ± 0.14 g CO_2 m^{-2} hr^{-1}).


a
Total Precipitation, mm
0
100
200
300
400
NOV_13
DEC_13
JAN_14
FEB_14
MAR_14
APR_14
MAY_14
JUN_14
JUL_14
AUG_14
SEP_14
OCT_14
NOV_14
DEC_14
JAN_15
FEB_15
MAR_15
APR_15
MAY_15
JUN_15
JUL_15
AUG_15
SEP_15
b
TWSA, cm
15
10
5
0
-5
-10
-15
c
Water Table Depth, cm
0
100
-200
○ FOREST
● OIL PALM

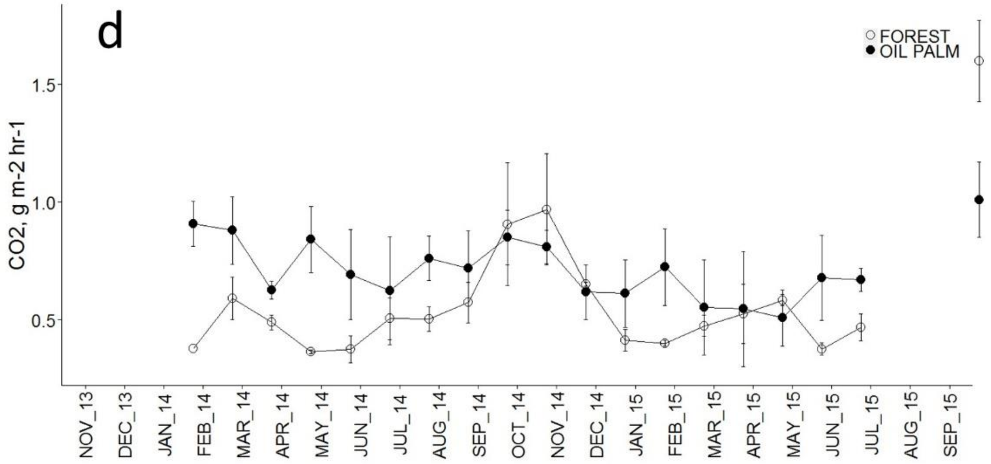


Figure 20. Monthly precipitation (a), GRACE TWSA (b), mean water table level (c) and mean total soil respiration in forest (solid circle) and oil palm (open circle) plots (d). Values in (b) represent the change in remotely sensed water storage at the sampling sites in centimeters liquid water equivalent. Error bars in (b) represent the scaled uncertainty associated with the 3° mascon estimate (Weise et al. 2016). Error bars in (c) and (d) represent standard error of the mean (n=3).

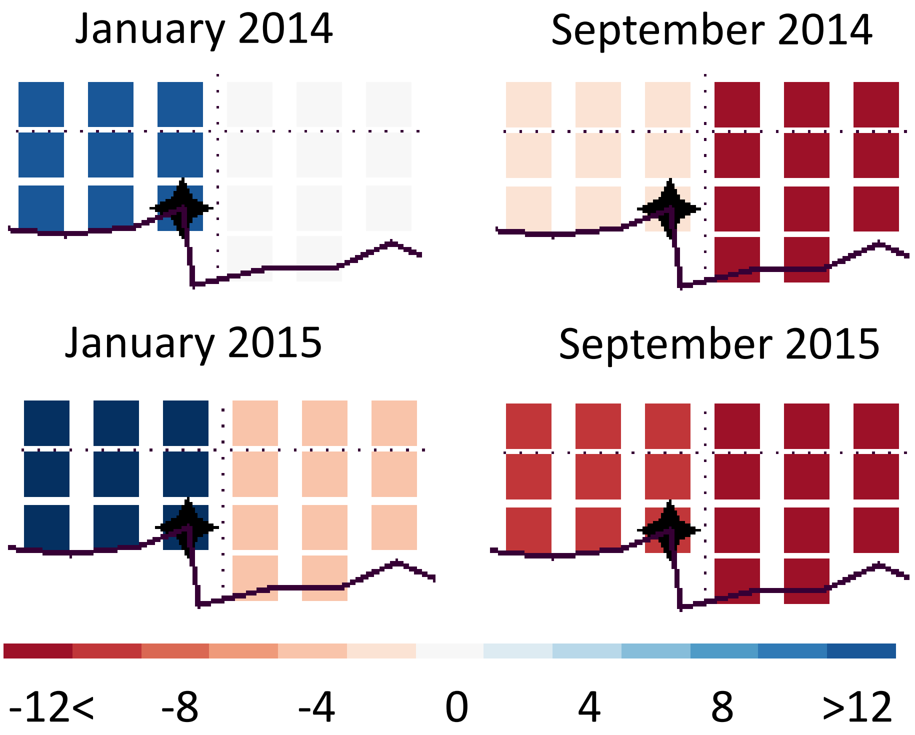


Figure 21. Gridded GRACE TWSA across southern Central Kalimantan, Indonesia during wet season in January 2014 and 2015 and dry season in September 2014 and 2015. Colors represent the change in water thickness (units = cm liquid water equivalent) relative to the January 2004 to

December 2009 average baseline. The grid cell covering our study site is marked with a star. Dotted lines indicate -2 latitude and 112 longitude.

Relationships among climate drivers, TWSA, and total soil respiration

TWSA increased logarithmically with increasing cumulative precipitation immediately before and during the GRACE measurement period (R^2=0.56, p<0.001, Figure 22a). TWSA was more strongly related to cumulative precipitation over 60 days than 30 days preceding the final day of the GRACE measurement period. Water table level also increased logarithmically with increasing cumulative precipitation in both forest (R^2=0.46, p=0.004) and oil palm (R^2=0.39, p=0.001), and was more strongly related to cumulative precipitation over 60 days than 30 days preceding the final day of field measurements. (Fig 22b). The data point corresponding to forest plot measurements collected in September 2015 (16 mm, 167.9 cm) was an outlier (Bonferroni adjusted p<0.01) with significant influence on the relationship between water table depth and soil respiration in forest (Cook's D=8).

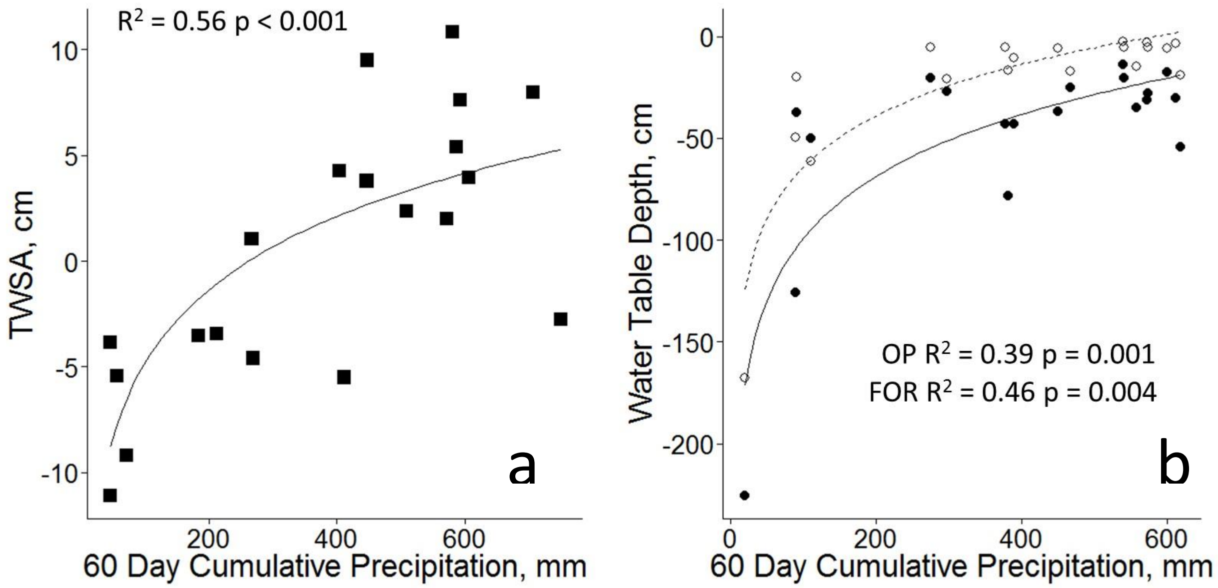


Figure 22. GRACE TWSA as a function of cumulative precipitation during the 60 days preceding the final day of the GRACE measurement period (a) and mean water table depth as a function of precipitation during the 60 days preceding the final day of monthly field

measurements (b) from January 2014 through September 2015 in oil palm (solid circle and solid line) and forest plots (open circle and dashed line).

Total soil respiration increased logarithmically with concurrently measured water table depth in both forest and oil palm (Figure 23). As the water table dropped further below the soil surface, soil respiration increased, in both oil palm (R^2=0.56, $p<0.01$) and forest (R^2=0.62, $p<0.01$). The data point corresponding to measurements collected in September 2015 in forest plots (167.9 cm, 1.54 g m^{-2} hr^{-1}) was an outlier (Bonferroni adjusted p=0.03) with marginally significant influence on the relationship between water table depth and soil respiration in forest (Cook's D=2.5).

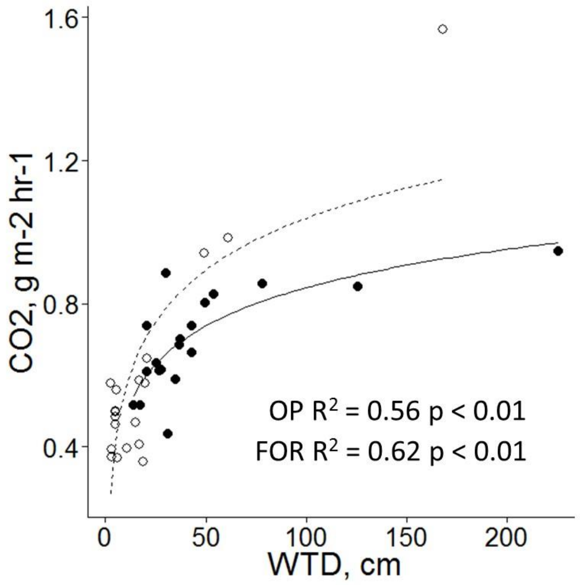


Figure 23. Mean total soil respiration as a function of mean water table depth from January 2014 through September 2015 in oil palm (solid circle and solid line) and forest plots (open circle and dashed line).

As water level approached the surface (and water table depth decreased), TWSA increased (R^2=0.39, p=0.01, Figure 24a). Total soil respiration declined with increasing TWSA, and the relationship was stronger than the relationship between TWSA and water table depth (R^2=0.47, $p<0.01$, Figure 24b).

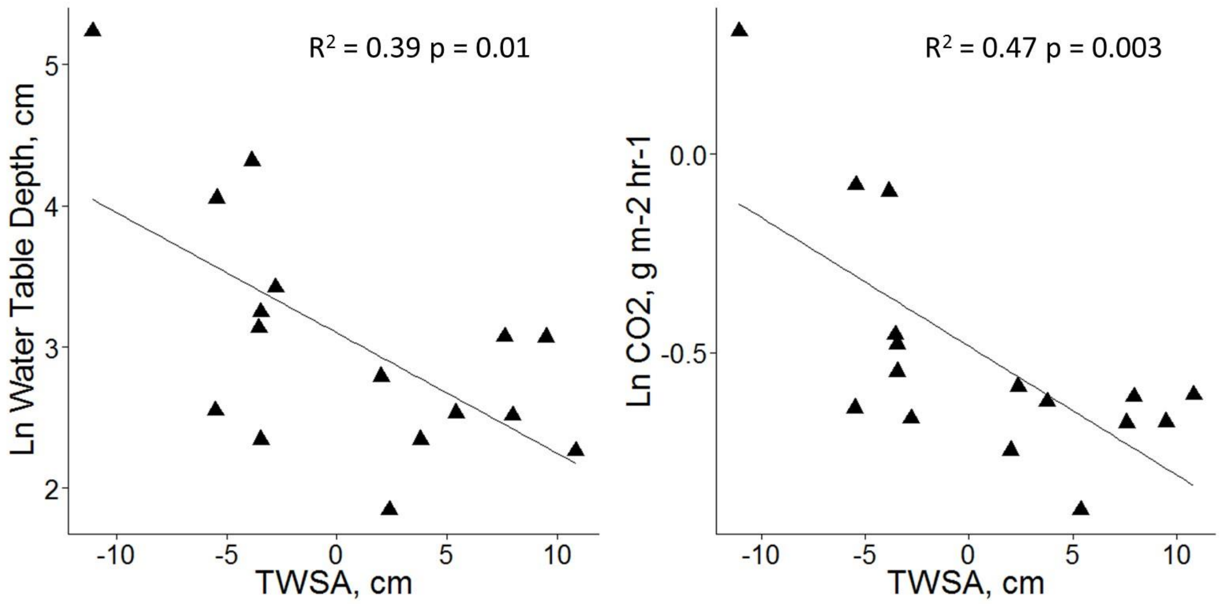


Figure 24. Weighted mean water table depth (a) and weighted mean soil respiration (b) as a function of GRACE TWSA from January 2014 through September 2015.

Discussion

Linking GRACE observations with total soil respiration

GRACE TWSA was well in phase with precipitation and water table depth (Figure 3). Water table depth, influenced by precipitation (Hirano et al. 2007), is a strong predictor of total soil respiration in our test site (Figure 23 and Swails et al. in preparation), and other tropical peatlands sites (Hirano et al. 2009; Jauhiainen et al. 2008). The significant relationship between GRACE TWSA and precipitation (Figure 22a), and water table depth (Figure 22a), indicates that GRACE data could be used to assess an important C flux from tropical peat soils. Indeed, we found a significant relationship between GRACE TWSA and total soil respiration in our test site (Figure 24b).

Understanding the hydrological processes driving variation in soil water storage is important for interpreting relationships among precipitation, GRACE, and water storage in tropical peatlands. GRACE is related to changes in water storage, which is a function of precipitation, but also evapotranspiration and discharge, which were not accounted for in our study. Relating GRACE TWSA to soil water status and total soil respiration on the ground is constrained by many factors. For example, TWSA reported for March 2014 was strongly negative. Despite extremely high rainfall in the latter half of March 2014, because the period followed two relatively dry months, TWSA remained negative for April, and it did not become positive again until May 2014. These data indicate that ground water reservoirs required several months of rainfall to recharge after the relatively dry conditions in January and February 2014. Another constraint on generating relationships among critical hydroclimatic parameters and soil respiration is the dearth of meteorological data. The precipitation recorded at Iskander Airport in Pangkalan Bun may not have been representative of the climatic conditions represented in the GRACE grid cell, which covers an area of approximately 3,136 km^2. The spatial resolution of the current product, at 0.5°, is fairly coarse. Finally, missing days in the data record due to instrument issues may have influenced the accuracy of TWSA observations. Generation of a good gravity field solution requires accumulation of satellite-to-satellite tracking data for about one month, and there were many days missing from the record. Beginning in 2011 the GRACE mission has shut down battery power for consecutive weeks approximately every six weeks to extend satellite lifetime. The anticipated GRACE follow-on mission will extend the GRACE time series with minimal data gaps while significantly improving on the accuracy and spatial resolution of the original mission (Fletchner et al. 2014).

A new way to assess a critical CO_2 flux from tropical peatlands

Lower TWSA, indicating drier conditions, was associated with higher landscape-scale soil respiration in our test site comprised of roughly 1/3 oil palm and 2/3 intact peat swamp forest. Using relationships among precipitation, GRACE TWSA, and total soil respiration, soil water storage, an important driver of respiration in tropical peat soils, could be related to seasonal and interannual climatic variation. Direct satellite based assessment of soil water status would better characterize spatial and temporal variability in total soil respiration in tropical peatlands compared to other existing satellite based approaches. For example, the Soil Moisture Active Passive (SMAP) mission L4-C product for monitoring terrestrial ecosystem – atmosphere CO_2 exchange achieves 9 km resolution (Jones et al. 2016) compared to 0.5 degree resolution with GRACE JPL-RL05. SMAP, while useful for assessing soil water status in other parts of the world (Piepmeier et al. 2017), cannot be used in densely vegetated tropical peatlands. GRACE is uniquely appropriate for application in tropical peatlands in that it is able to "see through" dense vegetation, unlike SMAP. Satellite based rainfall data such as the Tropical Rainfall Measurement (TRMM) can be used in the tropics to model soil water storage, and achieves higher spatial resolution than GRACE (e.g. 0.25^o for TRMM). However satellite based rainfall products are not measures of soil water storage, and may underestimate rainfall in Southeast Asia during dry months (Vernimmen et al. 2012).

Several issues complicate the application of GRACE data for assessment of the C cycle in tropical peatlands. Total soil respiration includes both heterotrophic and autotrophic contributions, but only heterotrophic respiration is directly linked to peat decomposition. The literature indicates that anywhere from 50-90% of the flux is likely due to heterotrophic respiration (Comeau et al. 2016). Furthermore, peat C storage or loss results from the balance of C entering the peat – litterfall, root mortality, and exudates, and C leaving the peat – heterotrophic respiration, dissolved organic carbon, methane, and fire, if any. Also, GRACE data are coarse, and grid level TWSA represents the contribution of changes in water storage in both undrained peat forest and drained oil palm. As we have done here, using land cover data, GRACE grid level data could be weighted to represent coverage by forest and oil palm to better model soil water storage (the proxy) or total soil respiration (the ultimate target) with TWSA observations. Finally, total soil respiration within a specific land use in tropical peatlands responds to multiple factors in addition to water table depth, such as soil moisture, temperature, soil organic matter quality, and nutrients. Ultimately, a multi-factor model could be developed linking remotely sensed measures with ground measurements to scale up assessment of soil respiration in tropical peatlands. With further work to account for other critical C fluxes, using GRACE data shows great promise for providing an alternative approach for understanding the role of tropical peatlands in the global C cycle.

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CHAPTER SIX

Synthesis

Available estimates indicate that tropical peatlands contribute substantially to anthropogenic emissions from land-use and land-use change, but controls on GHG emissions from tropical peat remain poorly understood. Although water table level is considered the primary control on microbial decomposition of peat, and therefore the driver of net soil C uptake or emissions from these ecosystems, results are inconsistent among land-uses and sites. Clearly, emissions depend on more than drainage status. Additionally, conversion, drainage, and management of peatlands for agricultural production also impacts peatland emissions of CH_4 and N_2O, GHGs with much higher global warming potential than CO_2. To accurately characterize GHG emissions from land-use change in peatlands, a full accounting of GHG sources and sinks is needed, with adequate consideration of spatial and temporal drivers controlling GHG emissions from peat soils.

In my dissertation, I focused on one of the main components of the peat C budget, soil respiration. The response of total soil respiration to climatic variability in the field experiment provided insight into how C emissions from peat may change in both forest and oil palm under a potential future climate regime (Chapter 2). At the study site in a Central Kalimantan peatland, total soil respiration was tightly linked with water table level. In forest plots, total soil respiration was highly responsive to water table depth, particularly in hollows. During dry months, when cumulative rainfall was less than 100 mm per month, total soil respiration increased as the water table level fell further below the soil surface. Oil palm plots, with lower water table level than forest plots overall, had higher cumulative total soil respiration during the monitoring period, and low sensitivity to change in water table level. However, during the El Niño event in September 2015, when water table levels were lower than in September in the previous year in both land uses, total soil respiration was higher in forest than in oil palm. Assuming that the contribution of heterotrophic respiration contributed approximately 50% of total respiration in forest and 70% in oil palm, as it did during a year with normal precipitation, during the El Niño event heterotrophic respiration from peat decomposition was roughly equal in the two land uses. In a warmer world with more frequent and severe El Niño events, CO_2 emissions from undrained peat swamp forests could rival those from drained tropical peatlands.

The incubation experiments provided insight into how C emissions from drained oil palm plantations may change over time under the current and potential future climate regime. Lower organic matter quality and nutrient availability in oil palm soils than soils from undrained forest is consistent with the literature. Multiple processes likely explain the decline in soil organic matter quality and nutrients in oil palm plantations, including enhanced microbial decomposition of peat and leaching as well as fires. However, the link between differences in peat soil properties across land-uses and sites and rates of peat decomposition has not been explored previously in the tropics. To test the influence of soil organic matter quality and nutrients over a broader range of values, I included in the experiment peat samples from the industrial oil palm plantation in Sumatra in addition to the soils from the oil palm and forest sites in Kalimantan. Differences in peat soil organic matter quality and nutrients, particularly ratios of aromatic:aliphatic and C:N, explained differences in rates of CO_2 production from soils incubated at the same moisture level and temperature. Forest soils, with lower aromatic:aliphatic and C:N ratios, had more labile carbon and available N. These soils decomposed faster, producing more CO_2 than oil palm soils. I interpret these results to suggest that soon after peat forest conversion to oil palm, high quality organic matter is available, and once aerated, it is readily decomposed. Consequently, CO_2 emissions from microbial decomposition of peat are high in the early years of an oil palm plantation. Increased CO_2 production by soils in response to amendment with labile C (glucose) and mineral N and P confirmed the relationship between microbial respiration and labile C and nutrients in these soils (Chapter 3). The results suggest that substrate driven rates of CO_2 production by drained peat soils in oil palm plantations may decline over time as nutrients are depleted, labile carbon is consumed, and recalcitrant organic matter accumulates. As CO_2 emissions from artificially drained peat soils decline with oil palm plantation age, increased CO_2 emissions from climate driven drying of undrained peat swamp forest may become an even more import source of GHG emissions (Chapter 2). This potential switch from land use change to climate change as a driver, and from converted peatlands to native peat swamp forest as a locus of substantial GHG emissions, is an area ripe for future research.

Like total soil respiration, CH_4 emissions from peat soils were tightly linked to water table level at the study site. CH_4 flux increased sharply in forest plots during wet months as the water table level rose closer to the soil surface. In oil palm plots the water table level remained well below the soil surface on average, and CH_4 emissions were unresponsive to changes in water table level there. Although CH_4 emissions were lower in oil palm than forest, decreased CH_4 emissions were outweighed by increased CO_2 emissions from enhanced decomposition of peat soils. This result is in agreement with the literature. On the other hand, previous observations of N_2O emissions from peat soils post-conversion were inconsistent. Some studies showed increased N_2O emissions as expected (Furukawa *et al.*, 2005; Takakai *et al.*, 2006), and other studies showed no effect on N_2O emissions (Inubushi *et al.*, 2003; van Lent *et al.*, 2015) or decreased N_2O emissions (Hadi *et al.*, 2005). With repeated monthly measurements over a period that spanned almost two years, I found that N_2O emissions were higher in oil palm plantations than forest. These results indicate that increased N_2O emissions can make a small but significant contribution to increased GHG emissions in oil palm plantations, and N_2O emissions should not be neglected in peatland GHG budgets. However, overall, contributions from CH_4 and N_2O were much smaller components of the GHG budget in the Kalimantan forest and oil palm plots compared to CO_2 (Chapter 4).

Remote sensing is a powerful tool for scaling up ground observations over space and time. The robust relationships among GRACE TWSA, water table level, and total soil respiration at the study site in Kalimantan indicate that GRACE provides a promising approach for assessing CO_2 emissions from tropical peatlands at broad spatial and temporal scales. At present, the spatial resolution of GRACE data is a limitation on robust estimates of GHG emissions from peatlands. However, downscaling techniques and more widespread field measurements for calibration may improve GRACE-based estimates of GHG emissions at regional or global scales. Furthermore the GRACE follow-on emissions, with expected launch in 2018, will improve upon spatial resolution of the data from original mission. Partitioning of heterotrophic and autotrophic respiration in forest and oil palm over a wide range of climatic conditions with more extensive sampling across the region is needed to understand how these two components of total respiration respond to extreme drying. Only heterotrophic respiration actively contributes to reduced C storage by peat soils, and is thus more important for climate change impacts than heterotrophic emissions. More comprehensive accounting that allows consideration of multiple drivers (peat substrate quality in addition to climate drivers) and time frames (pre- to early to late post-conversion) would improve understanding of how this important C sink is both contributing and responding to global climate change. This dissertation makes a substantial contribution to filling this need.

APPENDIX

Table A1. Trace elements in the peat soil profile in forest and oil palm (n=3 per depth interval). Mean values are presented with standard error. a and b indicate significant differences between forest and oil palm at the same depth. No letters are displayed in the absence of a significant difference.

Property	Depth (cm)	Forest		Oil Palm	
Ca (mg kg^{-1})	0-5	139.8	±36.8	281.7	±136.1
	10-20	86.9	±8.3	287.7	±61.6
	20-30	75.0		298.2	
	30-50	73.3		233.3	
	50-100	58.8			
Mg (mg kg^{-1})	0-10	61.6	±11.3	30.9	±5.8
	10-20	42.6	±3.3 [a]	23.6	±3.7 [b]
	20-30	38.0		23.7	
	30-50	28.6		20.1	
	50-100	18.5			
S (mg kg^{-1})	0-10	37.7	±20.8	20.6	±5.3
	10-20	42.7	±27.6	18.9	±3.7
	20-30	12.9		23.7	
	30-50	12.0		31.4	
	50-100	10.7			
Al (mg kg^{-1})	0-10	1,140	±275	834	±168
	10-20	1,316	±286	685	±50
	20-30	1,054		686	
	30-50	1,021		675	
	50-100	877			
Fe (mg kg^{-1})	0-10	77.7	±55.7	113.1	±35.9
	10-20	70.6	±53.8	74.3	±15.1
	20-30	14.0		51.3	
	30-50	9.7		37.9	
	50-100	2.8			
Na (mg kg^{-1})	0-10	25.6	±2.3	23.9	±1.6
	10-20	25.9	±2.3	22.9	±2.1
	20-30	24.1		19.9	
	30-50	20.6		18.4	
	50-100	17.9			
Cu (mg kg^{-1})	0-10	0.75	±0.16	0.80	±0.16
	10-20	0.86	±0.24	0.63	±0.03
	20-30	0.75		0.49	
	30-50	0.73		0.50	
	50-100	0.62			

Zn (mg kg^{-1})	0-10	1.20	±0.20	1.13	±0.18
	10-20	0.94	±0.14	0.71	±0.09
	20-30	0.91		0.76	
	30-50	0.64		0.62	
	50-100	0.52			