DR. ALISON HOYT (Orcid ID : 0000-0003-0813-5084)

DR. ALEXANDER R COBB (Orcid ID : 0000-0002-3128-3002)

Article type : Primary Research Articles

Corresponding Author Email ID: ahoyt@mit.edu

CO_2 emissions from an undrained tropical peatland: Interacting influences of temperature, shading and water table depth

Alison M. Hoyt[1,a], Laure Gandois[2], Jangarun Eri[3,c], Fuu Ming Kai[4,b], Charles F. Harvey[1,4,d], Alexander R. Cobb[4,d]

[1] Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, Massachusetts, 02139 USA

[2] EcoLab (Laboratoire Écologie fonctionnelle et Environnement), Université de Toulouse, CNRS, INPT, UPS, Toulouse, France

[3] Forestry Department, Ministry of Industry and Primary Resources, Jalan Menteri Besar, Bandar Seri Begawan BB3910, Brunei Darussalam

[4] Center for Environmental Sensing and Modeling, Singapore-MIT Alliance for Research and Technology, 138602 Singapore

[a] Present address: Max Planck Institute for Biogeochemistry, 07745 Jena Germany

[b] Present address: Gas Metrology Laboratory, National Metrology Center, Agency for Science, Technology and Research, 118221 Singapore

[c] Present address: Forestry Department, Ministry of Primary Resources and Tourism, Jalan Menteri Besar, Bandar Seri Begawan BB3910, Brunei Darussalam

[d] C.F.H. and A.R.C. should be considered joint senior author

Abstract

Emission of CO_2 from tropical peatlands is an important component of the global carbon budget. Over days to months, these fluxes are largely controlled by water table depth. However, the diurnal cycle is less well understood, in part, because most measurements have been collected daily at midday. We used an automated chamber system to make hourly measurements of peat surface CO_2 emissions from chambers root-cut to 30cm. We then used these data to disentangle the relationship between temperature, water table, and heterotrophic respiration (R_{het}). We made two central observations. First, we found strong diurnal cycles in CO_2 flux and near-surface peat temperature (<10 cm depth), both peaking at midday. The magnitude of diurnal oscillations was strongly influenced by shading and water table depth, highlighting the limitations of relying on daytime measurements and/or a single correction factor to remove daytime bias in flux measurements. Second, we found mean daily R_{het} had a strong linear relation to the depth of the water table and under flooded conditions, R_{het} was small and constant. We used this relationship between R_{het} and water table depth to estimate carbon export from both R_{het} and DOC over the course of a year based on water table records. R_{het} dominates annual carbon export, demonstrating the potential for peatland drainage to increase regional CO_2 emissions. Finally, we discuss an apparent incompatibility between hourly and daily-average observations of CO_2 flux, water table and temperature: water table and daily average flux data suggest that CO_2 is produced across the entire unsaturated peat profile, whereas temperature and hourly flux data appear to suggest that CO_2 fluxes are controlled by very near surface peat. We explore how temperature, moisture, and gas transport related mechanisms could cause mean CO_2 emissions to increase linearly with water table depth but also have a large diurnal cycle.

Keywords: heterotrophic respiration, CO_2 flux, diurnal cycle, soil temperature, closed dynamic chamber technique, tropical peatland, Southeast Asia

Introduction

There are 24.8 Mha of tropical peatlands in Southeast Asia that sequester 68.5 GtC (gigatons of carbon; Page *et al.*, 2011a). Existing peat deposits in Southeast Asia began to accumulate around 15 ka (kiloannum BP), and expanded rapidly in coastal areas following the last sea level highstand at about 4.5 ka (Dommain *et al.*, 2014). Across Southeast Asia, this large store of carbon is being released to the atmosphere as CO_2 as peatlands are deforested and drained (Hooijer *et al.*, 2010). Conversion and deforestation rates are high, and in 2015, only 6.4% of the 15.7 Mha of peatlands in Sumatra, Borneo and Peninsular Malaysia remained as pristine peat swamp forest (Miettinen *et al.*, 2016).

Drainage of peatlands releases sequestered carbon to the atmosphere. In natural peatlands, peat soil accumulates under waterlogged conditions as the rate of plant productivity exceeds the rate of decomposition due to a lack of oxygen available for decomposition. When the water table is lowered, either seasonally or through drainage projects, oxygen becomes available for aerobic decomposition of organic matter. The resulting release of CO_2 to the atmosphere is both a significant source of greenhouse gases, and is responsible for long-term subsidence of the peat surface (Hooijer *et al.*, 2012). Emissions from peat oxidation excluding fires in 2015 were estimated to range from 132-159 MtC/yr, and cumulative carbon emissions since 1990 are estimated at 2.5 GtC (Miettinen *et al.*, 2017). The associated subsidence rates due to peat oxidation in drained peatlands can remain as high as 5 cm/yr for decades following drainage (Hooijer *et al.*, 2012). At these rates, many coastal peatland areas are in danger of subsiding below sea level.

Both subsidence-based estimates of carbon loss and measurements of CO_2 efflux with respiration chambers have found that peatland CO_2 emissions are strongly correlated with the average water table depth on weekly to monthly timescales (reviewed in Couwenberg *et al.*, 2010; Carlson *et al.*, 2015). However, some natural and physical processes are likely to cause changes in CO_2 fluxes on shorter timescales. Like other biological processes, decomposition is affected by temperature, which varies diurnally (Davidson & Janssens, 2006). Circadian patterns in assimilate transport to roots drive diurnal patterns in root exudation, which can create diurnal pattern in soil CO_2 flux (reviewed in Kuzyakov, 2006). The correlation between emissions and water table depth is clearly documented over longer timescales, but few studies have measured emissions at sub-diurnal timescales in tropical peatlands due to logistical challenges. Despite the clear long-term dependence of peat oxidation and the corresponding CO_2 efflux on water table depth, the relationships between temperature, water table and CO_2 emissions on shorter timescales remain unclear (Jauhiainen *et al.*, 2012).

Automated chambers have been used to capture CO_2 fluxes over the 24-hour cycle (Hirano *et al.*, 2009, 2014; Ishikura *et al.*, 2018a) in only a few of the more than 20 studies measuring CO_2 emissions from tropical peatlands in Southeast Asia. Instead, the majority of studies rely on manual measurements, most often collected at midday (e.g. Melling *et al.*, 2005; Jauhiainen *et al.*, 2014). Perhaps in part due to sparse datasets, efforts to characterize the diurnal cycle and temperature dependence of CO_2 fluxes have found mixed results. Hirano *et al.* (2009) found a clear midday peak in CO_2 emissions using automated chambers. Higher midday fluxes were also detected in manual chamber measurements over more limited time periods (1 day – two weeks) by Ali *et al.* (2006), Husnain *et al.* (2014), Marwanto & Agus (2014) and Comeau *et al.* (2016). However, Hergoualc'h *et al.* (2017) did not detect a diurnal cycle in CO_2 flux, and Ishikura *et al.* (2018) measured the lowest average hourly CO_2 fluxes at midday.

Levels of shading, precipitation and temperature are expected to change in the future as a result of changing climate and land use, and will influence rates of heterotrophic respiration (R_{het}) in tropical peatlands. Hourly measurements could yield valuable mechanistic insights about how R_{het} will respond to such changes. Soil respiration across ecosystems depends strongly on temperature (Lloyd & Taylor, 1994; Fang & Moncrieff, 2001; Davidson *et al.*, 2006; Tuomi *et al.*, 2008). In tropical peatlands, CO_2 emissions have been found to depend on water table depth, as well as temperature (Hirano *et al.*, 2009), shading (Jauhiainen *et al.*, 2014), and time of day (Ishikura *et al.*, 2018a). These observations have different implications for the primary mechanisms driving R_{het}, as well as the depth distribution of peat decomposition.

Here we use hourly measurements to explore the relationship between temperature, water table, shading and the diurnal cycle of peat CO_2 efflux. We find: (A) a clear relationship between daily mean R_{het} and water table depth, which enables accurate upscaling of soil respiration fluxes throughout the year based on water table alone; and (B) a strong diurnal cycle in CO_2 flux and peat-surface temperature, highlighting the bias that can result from use of daytime measurements alone. Finally, through physical calculations, we explore several mechanisms that could result in the daily mean flux increasing linearly with water table depth while also having a large diurnal cycle.

Methods

Measurement location, climate and land conversion history

Measurements were made in an undrained former timber concession in the Belait district of Brunei Darussalam, on the island of Borneo (Figure 1f; 114.362787°E, 4.405100°N; Site 1b within the Damit dome, 3.4km from the edge of the peat dome, as described in Gandois *et al.* (2013)). This site is an area of regenerating peatland that was logged by rail in 200 m x 200 m blocks from 1972-2010 but was not drained, and has been described in Kobayashi (1999), Gandois *et al.* (2013) and Gandois *et al.* (2014). Prior to logging, the site had a monodominant *Shorea albida* canopy. However, all but a few remnant trees were removed during logging, and the site now hosts mostly low-statured vegetation at varying stages of regeneration. Although the site was not drained, its vegetation resembles that of drained and degraded peatlands of Central Kalimantan (Blackham *et al.*, 2013; Ishikura *et al.*, 2018b): the tree species *Combretocarpus rotundatus*, a liana (*Uncaria* sp.), and ferns (*Nephrolepis* sp.) are common at the site. Figs (*Ficus* sp.) are locally abundant near the chamber site (Figure 1).

The woody peat at the site is highly organic, with a loss on ignition of 99% and percent carbon of 51% (Gandois *et al.*, 2013). The peat characteristics are expected to be very similar to those documented in the adjacent Mendaram peatland site, where the primarily fibric and humic woody peat has a dry bulk density of 0.072 ± 0.02 g cm^{-3} in the top 3.5m of the peat profile (Dommain *et al.*, 2015). The peat microtopography at the site is also similar to that at the adjacent Mendaram peatland site as described by Cobb *et al.* (2017), with local depressions separated by mounds created by the accumulation of organic matter around deadfall or the buttresses of live or dead trees (Figure 1; Figure S4).

Average precipitation measured at nearby Seria and Kuala Belait weather stations in 1947-2004 was 2880 mm/yr. The site is relatively aseasonal. Average precipitation was 139 mm in the driest month (March) over the same interval, well above the threshold of 60 mm/mo for a tropical dry season in the Köppen climate classification (Kottek *et al.*, 2006).

Flux Measurements

We used automated soil respiration chambers to measure fluxes of CO_2 from the peat surface. Measurements were taken hourly at four chambers using an automated chamber system (LI-8100 with LI-8150 multiplexer; LI-COR Biosciences). Opaque white chambers were 20cm in diameter and had a volume of 4076.1 cm^3. We measured fluxes from July – November 2012, in both dry and flooded conditions (measurements in two chambers 7/13/12-8/5/12; four chambers active from 8/7/12-11/23/12). The first chamber was located in a relatively open area, with ferns and low-lying regenerating vegetation, and received direct sunlight during the day. Three additional chambers were fully shaded, located beneath low tree canopy. All chambers were installed at low points within the variable peat topography, and none were located directly adjacent to trees, due to the practical consideration that cutting roots and anchoring collars immediately adjacent to trees, or in higher topographic positions, where thick woody roots dominate, was not feasible. The chambers were placed approximately 8 m apart along a north-south transect (Figure 1e).

All chambers were mounted on tall collars (approx. 30cm tall). These collars significantly increased the total measurement air volume, to 18688.1, 17258.0, 16781.3 and 19005.9 cm^3 respectively for the four chambers. While this could reduce mixing within the collar, it was necessary to avoid flooding of chamber electronics at the high water tables experienced at the site. Each chamber was anchored into the peat using four legs constructed from 1m lengths of 2” PVC pipe (Figure 1a-d).

Soil collars were installed in March 2012, four months prior to CO_2 flux measurements. This long waiting period was designed to ensure any spike in respiration from the input of fresh root material would have dissipated by the time measurements began. In tropical peatlands, a substantial component of the peat mass is composed of dead root material, and very high rates of root turnover have been documented (Brady, 1997; Wright *et al.*, 2011). As a result, it is likely that after four months, labile root material had fully decomposed, leaving behind root remnants similar to those found within the existing peat matrix. Collars were constructed from 8” grey PVC pipe and were inserted to 30cm depth, the anticipated maximum depth of the water table, after cutting a slot for the pipe into the peat with a straight hoe, and severing roots. Although the water table dropped to 36cm below the peat surface during the study period, the time the water table spent below the 30cm trenching depth was a small fraction of the study period (Figure 1). Although we cannot rule out a small contribution from root respiration, from roots below 30cm, or those which may have grown up into the chamber over the course of the study, we expect the CO_2 fluxes measured are dominated by, and representative of, heterotrophic respiration.

Flux Calculations

Soil CO_2 fluxes from the peat surface, *F*, were calculated from the rate of change *dC/dt* in the water-vapor corrected CO_2 mole fraction multiplied by the moles of dry gas *n* in the chamber loop, divided by the soil surface area *S*, according to:

$$F = \frac{ndC}{S\,dt} = \frac{10VP\left(1 - \frac{W}{1000}\right)}{RS(T + 273.15)}\frac{dC}{dt} \qquad [1]$$

where the CO_2 flux from the peat surface, *F* (µmol m^{-2} s^{-1}), depends on the total chamber volume adjusted for water table depth, *V* (cm^3), the pressure, *P* (kPa), the water vapor mole fraction, *W* (mmol mol^{-1}), the air temperature, *T* (°C), the soil surface area, *S* (cm^2) and the rate of change in the water-corrected CO_2 mole fraction, *dC/dt* (µmol mol^{-1}). *dC/dt* is calculated from the increase in CO_2 concentration during chamber closure (LI-8150 maunal, LI-COR, 2010). We obtained the chamber air temperature from the built-in temperature sensor of a barometric pressure logger (Barologger Gold, Solinst Canada Ltd.) suspended inside the collar of one of the shaded soil chambers because of failure of the built-in chamber air temperature thermistors. The radiation balance and thermal mass of the barometric pressure logger could result in slightly higher estimates of chamber air temperature during the day and lower temperatures at night than the built-in thermistors, and the volume of the logger slightly reduced the volume of the measurement loop (<1.5%). Although air temperature measurements for flux calculations were only made in a shaded chamber, uncertainty associated with the temperature in the sunny chamber had a negligible impact on the fluxes (approximately 1.7% change in fluxes for expected possible air temperature difference of 5°C, or up to 3.3% for 10°C). The fluxes reported here correct those reported in Cobb *et al.* (2017) which used data from the faulty temperature sensors, leading to a relative correction of approximately 20% greater fluxes.

Each flux measurement was made over a 6 minute chamber closure time. Chambers rested open during the remaining period between hourly measurements (54 minutes). Throughout the study period, and across chambers, we observed increases in the water vapor-corrected CO_2 mole fraction which showed no evidence of saturation, possibly because of the large total chamber and collar volume or short closure time (Livingston *et al.*, 2005; Kutzbach *et al.*, 2007; Heinemeyer & McNamara, 2011). Therefore, we calculated rates of change in water vapor-corrected CO_2 mole fraction (dC/dt) from a linear fit to the data from 45s to 359s. An example time series is shown in Figure S3. As a result of the highly linear data, only a negligible fraction of data had fits with an $R^2<0.95$. Fluxes calculated from these fits were excluded from further analysis (0.54% and 1.45% of data in July-Aug period; 1.15%, 0%, 0% and 0.08% of data in Aug-Nov period for four chambers respectively). Instrument failure in October resulted in a shorter time series for Chamber 2.

Water table and Temperature measurements

Throughout the CO_2 flux study period (July to November, 2012) we also measured the water table depth, groundwater temperature (Levelogger Gold; Solinst Canada Ltd.; sensor continually submerged at depth >35cm) and air temperature (Barologger Gold, Solinst Canada Ltd.) adjacent to or within the shaded chamber (Period 1; Table 1). Additional water table measurements were also made 4.1 km from our chamber measurement site at an adjacent pristine peatland (the Mendaram peatland) described in Gandois *et al.* (2013), Dommain *et al.* (2015) and Cobb *et al.* (2017) and were used for upscaling (Figure 3) and to partition data period 2 into wet and dry phases (Table 1; Figure S2) using a water table cutoff of 5cm below the peat surface. Due to their proximity and the similar undrained nature of the sites, both sites experience similar water table depths. The Mendaram water table time series was assembled from data from two piezometers 130m apart (in and downslope of survey transect: Cobb *et al.*, 2017 Figure 2e). All water table measurements, at both the Damit and Mendaram peatlands, were made relative to low points, or hollows, in the peat surface. Peat soil temperature measurements were later made at the peat surface, as well as 10cm and 25cm below the peat surface using TidbiT temperature loggers (Onset, USA) from November 2013 to March 2014 (Period 2; Table 1) adjacent to both a sunny and shaded chamber. Unfortunately concurrent measurements of peat CO_2 efflux and peat temperature are not available, due to corrosion of the peat temperature sensor during Period 1. However, these two measurement periods cover similar ranges of representative water table depths, so qualitative comparisons are possible.

Upscaling of Fluxes

We modelled the fluxes of carbon leaving the peat dome throughout the year based on their water table dependence and a time series of water table data. We used a linear fit to the flux chamber daily mean data to model the heterotrophic peat surface CO_2 emission from local depressions (hollows) similar to the sites of chamber installation. To estimate the overall flux per area across the site, including higher areas in the microtopography, we assumed that higher areas had a similar peat surface CO_2 emission vs. water table relationship to hollows, but that this distribution was vertically shifted by the difference in peat surface height, based on similar findings reported by Hirano et al (2009) for hummocks and hollows in Central Kalimantan. Because the microtopography at the site resembles that of the adjacent Mendaram site, we used the results of our earlier theodolite survey at that site (Cobb *et al.*, 2017) to obtain the average height of the peat surface above the hollows for upscaling, by calculating the mean vertical offset between the peat surface interpolated between survey points and a smooth reference surface fit through local minima in the peat surface (Cobb *et al.*, 2017; Figure S4). We did not take the fraction of shaded area into account when upscaling as mean daily CO_2 efflux was very similar in the sunny and shaded chambers (Results).

We also estimated the total DOC export across different water table depths (Figure 3c) by using the relationship between runoff and water table developed by Cobb (Equation 5 and "SI Hydrologic Budget for Our Site" in Cobb *et al.*, 2017). We assumed this runoff carried a constant average DOC concentration of 75mgC/L, based on repeated measurements of shallow porewater at the site (Gandois *et al.*, 2013). We used three years of water table measurements from the nearby and similarly undrained Mendaram peatland site, where a longer continuous measurement time series was available. The data period from Feb 2012 – Feb 2015 included both dry and wet conditions, capturing the end of La Niña in early 2012, and the beginning of El Niño conditions in late 2014 and early 2015 (NOAA, 2019).

Oxygen Diffusion Calculations

We calculated the potential oxygen availability in the peat based on a diffusion equation. The oxygen profile vs depth z is described by the 1-D diffusion equation with a constant decomposition rate coefficient k:

$$d\frac{d^2C(z)}{dz^2} = -kC(z) \quad [2]$$

We assumed that oxygen consumption below the water table was negligible, which implies a zero gradient boundary at the depth of the water table L and yields the solution:

$$C(z) = C_0 \frac{\cosh\left[\sqrt{\frac{k}{d}}(L-z)\right]}{\cosh\left[\sqrt{\frac{k}{d}}L\right]} \quad [3]$$

where C_0 is the oxygen concentration in air (9.4 moles/m^3) and d is the effective diffusion coefficient of oxygen. We calculated a decomposition rate coefficient k [day^{-1}] for each day by first solving for the diffusive flux $q = d\frac{dC}{dz}$ at the peat surface, $q = C_0\sqrt{dk}\tanh\left[\sqrt{\frac{k}{d}}L\right]$, then setting q equal to the measured average flux for the day, and solving for k assuming an effective oxygen diffusion coefficient of 0.5 m^2/day, the coefficient in air (1.5 m^2/day) reduced by a tortuosity of 3 (Cussler, 1997; Rezanezhad *et al.*, 2010; Gharedaghloo *et al.*, 2018). Because the daily average flux q increased nearly linearly with water table depth L, the calculated value of k remained relatively uniform over the study period. These k values were compared to decomposition rates derived from incubation experiments (e.g. Jauhiainen *et al.*, 2016) by multiplying the rate of CO_2 production during the incubation by the dry bulk density of the peat.

<u>Results</u>

Water table

The study period (July-Nov 2012) included both wet and dry periods, capturing the full range of typical conditions for this undrained site. Beginning with dry conditions in August, the water table rose over the course of the measurements (Figure 2; Figure S1). Water table depth ranged from 36cm below the peat surface to 20cm above the peat surface. This is representative of conditions at the nearby pristine site (Mendaram); the water table rarely drops more than 20-30 cm below the peat surface (Figure 3).

Air and Soil Temperature

Air temperatures ranged from 20.8-34.8°C over the period of chamber measurements (Aug-Nov 2012), with a daily mean of 25.3 ± 2.2°C. The daily range in air temperature was dependent on the water table depth, with the largest diurnal fluctuations in temperature occurring when the water table was lowest (Figure 4). As the water table rose, the diurnal temperature range decreased (Figure 4h).

Temperatures measured at the peat surface followed a similar diurnal cycle. The daily peaks in temperature were strongest under dry conditions. Measured temperature increases were also larger in the sun than in the shaded chamber. The largest diurnal swings in peat surface temperature recorded, 49ºC at midday and 22ºC overnight, were found at the sunny location when the water table is low. At high water levels, temperature oscillations at the surface peat were damped, but not delayed. At depth, soil temperature fluctuations were buffered and lagged relative to the surface peat. Temperature fluctuations 10 cm and 25 cm below the peat surface were small (Figure 4c-f).

However, despite these differences in the diurnal peat temperature, there was little change in the mean daily air temperature over the study period (Figure 4h). Similarly, the mean peat temperature measurements made during Period 2 (Nov 2013-Mar 2014; Figure S2) were remarkably uniform across locations and depths, ranging between 24.9-25.1°C (Figure 4). High peat temperatures during the day were offset by cooler temperatures at night so that the daily average changed little from day to day even as oscillations increased in magnitude with the water table depth. Daily mean peat temperatures were similar across depths and shading conditions. Where diurnal temperature oscillations were largest (surface measurement of sunny chamber) the daily mean peat temperature was 25.1±1.6°C. Where oscillations were negligible (25 cm below surface, shaded chamber), the daily mean peat temperature was nearly constant at 24.9±0.7°C.

The mean groundwater temperature measured at the site is 25.0±0.4°C, essentially stable at the annual mean (measured Mar 2014-Sept 2015).

Peat surface CO_2 emission

Daily mean fluxes ranged from 0.5-8 μmol/m^2/s and closely followed trends in the water table (Figure 2). When the water table was at, or above, the local peat surface, the CO_2 flux from the peat or water surface was small, with a daily mean value of 0.4 μmol/m^2/s. The daily mean flux increased when the water table fell below the local peat surface, growing to ~6 μmol/m^2/s when the water table depth was 30 cm. The increase in daily mean flux when the water table was below the surface was nearly linear (R^2 = 0.92; Figure 3). Fluxes were highest under dry conditions in July and August and decreased over the measurement period (Figure S1).

Measured hourly CO_2 flux was variable and showed a strong diurnal pattern (Figure 2b, 2d, Figure 4), with maximum CO_2 fluxes observed at midday. The amplitude of the diurnal cycle increased as the water table dropped. Under the driest conditions, this effect was strongest, and CO_2 flux reached a clearly defined maximum at mid-day when the temperature was highest (with daily maximums 120% and 276% of the daily mean in the shade and sun respectively for water table depths >30cm; Figure 4a,b & Figure 5). In contrast, at higher water tables, the diurnal oscillations in CO_2 flux became less pronounced (with daily maximums 106% (shade) and 134% (sun) of the daily mean for water table depths of 5-20cm; Figure 4). Under flooded conditions (water table < 5 cm below surface), fluxes were low and stable, and slightly lower during the day than at night (Figure 5). This diurnal pattern was most pronounced in the sun chamber (Chamber 1; Figure 2 & 4). Less pronounced daily oscillations were observed in the shaded chambers during dry periods (Chambers 2-4; Figure 2 & 4).

Upscaling of Fluxes

Over three years from Feb 2012- Feb 2015, the upscaled heterotrophic CO_2 emission from our measurements of peat surface hollows was 20 $MgCO_2$/ha/yr, and our calculated CO_2 emission from R_{het} across the entire peat dome was 28 $MgCO_2$/ha/yr (Figure 3), based on an average height of peat above hollows of 4.8 cm (Figure S4). This value is a lower bound because we calculate nearly zero flux when the water table is at the average height of 4.8cm or above, but in fact there is still flux where the peat surface is higher than the average. Calculated carbon export by DOC was 0.8 $MgCO_2$/ha/yr (Figure 3).

Oxygen Diffusion Calculations

Calculation using equation [3] shows that the oxygen concentration just above the water table is reduced by 0.5% relative to oxygen at the peat surface when the water table is at a depth of 30 cm. The calculated decomposition rate coefficient *k* yielding the mean daily surface fluxes with this water table depth and uniform decomposition above the water table was ~1.8×10^{-5} µmol cm^{-3} s^{-1}.

Discussion

We observed (A) a tight correlation between daily average R_{het} and water table depth, and (B) strong diurnal oscillations in CO_2 flux and surface peat temperature. We first discuss the relationship between daily average R_{het} and water table depth, and apply this relationship to estimate carbon loss from the peat dome from water table records. We then explore the diurnal oscillations in CO_2 flux and surface-peat temperature. In section (C) we attempt to reconcile the underlying mechanisms responsible for these two key observations. Finally, we discuss the limitations of our approach and the implications of our findings (sections D and E).

A) Long-Term: Relation between Daily Average CO_2 Flux and Water Table Depth

(i) Heterotrophic respiration is proportional to water table depth

We observe a nearly linear relationship between water table and daily average CO_2 flux when the water level is below the peat surface, and small uniform fluxes when the peat is flooded (Figure 2). This simple behavior agrees closely with the results of Hirano *et al.* (2009) in a non-drained forest in southern Borneo, where seasonality in rainfall is stronger (Gastaldo, 2010). We cannot test whether the flux plateaus to a nearly constant value after the water table falls deeper than 30 cm, as shown in Hirano *et al*. (2009), because the water table at our undrained site rarely fell below 30 cm during the study.

The simple empirical relation of R_{het} to water table depth provides a link between hydrology and carbon dynamics that is useful in applications ranging from long-term models of peat geomorphology, to prediction of peat surface subsidence, to upscaling of regional CO_2 emissions (next section). Cobb *et al.* (2017) used a linear relation of peat loss (and accumulation) to water table depth to simulate the growth of peat domes over millennia. Although this model includes input of new organic material from plants, the simple linear relation between heterotrophic decomposition and water table described here is consistent with a linear net accumulation model. Hooijer *et al.* (2010) used a similar relationship to forecast CO_2 emissions from peatland drainage across Southeast Asia to 2100. Data compilations by Hooijer *et al.* (2010) and Carlson *et al.* (2015) found that heterotrophic respiration and total carbon loss increase linearly with falling water table in tropical peatlands drained for agriculture.

(ii) Why is mean daily R_{het} so strongly correlated with water table depth?

One simple explanation for the strong relationship between mean daily R_{het} and water table depth is that a falling water table exposes additional peat to oxic conditions, which then decomposes at a uniform daily average rate. This explanation requires that oxygen is available throughout the unsaturated peat profile. We tested the plausibility of this assumption with a simple calculation of the rate of oxygen diffusion into the peat (Methods). This calculation shows that sufficient oxygen would be available to support decomposition anywhere above the water table at all water table depths measured in this study (oxygen concentration reduced by less than 0.5% with water table at 30 cm). Our calculations are robust because the only adjustable parameter is the effective diffusion coefficient of CO_2 in soil gas, and it would have to be more than an order of magnitude smaller to qualitatively change the conclusion. Additionally, the calculated decomposition rate coefficient (~1.8×10^{-5} µmol cm^{-3} s^{-1}) falls within the range of values derived from tropical peat incubations by Jauhiainen *et al.*, 2016 (approximately 1×10^{-5} to 4×10^{-5} µmol cm^{-3} s^{-1}), and is broadly consistent with other incubation studies (Murayama & Bakar, 1996a, 1996b). Although this result suggests there is sufficient oxygen to support uniform decomposition throughout the peat profile, it does not provide an explanation for the daily oscillations in CO_2 efflux. Other possible mechanisms are explored in Section C.

(iii) Upscaling CO_2 and DOC fluxes from timeseries of water table dynamics

The relation of R_{het} to water table facilitates temporal and spatial upscaling, because water table depths are more easily monitored than is R_{het} over long time periods. Our calculations of overall fluxes from R_{het} and DOC export showed that heterotrophic respiration from the peat surface is the dominant mechanism for carbon export from the peat at low water table levels, whereas DOC export increases in importance when the water table is high (Figure 3). At high water levels, methane emissions from the peat surface may also play a role (Couwenberg *et al.*, 2010). Because water table dynamics are nearly uniform across the peat dome (Cobb et al, 2017), these results upscale measurements of local water table dynamics to estimate carbon fluxes across the entire dome.

At this site, the water table spends most of the time within 10 cm of the peat surface, high enough that R_{het} is small, but low enough that runoff, and hence DOC exports, are also small (histogram, Figure 3). Thus, the water table is most often at a depth that minimizes organic carbon loss and favors peat accumulation. Other studies on a variety of land uses (secondary forest, oil palm, other agriculture) have shown mostly higher annual CO_2 fluxes ranging from 26-102 $MgCO_2$/ha/yr (reviewed in Page *et al.*, 2011b). Although for a given water table depth we measure similar hourly fluxes to other studies, the total annual flux at our nondrained site (28 $MgCO_2$/ha/yr) is at the low end of this range due to the shallower average water table.

B) Diurnal Cycles: Temperature and Heterotrophic CO_2 Flux

(i) Diurnal cycle in temperature and CO_2 flux

Hourly measurements of air temperature, peat temperature, and CO_2 flux all followed a very similar diurnal cycle (Figure 4). We observed strong temperature oscillations in the surface peat, particularly in the sun and at low water tables. Deeper in the peat, temperature oscillations were both damped and delayed relative to surface peat. These trends in peat temperature are consistent with measurements by Jauhiainen *et al.* (2014), which also showed temperature oscillations that were smaller and increasingly lagged with depth (oscillation amplitude of <1ºC at 30 cm and below).

The strong diurnal cycle in peat surface CO_2 flux closely mirrored trends in peat temperature (Figure 4). The midday maximum in CO_2 flux coincided with the midday maximum in air and peat surface temperatures. This peak in CO_2 flux was sharpest for the sunny chamber, which also experienced the highest midday peat temperatures. Additionally, the largest temperature oscillations, both in the air and in the peat, occurred under dry conditions, when the largest diurnal peak in average CO_2 flux was also observed. This qualitative relationship suggests the diurnal cycle in the peat CO_2 flux is primarily driven by changes in peat temperature.

The magnitude of the diurnal cycle of temperature and CO_2 flux was smaller in the shaded chambers. This is consistent with shading experiments performed by Jauhiainen *et al.* (2014), who found larger diurnal fluctuations in temperature and CO_2 flux at unshaded sites than at shaded sites. Despite this large difference in daytime emissions, and in contrast to Jauhiainen *et al.* (2014), we found no evidence that the mean daily heterotrophic CO_2 emissions were different in the sun and shade (Figure 2) and observed very similar mean CO_2 flux values at each chamber for a given water table depth.

(ii) What drives the strong diurnal oscillations in CO_2 flux?

The similarity between daily patterns of CO_2 flux and peat temperature suggests changes in hourly CO_2 flux are driven by changes in peat temperature, either through direct or indirect mechanisms. The simplest explanation is that a large fraction of decomposition occurs near the surface and is driven by changes in the temperature of the shallow peat. Our data show that, for a reasonable Q_{10} value of less than 3 (Brady, 1997; Davidson *et al.*, 2006), only the very surface of the peat could produce oscillations in R_{het} of the amplitude observed in the peat surface CO_2 efflux. The much smaller temperature oscillations measured at 10 cm depth cannot produce such large oscillations in CO_2 production for any reasonable Q_{10} value. Thus, temperature-dependent decomposition can only fully explain daily flux oscillations if flux is dominated by decomposition in near-surface peat. Other studies have observed similar diurnal temperature fluctuations (Hirano *et al.*, 2009, 2014, Jauhiainen *et al.*, 2012, 2014). As a result of their observations, Jauhiainen *et al.* (2012, 2014) suggested that peat oxidation was concentrated in the upper 10cm of the peat profile, perhaps due to the higher concentrations of oxygen and labile carbon available for heterotrophic decomposition. However, we note that it is more difficult to explain the increase in CO_2 flux with depth of water table if decomposition is concentrated in the surface peat. Other possible mechanisms are explored in Section C.

(iii) Importance of hourly measurements

This dataset highlights the need for measurements around the diurnal cycle to accurately estimate daily mean CO_2 efflux. Our observations, and similar findings from other studies that employed automated chambers (Hirano *et al.*, 2009, 2014; Ishikura *et al.*, 2018a), show that it is very difficult to interpret CO_2 flux measurements taken only during part of the day because of large diurnal oscillations. Due to resource limitations, most measurements of CO_2 fluxes from tropical peatlands have been made with manual chambers, usually during daylight, and often at midday. The large daytime fluxes we observed, up to 180% above the diurnal average (Figure 5), would bias emissions estimates if measurements were made only during the day. These results demonstrate the importance of considering the diurnal cycle in experimental design. Use of a correction factor to compute mean fluxes from daytime measurements, as applied in Jauhiainen *et al.*, 2012, may provide a practical alternative to automated measurements (Jauhiainen *et al.*, 2012). However, our results suggest that such factors will depend on the water level regime at each site and will vary over time.

In particular, care should be taken when interpreting daytime flux measurements from unshaded open, degraded or logged peatlands, where diurnal fluctuations in peat temperature and CO_2 flux may be large (Figure 4; Jauhiainen *et al.*, 2014). The Damit peat dome studied here was selectively logged and retains scattered forest cover and areas of shade. However, other degraded peatlands may be totally open, or have more limited fern or shrub cover. Under these conditions, a pronounced diurnal cycle could strongly bias measurements. For example, in this study, midday measurements made at the sunny chamber at water table levels deeper than 20 cm are twice the mean daily flux (Figure 5). In other cases, day-time measurements could also underestimate CO_2 fluxes, as observed by Ishikura *et al.* (2018).

(iv) Thermal buffering and longer-term temperature stability

Despite the temperature oscillations we observed, the mean peat temperature over the study period was remarkably uniform across locations and depths, not differing by more than 0.2°C (Figure 4). Higher temperatures in the day were balanced by lower temperatures at night. Similarly, the mean air temperature (25.3 ± 2.2°C) and groundwater temperatures (25.0±0.4°C) were very stable. As a result of the uniformity of mean daily temperature, temperature explained little of the variability in mean daily R_{het}, which was driven instead by the level of the water table (Figure 2).

Stable temperatures are maintained in large part by the thermal capacity of the underlying groundwater. When the water table is near the surface, the heat capacity of the groundwater dampens diurnal temperature variations; when the water table is lower, surface temperature oscillations increase. However, the diurnal average remains close to the groundwater temperature.

The greater temperature oscillations at the open sunny site indicate the importance of radiation. During the day, the peat surface is heated by direct sunlight to much higher temperatures than the shady locations; at night the open canopy allows radiative cooling of the peat surface, offsetting higher daytime temperatures by the lowest nighttime temperatures recorded in our study. Lower cloud cover during drier periods could also contribute to the larger temperature fluctuations observed when the water table was low, by increasing both radiative heating during the day and radiative cooling at night.

C) Water Table and Temperature: Towards a Mechanistic Understanding of CO_2 Flux

We observed (A) a linear increase in CO_2 flux with water table depth below the peat surface, and (B) a large diurnal oscillation in CO_2 flux, correlated with oscillation in peat surface temperature. Other studies of tropical peatland CO_2 flux with chambers have shown the same basic phenomena (e.g., Jauhiainen *et al.*, 2012, 2014; Hirano *et al.*, 2014). There is a simple explanation for each observation (A, B), but these simple explanations are not compatible. The widely-observed depth dependence of emissions on water table depth (A) invites the simple explanation that decomposition occurs at the same rate throughout the aerobic part of the soil profile above the water table. Diurnal swings in emissions accompanying fluctuations in surface soil temperature (B) suggest a different simple model: that decomposition is concentrated in the near-surface peat. In this simple model, the diurnal fluctuations in temperature in the near-surface soil drive diurnal changes in decomposition rates because of the temperature dependence of decomposition. Each observation falsifies the simplest model for the other, implying that other mechanisms governing soil gas exchange need to be considered to understand peat decomposition. If we picture decomposition as uniform through the aerobic zone (simple explanation A), how can emissions be 280% of the mean at mid-day (Figure 5), though large temperature fluctuations are limited to near-surface peat (Figure 4; observation B)? On the other hand, if we believe that emissions are dominated by decomposition in the near-surface peat (simple explanation B), why do average emissions continue to increase as the water table recedes to greater depths (observation A)? Although similar observations have been made before, there has not been a systematic effort to reconcile the conflicting implications of these statements.

In this section we explore three mechanisms that could help answer these questions and explain both observations A and B (Figure 6). First (i), we explore the possibility that the increase in temperature oscillations at deeper water tables might promote more near-surface decomposition. In this way, increasing water table depth would indirectly increase daily average R_{het}. Second (ii), soil moisture could play a role in enhancing near-surface decomposition as the water table drops. For example, as the water table falls, the aerobic peat above the water table dries out, which could increase the rate of decomposition per volume of exposed peat. Finally (iii), it is also possible that the daily oscillations in CO_2 flux reflect daily shifts in physical transport processes that drive CO_2 out of the surface, rather than changes in decomposition rates. Determining the roles of these mechanisms would provide insight into the physical and biological mechanisms that control R_{het}, and could improve predictions of peat decomposition under different temperature and water conditions.

(i) Oscillating temperatures drive higher R_{het} because of nonlinearity

The effect of temperature on respiration is typically represented using the Q_{10} formulation. Because the Q_{10} formulation is nonlinear and convex, a greater range in temperature, even at the same daily mean, could lead to a greater mean daily respiration rate. Could larger temperature oscillations at low water tables drive both larger oscillations in fluxes and larger daily mean fluxes from near-surface peat, explaining both observations A and B?

The ratio of the average decomposition rate over a day, $\overline{R(T(\tau))}$, to the decomposition rate with the daily average temperature $R(\overline{T})$, is:

$$\frac{\overline{R(T(\tau))}}{R(\overline{T})} = \frac{1}{24}\int_{0}^{24} Q_{10}{}^{(T(\tau)\,-\,\overline{T})/10} d\tau \qquad [4]$$

where T is temperature, $\overline{T}$ is the average temperature over the day, and τ is the hour of the day. For the shady locations, where the oscillations span 24° to 30° with a mean of 25º, and with Q_{10} set to 3 as an upper bound, equation [4] indicates an increase in mean daily flux of 10% caused by oscillations, compared to the flux without oscillations. However, we observed a mean daily flux about 10 times greater when the water table was at its lowest at both the sunny and shady locations, indicating an increase in mean CO_2 flux of about 1000%. Therefore, nonlinear dependence of decomposition on temperature alone cannot explain the strong increase in CO_2 flux as the water table falls with a reasonable value of Q_{10}.

(ii) Moisture controls on R_{het}

Soil heterotrophic respiration in unsaturated soil generally depends on both moisture and temperature (Moyano *et al.* 2013). As the water table drops, soil moisture in the unsaturated zone will also decrease. If this decrease in soil moisture causes a substantial increase in decomposition of surface peat, this could explain both higher average fluxes at low water tables (A) and large diurnal oscillations in fluxes (B).

Heterotrophic respiration is typically greatest at intermediate soil moisture, and lower at very low and very high water contents (Moyano *et al.* 2013). Decomposition of near-surface peat could begin to be reduced by desiccation at very low water tables (e.g. Hirano *et al.*, 2009; Ishikura *et al.*, 2018), leading to a plateau in peat decomposition rates. In contrast, at wetter sites like this one, surface peat decomposition could increase monotonically with drying over the range of soil moisture contents. Experiments with a carbon-rich (60-70%) northern soil (Wickland & Neff, 2008) show that microbial respiration increases by ~20% from saturated to 75% saturation. Moyano *et al.* (2013) describe a variety of mechanisms for increased respiration with desaturation, including greater diffusion of oxygen in the gas phase and decreased predation by microorganisms that can no longer find connected water pathways between soil aggregates. To conclusively characterize this mechanism would require both detailed characterization of the moisture profile above the water table and incubation experiments to characterize how moisture content affects decomposition.

(iii) Temperature-dependent transport processes

An alternative mechanism that could help explain observations (A) and (B) is that daily temperature oscillations could drive cycles in CO_2 transport. If diurnal oscillations in CO_2 fluxes are partly accounted for by changes in transport of CO_2 out of the peat, decomposition could occur deeper in the soil profile than implied if varying CO_2 production is explained entirely by a Q_{10} mechanism. Ishikura *et al.* (2018) invoked physical transport processes to explain their observation of flux oscillations peaking at night. Oscillating temperature may drive advective and diffusive fluxes from the peat surface through a variety of mechanisms. As the peat warms, soil gas expands, driving a gas flux from the peat surface. The maximum shallow temperature swing at the sunny location drives an expansion of the gas volume in the near-surface peat by about 12%, 7% from thermal expansion of gas and 5% from evaporation of water. As the peat heats, this gas expansion can increase flux by both pushing CO_2 from the peat and increasing the gradient driving CO_2 diffusion from the peat; when the peat cools at night, both processes reverse, cooling gas contracts and water vapor condenses. To a lesser degree, shifts in the solubility of CO_2 and diffusion coefficients with temperature will also increase daytime and decrease nighttime fluxes from the peat surface. Determining the importance of these physical processes in the diurnal pattern of flux measured at the peat surface, and the interactions of these processes, would require a detailed numerical model of gas behavior in the peat column that is beyond the scope of this paper. Here, we point out that such physical processes may create daily oscillations in flux independent of decomposition processes.

D) Limitations

Despite the strong trends we observe, we recognize a number of methodological limitations to our chamber-based approach. The chamber and collar design inherently modify local conditions. In particular, the root exclusion method may greatly affect decomposition processes, as soil moisture, temperature, and carbon and nutrient cycling are disrupted by the absence of roots. Thus measurements of R_{het} in root-cut conditions may differ substantially from rates of R_{het} in undisturbed conditions (reviewed in Kuzyakov, 2006, 2010), although some evidence suggests that enhancement or inhibition of decomposition by roots may be limited in highly organic soils (Linkosalmi *et al.*, 2015). Additionally, the tall collar design could affect air flow. Due to the dense understory of regenerating vegetation and remnant small trees, wind movement near the surface is usually limited at the site, but localized convective transport could play a more important role and may be affected by the tall collar design (Ishikura *et al.*, 2018a). Shrinkage of the peat near collars could also modify local gas transport, though there was no visible evidence of gaps near collars. Finally, flux and peat temperature measurements were made over two consecutive but non-overlapping time periods. Although simultaneous measurements of both variables would give more precise results, qualitative findings would most likely be similar because both time periods included a similar range of water table depths and diurnal oscillation in temperature and CO_2 flux were highly regular.

E) Conclusions and Implications for Further Work

In summary, we find CO_2 flux is strongly dependent on water table depth over days to months (A), and has a pronounced diurnal oscillation which follows peat temperature at hourly timescales (B). A satisfactory model for heterotrophic respiration in peat must account for both observations A and B (Figure 5). We explored three mechanisms that could help account for both the increase in average emissions at low water tables and the diurnal oscillation in fluxes: (i) the nonlinear effect of temperature on respiration (Q_{10}); (ii) decreased soil moisture in surface peat at low water tables; and (iii) temperature-dependent transport of soil gas.

Of these three mechanisms, (i) the nonlinear relationship between temperature and decomposition is insufficient to explain the observed data. However, (ii) physical transport mechanisms, and (iii) increased near-surface decomposition due to changes in soil moisture remain plausible. Both mechanisms emphasize the important indirect control of water table depth on heterotrophic respiration. A mix of these two mechanisms is likely, although we are unable to quantify their role here. To conclusively resolve this issue would require detailed depth profile measurements of CO_2, combined with a model to disentangle the effects of CO_2 transport and production.

Our observations also have important practical implications. The strong diurnal cycle in CO_2 flux suggests that if manual chamber measurements are limited to midday, they may significantly overestimate mean daily fluxes under some conditions, particularly in open degraded peatlands. This highlights the importance of making hourly measurements, and/or determining correction factors to less frequent measurements. Finally, our upscaling of both carbon export as DOC and R_{het} based on water table time series suggests that drainage will continue to be the most important driver of CO_2 fluxes from tropical peatlands in the region. These findings show that hourly measurements are an important foundation for quantification of the carbon budget of tropical peatlands.

Acknowledgements

We thank Mahmud Yussof of Brunei Darussalam Heart of Borneo Center and the Brunei Darussalam Ministry of Industry and Primary Resources for their support of this project; Hajah Jamilah Jalil and Joffre Ali Ahmad of the Brunei Darussalam Forestry Department for facilitation of field work and release of staff; Amy Chua for project support; Bernard Jun Long Ng, Jefferey Muli Anak Incham, Ramasamy Anak Zulkiflee, and Haji Bohari Bin Haji Idi for field assistance; and Lucy Hutyra for technical guidance. This research was supported by the National Research Foundation Singapore through the Singapore–MIT Alliance for Research and Technology's Center for Environmental Sensing and Modeling interdisciplinary research program, by the US National Science Foundation under Grants 1114155 and 1114161 (to C.F.H.), and by a grant from the Environmental Solutions Initiative at Massachusetts Institute of Technology.

References

Ali M, Taylor D, Inubushi K (2006) Effects of environmental variations on CO_2 efflux from a tropical peatland in Eastern Sumatra. *Wetlands*, **26**, 612–618.

Blackham G V, Thomas A, Webb EL, Corlett RT (2013) Seed rain into a degraded tropical peatland in Central Kalimantan, Indonesia. *Biological Conservation*, **167**, 215–223.

Brady MA (1997) *Organic Matter Dynamics of Coastal Peat Deposits in Sumatra, Indonesia*. PhD thesis, The University of British Columbia.

Carlson KM, Goodman LK, May-Tobin CC (2015) Modeling relationships between water table depth and peat soil carbon loss in Southeast Asian plantations. *Environmental Research Letters*, **10**, 074006.

Cobb AR, Hoyt AM, Gandois L, Eri J, Dommain R, Salim KA, Kai FM, Su'ut NSH, Harvey CF (2017) How temporal patterns in rainfall determine the geomorphology and carbon fluxes of tropical peatlands. *Proceedings of the National Academy of Sciences*, **114**, E5187–E5196.

Comeau L-P, Hergoualc'h K, Hartill J, Smith J, Verchot L V, Peak D, Salim AM (2016) How do the heterotrophic and the total soil respiration of an oil palm plantation on peat respond to nitrogen fertilizer application? *Geoderma*, **268**, 41–51.

Couwenberg J, Dommain RR, Joosten H (2010) Greenhouse gas fluxes from tropical peatlands in south-east Asia. *Global Change Biology*, **16**, 1715–1732.

Cussler EL (1997) *Diffusion: Mass Transfer in Fluid Systems*, 2nd Editio edn. Cambridge University Press, New York, 45078 pp.

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.

Davidson EA, Janssens IA, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. *Global Change Biology*, **12**, 154–164.

Dommain R, Couwenberg J, Glaser PH, Joosten H, Suryadiputra INN (2014) Carbon storage and release in Indonesian peatlands since the last deglaciation. *Quaternary Science Reviews*, **97**, 1–32.

Dommain R, Cobb AR, Joosten H et al. (2015) Forest dynamics and tip-up pools drive pulses of high carbon accumulation rates in a tropical peat dome in Borneo (Southeast Asia). *Journal of Geophysical Research: Biogeosciences*, **120**, 617–640.

Fang C, Moncrieff JB (2001) The dependence of soil CO_2 efflux on temperature. *Soil Biology and Biochemistry*, **33**, 155–165.

Gandois L, Cobb AR, Hei IC, Lim LBL, Salim KA, Harvey CF (2013) Impact of deforestation on solid and dissolved organic matter characteristics of tropical peat forests: implications for carbon release. *Biogeochemistry*, **114**, 183–199.

Gandois L, Teisserenc R, Cobb AR et al. (2014) Origin, composition, and transformation of dissolved organic matter in tropical peatlands. *Geochimica et Cosmochimica Acta*, **137**, 35–47.

Gastaldo RA (2010) Peat or no peat: Why do the Rajang and Mahakam Deltas differ? *International Journal of Coal Geology*, **83**, 162–172.

Gharedaghloo B, Price JS, Rezanezhad F, Quinton WL (2018) Evaluating the hydraulic and transport properties of peat soil using pore network modeling and X-ray micro computed tomography. *Journal of Hydrology*, **561**, 494–508.

Heinemeyer A, McNamara NP (2011) Comparing the closed static versus the closed dynamic chamber flux methodology: Implications for soil respiration studies. *Plant Soil*, **346**, 145–151.

Hergoualc'h K, Hendry DT, Murdiyarso D, Verchot LV (2017) Total and heterotrophic soil respiration in a swamp forest and oil palm plantations on peat in Central Kalimantan, Indonesia. *Biogeochemistry*, **135**, 203–220.

Hirano T, Jauhiainen J, Inoue T, Takahashi H (2009) Controls on the carbon balance of tropical peatlands. *Ecosystems*, **12**, 873–887.

Hirano T, Kusin K, Limin S, Osaki M (2014) Carbon dioxide emissions through oxidative peat decomposition on a burnt tropical peatland. *Global Change Biology*, **20**, 555–565.

Hooijer A, Page S, Canadell JG, Silvius M, Kwadijk J, Wösten H, Jauhiainen J (2010) Current and future CO_2 emissions from drained peatlands in Southeast Asia. *Biogeosciences*, **7**, 1505–1514.

Hooijer A, Page S, Jauhiainen J, Lee WA, Lu XX, Idris A, Anshari G (2012) Subsidence and carbon loss in drained tropical peatlands. *Biogeosciences*, **9**, 1053–1071.

Husnain H, Wigena IGP, Dariah A, Marwanto S, Setyanto P, Agus F (2014) CO_2 emissions from tropical drained peat in Sumatra, Indonesia. *Mitigation and Adaptation Strategies for Global Change*, **19**, 845–862.

Ishikura K, Hirano T, Okimoto Y et al. (2018a) Soil carbon dioxide emissions due to oxidative peat decomposition in an oil palm plantation on tropical peat. *Agriculture, Ecosystems and Environment*, **254**, 202–212.

Ishikura K, Darung U, Inoue T, Hatano R (2018b) Variation in soil properties regulate greenhouse gas fluxes and global warming potential in three land use types on tropical peat. *Atmosphere*, **9**, 1–14.

Jauhiainen J, Limin S, Silvennoinen H, Vasander H (2008) Carbon dioxide and methane fluxes in drained tropical peat before and after hydrological restoration. *Ecology*, **89**, 3503–3514.

Jauhiainen J, Hooijer A, Page SE (2012) Carbon dioxide emissions from an *Acacia* plantation on peatland in Sumatra , Indonesia. *Biogeosciences*, **9**, 617–630.

Jauhiainen J, Kerojoki O, Silvennoinen H, Limin S, Vasander H (2014) Heterotrophic respiration in drained tropical peat is greatly affected by temperature—a passive ecosystem cooling experiment. *Environmental Research Letters*, **9**, 105013.

Jauhiainen J, Silvennoinen H, Könönen M, Limin S, Vasander H (2016) Management driven changes in carbon mineralization dynamics of tropical peat. *Biogeochemistry*, **129**, 115–132.

Kobayashi S (1999) Initial phase of secondary succession in the exploited peat swamp forest (*Shorea albida*) at Sungai Damit, Belait in Brunei Darussalam. In: *Proceedings of the International Symposium on Tropical Peatlands (ISTP)*, pp. 205–214. Bogor.

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World Map of the Köppen-Geiger climate classification updated. **15**, 259–263.

Kutzbach L, Schneider J, Sachs T et al. (2007) CO_2 flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression. *Biogeosciences*, **4**, 1005–1025.

Kuzyakov Y (2006) Sources of CO_2 efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry*, **38**, 425–448.

Kuzyakov Y (2010) Priming effects: Interactions between living and dead organic matter. *Soil Biology and Biochemistry*, **42**, 1363–1371.

LI-COR (2010) LI-8100A Automated Soil CO_2 Flux System & LI-8150 Multiplexer Instruction Manual.

Linkosalmi M, Pumpanen J, Biasi C et al. (2015) Studying the impact of living roots on the decomposition of soil organic matter in two different forestry-drained peatlands. *Plant Soil*, **396**, 59–72.

Livingston GP, Hutchinson GL, Spartalian K (2005) Diffusion theory improves chamber-based measurements of trace gas emissions. **32**, L24817.

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Marwanto S, Agus F (2014) Is CO_2 flux from oil palm plantations on peatland controlled by soil moisture and/or soil and air temperatures? *Mitigation and Adaptation Strategies for Global Change*, **19**, 809–819.

Melling L, Hatano R, Goh KJ (2005) Soil CO_2 flux from three ecosystems in tropical peatland of Sarawak , Malaysia. *Tellus*, **57B**, 1–11.

Miettinen J, Shi C, Liew SC (2016) Land cover distribution in the peatlands of Peninsular Malaysia, Sumatra and Borneo in 2015 with changes since 1990. *Global Ecology and Conservation*, **6**, 67–78.

Miettinen J, Hooijer A, Vernimmen R, Liew SC, Page SE (2017) From carbon sink to carbon source: extensive peat oxidation in insular Southeast Asia since 1990. *Environmental Research Letters*, **12**, 024014.

Moyano FE, Manzoni S, Chenu C (2013) Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biology and Biochemistry*, **59**, 72–85.

Murayama S, Bakar ZA (1996a) Decomposition of tropical peat soils: 1. Decomposition kinetics of organic matter of peat soils. *Japan Agricultural Research Quarterly*, **30**, 145–151.

Murayama S, Bakar ZA (1996b) Decomposition of tropical peat soils: 2. Estimation of in-situ decomposition by measurement of CO_2 flux. *Japan Agricultural Research Quarterly*, **30**, 153–158.

NOAA (2019) Cold & warm episodes by season, Oceanic Niño Index. *National Centers for Environmental Prediction*, 8–10.

Page SE, Rieley JO, Banks CJ (2011a) Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, **17**, 798–818.

Page SE, Morrison R, Malins C, Hooijer A, Rieley JO, Jauhiainen J (2011b) *Review of Peat Surface*

Greenhouse Gas Emissions from Oil Palm Plantations in Southeast Asia.

Rezanezhad F, Quinton W, Price J, Elliot T, Elrick D, Shook K (2010) Influence of pore size and geometry on peat unsaturated hydraulic conductivity computed from 3D computed tomography image analysis. *Hydrological Processes*, **24**, 2983–2994.

Tuomi M, Vanhala P, Karhu K, Fritze H, Liski J (2008) Heterotrophic soil respiration-Comparison of different models describing its temperature dependence. *Ecological Modelling*, **211**, 182–190.

Wickland KP, Neff JC (2008) Decomposition of soil organic matter from boreal black spruce forest: Environmental and chemical controls. *Biogeochemistry*, **87**, 29–47.

Wright EL, Black CR, Cheesman AW, Drage T, Large D, Turner BL, Sjögersten S (2011) Contribution of subsurface peat to CO_2 and CH_4 fluxes in a neotropical peatland. *Global Change Biology*, **17**, 2867–2881.

<u>Tables:</u>

Timing	Measurements Conducted
Period 1: **Jul 2012 – Nov 2012**	• CO_2 Flux: Sun • CO_2 Flux: Shade • Water table and precipitation • Air temperature
Period 2: **Nov 2013 – Mar 2014**	• Peat temperature: Sun • Peat temperature: Shade • Air temperature • Water table at the nearby Mendaram peatland (2012-2015)

Table 1. Timeline of measurements. Measurements were conducted over two study periods. CO_2 Flux measurements were conducted during the first period. Peat temperature was measured during the second study period.

Figure Captions:

Figure 1. Chamber Locations. (a) Sunny chamber (chamber 1). (b-d) Shaded chambers (chambers 2, 3 & 4 respectively) (e) Schematic of chamber layout. Circles indicate chamber locations (C1-C4), the triangle indicates the location of ground water measurements (GWL), the small square indicates the location of the infrared gas analyzer (IRGA), the large square indicates the solar power supply and the star indicates a large remnant *Shorea albida* tree (SA). Precipitation was measured on the roof of the solar power supply. (f) Map of insular Southeast Asia with peatland area (grey) and study site in Brunei Darussalam (black star) indicated.

Figure 2. CO_2 Flux and Water Table Measurements. (a) CO_2 flux (R_{het}) vs water table depth. Colored dots represent hourly measurements at each individual chamber. Large black circles represent the daily mean across all chambers. Data from August-November shown. The y-axis is truncated for clarity, so the highest hourly measurements do not appear. (b) Timeseries of individual chamber hourly measurements of CO_2 efflux (colored) and daily mean values (black). (c) Time series of water table depth over study period 1, covering the typical range of conditions experienced at this nondrained site. (d) Time series inset shows diurnal cycle over the course of a week. Daytime peaks are largest in the sun (Chamber 1).

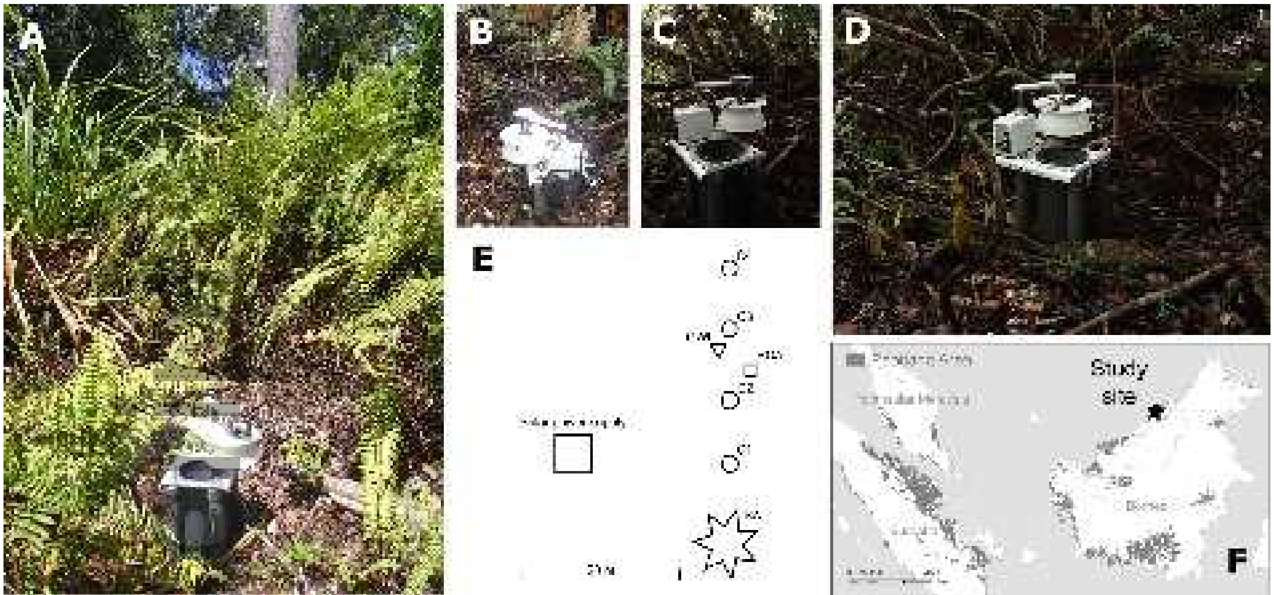
Figure 3. Upscaling CO_2 and DOC Fluxes. (a) Time series of calculated mean daily heterotrophic respiration (R_{het}) from hollows (dark grey), R_{het} from across the peat dome (light grey; calculated using a topographic offset of 4.8cm), and DOC export. Y-axis truncates peak DOC export of 46µmol/m^2/s in Mar 2012. (b) Fitted carbon loss by heterotrophic respiration (R_{het}) from hollows (R^2 = 0.92), calculated R_{het} from across the peat dome, calculated DOC export, and measured daily mean CO_2 flux vs. water table depth are shown on the right axis (truncated for visibility). A histogram of water table depth at the site is shown on the left axis. The water table spends most of the time near the surface where both DOC export and CO_2 emissions are small, perhaps facilitating peat stability. (c) Measured time series of water table depth from Feb 6, 2012-Feb 6, 2015 from the nearby undrained Mendaram peatland used for upscaling.

Figure 4. Diurnal Cycle. (a & b) R_{het} flux vs time of day. Hourly measurements are aggregated for water table depth ranges for sun and shaded chambers. (c, d, e & f): Hourly measurements of peat temperature at different depths in the soil for sun, shade, wet and dry conditions. Largest diurnal oscillations are seen

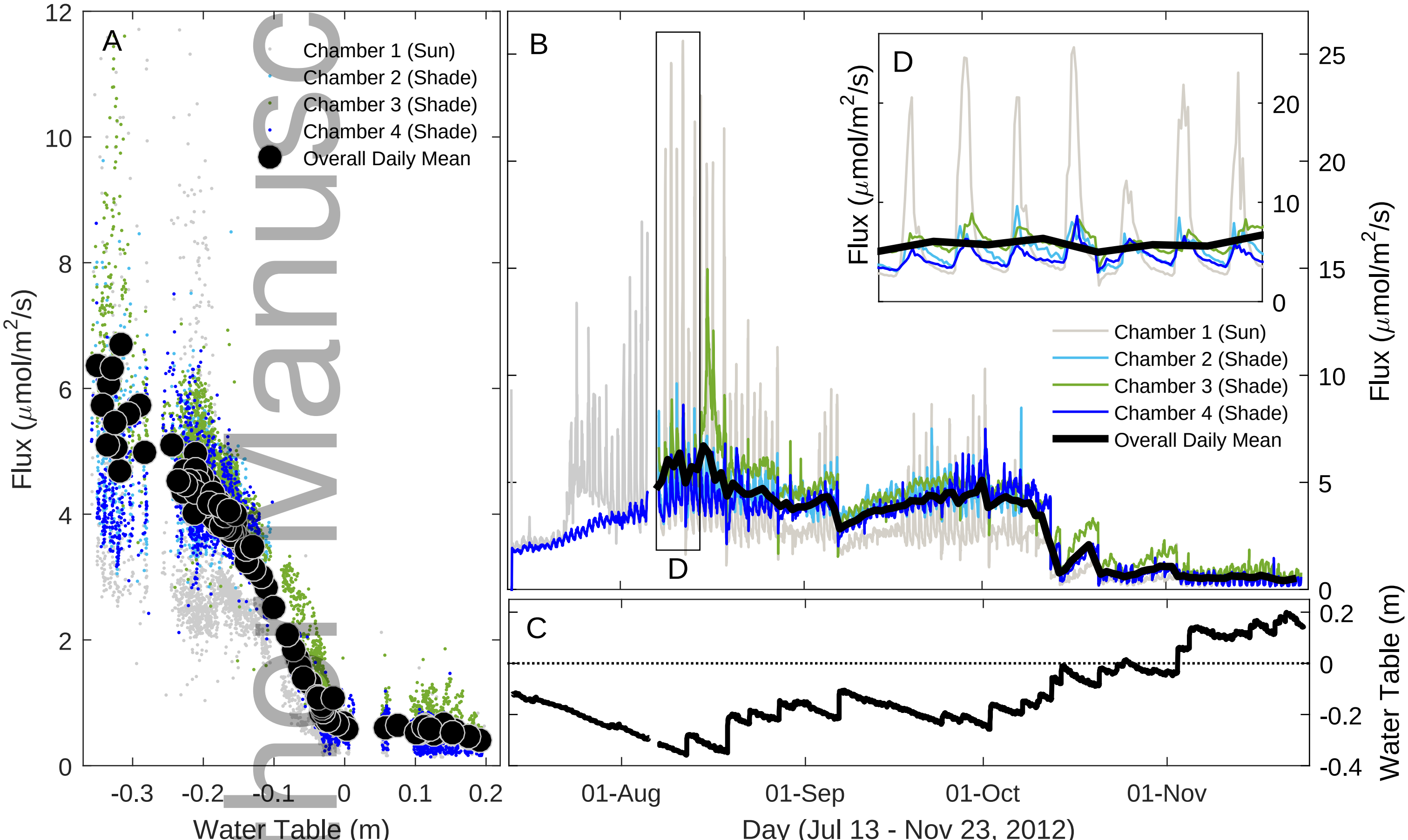
under dry conditions in the sun. Wet/dry cutoff is 5cm below the peat surface (Figure S2). g) Hourly air temperature averaged across days. Oscillations are greatest under dry conditions. h) Air temperature maximum, mean and minimum vs. water table depth.

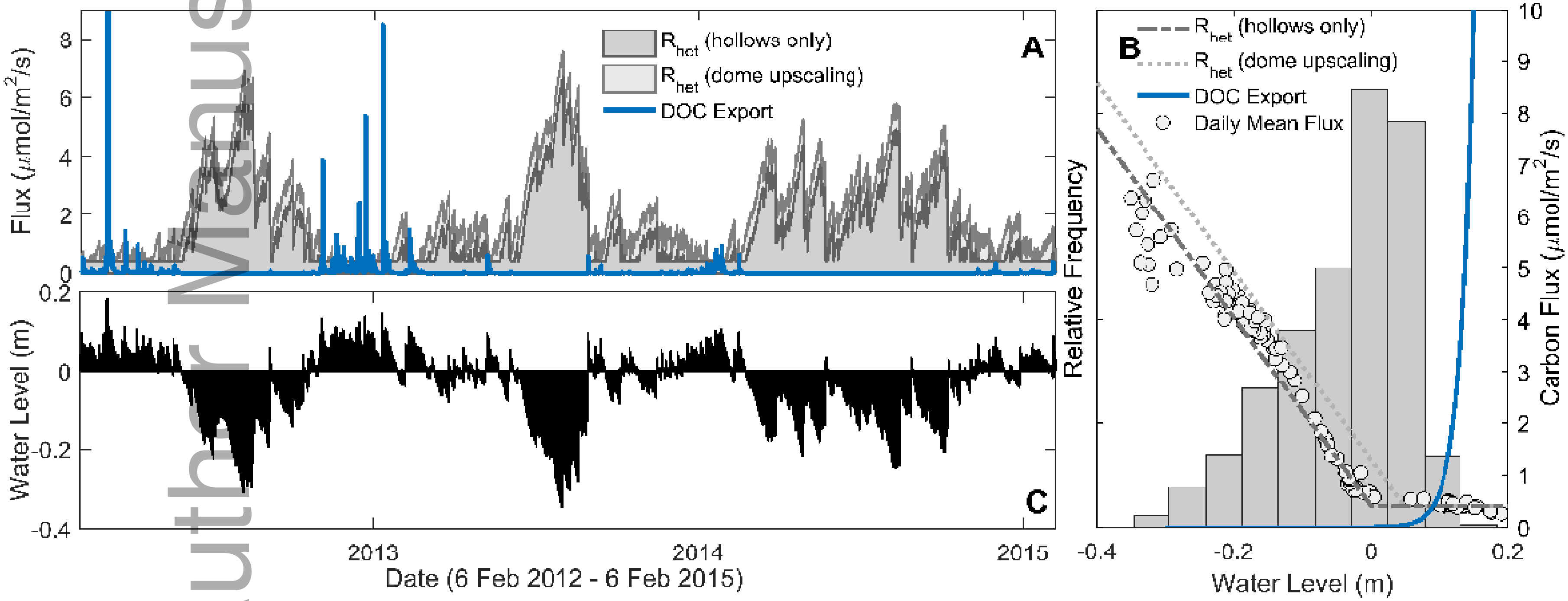
Figure 5. Hourly measurements as a percentage of daily mean for (a) sun and (b) shade. Daytime measurements have the potential to significantly overestimate daily mean fluxes, particularly in the sun, and under relatively dry conditions.

Figure 6. Explaining key observations from chamber measurements in tropical peatlands. The relationship between mean daily CO_2 flux and water table depth explored in section A could be simply explained by uniform CO_2 production through the peat profile above the water table. The diurnal oscillations in CO_2 flux discussed in section B could be simply (but incompatibly) explained if CO_2 production is dominated by near-surface decomposition. Section C explores mechanisms that could account for both observations A and B.

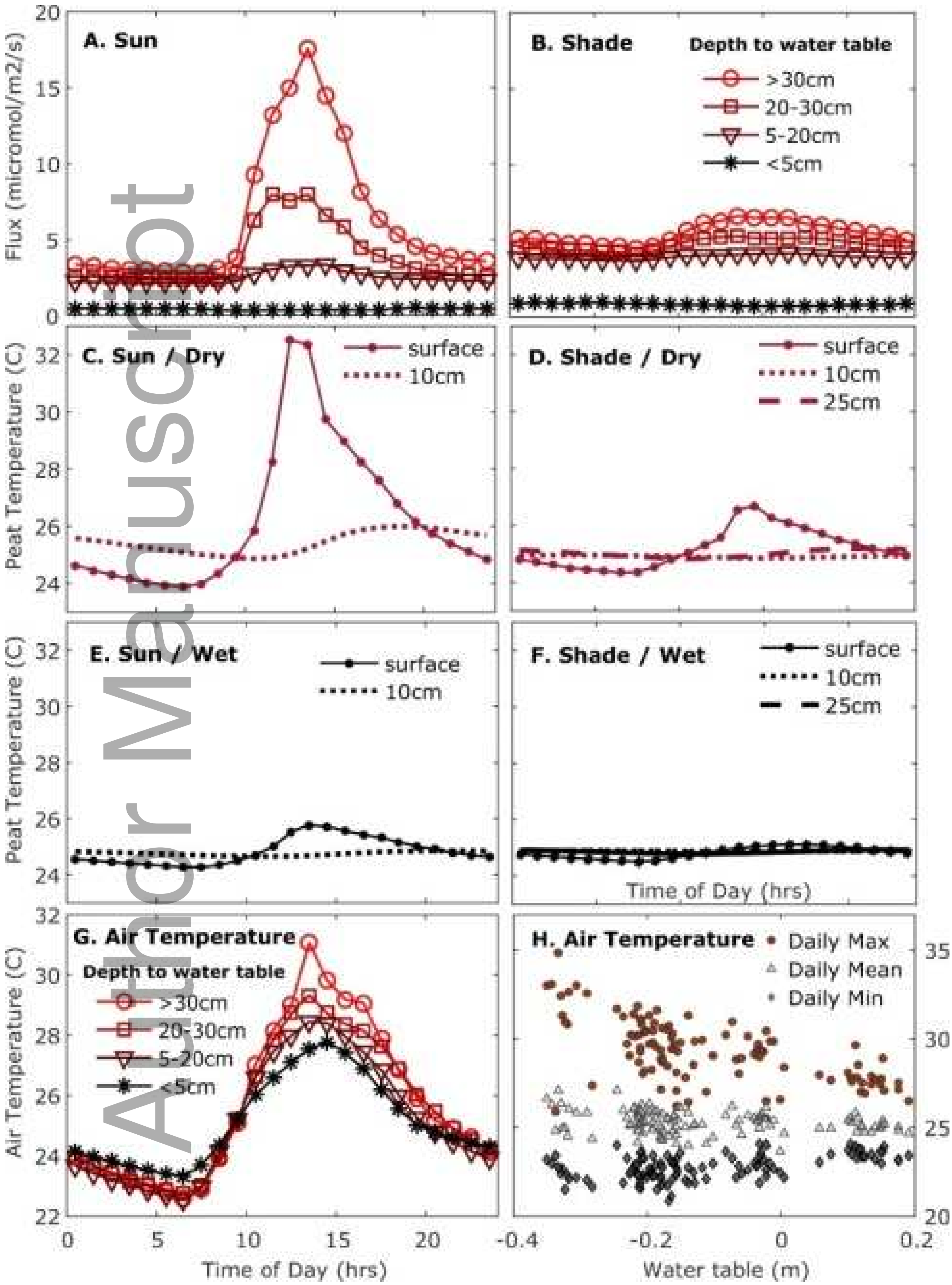


gcb_14702_f1.png

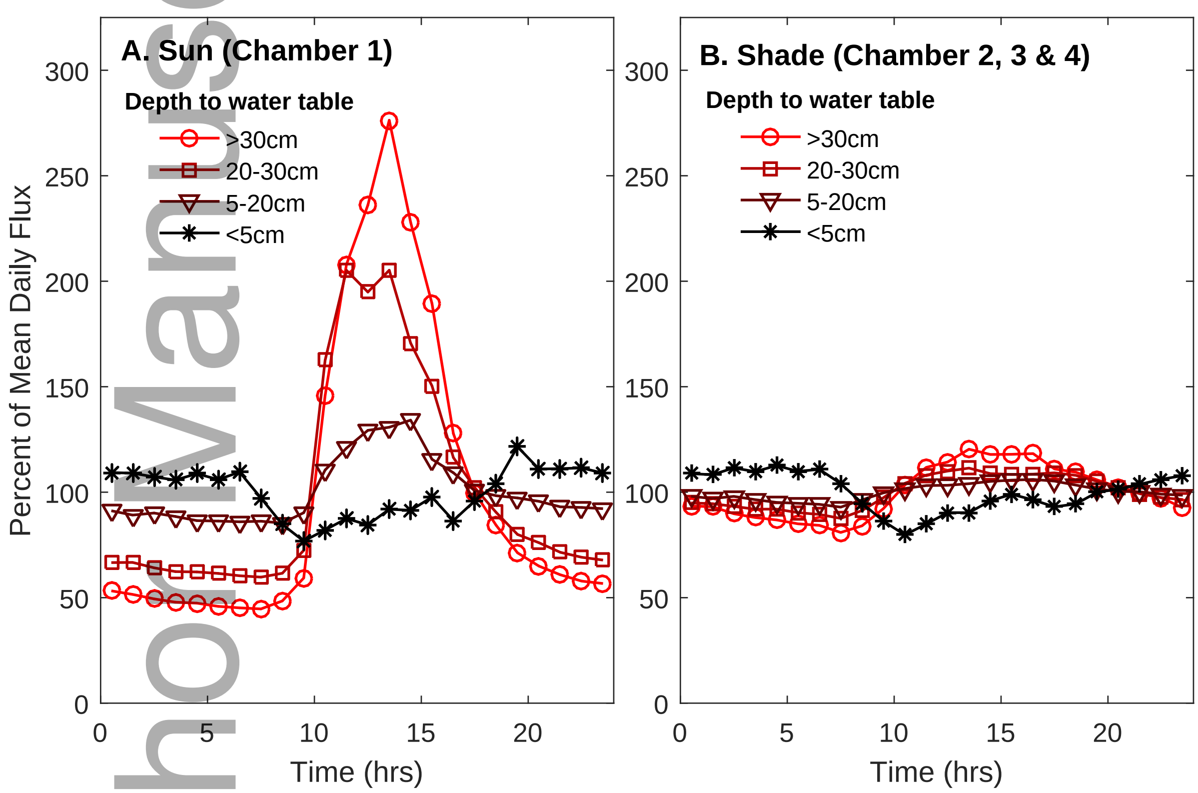

A
B
C
D
Chamber 1 (Sun)
Chamber 2 (Shade)
Chamber 3 (Shade)
Chamber 4 (Shade)
Overall Daily Mean
Flux (μmol/m2/s)
Water Table (m)
Day (Jul 13 - Nov 23, 2012)
01-Aug
01-Sep
01-Oct
01-Nov

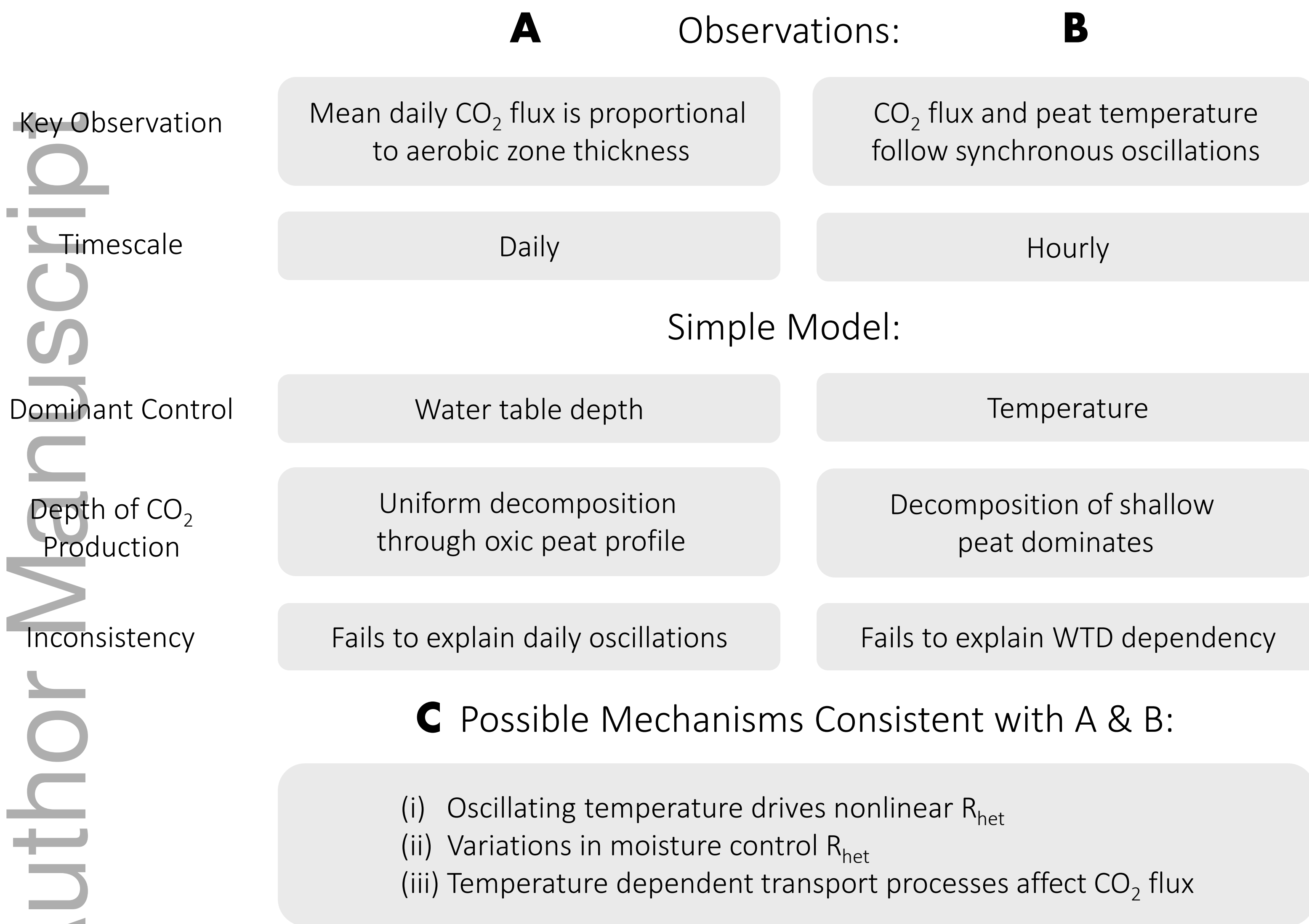


Flux (μmol/m²/s)
8
6
4
2
0
A
R_het (hollows only)
R_het (dome upscaling)
DOC Export
Water Level (m)
0.2
0
-0.2
-0.4
C
2013
2014
2015
Date (6 Feb 2012 - 6 Feb 2015)
B
R_het (hollows only)
R_het (dome upscaling)
DOC Export
Daily Mean Flux
Relative Frequency
Carbon Flux (μmol/m²/s)
10
9
8
7
6
5
4
3
2
1
0
-0.4
-0.2
0
0.2
Water Level (m)



gcb_14702_f4.png


A. Sun (Chamber 1)
Depth to water table
>30cm
20-30cm
5-20cm
<5cm
B. Shade (Chamber 2, 3 & 4)
Depth to water table
>30cm
20-30cm
5-20cm
<5cm
Percent of Mean Daily Flux
Time (hrs)
Time (hrs)
0
50
100
150
200
250
300
0
5
10
15
20


A
Observations:
B
Key Observation
Mean daily CO_2 flux is proportional to aerobic zone thickness
CO_2 flux and peat temperature follow synchronous oscillations
Timescale
Daily
Hourly
Simple Model:
Dominant Control
Water table depth
Temperature
Depth of CO_2 Production
Uniform decomposition through oxic peat profile
Decomposition of shallow peat dominates
Inconsistency
Fails to explain daily oscillations
Fails to explain WTD dependency
C Possible Mechanisms Consistent with A & B:
(i) Oscillating temperature drives nonlinear R_{het}
(ii) Variations in moisture control R_{het}
(iii) Temperature dependent transport processes affect CO_2 flux