



# Carbon Emissions From Oil Palm Plantations on Peat Soil

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Southeast Asian peatlands have undergone recent land use change with an increase in industrial agricultural plantations, including oil palm. Cultivating peatlands requires creating drainage ditches and other surface microforms (i.e., harvest paths, frond piles, cover plants, and next to the palm). However, it is currently unclear how these management actions affect rates of carbon losses from the peat. Here we report carbon fluxes from each of the different surface microforms measured monthly (soil CO<sub>2</sub> [total soil respiration  $-R_{tot}$ ] and stem CH<sub>4</sub>) and bimonthly (soil CH<sub>4</sub>, drain CO<sub>2</sub> and drain CH<sub>4</sub>). We calculated annual carbon fluxes and partitioned heterotrophic (R<sub>b</sub>) and root-rhizosphere respiration by sampling rhizosphere and root-free soil. Linear mixed effect models were used to determine which environmental factors best-predicted carbon fluxes, and to develop recommendations for management solutions that could reduce carbon losses. Carbon fluxes varied significantly between the different microforms; the greatest CO<sub>2</sub> fluxes were measured next to the palm and the greatest CH<sub>4</sub> fluxes were measured from the drainage ditches. Annual estimates of  $R_{tot},\,R_{h}$  and drain CO\_2 were 22.08  $\pm$  0.50, 17.75  $\pm$  1.54, and 1.5  $\pm$  0.10 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, respectively. R<sub>b</sub> varied between the two plantations: Sebungan averaged 11.43  $\pm$  1.37 Mg CO\_2-C ha^{-1} yr^{-1} and Sabaju averaged 24.08  $\pm$  1.42 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>. Net ecosystem CH<sub>4</sub> fluxes averaged 61.02  $\pm$  17.78 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>-similar to unmanaged swamp forests. The two plantations did not vary in overall CH<sub>4</sub> flux, but did vary in transport pathway. CH<sub>4</sub> fluxes from the soil, drains and stems followed a ratio of 50:50:0 from Sabaju (water table depth [WTD]:  $-0.49 \pm 0.004$  m) and 11:98:0 from Sebungan (WTD:  $-0.77 \pm 0.007$  m). R<sub>h</sub> dominated the peat carbon losses. WTD controlled variation in R<sub>h</sub> from Sebungan where the WTD was deeper. Air and soil temperature controlled variation in Sabaju, with greater fluxes from the harvest path, attributed to the absence of shade. These results suggest that shading the soil (e.g., through addition of frond piles) and raising the water table may be the most effective ways to reduce peat carbon loss from drained peat soils.

Keywords: oil palm, peat, peat oxidation, heterotrophic respiration, methane

# INTRODUCTION

Palm oil currently makes a significant contribution to feeding the world, which is expected to continue with increased population growth, and helps with climate change mitigation, for example through high rates of photosynthesis taking CO<sub>2</sub> from the atmosphere and it's use for bioenergy (Fowler et al., 2011; Fuss et al., 2016; IPCC, 2018; Meijaard et al., 2018). However, agriculture itself is not free from carbon emissions (Bajželj et al., 2014; Smith et al., 2014; Tubiello et al., 2015). Oil palm (Elaeis guineensis; the source of palm oil) plantations are grown on both industrial and small-holder scale throughout the tropics (FAOSTAT, 2019). Indonesia and Malaysia currently dominate both the production and export of palm oil (FAOSTAT, 2019; USDA, 2019). Since 1980, oil palm plantations have been established on peat soils in these countries, due to the decline in available suitable mineral soils, which are preferred (Silvius and Diemont, 2007; Corley and Tinker, 2008; Miettinen et al., 2016). However, oil palm plantations growing on peat soils are subject to debate concerning the magnitude of CO<sub>2</sub> and CH<sub>4</sub> losses from the peat (Evers et al., 2017; Wijedasa et al., 2017).

Southeast (SE) Asia has 24.7 Mha of peatlands, storing  $\sim$ 66 Gt C (Page et al., 2011; Miettinen et al., 2016). Industrial oil palm plantations are currently cultivated on 3.1 Mha of SE Asian peatlands (Miettinen et al., 2016). Undisturbed, these peatlands act as an overall long-term carbon sink, due to high water tables providing saturated conditions with low redox potentials (Dommain et al., 2015; Cobb et al., 2017; Hodgkins et al., 2018). Organic matter breaks down in these conditions through anaerobic degradation, releasing CH<sub>4</sub> to the atmosphere (Sundh et al., 1994; Arai et al., 2014; Sjögersten et al., 2014).

Modifying peatlands for agricultural management can alter the biogeochemistry and trace gas fluxes from these systems due to the introduction of artificial drainage ditches that lower the water table and create an aerated zone for root growth, raising the soil redox potential (Hirano et al., 2012; Mishra et al., 2014; Tonks et al., 2017). In these more oxic conditions, methanogenesis is inhibited and aerobic degradation pathways predominate, namely peat oxidation from heterotrophic respiration (Rh; Hooijer et al., 2012; Miettinen et al., 2017; Warren et al., 2017). Additionally, significant CO<sub>2</sub> and CH4 fluxes have been observed from the surface of drainage ditches in cultivated temperate and tropical peatlands (hereafter drain CO<sub>2</sub>, drain CH<sub>4</sub> and stem CH<sub>4</sub>; Teh et al., 2011; Jauhiainen and Silvennoinen, 2012). Tree stems have also been shown to act as a pathway for CH<sub>4</sub> transport from tropical peat swamp forests (Pangala et al., 2013, 2017).

Soil  $R_h$  and  $CH_4$  fluxes have been measured previously from oil palm plantations. Current estimates of  $R_h$  from oil palm plantations on peat suggest that these systems emit a mean flux of 12.2 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, with reported estimates ranging from 4.1 to 22.9 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> (Farmer, 2013; Melling et al., 2013; Dariah et al., 2014; Husnain et al., 2014; Comeau, 2016; Comeau et al., 2016; Hergoualc'h et al., 2017; Ishikura et al., 2018; Matysek et al., 2018). Only one study has quantified CH<sub>4</sub> from oil palm plantations, finding annual emissions of  $-0.2 \text{ kg CH}_4$ -C ha<sup>-1</sup> yr<sup>-1</sup>, suggesting that CH<sub>4</sub> oxidation may predominate in these drained ecosystems (Melling et al., 2005a).

Furthermore, existing studies of R<sub>h</sub> and soil CH<sub>4</sub> have failed to fully account for spatial heterogeneity of the trace gas fluxes in oil palm systems, despite the fact that biogeochemical processes are known to be highly variable in space and time (i.e., "hot spots" and "hot moments," sensu McClain et al., 2003). Oil palm plantations have different soil surface management microforms, namely highly compacted bare soil harvest paths, piles of decomposing fronds, rows of cover plants, and an extensive rhizosphere in the fertilizer circle around the palm (Manning, 2019; Manning et al., in preparation). R<sub>h</sub> and soil CH<sub>4</sub> measurements have predominantly been sampled from the harvest path only (Melling et al., 2005a, 2013; Farmer, 2013; Dariah et al., 2014; Hergoualc'h et al., 2017; Matysek et al., 2018). However, the frond piles and cover plants may give different results for R<sub>h</sub> and CH<sub>4</sub> due to potentially different environmental conditions.

Several CO<sub>2</sub> and CH<sub>4</sub> fluxes known to be important in temperate peatlands and tropical forest have not been measured in oil palm plantations on peat soils. In temperate peatlands, drainage ditches have been observed to act as hotspots for CH<sub>4</sub> emissions, making a disproportionately large contribution to net ecosystem exchange (Minkkinen and Laine, 2006; Schrier-Uijl et al., 2010; Teh et al., 2011). Similarly the absence of stem CH<sub>4</sub> may signify the oversight of a notable CH<sub>4</sub> loss from oil palm plantations; it has been found that stem fluxes contribute between 62-87% (Brunei) and 42-53% (Amazon) of ecosystem CH<sub>4</sub> fluxes from mature trees in swamp forests (Pangala et al., 2013, 2017), and may therefore represent an important but so far unexplored transport pathway for CH<sub>4</sub> emission in oil palm systems.

Here we report CO2 (Rtot, Rh and drain) and CH4 (soil, drain and stem) fluxes from two mature oil palm plantations established on peat soils in Sarawak, Malaysian Borneo. Autotrophic fluxes (R<sub>a</sub> and stem CO<sub>2</sub>) are noted due to being measured simultaneously. We include a wide spatial resolution, sampling CO<sub>2</sub> and CH<sub>4</sub> from all major surface microforms (i.e., next to palms, harvest paths, frond piles, cover plants, drainage ditches, and tree stems). Temporal trends in fluxes were determined by sampling at monthly (soil CO<sub>2</sub> and stem fluxes) or bi-monthly (soil CH4 and drain fluxes) intervals. Lastly, we upscaled our surface fluxes and estimates of peat oxidation (i.e., R<sub>b</sub>) to the plantation-level using proportional surface areaweighting and temporal integration. The overarching goal of this research was to determine rates of carbon losses that are broadly representative of production systems of this kind elsewhere in Southeast Asia, with a view to presenting effective solutions to reduce these carbon losses. During the course of this work we explored the following research questions:

- 1. Do CO<sub>2</sub> and CH<sub>4</sub> fluxes vary spatially and temporally in oil palm plantations?
- 2. What are the annual rates of R<sub>h</sub>, drain CO<sub>2</sub>, soil CH<sub>4</sub>, drain CH<sub>4</sub> and stem CH<sub>4</sub> from oil palm plantations on peat soil—both individually and combined as total peat carbon losses?
- 3. What are the relationships between key environmental factors and trace gas fluxes?
- 4. Do opportunities exist to minimize or mitigate CO<sub>2</sub> and CH<sub>4</sub> fluxes, based on our understanding of the drivers of trace gas exchange in this system?

#### Oil Palm Plantation Carbon Emissions

# **METHODS**

### **Site Description**

Data were collected from Sabaju (latitude  $003^{\circ} 12'$  N, longitude  $113^{\circ} 30'$  E) and Sebungan (latitude  $003^{\circ} 09'$  N, longitude  $113^{\circ} 21'$  E) oil palm plantations in Sarawak, Malaysia. Sabaju and Sebungan Estates have been established on peat soils broadly classified as histosols (FAO, 2006). The peat depth was measured to be 3.0 m at Sabaju and 4.0 m at Sebungan. The mean annual precipitation was ~3,200 mm (MET Malaysia, 2017). The northeast monsoon from October to January has the most rainfall, with a slightly drier southwest monsoon between May and August (MET Malaysia, 2017). The two principal dry seasons fall between February to April and in September. The mean annual temperature was 26.5°C (MET Malaysia, 2017).

Prior to planting, the land use was a mixed species swamp forest, which had been heavily logged. The land was converted to a plantation in 2006 and the palms were on their first crop rotation. The palms were 8 years old when measurements began. The plantations were laid out systematically with  $\sim$ 35 ha blocks and drainage ditches every 28 m leading to a larger ditch running down the center of the block. Palms were planted every 8 m in rows that were 8 m apart, with a planting density of 160 palms per ha. Within the palm blocks, four different surface management microforms were present and two different drain types (**Figure 1**):

- By palm or fertilizer circle—the ring of soil around the palm where the majority of oil palm roots grow and the fertilizer is applied.
- Harvest path—frequently weeded soil between the rows of palms and around the palms to allow access for workers.
- Frond pile—the location of the decomposing, harvested fronds.
- Cover plants—an area where weeds were left to grow freely.
- Field drains—small, 1.5 m wide drains dug every four rows of palms.
- Collection drains—larger, 3 m wide drains running down the center of the plantation blocks.

# **Experimental Design**

Six one hectare plots were established, three in Sabaju and three in Sebungan. Within each plot, three subplots were randomly placed. In each subplot, soil surface collars made from PVC plastic of dimensions 10 cm deep by 10.5 cm diameter were installed to 5 cm depth to measure from the harvest path, underneath a frond pile, in the cover plants and adjacent to three palms in order to take  $CO_2$  and  $CH_4$  measurements. Collars were installed 6 months prior to the commencement of sampling in order to avoid disturbance effects associated with chamber base installation (Varner et al., 2003).

A location was selected to sample the drain fluxes from both the field drain and the collection drain within each subplot. Soil surface collars of 10 cm depth and 10.5 cm diameter were installed into the base of each ditch to 5 cm, to prepare for sampling months when the drains were dry. Floating chambers were made for sampling when there was water in the drains (**Figure 2A**; Kent, 2018). Here two holes were drilled into plastic mixing bowls (30 cm rim diameter) and lengths of Tygon tubing (2.5 m long, 3 mm inner diameter) were attached to each hole using Swagelok fittings. Aluminum foil was taped over the bowls to prevent light from penetrating and foam cylinders were attached to the bowls to help them float.

Stem fluxes were only taken from one plot in Sabaju and one plot in Sebungan, due to time and resource limitations, adapting the chamber methodology used by Pangala et al. (2013) and Siegenthaler et al. (2016) to suit oil palms (Figure 2B; Figure S1; Manning, 2019). Here, five palms were selected from each plot, including three that had soil collars next to them. Permanent chamber bases were glued onto the palm surfaces-these were made out of 3 cm wide and 6 cm thick strips of neoprene, attached at 0.2 m and 0.7 m height. Expandable polyurethane (PU) foam was applied to the stem, filling any gaps between the neoprene strips and the palm surface that had been created by the uneven distribution of frond bases. Extra neoprene blocks were randomly placed inside the chamber base area to help maintain an even volume inside the chamber. The chamber itself consisted of a  $2.5 \text{ m} \times 0.75 \text{ m} \times 0.003 \text{ m}$  sheet of plastic, which was wrapped around the chamber base and fixed in place using two ratchet straps to attach the sheet to the neoprene strips, with a third ratchet strap around the middle of the chamber to keep the sheet closed. Prior to attachment, six fans (12 VDC 120 mm computer case fans; flow  $\sim$ 200 CFM) were distributed within the chamber base. After attaching the chamber, the chamber was wrapped first in plastic wrap to make it gas tight, and then in black plastic sheeting to block sunlight and prevent any photosynthesis. Furthermore, the palm stems were regularly cleaned of vegetation at least one week prior to flux measurement.

# **Determining the Chamber Volumes**

The soil chamber volume was determined by multiplying the height of the chamber (15 cm) with the surface area (radius 5.5 cm). Prior to each measurement, the depth of the collar was measured and included in the volume calculations. The floating drain chamber volume was 7 L. The volume inside the drain chamber did not change when the chamber was placed on the water.

The stem chamber volume needed to be calculated for each measurement due to the uneven surface of the palms and the chamber being flexible rather than rigid. Equation (1) was used to determine the stem chamber volume:

$$V = dh\pi (R + r) \tag{1}$$

where *V* is the volume of the chamber, *d* is the mean depth of the chamber base (i.e., radially outwards from palm), *h* is the internal (vertical) height of each chamber, *R* is the radius of the outer chamber surface (i.e., that of the plastic sheet), and *r* is the radius of the inner chamber surface (i.e., the radius of the stem). Multiple measurements were made of *d*, *h*, *R*, and *r* for each palm and the mean values were used in this equation. More information can be found in Manning (2019).

### Flux Measurements

Flux measurements were made using the static chamber approach (Livingston and Hutchinson, 1995). Soil and drain CO<sub>2</sub>



and  $CH_4$  fluxes were collected between June 2015 and May 2016 and stem fluxes were collected from May 2016 to May 2017. The fluxes were measured at different times due to limitations in resource availabilities. Soil, drain and stem fluxes were measured at the same time in May 2016 to ensure comparability. Furthermore, the different instruments were calibrated against each other to ensure compatibility (Manning, 2019).

 $R_{tot}$  measurements were made using an EGM-4 and SRC-1 chamber (PP Systems; Hansatech Instruments, Amesbury, USA). Two recordings were made in duplicate (one immediately after the other) and averaged during data processing because the EGM did not always save one of the recordings. For each replicate measurement, CO<sub>2</sub> concentrations were measured over a 2 min enclosure period, with concentrations recorded at 3 s intervals, or until an increase of 100 ppm CO<sub>2</sub> had been observed.

Measurements were then made monthly for 12 months (per month n = 54 for by palm fluxes and n = 18 for each of the harvest path, frond pile and cover plants fluxes). Extra fluxes were measured next to the palm because of high variability in both R<sub>tot</sub>, root biomass and R<sub>a</sub>, and the desire to accurately capture plantation R<sub>tot</sub> fluxes (Manning, 2019; Manning et al., in preparation).

Soil CH<sub>4</sub>, drain CO<sub>2</sub>, and drain CH<sub>4</sub> measurements were made using syringe sampling (soil CO<sub>2</sub> data were also obtained using this method but the EGM data are presented due to a larger dataset). Static chambers were placed on the soil collars and floating chambers were deployed on drains when there was water present, otherwise static chambers were used on the drain surface. These chambers were left in place for 40 min, and 30 ml samples were collected with syringes every 0, 10,



**FIGURE 2** | Chambers adapted for this study: **(A)** a floating chamber to measure  $CO_2$  and  $CH_4$  fluxes from the drainage ditches, and **(B)** a novel stem chamber to measure stem  $CO_2$  and  $CH_4$ .

20, 30, and 40 min. These samples were transferred into 20 ml pre-evacuated vials, which had been sealed with chlorobutyl rubber septa and aluminum seals (Sigma-Aldrich, Dorset, UK), and the over-pressurized vials were shipped to the UK for analysis. Measurements were made in August 2016, September 2016, November 2016, January 2017, March 2017, and May 2017 providing per month n = 18 for each location. The air samples were sent to St. Andrews University for analysis where samples were manually injected into a Thermo TraceGC Ultra Gas Chromatograph, which was fitted with a FID and methanizer for determination of CO2 (Thermo Electro Corporation). August 2016 samples were analyzed at the University of Aberdeen on an Agilent 6890 Gas Chromatograph Analyser, fitted with an FID (Agilent). The two different analysers were cross-calibrated with three different BOC standards, which comprised of mixes of CO2 and CH<sub>4</sub> in different concentrations (Manning, 2019).

Stem  $CO_2$  and  $CH_4$  fluxes were measured using a Los Gatos UGGA (Ultraportable Greenhouse Gas Analyzer; Los Gatos Research Inc, San Jose, California, USA). This UGGA was attached to the chamber by 2 m long tubing and data were

continuously measured for 10 min at a frequency of 1 Hz. Data were stored on the field laptop and the dry air ppm were reported.

#### **Environmental Measurements**

Ancillary measurements were made during and just after the completion of flux measurements. Ambient air temperature was measured at the same time as all flux measurements, using a thermometer (LCD Digital Thermometer, ATP Instrumentation, Leicestershire, UK; precision:  $\pm 1^{\circ}$ C). Soil temperature and soil moisture measurements at 0-10 cm depth were taken following the completion of soil CO<sub>2</sub> and CH<sub>4</sub> sampling, adjacent to the soil collars, with soil moisture measured using an ML3-probe and HH2 moisture meter (Delta-T, Cambridge, UK; precision for soil moisture:  $\pm 1\%$ ). Soil moisture measurements at 0–10, 10–20, 20– 30, and 30-40 cm intervals were made next to a subset of soil collars following each measurement, namely at one subplot in each plot, using a PR2-probe and HH2 moisture meter (Delta-T, Cambridge, UK; precision:  $\pm 4\%$ ). If soil collars were being used to measure drain fluxes, soil temperature and soil moisture at 0-10 cm were also sampled from the peat at the base of the drain following the completion of the flux measurement. When floating chambers were being used to measure drain fluxes, water temperature was measured following the completion of the flux measurement, using the same thermometer as used for air and soil temperature. Stem temperature was measured using a Fluke 62 Max Infrared Thermometer (MEA, Dubai, United Arab Emirates; precision:  $\pm 2^{\circ}$ C). Throughout the study climate data were collected from two weather stations (Davis Vantage Pro2 Plus, Hayward, California, USA), one on each plantation. Measurements from these weather stations include precipitation, air temperature, UV index, and air humidity (precisions:  $\pm 4\%$ ,  $\pm 0.3^{\circ}$ C,  $\pm 5$  and  $\pm 2\%$ , respectively).

Water table depth (WTD) and the depth of the water in the drains (drain water depth) were both measured after the flux measurements were completed. To prepare for WTD measurements from the soil, PVC pipes of 3 m length and 5 cm diameter had holes drilled into them at 10 cm intervals along the pipe, in all four directions. These pipes were then installed into the peat to depths of 2.5 m 1 month prior to the commencement of flux measurement. WTD was then measured by inserting a 2.5 cm diameter pipe with a measuring tape attached to it into the PVC pipe. Drain water depth was measured using a pipe with a measuring tape attached to it, which was lowered into the drain until it reached the bottom of the drain. If the drain was dry when CO<sub>2</sub> and CH<sub>4</sub> fluxes had been measured from the drain surface, the WTD was measured by digging a hole 0.5 m away from the flux collar from the drain surface to the water table and measuring this distance.

### **Calculating Fluxes**

Fluxes were calculated using the HMR package in R version 2.15.1 (http://www.R-project.org; Pedersen et al., 2010). Here linear and non-linear regressions were applied to the fluxes in accordance with the HMR methodology, whereby both options were calculated and the fit with the lowest standard error was used. All of the data were included for the flux calculations when the data were collected by the EGM. The vial  $CO_2$  data were first plotted in conjunction with  $CH_4$  to determine whether any of the

vials had leaked, before the HMR function was applied, with the leaked vials being excluded from the analysis. The units of the HMR outputs are  $\mu L m^{-2} s^{-1}$ . These units were converted to Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> or kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> using Equation (2):

$$F = \frac{\Delta_c PVMY}{\Delta_t TAR} \tag{2}$$

where *F* is the C flux,  $\Delta_C$  is the change in CO<sub>2</sub> or CH<sub>4</sub> concentration over the measurements period (ppm),  $\Delta_t$  is the duration of the measurement period (s), *P* is pressure (mb), *T* is temperature (K), *V* is volume (m<sup>3</sup>), *A* is surface area of the soil (m<sup>2</sup>), *R* is the Universal Gas Constant 8.31432 J mol<sup>-1</sup> K<sup>-1</sup>, *M* is the relative molecular mass of CO<sub>2</sub> or CH<sub>4</sub> and *Y* is the conversion to upscale the flux to annual emissions.

#### **Upscaling to Annual Flux Estimates**

Annual flux estimates were upscaled using spatial and temporal weighting. Fluxes from the soil and drain microforms were spatially weighted by multiplying the mean CO<sub>2</sub> or CH<sub>4</sub> flux by the proportional area of the microform (**Tables S1, S2**). Stem fluxes were first upscaled to the plot level fluxes (F'), expressed as Mg CO<sub>2</sub>-C ha<sup>-1</sup> or kg CH<sub>4</sub>-C ha<sup>-1</sup> soil—first the flux (F) was multiplied by the surface area (A) of each palm to calculate the mean stem flux ( $A^{-1}$ ) and then  $A^{-1}$  was then multiplied by the planting density (166 palm ha<sup>-1</sup>) to get the per hectare stem carbon flux. Second, each spatially weighted flux (F') was linearly interpolated between months using Equation (3):

$$F^* = \frac{1}{2} \left( F'_{t_1} + F'_{t_2} \right) (t_2 - t_1) \tag{3}$$

where  $t_1$  and  $t_2$  are the timings of the measurements in days. These temporally weighted fluxes  $F^*$  were subsequently summed over one year to produce annual flux estimates ( $F_{tot}$ ). The microform annual estimates were summed to provide component and plantation flux estimates.

### Calculating Peat Oxidation Rates (R<sub>h</sub>)

The rate of peat oxidation (i.e.,  $R_h$ ) was calculated by sampling root-free soil 4 m away from the palms, based on prior work by Manning et al. (in preparation), where roots and  $R_{tot}$  were measured in transects at 0, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5, and 4 m distance from the palm, going into the harvest path, frond piles and cover plants, to 0.3 m depth. Root biomass was found to be negligible further than 1.0 m away from the palm and  $R_{tot}$ did not vary with increasing distance more than 0.75 m distance from the palm (Manning et al., in preparation). Therefore, at this site the contribution of  $R_a$  to  $R_{tot}$  was considered to be negligible more than 1 m from the palm and sites were chosen for  $R_h$  measurements exactly 4 m away from the palms (halfway between two palms).

A range of  $R_h$  values were proposed, assuming: (1) the harvest path only provided true  $R_h$  estimates, (2) the harvest path and frond pile gave  $R_h$  estimates, and (3) assuming that surface  $R_{tot}$  fluxes measured from the harvest path, frond pile and cover plants only contributed to  $R_h$ . We estimated  $R_h$  using this range of methods because peat oxidation occurs at all of these different microforms and potentially at different rates due to variations between the microclimates. These estimates of  $R_h$  were extrapolated to the plantation level by area-weighting each flux by the proportional surface area of its microform. For methods (1) and (2) the flux measured from the harvest path was used to represent  $R_h$  from the microforms that were not included in the specific  $R_h$  calculation, when spatially upscaling. In all three methods the harvest path flux was also assumed to represent the rate of  $R_h$  for the area next to the palm.

### **Statistical Analyses**

All statistical analyses were done in R (version 3.5.1). Kruskal-Wallis tests were used to test whether there were significant variations in the  $CO_2$  and  $CH_4$  fluxes between the two different plantations, the three plots within each plantation, the three subplots within each plot and the different surface microforms. Kruskal-Wallis tests were used to test for significant variation in the  $CO_2$  and  $CH_4$  fluxes between the months. *Post-hoc* multiple comparisons tests were performed using the R package pgirmess (Giraudoux et al., 2018).

 $CO_2$  and  $CH_4$  measurements were modeled as a function of environmental variables using Gaussian linear mixed effect models from the nlme package in R (Pinheiro et al., 2017). Log or square root transformations of  $CO_2$  and  $CH_4$  measurements were sometimes necessary to normalize model residuals. The random effect structure and correlation structure, the latter used to take into account seasonality, were determined by comparing model residual plots. Fixed effect variables were chosen by top down selection, with the non-significant variables removed one by one from models using the ANOVA function (see **Data Sheets 1–5**, for the selection processes for the fixed effects in each model). The following five models were used for this study, with \* used to denote significant interactions between variables:

```
R_h = lme (log(R_h) \sim Plantation x Microform x Soil moisture (0 - 10 cm))
     +Plantation x Microform x Soil temperature + Air temperature +
     +Plantation x WTD,
     random = \sim 1|Plantation/Plot/Subplot,
     correlation = corCompSymm (form = \sim 1|
     Plantation/Plot/Subplot/Microform),
     weights = varIdent (form = \sim 1|Plantation x Microform))
                                                                         (4)
Soil CH_4 = lme(sqrt(CH_4 + 2.71) \sim Plantation x Microform x Soil moisture
     (30 - 40 \text{ cm}) \times WTD + Plantation \times Soil temperature}
     + Soil moisture (0 - 10 cm),
     random = \sim 1 | Plantation/Plot/Subplot,
                                                                         (5)
     weights = varIdent (form = \sim 1|Plantation x Microform))
Drain CO_2 = lme (log(CO_2) \sim Microform,
     random = \sim 1|Plantation/Plot/Subplot,
     correlation = corCompSymm (form = \sim 1)
     Plantation/Plot/Subplot/Microform),
     weights = varIdent (form = \sim 1|Plantation x Microform))
                                                                         (6)
Drain CH_4 = lme (CH_4 \sim Air temperature,
     random = \sim 1|Plantation/Plot/Subplot,
     correlation = corCompSymm (form = \sim 1|
     Plantation/Plot/Subplot/Microform),
     weights = varIdent (form = \sim 1|Plantation x Microform))
                                                                         (7)
```

 $StemCH_4 = lme (CH_4 \sim Mean monthly relative humidity x Plantation x Palm + WTD + Plantation x Palm x Soil moisture + Mean monthly relative humidity x Soil temperature + Air temperature x Plantation, random = ~1|Plantation/Palm) (8)$ 

## RESULTS

#### **Environmental Variables**

Precipitation, relative humidity and air temperature were measured from weather stations in Sabaju (November 2015-March 2017) and Sebungan (June 2015-March 2017). Annual means for climate variables can be found in Table 1. Annual precipitation was recorded at 2,015 mm in Sabaju, using an average of moving annual sums of the data available. Precipitation records from Sebungan were unreliable due to equipment failure. The dry season consisted of February, March and May-all of which recorded <100 mm rain in Sabaju. Collectively, the rainy season had significantly more rainfall than the dry season, averaging 216  $\pm$  25 mm/month in the rainy season and 90  $\pm$  46 mm/month in the dry season (Kruskal-Wallis: chi-squared = 4.5; d.f. = 1; p = 0.03). Relative humidity was significantly higher in Sabaju than in Sebungan in both measurement periods (2015-2016: Kruskal-Wallis: chi-squared = 6.2; d.f. = 1; p = 0.01; 2016–2017: Kruskal-Wallis: chisquared = 12.8; d.f. = 1; p < 0.0001). Using averages taken between November 2015 and January 2017, where there were complete records of relative humidity from both plantations, relative humidity was significantly higher in the rainy season (88.0  $\pm$  0.5%) than in the dry season (87.3  $\pm$  1.1%; Kruskal-Wallis: chi-squared = 6.5; df = 1; p = 0.01). Annual mean air temperatures measured from the weather stations were the same for both plantations, in both measurement periods. Air temperature measured at the time and location of the soil flux sampling was significantly higher in Sabaju than in Sebungan (Sabaju:  $30.7 \pm 0.1^{\circ}$ C; Sebungan:  $29.2 \pm 0.1^{\circ}$ C; Kruskal-Wallis: chi-squared = 109.7; d.f. = 1; p < 0.0001). Air temperature measured at the same time as the stem fluxes was not significantly different between the two plantations. Air temperature did not vary significantly between the rainy and dry seasons.

WTD varied between the two plantations during 2015-2016 but not during 2016-2017 (Table 1; Table S3). During 2015-2016, when the soil and drain measurements were made, mean WTD was  $-0.49\pm0.0041\,m$  in Sabaju and  $-0.76\pm0.0072\,m$ in Sebungan, which were significantly different (Kruskal-Wallis: chi-squared = 789.2; d.f. = 1; *p* < 0.0001). During 2016–2017, when the stem measurements were made, monthly mean WTD was  $-0.46 \pm 0.16$  m for Sabaju and  $-0.43 \pm 0.16$  m for Sebungan, which were not significantly different. Seasonal variation was observed in WTD; WTD was significantly higher in the dry season than in the rainy season in both measurement periods  $(2015-2016: dry season: -0.72 \pm 0.00048 m; rainy season: -0.61$  $\pm$  0.00046 m; Kruskal-Wallis: chi-squared = 50.11; d.f. = 1; p < 0.001; 2016–2017: dry season:  $-0.49 \pm 0.02$  m; rainy season:  $-0.42 \pm 0.02$  m; Kruskal-Wallis: chi-squared = 5.68; d.f. = 1; p = 0.017).

In addition to climate and WTD measurements, different environmental measurements were made at the time of flux sampling, with annual averages reported in Table 1. Of particular interest are soil temperature and soil moisture, which varied significantly between the two plantations and between the different surface microforms. Soil temperature was significantly higher in Sabaju than in Sebungan (Kruskal-Wallis: chi-squared = 185.9; d.f. = 1; p < 0.0001) and varied significantly between the different surface microforms (Kruskal-Wallis: chi-squared = 253.7; d.f. = 3; p < 0.0001). Soil temperature was highest next to the palm and lowest beneath the frond piles, decreasing in order by palm > harvest path > cover plants > frond pile. Soil temperature was also significantly higher in the dry season  $(29.4 \pm 0.05^{\circ}\text{C})$  than the rainy season  $(28.1 \pm 0.05^{\circ}\text{C};$  Kruskal-Wallis: chi-squared = 29.2; d.f. = 1; p < 0.001). This seasonality was measured in both plantations (Sabaju Kruskal-Wallis: chisquared = 10.60; d.f. = 1; p = 0.0011; Sebungan Kruskal-Wallis: chi-squared = 30.31; d.f. = 1; p < 0.001).

Soil moisture was significantly greater in Sebungan than in Sabaju (Kruskal-Wallis: chi-squared = 15.8; d.f. = 1; p < 0.0001). Soil moisture varied significantly between the different surface microforms (Kruskal-Wallis: chi-squared = 840.0; d.f. = 3; p < 0.0001). Soil moisture was consistently drier next to the palm than in the other microforms, decreasing in order harvest path > frond pile > cover plants > by palm, although soil moisture was highest in the frond pile in Sabaju and the harvest path in Sebungan. Soil moisture was significantly greater in the rainy season than in the dry season, with a mean of  $39.4 \pm 1.1\%$  in the rainy season and  $32.4 \pm 1.0\%$  in the dry season (Kruskal-Wallis: chi-squared = 23.8; d.f. = 1; p < 0.001). This relationship was seen in the different microforms, at the different plantations and in the different microforms at each plantation.

### Spatial Variability in CO<sub>2</sub> and CH<sub>4</sub> Fluxes

The CO<sub>2</sub> fluxes are summarized in **Table 2**. Mean R<sub>tot</sub> was recorded as  $0.83 \pm 0.048 \text{ g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$ . Drain CO<sub>2</sub> averaged  $0.14 \pm 0.0012 \text{ g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$ . Mean stem respiration was  $0.23 \text{ g} \pm 0.012 \text{ CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$ . There was no significant difference in the overall mean CO<sub>2</sub> flux between the plantations.

Significant differences were seen in the magnitude of the CO<sub>2</sub> fluxes between the different surface microforms (**Figure 3**). Considering the plantations together, Rtot measured next to the palm gave the highest CO<sub>2</sub> flux from the plantation (Kruskal-Wallis: chi-squared = 1,555.5; d.f. = 6; p < 0.0001). Within each plantation, we found differences in the magnitude of CO<sub>2</sub> flux from each microform (Sabaju: Kruskal-Wallis: chi-squared = 572.6; d.f. = 6; p < 0.0001; Sebungan: Kruskal-Wallis: chisquared = 1,078.6; d.f. = 6; p < 0.0001). For example, in Sabaju, the harvest path Rtot was significantly higher than Rtot measured from the frond piles and cover plants-although they themselves did not differ (multiple comparison test for Kruskal-Wallis:  $p \leq 0.05$ ). Drain fluxes were lower than soil fluxes but not significantly different to stem CO<sub>2</sub> (multiple comparison test for Kruskal-Wallis:  $p \le 0.05$ ). Stem CO<sub>2</sub> fluxes were significantly lower than R<sub>tot</sub> from next to the palm, the harvest path and beneath the frond piles, but not the cover plants (multiple comparison test for Kruskal-Wallis:  $p \le 0.05$ ).

TABLE 1 | Mean environmental variables measured from the two plantations, both combined and from Sabaju and Sebungan individually.

Variable	Microform	Combined	Sabaju	Sebungan
ENVIRONMENTAL MEASUREMENTS TAKEN ALONG	SIDE ALL FLUXES			
Relative humidity (2015–2016)	All	88.2 (0.4)	89.9 (0.3) <sup>a</sup>	87.2 (0.4) <sup>b</sup>
Relative humidity (2016–2017)	All	87.2 (0.5)	89.4 (0.3) <sup>a</sup>	85.1 (0.3) <sup>b</sup>
Air temperature (2015–2016)—weather station	All	27.3 (0.1)	27.4 (0.2)	27.3 (0.1)
Air temperature (2015–2016)—next to measurement	All	29.9 (0.1)	30.7 (0.1) <sup>a</sup>	29.2 (0.1) <sup>b</sup>
Air temperature (2016–2017)—weather station	All	27.0 (0.1)	27.0 (0.1)	27.0 (0.1)
Air temperature (2016–2017)—next to measurement	All	27.2 (0.04)	27.1 (0.1)	27.2 (0.1)
WTD (2015–2016)	All	-0.62 (0.005)	-0.49 (0.004) <sup>a</sup>	-0.76 (0.007) <sup>b</sup>
WTD (2016–2017)	All	-0.46 (0.16)	-0.47 (0.16)	-0.43 (0.16)
ENVIRONMENTAL MEASUREMENTS TAKEN ALONG	SIDE SOIL FLUXES			
Soil temperature (2015–2016)	All	28.2 (0.03)	28.7 (0.05) <sup>a</sup>	27.8 (0.02) <sup>b</sup>
	By palm	28.7 (0.04) <sup>m</sup>	29.3 (0.08) <sup>r</sup>	28.2 (0.03) <sup>w</sup>
	Away from palm	27.7 (0.02)	28.1 (0.03)	27.4 (0.03)
	Harvest path	28.1 (0.04) <sup>n</sup>	28.6 (0.7) <sup>s</sup>	27.6 (0.04) <sup>x</sup>
	Frond pile	27.5 (0.04)°	27.8 (0.6) <sup>t</sup>	27.2 (0.04) <sup>y</sup>
	Cover plants	27.7 (0.03)°	28.0 (0.04) <sup>t</sup>	27.4 (0.05) <sup>x</sup>
Soil moisture (2015–2016)	All	36.9 (0.4)	33.6 (0.6)	40.2 (0.6)
	By palm	14.7 (0.2) <sup>m</sup>	12.4 (0.3) <sup>m</sup>	16.9 (0.4) <sup>x</sup>
	Away from palm	58.5 (0.5)	53.4 (0.6)	63.2 (0.7)
	Harvest path	64.0 (0.8) <sup>n</sup>	57.8 (0.9) <sup>n</sup>	70.1 (1.1) <sup>y</sup>
	Frond pile	58.5 (0.7) <sup>n</sup>	61.6 (1.0) <sup>n</sup>	55.4 (1.0) <sup>y</sup>
	Cover plants	48.7 (0.8)°	40.3 (1.1)°	57.0 (1.1) <sup>y</sup>
ENVIRONMENTAL MEASUREMENTS TAKEN ALONG	SIDE DRAIN FLUXES			
Drain depth	Collection drain	31.0 (0.03)	34.2 (0.04)	27.6 (0.04)
	Field drain	19.9 (0.01)	24.1 (0.01) <sup>a</sup>	15.5 (0.02) <sup>b</sup>
Water temperature	Collection drain	27.7 (0.1)	28.3 (0.2) <sup>a</sup>	27.3 (0.2) <sup>b</sup>
	Field drain	27.3 (0.9)	27.4 (0.1)	27.2 (0.2)
ENVIRONMENTAL MEASUREMENTS TAKEN ALONG	SIDE STEM MEASUREMENT	TS		
Stem temperature	Palm	32.4 (0.4)	31.8 (0.5)	33.1 (0.7)
Soil temperature (2016–2016)	By palm	28.7 (0.1)	28.7 (0.2)	28.7 (0.2)
Soil moisture (2016–2016)	By palm	22.0 (1.3)	29.4 (1.7) <sup>a</sup>	14.7 (1.3) <sup>b</sup>

Standard errors are in brackets. Relative humidity units are in %, temperature units are in °C, WTD units are in m and soil moisture units are in %. Plantations with significantly different parameters have been denoted by suffix m, n, and o when considered collectively, or r, s, and t in Sabaju and w, x, and y in Sebungan when considered individually.

In contrast, in Sebungan, frond pile R<sub>tot</sub> was significantly higher than the field drain CO<sub>2</sub> flux, but otherwise the soil, drain and stem fluxes did not differ significantly, apart from the high R<sub>tot</sub> fluxes measured next to the palms (multiple comparison test for Kruskal-Wallis:  $p \leq 0.05$ ).

Summaries of the CH<sub>4</sub> fluxes are presented in **Table 2**. The mean soil CH<sub>4</sub> flux was  $0.29 \pm 0.047$  mg CH<sub>4</sub>-C m<sup>-2</sup> hr<sup>-1</sup>. The mean drain CH<sub>4</sub> flux was  $4.24 \pm 1.64$  mg CH<sub>4</sub>-C m<sup>-2</sup> hr<sup>-1</sup>. The stem CH<sub>4</sub> flux averaged  $0.043 \pm 0.0056$  mg CH<sub>4</sub>-C m<sup>-2</sup> hr<sup>-1</sup>. We did not observe a significant difference in the overall CH<sub>4</sub> flux when comparing all the CH<sub>4</sub> fluxes from the two plantations.

CH<sub>4</sub> fluxes varied significantly among the different surface microforms (**Figure 3**; Kruskal-Wallis: chi-squared = 258.79; d.f. = 6; p < 0.0001). Multiple comparisons tests indicate that the CH<sub>4</sub> fluxes from different microforms fell into one of two groups; the first (lower emission) group consisted of the harvest path, frond pile, cover plants and stem fluxes, while the second (higher

emission) group consisted of the by palm, collection drain and field drain fluxes (multiple comparison test for Kruskal-Wallis:  $p \leq 0.05$ ). This trend was the same in both plantations.

# Temporal Variability in CO<sub>2</sub> and CH<sub>4</sub> Fluxes

Seasonal trends were observed in trace gas fluxes between the rainy and dry seasons. CO<sub>2</sub> fluxes varied between the rainy and dry seasons, but this trend was not statistically significant. The rainy season flux averaged 0.74  $\pm$  0.054 g CO<sub>2</sub>-C m<sup>-2</sup> hr<sup>-1</sup> and the dry season flux averaged 0.94  $\pm$  0.081 g CO<sub>2</sub>-C m<sup>-2</sup> hr<sup>-1</sup>.

Disaggregating the data by microform showed that each microform had different trends with respect to CO<sub>2</sub> fluxes (**Figure 4**). R<sub>tot</sub> measured next to the palm was significantly higher in the dry season than in the rainy season (Kruskal-Wallis: chi-squared = 25.6; d.f. = 11; p < 0.0001). R<sub>tot</sub> measured from the harvest path, frond piles and cover plants did not vary significantly between the rainy and dry seasons. Significantly

	CO <sub>2</sub> (g CO <sub>2</sub> -C m <sup>-2</sup> hr <sup>-1</sup> )			$CH_4$ (mg $CH_4$ -C $m^{-2}$ $hr^{-1}$ )				
	Mean (S.E.)	Min	Max	n	Mean (S.E.)	Min	Max	n
COMBINE	D							
Soil	0.83 (0.048)	0.0044	36.62	1233	0.29 (0.047)	-2.70	15.47	461
Drain	0.14 (0.0012)	0.0016	1.70	280	4.24 (1.64)	-128.87	162.66	165
Stem	0.23 (0.012)	0.000022	0.96	130	0.043 (0.0056)	-0.016	0.44	130
SABAJU								
Soil	0.82 (0.052)	0.029	12.89	587	0.40 (0.087)	-1.77	15.48	237
Drain	0.14 (0.018)	0.0020	1.70	142	5.13 (2.44)	-128.87	110.81	89
Stem	0.24 (0.017)	0.000022	0.89	65	0.048 (0.010)	-0.016	0.44	65
SEBUNG/	AN .							
Soil	0.85 (0.083)	0.044	36.62	646	0.17 (0.030)	-2.70	3.51	224
Drain	0.14 (0.015)	0.0016	1.12	138	3.19 (2.15)	-0.015	162.66	76
Stem	0.23 (0.018)	0.013	0.96	65	0.038 (0.0045)	0.0012	0.15	65

TABLE 2 | Summaries of the mean, minimum, maximum and number of CO2 and CH4 fluxes measured in this study.

Standard errors of the mean are included in brackets. Fluxes are presented that were measured from the soil, drain and stem surfaces from both plantations combined, or when the plantations were considered separately.



**FIGURE 3** |  $CO_2$  and  $CH_4$  fluxes from the different microforms in Sabaju and Sebungan. Microform acronyms are in the top left of each panel and are: BP - by palm; HP - harvest path; FP - frond pile; CP - cover plants; CD - collection drain; FD - field drain; and S - stem. (A) the median and interquartile range for  $CO_2$  fluxes from Sabaju and (B) Sebungan, and (C) the median and interquartile range for  $CH_4$  fluxes from Sabaju and (D) Sebungan. Outliers were excluded from the graph for visual clarity.





**FIGURE 4** | each panel and are: BP - by palm; HP - harvest path; FP - frond pile; CP - cover plants; CD - collection drain; FD - field drain; and S - stem. Furthermore, the lines for by palm fluxes are plotted in black, the lines for harvest path, frond pile, and cover plants are plotted in brown, the drain fluxes are plotted in blue and the stem fluxes are plotted in green. The shaded gray areas signify the rainy seasons and the white areas signify the dry seasons. Standard errors are shown with bars. Data are presented for 2015–2016, apart from stem data which are presented for 2016–2017. Note the different y-axis scales.

more CO<sub>2</sub> was measured from the surfaces of the drainage ditches in the rainy season than in the dry season (Kruskal-Wallis: chi-squared = 11.54; d.f. = 1; p < 0.0001). Splitting the drains, the larger collection drains had significant seasonal variation in CO<sub>2</sub> fluxes (Kruskal-Wallis: chi-squared = 8.1; d.f. = 1; p = 0.004), with higher CO<sub>2</sub> fluxes in the rainy season than the dry season (multiple comparison test for Kruskal-Wallis:  $p \le 0.05$ ) and the smaller field drains did not. Stem CO<sub>2</sub> did not show significant variation between the rainy and dry seasons.

Collectively, CH<sub>4</sub> fluxes did not vary significantly between rainy and dry seasons, although the rainy season flux averaged  $0.76 \pm 0.17 \text{ mg CH}_4\text{-C} \text{ m}^{-2} \text{ hr}^{-1}$  and the dry season flux averaged  $2.27 \pm 1.14 \text{ mg CH}_4\text{-C} \text{ m}^{-2} \text{ hr}^{-1}$ . Soil and stem CH<sub>4</sub> fluxes did not show significant variation between the rainy and dry seasons at the different plantations. Drain CH<sub>4</sub> fluxes were significantly higher in the rainy season than in the dry season (**Figure 4**; Kruskal-Wallis: chi-squared = 4.33; d.f. = 1; p = 0.04). Considering the plantations separately, there was no significant difference between the rainy and dry seasons in the different microforms or locations.

#### Annual Estimates of CO<sub>2</sub> and CH<sub>4</sub> Flux

Annual estimates of CO<sub>2</sub> fluxes were produced for the plantations both together and separately (**Table 3**). Combining R<sub>tot</sub> and drain CO<sub>2</sub> fluxes to give the total CO<sub>2</sub> flux from the ground surfaces gave an average of  $23.57 \pm 0.50$  Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>. Sabaju and Sebungan differed in their annual combined R<sub>tot</sub> and drain CO<sub>2</sub> flux. Sabaju was estimated to produce 29.54  $\pm$  0.47 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> and Sebungan was estimated to produce 17.62  $\pm$  0.53 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>. The plantations differed in this CO<sub>2</sub> flux because of the contribution from the harvest path at each plantation; Sebungan averaged 9.21  $\pm$  1.40 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> from the harvest path, while Sabaju emitted 20.19  $\pm$  1.33 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>.

Annual estimates of CH<sub>4</sub> fluxes were calculated, collectively for both plantations and individually, with very little difference between the total CH<sub>4</sub> flux (**Table 4**). Combined, the annual CH<sub>4</sub> flux from oil palm plantations, including soil, drain and stem fluxes, was 61.02  $\pm$  17.78 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>. In Sabaju, the annual CH<sub>4</sub> flux was 60.84  $\pm$  4.35 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> and in Sebungan the annual CH<sub>4</sub> flux was 61.19  $\pm$  25.28 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>.

# Partitioning R<sub>tot</sub> Into R<sub>h</sub> and R<sub>a</sub>

 $R_{tot}$  was partitioned into  $R_h$  and  $R_a$  at both plantations (**Table 5**). Collectively,  $R_h$  ranged from 17.61 to 17.89 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> and  $R_a$  ranged from 4.19 to 4.47 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>. Plantation  $R_a$  increased from 4.71 to 4.99 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> when stem respiration was included.  $R_h$  varied between the two plantations;  $R_h$  in Sabaju ranged from 23.89 to 24.39 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, while in Sebungan it ranged from 11.13 to 11.81 Mg CO<sub>2</sub>-C ha<sup>-1</sup>

yr<sup>-1</sup>. Considering the plantations separately, R<sub>a</sub> ranged from 3.10 to 3.60 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> in Sabaju and from 4.36 to 5.04 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> in Sebungan. When stem respiration was combined with soil R<sub>a</sub>, plantation R<sub>a</sub> increased to range from 3.52 to 4.02 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> in Sabaju and from 4.98 to 5.66 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> in Sebungan.

# Plantation Peat Carbon Losses and Percentage Contributions

Plantation peat carbon losses were comprised of  $R_h$ , drain  $CO_2$ , soil  $CH_4$ , drain  $CH_4$ , and stem  $CH_4$  components and were estimated in  $CO_{2-eq}$ . Overall plantation carbon losses ranged from 72.35  $\pm$  0.14 to 73.38  $\pm$  0.16 Mg  $CO_{2-eq}$  ha^{-1} yr^{-1}. Plantation carbon losses varied between the two plantations. In Sabaju, the plantation carbon losses ranged from 95.58  $\pm$  0.14 to 97.41  $\pm$  0.17 Mg  $CO_{2-eq}$  ha^{-1} yr^{-1}. In Sebungan, the plantation carbon losses ranged from 48.37  $\pm$  0.16 to 50.86  $\pm$  0.19 Mg  $CO_{2-eq}$  ha^{-1} yr^{-1}.

Breaking the carbon losses down by component showed that 92% of the CO<sub>2</sub> produced through  $R_h$  and drain CO<sub>2</sub> pathways came from soils and 8% came from the drains (**Table 6**). This was similar for both plantations. In Sabaju, 94% of the CO<sub>2</sub> produced through  $R_h$  or drain CO<sub>2</sub> came from  $R_h$  and 6% came from drain CO<sub>2</sub>. In Sebungan, 89% of the CO<sub>2</sub> produced through  $R_h$  or drain CO<sub>2</sub> came from  $R_h$  and 11% came from drain CO<sub>2</sub>.

The CH<sub>4</sub> losses showed different component contributions to CO<sub>2</sub> (**Table 6**). Overall, 30% of CH<sub>4</sub> fluxes came from the soil and 70% of plantation CH<sub>4</sub> fluxes came from the drainage ditches. Stem CH<sub>4</sub> fluxes gave negligible contributions. The CH<sub>4</sub> pathways varied between the two plantations. In Sabaju, 50% of the plantation CH<sub>4</sub> flux was measured from the soil surface and 50% was recorded from the drainage ditches. In Sebungan, 11% of the plantation CH<sub>4</sub> flux came from the soil and 89% came from the drainage ditches.

In order to isolate which pathways were dominating the plantation peat carbon losses, the fluxes were compared in  $CO_{2-eq}$  (**Table 6**). Considering the soil component in isolation, 99% of soil peat carbon losses were attributable to  $R_h$  and 1% to  $CH_4$ . Considering the drain carbon fluxes, 78% of the carbon losses came through drain  $CO_2$  and 22% of the carbon measured from the drain surfaces came from drain  $CH_4$ .

Overall, 89% of plantation peat carbon losses came from  $R_h$ , 8% came from drain  $CO_2$ , 1% from soil  $CH_4$ , 2% from drain  $CH_4$ , and 0% from stem  $CH_4$ ; 90% of plantation carbon losses came from the soil and 10% from drainage ditches (**Table 6**). In Sabaju, 92% of plantation peat carbon losses were attributable to  $R_h$ , 6% to drain  $CO_2$ , 1% to soil  $CH_4$ , 1% to drain  $CH_4$ , and 0% to stem  $CH_4$ ; 93% of peat carbon losses came from the soil and 7% from the drainage ditches. In Sebungan, 84–85% of plantation carbon losses were from  $R_h$ , 10–11% were from

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Location	Combined	n	Sabaju	п	Sebungan	n
INDIVIDUAL MICROFORM						
By palm	4.99 (0.73)	616	5.11 (0.68)	293	4.87 (0.78)	323
Harvest path	14.70 (1.36)	207	20.19 (1.33)	99	9.21 (1.40)	108
Frond pile	1.04 (0.17)	206	1.13 (0.19)	98	0.96 (0.13)	108
Cover plants	1.34 (0.26)	204	1.55 (0.20)	97	1.14 (0.32)	107
Collection drain	0.42 (0.02)	107	0.32 (0.03)	54	0.53 (0.00)	53
Field drain	1.08 (0.15)	173	1.24 (0.22)	88	0.91 (0.03)	85
Stem	0.52 (0.01)	130	0.42 (0.05)	65	0.62 (0.08)	65
COMPONENT SUMS						
Sum (R <sub>tot</sub> )	22.08 (0.77)	1233	27.98 (0.73)	587	16.17 (0.81)	646
Sum (drain CO <sub>2</sub> )	1.50 (0.10)	280	1.56 (0.14)	142	1.44 (0.02)	138
Sum ( $R_{tot}$ + drain CO <sub>2</sub> )	23.57 (0.50)	1513	29.54 (0.47)	729	17.62 (0.53)	784
Sum ( $R_{tot}$ + drain CO <sub>2</sub> + stem CO <sub>2</sub> )	24.09 (0.48)	1643	29.96 (0.45)	794	18.24 (0.51)	849

Temporally and spatially weighted fluxes are presented for each individual microform. The sums of the different surface components ( $R_{tot}$  + drain CO<sub>2</sub> and  $R_{tot}$  + drain CO<sub>2</sub> + stem CO<sub>2</sub>) are included. All flux values are given in Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>. Standard errors are in brackets.

TABLE 4 Annual upscaled CH<sub>4</sub> fluxes from the different surface microforms sampled at both plantations and at Sabaju and Sebungan individually.

Location	Combined	n	Sabaju	n	Sebungan	n
INDIVIDUAL MICROFORM						
By palm	0.18 (0.31)	171	0.29 (0.44)	85	0.07 (0.040)	86
Harvest path	17.35 (6.30)	95	29.38 (8.53)	52	5.31 (0.74)	43
Frond pile	0.36 (0.06)	97	0.17 (0.02)	49	0.56 (0.08)	48
Cover plants	0.53 (0.15)	98	0.55 (0.14)	51	0.50 (0.17)	47
Collection drain	14.37 (2.09)	70	22.71 (2.06)	34	6.03 (2.12)	36
Field drain	28.14 (46.00)	95	7.67 (6.49)	55	48.62 (71.71)	40
Stem	0.09 (0.01)	130	0.08 (0.04)	65	0.11 (0.02)	65
COMPONENT SUMS						
Sum (soil CH <sub>4</sub> )	18.41 (2.88)	461	30.39 (4.02)	237	6.44 (0.34)	224
Sum (drain CH <sub>4</sub> )	42.51 (34.72)	165	30.38 (5.24)	89	54.64 (51.43)	76
Sum (soil $CH_4$ + drain $CH_4$ )	60.93 (17.92)	626	60.76 (4.39)	326	61.08 (25.49)	300
Sum (soil $CH_4$ + drain $CH_4$ + stem $CH_4$ )	61.02 (17.78)	756	60.84 (4.35)	391	61.19 (25.28)	365

Temporally and spatially weighted fluxes are presented for each individual microform. The sums of the different surface components (soil  $CH_4$  + drain  $CH_4$  and soil  $CH_4$  + drain  $CH_4$  + drain C

drain CO<sub>2</sub>, 0% from soil CH<sub>4</sub>, 4% from drain CH<sub>4</sub>, and 0% from stem CH<sub>4</sub>; 85–86% came from the soil and 14–15% from the drainage ditches.

# Environmental Models for CO<sub>2</sub> and CH<sub>4</sub> Losses

 $R_h$ , the most dominant component in the peat carbon losses, was controlled by variations in air temperature, WTD, soil temperature, and soil moisture (**Table S4**).  $R_h$  increased as air temperature increased (**Figure 5**). Whilst the interaction between air temperature and plantation was not significant, the rate of increase in  $R_h$  as air temperature increased was predicted to be almost three times greater in Sabaju than in Sebungan (**Table S5**). Unexpectedly,  $R_h$  increased as WTD rose, with a modeled increase of 0.75 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> for every 10 cm decrease in WTD. The interaction between WTD and plantation was significant, with opposite relationships seen in both plantations (Figure 5). In Sabaju, R<sub>h</sub> increased by 0.85 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> for every 10 cm rise in WTD. R<sub>h</sub> increased in Sebungan as the WTD was lowered, by a modeled rate of -0.29 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> for every 10 cm drawdown of WTD.

Overall,  $R_h$  increased as soil temperature increased and  $R_h$  increased as soil moisture decreased (**Tables S4, S5**). Soil temperature and soil moisture had significant relationships with  $R_h$  when their individual interactions with plantation and microform were included in the model. Considering the plantations together and the microforms separately, the harvest path increased in  $R_h$  as soil temperature increased, and the frond pile and cover plants decreased in  $R_h$  as soil temperature increased, when the plantations were considered separately. In Sabaju when the plantations were considered separately. In Sabaju,  $R_h$  increased when soil temperature increased throughout the

TABLE 5 | Rtot, Rh and Ra estimates from both plantations combined, and Sabaju and Sebungan considered individually.

Partitioning method	R <sub>tot</sub>	R <sub>h</sub>	Ra
COMBINED			
(1) Partitioned using harvest path fluxes	22.08 (0.77)	17.76 (1.65)	4.32 (0.95)
(2) Partitioned using harvest path and frond pile fluxes	22.08 (0.77)	17.61 (1.09)	4.47 (0.86)
(3) Partitioned using harvest path, frond pile and cover plants fluxes	22.08 (0.77)	17.89 (0.85)	4.19 (0.80)
SABAJU			
(1) Partitioned using harvest path fluxes	27.49 (0.73)	24.39 (1.61)	3.10 (0.91)
(2) Partitioned using harvest path and frond pile fluxes	27.49 (0.73)	23.89 (1.07)	3.60 (0.83)
(3) Partitioned using harvest path, frond pile, and cover plants fluxes	27.49 (0.73)	23.97 (0.82)	3.52 (0.77)
SEBUNGAN			
(1) Partitioned using harvest path fluxes	16.17 (0.81)	11.13 (1.69)	5.04 (0.98)
(2) Partitioned using harvest path and frond pile fluxes	16.17 (0.81)	11.34 (1.12)	4.83 (0.89)
(3) Partitioned using harvest path, frond pile and cover plants fluxes	16.17 (0.81)	11.81 (0.87)	4.36 (0.82)

 $R_{tot}$  has been partitioned into  $R_h$  and  $R_a$  using three methods: partitioning method one has been estimated from harvest path fluxes only; partitioning method two has been estimated from harvest path and frond pile fluxes only; and partitioning method three has been estimated from harvest path, frond pile and cover plants fluxes only. Spatially weighted results are presented in Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> for each flux. Standard errors are in brackets.

microforms. Increasing soil moisture decreased the rate of  $R_h$ , with the greatest effect beneath the frond pile, followed by the harvest path and then the cover plants. This trend was also observed when the microforms in Sebungan were considered in isolation. In Sabaju, rates of  $R_h$  decreased as soil moisture increased in the cover plants but not in the harvest path and frond piles.

Soil CH<sub>4</sub> was controlled by soil moisture between 0 and 10 cm, soil moisture between 30 and 40 cm, WTD and soil temperature (Table S6). Soil CH4 increased as soil moisture between 0 and 10 cm increased (Table S5). The interaction between plantation, microform, WTD and soil moisture between 30 and 40 cm also significantly explained the variation in soil CH<sub>4</sub>. Here the expected relationship of soil CH<sub>4</sub> increasing as WTD decreased was observed in the harvest path and next to the palm. This trend was seen when considering the plantations together or in Sabaju. In Sebungan, soil CH4 was modeled to increase as WTD decreased in the frond piles and cover plants. The opposite relationship was seen in the other microforms. Similarly, variation was seen in the relationship between soil CH<sub>4</sub> and soil moisture between 30 and 40 cm. Soil CH<sub>4</sub> increased as soil moisture between 30 and 40 cm increased in the harvest path, frond pile and next to the palm, with the opposite relationship in the cover plants. In Sabaju, soil CH<sub>4</sub> increased as soil moisture between 30 and 40 cm increased in the harvest path and by the palm. In Sebungan, soil CH<sub>4</sub> increased as soil moisture between 30 and 40 cm increased in the frond pile and cover plants. Soil CH<sub>4</sub> increased as soil temperature decreased. The interaction between soil temperature and plantation was significant, with the rate of soil CH<sub>4</sub> increasing twice as quickly in Sabaju than in Sebungan when soil temperature decreased.

Drain  $CO_2$  and drain  $CH_4$  had different environmental relationships (**Tables S5, S7**). Drain  $CO_2$  did not have a significant relationship with any of the environmental variables measured in this study, but did vary significantly depending on the size of the microform. Overall, the field drain had a

greater drain CO<sub>2</sub> flux. Drain CH<sub>4</sub> increased significantly as air temperature increased. This was seen at both plantations.

Stem CH<sub>4</sub> was explained by variations in monthly relative humidity, WTD, soil moisture, air temperature and soil temperature (Table S8). Stem CH<sub>4</sub> decreased as monthly relative humidity increased (Table S5). This relationship was seen on both plantations and the interaction between the individual palms within each plantation with monthly relative humidity was significant. Stem CH<sub>4</sub> increased as WTD increased. This was also seen at both plantations. For soil moisture, air temperature and soil temperature, opposite trends were seen between the two plantations. Stem CH<sub>4</sub> increased as soil moisture increased, this trend was the same when the plantations were considered together and also in Sebungan when the plantations were considered separately, but not in Sabaju. Stem CH<sub>4</sub> increased as air temperature and soil temperature increased, when both plantations were considered together. These trends were seen in Sebungan but not in Sabaju when the plantations were considered separately.

# DISCUSSION

# Carbon Fluxes Vary Spatially in Managed Tropical Peatlands

 $\rm CO_2$  and  $\rm CH_4$  fluxes varied significantly when measured from different surface microforms in two oil palm plantations on peat soil. The highest soil  $\rm CO_2$  and  $\rm CH_4$  fluxes were measured next to the palms. This pattern was attributed to the high density of roots in the palm rhizosphere; root biomass was greatest within the immediate 1 m radius around each palm, and decreased with increasing distance from the palm (Farmer, 2013; Dariah et al., 2014; Manning, 2019; Manning et al., in preparation). In these studies  $\rm R_{tot}$  and soil respiration were measured at consistent intervals from the palm into the harvest path (Farmer, 2013; Dariah et al., 2014), frond pile and cover plants (Manning, 2019; Manning et al., in preparation) from mature oil palm plantations in Jambi, Indonesia (Farmer, 2013; Dariah et al., 2014) and TABLE 6 Percentage contributions of the soil, drain, and stem components to plantation CO2, CH4 and CO2-eq fluxes.

	Combined	Sabaju	Sebungan				
PLANTATION CO <sub>2</sub> CONTRIBUTIONS PER COMPONENT FLUX (EXCLUDING R <sub>a</sub> )							
Soil: Plantation carbon losses	92%	94%	89%				
Drain: Plantation carbon losses	8%	6%	11%				
Stem: Plantation carbon losses	-	-	_				
Total	100%	100%	100%				
PLANTATION CH <sub>4</sub> CONTRIBUTIONS PER	COMPONENT FLUX						
Soil: Plantation carbon losses	30%	50%	11%				
Drain: Plantation carbon losses	70%	50%	89%				
Stem: Plantation carbon losses	0%	0%	0%				
Total	100%	100%	100%				
CONTRIBUTION OF CO2 AND CH4 TO EA	CH COMPONENT						
Soil $(R_h + CH_4)$	99% CO <sub>2</sub> , 1% CH <sub>4</sub>	99% CO <sub>2</sub> , 1% CH <sub>4</sub>	99% CO <sub>2</sub> , 1% CH <sub>4</sub>				
Drain	78% CO <sub>2</sub> , 22% CH <sub>4</sub>	83% CO <sub>2</sub> , 17% CH <sub>4</sub>	72% CO <sub>2</sub> , 28% CH <sub>4</sub>				
Stem (CH <sub>4</sub> only)	0% CO <sub>2</sub> , 100% CH <sub>4</sub>	0% CO <sub>2</sub> , 100% CH <sub>4</sub>	0% CO <sub>2</sub> , 100% CH <sub>4</sub>				
Plantation carbon losses	97% CO <sub>2</sub> , 3% CH <sub>4</sub>	98% CO <sub>2</sub> , 2% CH <sub>4</sub>	95–96% CO <sub>2</sub> , 4–5% CH <sub>4</sub>				
PLANTATION CO2 AND CH4 CONTRIBUTI	ONS PER COMPONENT						
Soil: Plantation carbon losses	90%	93%	85–86%				
Drain: Plantation carbon losses	10%	7%	14–15%				
Stem: Plantation carbon losses	0%	0%	0%				
Total	100%	100%	100%				
OVERALL CO2 OR CH4 CONTRIBUTION T	O PLANTATION CARBON LOSSES, PE	R COMPONENT					
R <sub>h</sub> : Plantation carbon losses	89% CO <sub>2</sub>	92% CO <sub>2</sub>	84–85% CO <sub>2</sub>				
Drain CO2: Plantation carbon losses	8% CO <sub>2</sub>	6% CO <sub>2</sub>	10-11% CO <sub>2</sub>				
Soil CH <sub>4</sub> : Plantation carbon losses	1% CH <sub>4</sub>	1% CH <sub>4</sub>	0% CH <sub>4</sub>				
Drain CH <sub>4</sub> : Plantation carbon losses	2% CH <sub>4</sub>	1% CH <sub>4</sub>	4% CH <sub>4</sub>				
Stem CH <sub>4</sub> : Plantation carbon losses	0% CH <sub>4</sub>	0% CH <sub>4</sub>	0% CH <sub>4</sub>				
Total	100% CO <sub>2-eq</sub>	100% CO <sub>2-eq</sub>	100% CO <sub>2-eq</sub>				

Firstly, the percentage contribution of peat  $CO_2$  carbon losses to the total plantation  $CO_2$  losses by soil, drain and stem components are presented ( $R_a$  and stem  $CO_2$  are not included). Secondly, the percentage contribution of net peat  $CH_4$  to the total plantation net  $CH_4$  flux by soil, drain and stem components are presented. Thirdly, the percentage contribution of  $CO_2$  and  $CH_4$  to each component and for the overall plantation carbon losses are presented, when the  $CO_2$  and  $CH_4$  fluxes have been combined in  $CO_{2-eq}$ . Here plantation carbon losses are defined as the sum of  $R_h$ , drain  $CO_2$ , soil  $CH_4$ , drain  $CH_4$  and stem  $CH_4$ . Fourthly, the percentage contribution of the combined  $CO_2$  and  $CH_4$  fluxes in  $CO_{2-eq}$ . The plantation carbon losses by soil, drain and stem components are presented. Finally, the percentage contributions of individual  $CO_2$  and  $CH_4$  fluxes to overall plantation carbon losses by soil, drain, and stem components are presented. Finally, the percentage contributions of individual  $CO_2$  and  $CH_4$  fluxes to overall plantation carbon losses by soil, drain, and stem components are considered together and separately.

this plantation (Manning, 2019; Manning et al., in preparation). Respiration from root biomass has been shown to drive high  $R_{tot}$  rates next to the palm, with a progressive decline in  $R_{tot}$  with increasing distance from each palm (Farmer, 2013; Dariah et al., 2014; Manning, 2019; Manning et al., in preparation). Likewise, high CH<sub>4</sub> fluxes from the rhizosphere could be due to a number of causes, including accelerated organic matter turnover facilitated by the metabolism of root exudates (Girkin et al., 2018a,b), or transport of CH<sub>4</sub> from deeper in the profile via porous tissues in the roots.

Outside the palm rhizosphere (i.e., >1 m distance from the palm), different soil surface management practices appeared to influence R<sub>tot</sub> but not CH<sub>4</sub>. R<sub>tot</sub> was significantly higher in the harvest path than from either the frond piles or beneath the cover plants. There was no significant difference in CH<sub>4</sub> measured from these microforms. Considering the plantations separately gave different trends for R<sub>tot</sub>, but did not change the pattern of CH<sub>4</sub>. For example, in Sebungan, there was no significant difference in R<sub>tot</sub> between the non-rhizosphere fluxes. In contrast, in Sabaju the harvest path had significantly higher R<sub>tot</sub> than the frond pile

and cover plants. These differences in  $R_{tot}$  among microforms are noteworthy because few other studies consider the effects of surface management practices on  $R_{tot}$ , with the exception of work by Arifin et al. (2015), who also found that  $R_{tot}$  was significantly lower when measured from beneath cover plants than from the harvest path. These differences in  $R_{tot}$  among microforms are significant because they have direct bearing not only predicting and upscaling land-atmosphere fluxes, but also because they provide insight into how soil surface management practices are affecting soil CO<sub>2</sub> and CH<sub>4</sub> dynamics.

Drainage ditches made a substantial contribution to landatmosphere  $CO_2$  and  $CH_4$  fluxes, particularly with respect to  $CH_4$ . Drain  $CH_4$  was significantly higher than  $CH_4$  fluxes from all soil microforms, with the exception of the  $CH_4$  flux measured next to the palm. Comparing our drain data against other datasets, we found that our  $CH_4$  fluxes fell within the range observed in drained peatlands and drained *Acacia sp.* plantations in Kalimantan (Jauhiainen and Silvennoinen, 2012). These high drain  $CH_4$  fluxes could be attributable to the photochemical or microbial breakdown of DOC, or lateral transport of dissolved



 $CH_4$  produced in the peat into surface waters (Billett and Moore, 2008; Teh et al., 2011; Cory et al., 2014; Logue et al., 2016). These data are significant because there are currently no published data on drain  $CO_2$  and  $CH_4$  fluxes from oil palm plantation drainage ditches, and they have implications for extrapolating both plot-level  $CO_2$  and  $CH_4$  fluxes to larger spatial scales. In particular, the estimates of  $CO_2$  and  $CH_4$  fluxes based on straight mean averaging or non-spatially explicit sampling may tend to overestimate the net release of  $CO_2$  to the atmosphere and underestimate the net release of  $CH_4$  from tropical peatlands, given that drainage ditches form a small but significant portion of the landscape.

Stem respiration fell within a similar range to drain  $CO_2$ and the R<sub>tot</sub> fluxes when excluding the high fluxes next to the palm. Once again, disaggregation of the dataset by plantation revealed local differences in stem respiration relative to other  $CO_2$ -emitting processes. Stem respiration was lower in Sabaju than in Sebungan. Furthermore, in Sabaju, stem respiration was significantly lower than  $R_{tot}$  measurements taken from next to the palm, the harvest path and the frond pile. In contrast, in Sebungan, stem respiration was similar to all other soil fluxes with the exception of  $R_{tot}$  measured next to the palm. We believe that these local differences in stem respiration may reflect differences in productivity between the two plantations. Generally, stem respiration correlates with photosynthetic rate (Yang et al., 2016); hence, the higher stem respiration in Sebungan may reflect that this plantation shows higher rates of CO<sub>2</sub> uptake and growth than Sabaju, evidenced by higher rates of net primary productivity, larger fronds and formation of a denser, more closed canopy.

Stem CH<sub>4</sub> fluxes were recorded from the palms in both plantations, with lower CH<sub>4</sub> fluxes than those reported from the soil or drain surfaces, by factors of 22 and 200, respectively. Stem CH<sub>4</sub> has been recorded from the stems of tropical trees growing in swamp forests in Brunei and the Amazon (Pangala et al., 2013, 2017). Stem fluxes from Brunei ranged between similar magnitudes to the stem fluxes measured at this site (here:

-0.016-0.440 mg CH<sub>4</sub>-C m<sup>-2</sup> hr<sup>-1</sup>; Brunei: 0.013-0.139 mg CH<sub>4</sub>-C m<sup>-2</sup> hr<sup>-1</sup>) when the fluxes were considered per m<sup>-2</sup> of stem surface area (Pangala et al., 2013). Stem fluxes in the Amazon were considerably higher than the stem fluxes in Borneo (0.248-435.75 mg CH<sub>4</sub>-C m<sup>-2</sup> hr<sup>-1</sup>; Pangala et al., 2017). Stem CH<sub>4</sub> has been shown to correlate with rates of evapotranspiration (Pangala et al., 2014). We propose that the similar rates of relative humidity between Sarawak and Brunei may contribute to the similarities in range of fluxes from the stems of plants at these sites. The CH<sub>4</sub> oxidation reported from this site was measured four times and only when relative humidity exceeded 93% (Manning, 2019). We suggest that this may be due to methanotrophs on the palm surface, that are normally masked from stem CH<sub>4</sub> fluxes, but observable when high relative humidity prevents transpiration (Raghoebarsing et al., 2005).

### **Temporal Variation in Carbon Fluxes**

Both  $CO_2$  and  $CH_4$  fluxes were greater in the dry season than the rainy season, but these differences were not statistically significant. In this region, two rainy seasons occur, with the main rainy season between October and January, and a secondary rainy season between May and August. Dry season falls from February to April and in September.

Considering the surface microforms separately, significant seasonal variation was seen from  $R_{tot}$  measured next to the palm, with higher fluxes in the dry season than in the rainy season.  $R_{tot}$  next to the palm was predominately attributed to  $R_a$  (Farmer, 2013; Dariah et al., 2014; Manning et al., in preparation). Stem respiration gave similar overall trends to by palm  $R_{tot}$ , but differences were not statistically significant. Overall these fluxes, dominated by autotrophic processes, suggest strong seasonal growth from the palms, with more photosynthetic activity in the dry season than in the rainy season. Seasonality has been recorded from  $R_{tot}$  next to the palm in other plantations (Comeau, 2016; Hergoualc'h et al., 2017), as well as from  $R_a$  sampled from the edge of the canopy (Melling et al., 2013).

In contrast,  $R_{tot}$  measured from the harvest path, frond pile and cover plants did not show significant seasonal variation.  $R_{tot}$  fluxes measured from these locations were dominated by  $R_h$ .  $R_h$  was shown to have significant seasonality in a rubber plantation in Kalimantan, Indonesia growing on peat soil, where the seasonality in  $R_h$  was driven by seasonal changes in WTD (Wakhid et al., 2017). Similar to this study, those on other oil palm plantations have not found significant seasonality in  $R_h$ (Comeau, 2016; Hergoualc'h et al., 2017). The lack of apparent seasonality in  $R_h$  from oil palm plantations could be due to reduced variability in the environmental variables driving  $R_h$ . For example, Melling et al. (2013) found that  $R_h$  varied in the forest due to variations in WTD but not in the oil palm plantation where the WTD was more consistent.

Drain  $CO_2$  and  $CH_4$  fluxes showed seasonality; drain  $CO_2$  fluxes were significantly higher in the rainy season than the dry season and drain  $CH_4$  fluxes were significantly higher in the dry season than in the rainy season. Cook et al. (2018) found that drain discharge varied seasonally but total organic carbon (DOC plus particulate organic carbon) concentrations in the drains did not vary seasonally from Sabaju and Sebungan. Billett and Moore

(2008) found that drain  $\rm CO_2$  increased when flow rate increased, whilst DOC concentrations remained consistent regardless of flow rate.

# Peat Oxidation Rates and Major Loss Pathways?

 $R_{\rm h}$  was estimated to range from 17.61  $\pm$  1.65 to 17.89  $\pm$  $0.85 \text{ Mg CO}_2\text{-C} \text{ ha}^{-1} \text{ yr}^{-1}$  (mean:  $17.75 \pm 1.54 \text{ Mg CO}_2\text{-C}$  $ha^{-1} yr^{-1}$ ). For these calculations,  $R_h$  was partitioned from  $R_{tot}$ using the distance from palm approach, as this was deemed sufficient in these plantations (Manning, 2019; Manning et al., in preparation). We present a range of estimates that include (1) only the harvest path-comprising of bare soil and often the only microform measured in Rh studies; (2) the harvest path and the frond pile-the latter being bare soil covered in dead fronds; (3) the harvest path, frond pile and cover plantswith the cover plants being included, despite the presence of cover plant roots, due to the increased Rh being potentially from priming, as opposed to R<sub>a</sub> or decomposition from the cover plants (Manning et al., in preparation). In this study the lowest Rh estimate was obtained from when the harvest path and frond pile were both included in the calculations and the highest estimate came from when the cover plants were included as well. However, the estimates did not vary significantly regardless of which microforms were included.

R<sub>h</sub> estimates from Sebungan were found to range from 11.13  $\pm$  1.69 to 11.81  $\pm$  0.87 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> (mean: 11.43  $\pm$  1.37 Mg CO2-C  $ha^{-1}~yr^{-1})$  and  $R_h$  from Sabaju was measured ranging between 23.89  $\pm$  1.07 and 24.39  $\pm$  1.61 Mg  $CO_2$ -C ha<sup>-1</sup> yr<sup>-1</sup> (mean: 24.08  $\pm$  1.42 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>). In these estimates R<sub>h</sub> was lowest from Sebungan when the harvest path only was measured, and highest when the cover plants were included. In Sabaju the lowest Rh estimate used the harvest path and frond pile data and the highest R<sub>h</sub> estimate only used the harvest path results. The Sebungan Rh estimate fell within the reported range of R<sub>h</sub> from oil palm plantations (4.1 to 22.9 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, but the Sabaju estimate was greater than this range (Farmer, 2013; Melling et al., 2013; Dariah et al., 2014; Husnain et al., 2014; Comeau, 2016; Comeau et al., 2016; Hergoualc'h et al., 2017; Ishikura et al., 2018; Matysek et al., 2018).

These data are relevant to policy because they suggest that the IPCC emissions factor for  $R_h$  is underestimated. For example, whilst  $R_h$  estimates from Sebungan have been shown to be similar to the IPCC (2014) emissions factor of 11 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>,  $R_h$  from Sabaju is at least twice as large. This has implications when upscaling—estimating the  $R_h$  emissions from industrial oil palm plantations using the areal extent of plantations given in Miettinen et al. (2016) increases predicted  $R_h$  from 34.1 Tg CO<sub>2</sub>-C yr<sup>-1</sup> if the IPCC emission factor is used to 55.8 Tg CO<sub>2</sub>-C yr<sup>-1</sup>

Another important policy-relevant finding is that areaweighted CH<sub>4</sub> fluxes from these managed systems are similar to swamp forests in SE Asia, suggesting that drainage has not diminished the CH<sub>4</sub> emissions potential of these systems. Annual estimates of CH<sub>4</sub> were  $61.02 \pm 17.78 \text{ kg} \text{ CH}_4\text{-C} \text{ ha}^{-1} \text{ yr}^{-1}$ 

Oil Palm Plantation Carbon Emissions

including soil, drain and stem fluxes. Sabaju and Sebungan produced similar rates of CH4 of 60.84  $\pm$  4.35 kg CH4-C  $ha^{-1}$  $yr^{-1}$  and 61.19  $\pm$  25.28 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, respectively. Annual estimates from forest CH<sub>4</sub> have been shown to range between 0.2 and 72 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> from Malaysian, Indonesian and Brunei peatlands (Inubushi et al., 1998, 2003; Furukawa et al., 2005; Hadi et al., 2005; Jauhiainen et al., 2005; Melling et al., 2005b; Hirano et al., 2009; Pangala et al., 2013). The results from this study are potentially controversial because current conceptual ideas of peatland drainage predict a net reduction in CH<sub>4</sub> emission linked to peatland drainage (Jauhiainen et al., 2005, 2008; Lai, 2009; Couwenberg et al., 2010). This is reflected in the IPCC (2014) emissions factors for oil palm plantations that are 0 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> from the peat soil and 45.18 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> from the drainage ditches. The results from this study show that draining peat does not reduce CH<sub>4</sub> fluxes. The high CH<sub>4</sub> fluxes from the drains suggest that either the drain sediments have increased rates of CH<sub>4</sub> production, or that the CH<sub>4</sub> transported in the water may be carried to the drains before being egressed, rather than diffusing through the soil and being oxidized by methanotrophs (Müller et al., 2015; Evans et al., 2016).

Combining rates of R<sub>h</sub>, drain CO<sub>2</sub>, soil CH<sub>4</sub>, drain CH<sub>4</sub>, and stem CH<sub>4</sub> in CO<sub>2-eq</sub> gave overall plantation peat carbon losses. Here, net peat carbon losses averaged across plantations ranged between 72.35  $\pm$  0.14 and 73.38  $\pm$  0.16 Mg CO<sub>2-eq</sub> ha<sup>-1</sup>  $yr^{-1}$ . Of this flux, 89% was attributed to  $R_h$ . Drain CO<sub>2</sub> was the next largest driver, contributing 8% of the plantation carbon losses. CH<sub>4</sub> contributed 2, 1, and 0% to plantation carbon losses for drain, soil and stem fluxes, respectively. We suggest this particularly low contribution from palm stems is due to two factors: (1) a strong gradient for CH<sub>4</sub> transport to the atmosphere through the drainage ditches, and (2) the low density of palms growing on the soil. As previously mentioned, the measured stem CH<sub>4</sub> fluxes were in the same range as the stem fluxes from trees in a swamp forest in Brunei (Pangala et al., 2013). Following upscaling the stem CH<sub>4</sub> fluxes from Brunei were 10-23 times greater than the stem CH<sub>4</sub> fluxes measured here (Pangala et al., 2013). However, the swamp forest trees were taller and more densely populated than oil palms, allowing for a greater overall stem surface area and therefore a greater total plot-scale stem CH<sub>4</sub>. Similarly, the total contribution of tree stem CH<sub>4</sub> to plotscale CH<sub>4</sub> was 62-87% of the total ecosystem flux-but there were no drainage ditches in the forest plot, meaning that stem fluxes had a greater overall representation (Pangala et al., 2013). Excluding the drainage ditches from the estimates in this study increased the stem contribution to 0.5%.

Sabaju and Sebungan differed in their overall net peat carbon losses. Sabaju produced double the amount of peat carbon losses compared to Sebungan, with peat carbon losses ranging between 95.58  $\pm$  0.14 and 97.41  $\pm$  0.17 Mg CO<sub>2-eq</sub> ha<sup>-1</sup> yr<sup>-1</sup> in Sabaju. In Sebungan, net peat carbon losses fell within the range of 48.37  $\pm$  0.16 to 50.86  $\pm$  0.19 Mg CO<sub>2-eq</sub> ha<sup>-1</sup> yr<sup>-1</sup>. Sabaju and Sebungan peat carbon losses were made up from slightly different proportions of CO<sub>2</sub> and CH<sub>4</sub>. R<sub>h</sub> dominated the proportional losses of peat carbon in Sabaju; 92% of the total flux was from R<sub>h</sub>, 6% from drain CO<sub>2</sub>, 1% from soil CH<sub>4</sub>, 1% from drain

CH<sub>4</sub>, and 0% from stem CH<sub>4</sub>. In Sebungan, R<sub>h</sub> was still the predominant peat carbon loss pathway, but the drain CO<sub>2</sub> and CH<sub>4</sub> fluxes doubled in contribution compared to Sabaju; 84–85% of plantation carbon losses in Sebungan was made up from R<sub>h</sub>, 10–11% was from drain CO<sub>2</sub>, 4% was from drain CH<sub>4</sub>, and 0% was from both soil and stem CH<sub>4</sub>.

# Role of Temperature and Water Table Depth in Modulating Carbon Fluxes

Air temperature, soil temperature, WTD and soil moisture controlled rates of  $R_h$ . WTD, soil moisture at 0–10 cm, soil moisture at 30–40 cm and soil temperature controlled soil CH<sub>4</sub> fluxes. Drain CO<sub>2</sub> did not correlate with the environmental variables measured in this study. Drain CH<sub>4</sub> was controlled by air temperature. Stem CH<sub>4</sub> had significant relationships with relative humidity, WTD, air temperature, soil temperature and soil moisture.

Air and soil temperatures have been shown to control the rate of R<sub>h</sub>, both on these plantations and in other studies (Jauhiainen et al., 2012; Farmer, 2013; Hergoualc'h et al., 2017). Temperature has been shown to increase the rate of R<sub>tot</sub> and R<sub>h</sub> due to increased activation energy for the chemical reactions (Lloyd and Taylor, 1994). Air temperature increased the rate of R<sub>h</sub> in both plantations and the model predicted it was at a three times greater rate in Sabaju than in Sebungan. This steeper gradient in Sabaju might explain why Sabaju was only 1.5°C warmer than Sebungan but rates of R<sub>h</sub> were twice as high. R<sub>h</sub> also increased as soil temperature increased in both plantations-with differences seen in the relationships between the microforms. As soil temperature increased, R<sub>h</sub> was predicted to increase in the harvest path and in the cover plants in Sabaju, which also did not always have a closed canopy, exposing the soil directly to the Sun. This relationship with temperature was not seen in the frond piles, potentially due to extra shading, a different microclimate and the interaction of other variables, such as moisture.

Hydrology also controlled rates of R<sub>h</sub>, with soil moisture and WTD acting as proxies for redox potential. Increasing soil moisture lowered the rate of R<sub>h</sub>, as supported by Farmer (2013), Comeau (2016) and Hergoualc'h et al. (2017). This was seen in every microform in Sebungan, particularly in the frond pile, and in the frond pile and cover plants in Sabaju. Rh increased as soil moisture increased in Sabaju, but the effect size was negligible. WTD had opposite relationships with R<sub>h</sub> at both plantations. Sebungan gave the expected relationship with R<sub>b</sub> increasing as the WTD lowered. This trend has also been seen by Hergoualc'h et al. (2017). However, Sabaju had the opposite relationship with WTD, with increasing WTD decreasing rates of R<sub>h</sub>. The WTD measurements made in Sebungan were deeper and had a wider range than those made in Sabaju. Within the WTD range sampled, the more labile carbon may have already been oxidized in Sabaju, with fresher labile carbon exposed at the deeper WTDs in Sebungan, explaining the variation in relationship with WTD (Hooijer et al., 2012).

Soil  $CH_4$  was controlled by soil temperature, soil moisture between 0 and 10 cm, soil moisture between 30 and 40 cm and WTD. Melling et al. (2005b) also found that soil temperature,

water filled pore space and WTD controlled soil CH<sub>4</sub> fluxes. Here, soil CH<sub>4</sub> increased as soil moisture between 0 and 10 cm increased. This result would be expected, as CH<sub>4</sub> is more likely to be produced in anoxic conditions. The interaction between soil CH<sub>4</sub>, soil moisture between 30 and 40 cm, plantation and location was significant. In the different plantations and at different microforms, the expected relationship of soil CH4 increasing as WTD increased and soil moisture between 30 and 40 cm increased was seen, but not in every microform. It would be expected that soil CH4 increased as WTD decreased and soil moisture between 30 and 40 cm increased due to a larger volume of anoxic conditions for methanogens to break the peat down, and a lower volume of oxic conditions for methanotrophs to break down the CH<sub>4</sub> (Iivama et al., 2012; Carlson et al., 2015). Soil moisture at 0-10 cm did not have a significant interaction with soil moisture between 30 and 40 cm or WTD. Furthermore, Manning (2019) found that surface soil moisture correlated with climatic trends and soil moisture between 30 and 40 cm was determined by WTD. We propose that redox potential nearer the surface of the peat is more important than WTD for soil CH<sub>4</sub> fluxes, with CH<sub>4</sub> oxidized to CO<sub>2</sub> regardless of WTD, if the surface of the peat does not inhibit methanotrophs. Finally, soil CH<sub>4</sub> increased as soil temperature decreased. This may be due to seasonality and soil temperatures being cooler when the peat was wetter.

Drain CO<sub>2</sub> and drain CH<sub>4</sub> were controlled by different variables. Drain CO<sub>2</sub>, produced from DOC, did not have a significant relationship with the environmental variables but did have a significant relationship with drain type, being higher in the smaller field drains than the larger collection drains. DOC was greater in Sebungan than Sabaju during this measurement period and this was associated with the increased WTD at time of measurement (Cook et al., 2018). This same relationship was not observed in this study for drain CO<sub>2</sub>. The smaller field drains may therefore have a higher drain CO<sub>2</sub> flux than the collection drains due to being the first drain that DOC reaches from the soil—after all the field drains feed into the collection drains. Drain CH<sub>4</sub> was controlled by the rate of air temperature in both plantations. This was presumably due to the increase in rate of diffusion for the CH<sub>4</sub> (Billett and Moore, 2008).

Stem CH<sub>4</sub> was controlled by relative humidity, WTD, air temperature, soil temperature and soil moisture. Stem CH<sub>4</sub> reduced as relative humidity increased. We hypothesize that this is due to reduced rates of evapotranspiration at higher relative humidities, from a reduced moisture gradient. Evapotraspiration has been shown to control the rates of stem CH<sub>4</sub> (Pangala et al., 2014). Slowing the rate of water through the xylem would reduce the speed of transport for dissolved CH<sub>4</sub> and thus reduce the rate of stem CH<sub>4</sub>. Increasing WTD increased the rate of stem CH<sub>4</sub>. This has been seen in a manipulation experiment by Pangala et al. (2014), who found that if there is soil volume between the WTD and plant roots, CH<sub>4</sub> is oxidized before it reaches the roots. Air temperature, soil temperature and soil moisture gave opposite relationships with stem CH<sub>4</sub> at each plantation, with stronger relationships in Sebungan where increasing air temperature, soil temperature and soil moisture all increased stem CH<sub>4</sub>. Increasing temperatures would be expected to increase the rate of methanogenesis, whilst increasing soil moisture would reduce the redox potential, also increasing methanogenesis or transport of stem  $CH_4$  to the roots (Pangala et al., 2014). These relationships were negative in Sabaju but had very small effects.

## **Mitigation Options**

The most effective way to reduce carbon losses from oil palm plantations on peat soil is to reduce the rate of R<sub>h</sub>. The strong influence of temperature and WTD on Rh suggest that means of controlling soil surface temperatures and WTD are the best means of mitigating carbon losses from the peat. For example, the impact of temperature could be reduced by providing better coverage of the soil surface-particularly when the plantation canopy has not closed. Here, in Sebungan the canopy was closed, soil and air temperatures were lower and the Rh flux was half the rate of Sabaju. In Sabaju, the canopy was open and air temperature increased the rate of R<sub>h</sub> at three times the extent in Sebungan. Covering the soil in Sabaju with frond piles lowered the mean soil temperature (harvest path: 28.6  $\pm$  0.7°C; frond pile:  $27.8 \pm 0.6^{\circ}$ C) and increased mean soil moisture (harvest path: 57.8  $\pm$  0.9%; frond pile 61.6  $\pm$  1.0%); both changes in environmental conditions have been shown to reduce the Rh flux. Jauhiainen et al. (2014) found that R<sub>h</sub> could be reduced by 30% if the tropical peat was shaded. Annual Rtot was 30% lower beneath the frond pile in Sabaju than from the harvest path-extending the shade could therefore reduce Sabaju Rh to range between  $16.9 \pm 1.61$  and  $17.4 \pm 0.82$  Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, reducing the plantation net carbon losses to between 69.59  $\pm$  0.62 and 71.75  $\pm$  $0.65 \text{ Mg CO}_{2-eq} \text{ ha}^{-1} \text{ yr}^{-1}.$ 

Raising the water table is also an effective way of suppressing  $R_h$ . This was particularly apparent in Sebungan, where the canopy was closed and temperatures were lower. Sebungan had a lower mean WTD than the RSPO recommendations at the time of measurement and thus fresh peat may have been exposed to heterotrophic bacteria, increasing the rate of  $R_h$  from Sebungan (Lim et al., 2012; Mishra et al., 2014; Carlson et al., 2015).

Furthermore, temperature control may be more important than WTD control. Sebungan had a lower WTD than Sabaju but Sabaju had higher rates of  $R_h$ . It would be expected that  $R_h$  decreased with WTD (Carlson et al., 2015). However, the result from Sabaju did not fit the trend. We propose this is due to the open canopy in Sabaju and thus there being no barrier for the Sun to heat up the peat and increase the rate of its decomposition.

# CONCLUSIONS

 $\rm CO_2$  and  $\rm CH_4$  fluxes vary spatially and temporally in oil palm plantations on peat soil.  $\rm R_{tot}$  and soil  $\rm CH_4$  fluxes were both higher next to the palm than from the "away from palm" soil surface microforms (the bare soil harvest path, beneath frond piles and beneath cover plants). Drain  $\rm CO_2$  did not differ significantly from the "away from palm"  $\rm R_{tot}$  fluxes but drain  $\rm CH_4$  was significantly greater than the "away from palm" soil  $\rm CH_4$  fluxes.  $\rm CH_4$  emitted through the palm stems, after being transported through the xylem from the soil, was measured at both plantations.  $\rm R_{tot}$  next to the palm, drain  $CO_2$  and drain  $CH_4$  showed seasonality. Here  $R_{tot}$  and drain  $CO_2$  were higher in the dry season than in the rainy season. Drain  $CH_4$  was higher in the rainy season than in the dry season.

Annual CO<sub>2</sub> fluxes varied between the two plantations but annual CH<sub>4</sub> fluxes did not—and were within the range of CH<sub>4</sub> reported from swamp forests in the literature—draining the peat did not reduce the CH<sub>4</sub> flux (here 61.02 ± 17.78 kg CH<sub>4</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>). R<sub>tot</sub> from Sabaju and Sebungan were 27.98 ± 0.73 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> and 16.17 ± 0.81 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup>, respectively. The larger flux in Sabaju was due to higher R<sub>h</sub> measurements: R<sub>h</sub> ranged from 23.89 ± 1.07 to 24.39 ± 1.61 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> in Sabaju and 11.13 ± 1.69 to 11.81 ± 0.87 Mg CO<sub>2</sub>-C ha<sup>-1</sup> yr<sup>-1</sup> in Sebungan.

Plantation carbon losses were dominated by  $R_h$ , with drain  $CO_2$ , soil  $CH_4$ , drain  $CH_4$  and stem  $CH_4$  also contributing, in order of proportion. In Sabaju the plantation carbon losses were between  $95.58\pm0.14$  and  $97.41\pm0.17$  Mg  $CO_{2-eq}$  ha^{-1} yr^{-1}, with 92% of the flux attributed to  $R_h$ . In Sebungan, the plantation carbon losses fell within the range of  $48.37\pm0.16$  and  $50.86\pm0.19$  Mg  $CO_{2-eq}$  ha^{-1} yr^{-1}, with 84–85% of the flux made up from  $R_h$ . Therefore, the optimal management strategies to reduce plantation carbon losses are to focus on reducing  $R_h$ .

We propose shading the peat and raising the WTD to reduce R<sub>h</sub>. In Sabaju, where the canopy was open, air temperature dominated the drivers of R<sub>h</sub>, with fluxes measured below the frond piles being 30% lower than fluxes measured from the bare soil harvest path. Temperatures were lower in Sebungan, attributed to a closed canopy, and rates of R<sub>h</sub> were also lower. In Sebungan, WTD had a significant effect on rates of R<sub>h</sub>. WTD was lower in Sebungan than in Sabaju, (Sabaju: -0.49 m; Sebungan: -0.77 m) providing a greater peat volume for R<sub>h</sub>.

### **AUTHOR CONTRIBUTIONS**

FM designed and conducted the study, performed the data analysis, and wrote the manuscript. TH and YT were integrally involved in the study design, data interpretation, and writing the

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manuscript. LK was involved in the study design, data collection, field support, and data interpretation. TC helped with the mixed model analysis.

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### SUPPLEMENTARY MATERIAL

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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