

# Total and heterotrophic soil respiration in a swamp forest and oil palm plantations on peat in Central Kalimantan, Indonesia

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Received: 24 May 2017 / Accepted: 18 July 2017 / Published online: 7 September 2017  
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**Abstract** Heterotrophic respiration is a major component of the soil C balance however we critically lack understanding of its variation upon conversion of peat swamp forests in tropical areas. Our research focused on a primary peat swamp forest and two oil palm plantations aged 1 (OP2012) and 6 years (OP2007). Total and heterotrophic soil respiration were monitored over 13 months in paired control and trenched plots. Spatial variability was taken into account by differentiating hummocks from hollows in the forest; close to palm from far from palm positions in the plantations. Annual total soil respiration was the

highest in the oldest plantation ( $13.8 \pm 0.3$  Mg C ha<sup>-1</sup> year<sup>-1</sup>) followed by the forest and youngest plantation ( $12.9 \pm 0.3$  and  $11.7 \pm 0.4$  Mg C ha<sup>-1</sup> year<sup>-1</sup>, respectively). In contrast, the contribution of heterotrophic to total respiration and annual heterotrophic respiration were lower in the forest ( $55.1 \pm 2.8\%$ ;  $7.1 \pm 0.4$  Mg C ha<sup>-1</sup> year<sup>-1</sup>) than in the plantations ( $82.5 \pm 5.8$  and  $61.0 \pm 2.3\%$ ;  $9.6 \pm 0.8$  and  $8.4 \pm 0.3$  Mg C ha<sup>-1</sup> year<sup>-1</sup> in the OP2012 and OP2007, respectively). The use of total soil respiration rates measured far from palms as an indicator of heterotrophic respiration, as proposed in the literature, overestimates peat and litter mineralization by around 21%. Preliminary budget estimates suggest that over the monitoring period, the peat was a net C source in all land uses; C loss in the plantations was more than twice the loss observed in the forest.

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Responsible Editor: Melany Fisk.

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**Keywords** CO<sub>2</sub> emissions · Greenhouse gas · Land-use change · Soil respiration partitioning · Trenching · Tropics

## Introduction

Indonesia is one of the main holders of peatlands in the tropics with an estimated area of 225,000 km<sup>2</sup> (Gumbrecht et al. 2017), of which about 14–18% is located in Central Kalimantan (Warren et al. 2017). Apart from being the habitat of rare species and providing

hydrological regulation services, Indonesian peat swamp forests play a prominent role as a global carbon (C) pool and sink. In their pristine status, they are estimated to store on average 220 Mg C ha<sup>-1</sup> in the phytomass (Hergoualc'h and Verchot 2011) and as much as 670 Mg C ha<sup>-1</sup> m<sup>-1</sup> depth of peat (Warren et al. 2012). Peat C stores have accumulated over millennia as the result of a simultaneous high primary productivity, and low decomposition rates in waterlogged conditions. While in some regions of Indonesia peat swamp forests are still accumulating peat, in others such as in Central Kalimantan, peat growth may have ceased following intensification of El Niño activity during the late Holocene (Dommain et al. 2011) although knowledge on current accumulation or loss rates is lacking.

Indonesian peat swamp forests have experienced continued deforestation and conversion over the past decades (Miettinen et al. 2016). The proportion of pristine and degraded peat swamp forest in Sumatra and Kalimantan fell from 76% in 1990, to 40% in 2007 and 29% in 2015. Kalimantan though has retained a higher proportion of peat forest (42%) than Sumatra (18%). Unsustainable logging activities, uncontrolled fires and unsupervised agricultural development have sequentially led to dramatic declines of the extent of peat swamp forests in these regions. Between 2007 and 2015, most converted forests (73%) were turned into smallholder fields and industrial plantations. Forest to industrial plantations was the main conversion type in Kalimantan (64% versus 4% for conversion to smallholder fields) whereas in Sumatra conversion by smallholders was substantial (30% versus 44% for conversion to industrial plantations). In Kalimantan newly established industrial plantations were mostly oil palm plantations (90%) (Miettinen et al. 2016). There is no information on land cover type to which smallholders converted forests, but oil palm plantations are also likely to represent the most dominant land use.

Peat forest conversion to oil palm plantation implies drastic vegetation cover changes and drainage of the land, which turns the potential C sink into a major source (Hergoualc'h and Verchot 2014). The conversion is estimated to release as much as 2216 Mg CO<sub>2</sub> eq ha<sup>-1</sup> over 25 years (Drösler et al. 2014; Hergoualc'h et al. 2017; Hergoualc'h and Verchot 2011); 50% of which are from peat decomposition; 26% from biomass changes and the rest corresponding

to one fire. Fires used for land-clearing can spread out of control and release massive emissions of greenhouse gases to the atmosphere; which is the cause of major international concern (Gaveau et al. 2014). Quantification of peat C losses from forest conversion requires knowledge of the main elements contributing to increase or decrease the pool size. Carbon enters the peat in the form of above and belowground litter, it leaves through peat and litter mineralization (or heterotrophic soil respiration—SRh), fires, methane emissions, and dissolved and particulate organic C (Hergoualc'h and Verchot 2014). SRh is a major source of C loss and a key component of the soil C balance in tropical peatlands (Hergoualc'h and Verchot 2014) however current assessments in forests and oil palm plantations on peat are based on a very limited number of studies (Dariah et al. 2014; Ishida et al. 2001; Melling et al. 2007). In addition, several studies evaluating peat C loss such as the study by Hooijer et al. (2010) have not dissociated total from heterotrophic soil respiration or total soil respiration from net CO<sub>2</sub> emissions. Soil respiration is made up of autotrophic respiration (by roots) and heterotrophic respiration (by microbes and soil fauna) however only the second component of the respiration contributes to peat C loss to the atmosphere (Bond-Lamberty and Thompson 2010; Hergoualc'h and Verchot 2011; Ryan and Law 2005). Although root respiration integrates heterotrophic activity in the rhizosphere, we don't consider this distinction in the current study.

Partitioning total soil respiration (SRt) into its autotrophic and heterotrophic components is difficult. For this, various methods have been developed and used under both laboratory and field conditions. These encompass root trenching, root biomass regression, tree girdling, measuring respiration of excised or living roots and incubation of root-free soil. Isotopic methods include continuous or pulse labeling of shoots in <sup>14</sup>CO<sub>2</sub>, air CO<sub>2</sub> enrichment, radiocarbon dating of soil CO<sub>2</sub>, bomb-<sup>14</sup>CO<sub>2</sub>, and <sup>18</sup>O of CO<sub>2</sub> (Kuzyakov 2006). All methods present biases and uncertainties. Isotopic methods allow non-destructive partitioning but are expensive and not always applicable (Ryan and Law 2005). Among the non-isotopic methods available, regression between root biomass and SRt in oil palm plantations on peat has proved to be weak (Dariah et al. 2014). Tree girdling often induces tree death (Kuzyakov 2006) and is thus problematic to implement in commercial oil palm plantations.

Extrapolating respiration rates of excised or living roots to field scales is complicated and usually considered as inexact (Kuzyakov 2006). The advantage of incubating soil mesocosms over trenching is the near absence of dead roots that can potentially contribute to increase SRh rates in trenching experiments (Hanson et al. 2000). Its disadvantage is the high disturbance of soil physical structure when removing roots and re-packing. Here we opted for the root trenching method to partition soil respiration in situ and characterize temporal variations of SRt and SRh.

We studied a primary peat swamp forest and two oil palm plantations on peat with different ages (1 year old—OP2012 and 6 year old—OP2007) in Central Kalimantan, Indonesia. We combined the trenching method with the dynamic closed chamber technique to measure total and heterotrophic soil respiration over 13 months (from June 2013 to June 2014). To account for variation along microtopographic and microclimatic gradients, we employed a spatially-stratified experimental design distinguishing hollows from hummocks in the forest, and close to palm from far from palm positions in the plantations. The distinction in the plantations also accounts for soil management differences between these areas as typically only areas near palms receive fertilizer applications. Concomitantly with soil respiration measurements, we monitored the key environmental variables known to influence flux variations. Our main objective was to quantify how soil C losses through SRh differed between a swamp forest and oil palm plantations on peat. The second objective was to evaluate the contribution of SRh to SRt for further use in studies monitoring SRt exclusively. Our third objective was to examine the control that environmental factors, including climatic and edaphic variables, can exert on SRt and SRh rates over time and across land uses.

## Materials and methods

### Study sites

The research was conducted in and around the national park of Tanjung Puting in the province of Central Kalimantan, Indonesia. The park is about 400,000 ha and is famous for its conservation and rehabilitation center for orangutans (*Pongo pygmaeus*, a peat swamp

forest endemic species), gibbons (*Hylobates* spp), red Langur (*Presbytis rubicunda*) and proboscis monkey (*Nasalis larvatus*). Long-term average annual temperature and rainfall in the area during 2004–2014 are 27 °C and 2058 mm, with no clear seasonal pattern (Swails et al. 2017).

The study included a forest site (2°49′21″S, 111°50′24″E) situated inside the national park and two oil palm plantations (OP2012, 2°47′39″S, 111°48′64″E; OP2007, 2°47′28″S, 111°48′7″E) located about six km away from the forest site across the Sekonyer river (Fig. 1). The forest site, locally known as Pesalat, was undrained and maintained in pristine conditions. It was dominated by Dipterocarpaceae (*Shorea ovalis*, *Vatica oblongifolia*), Tetrameristaceae (*Tetramerista glabra*) and Anacardiaceae (*Gluta rengas*). The forest floor was uneven with the presence of 20–30 cm tall hummocks around tree trunks and hollows in between hummocks. The hummocks which are formed of roots, accumulated decomposing litter and peat, remain above the water surface throughout the year whereas the water table level in hollows is much closer to the soil surface.

The two oil palm plantations of one (OP2012) and 6 (OP2007) year old were smallholder plantations (1–1.5 ha) located near the village of Bedaun. Lowering of the water table to improve palm productivity was implemented by excavating 57 and 100 cm deep drainage canals around the OP2012 and OP2007 plantations, respectively. Inorganic fertilizers were spread by hand to the plantations every three months, for an annual total of about 120–150 kg N, 70–85 kg P and 100–120 kg K ha<sup>-1</sup> (Swails et al. 2017). Weeds and pests were controlled by regularly applying herbicides within a 1–2 m radius from the palms. Both plantations were converted from primary forest which was cleared in 1989 by slashing and burning after extraction of the valuable timber. After the deforestation, shifting cultivation was practiced in the area for about 20 years with several cycles alternating 2 years of cropping (either rice or horticulture crops) and longer fallow periods. Thus, the sites underwent several land clearing fires, five at least. The OP2012 site was planted with palms in 2012 at a density of 153 palms ha<sup>-1</sup> (about 8.7 m between palms in a triangular design). Palms were planted at the OP2007 site in 2007 at a density of 196 palms ha<sup>-1</sup> (about 7.7 m between palms in a triangular design).



**Fig. 1** Location of the research area in Central Kalimantan, Indonesia. The sites include a primary peat swamp forest inside Tanjung Puting national park (yellow star), a 1 (OP2012) and a 6 (OP2007) year old oil palm plantation on peat (red stars). (Color figure online)

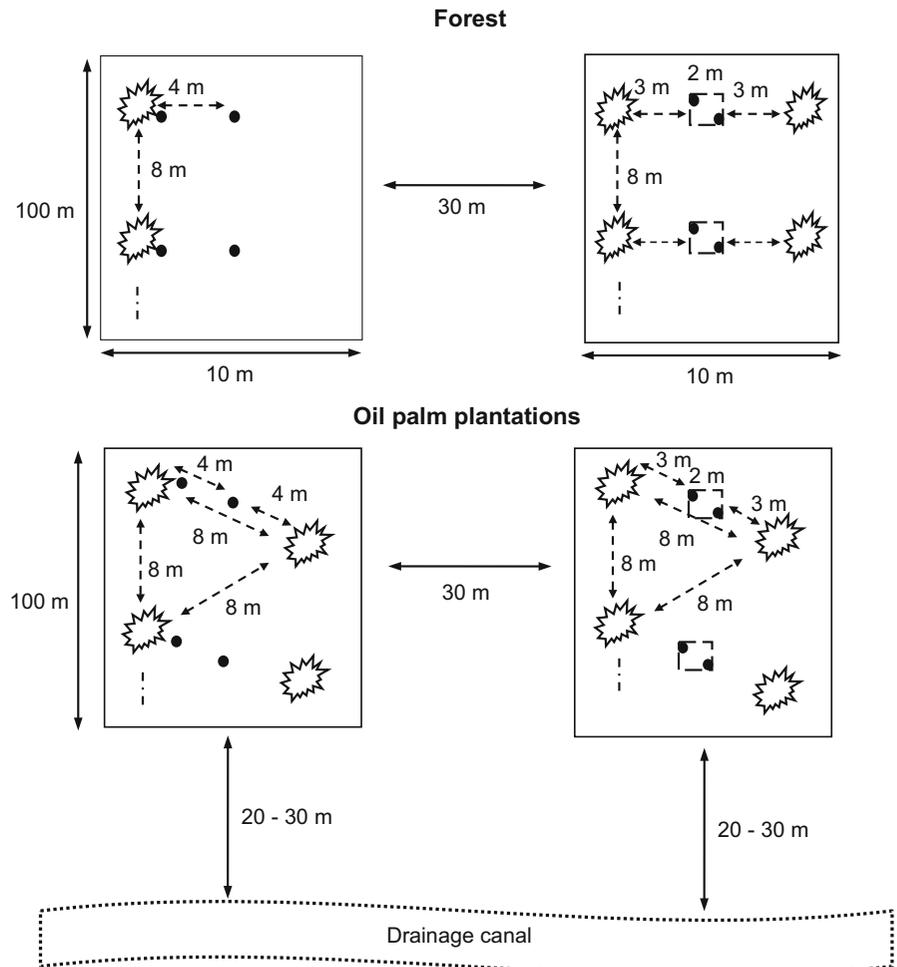
### Experimental design

At each of the three study sites a  $100 \times 50$  m area was delineated in which two  $100 \times 10$  m plots about 30 m apart were established; one to serve as a control and the second for trenching (Fig. 2). Control and trenched plots were used to measure total soil respiration (SRt) and heterotrophic respiration (SRh), respectively. The  $2 \times 2$  m<sup>2</sup> trenches were made using a chainsaw in June 2012; one year prior to the beginning of the measurements. They were one meter deep (depth at which no coarse roots were observed) and 0.2 m wide. We lined the inner side of the trenches with construction plastic and subsequently backfilled them. To ensure that new vegetation did not develop in the trenched plots, clipping at the surface was conducted monthly, a few days prior to CO<sub>2</sub> efflux measurement.

Considering the possibility of reinvasion of roots into root-free zones (Sayer and Tanner 2010) we recut the trenches in December 2013 (one and half year after initial trenching) at the forest and OP2012 sites. Re-trenching was not conducted at the OP2007 due to refusal by the owner who was concerned about potential damage to the plantation. Re-trenching was performed similarly to initial trenching and new construction plastic lining the trenches were installed.

Each control plot was divided into twelve subplots comprising each two spatial positions. In the forest these positions coincided with a hummock surrounding a tree (CT) and a hollow in between trees (FT). In the oil palm plantations, the spatial positions were stratified according to the distance to a palm, one being close to a palm (CT) and the other one far from a palm (FT). The CT position, about 0.3 m from the palm, is

**Fig. 2** Experimental design implemented for assessing total and heterotrophic soil respiration in the forest (*top*) and oil palm plantations (*bottom*). The collars (*black circle*) where total soil respiration was monitored were placed close to tree/palm and far from tree/palm in control plots (*left*). Those where heterotrophic soil respiration was measured were located in trenched plots (*right, squares with dashed lines*) and far from tree/palm to avoid root presence



where fertilizer is usually applied and the FT position was set at mid-distance between two palms (i.e. at about 4 m from the palm trunk). Each trenching plot was also divided into twelve trenched subplots comprising each two sampling positions. The trenched subplots were located about 3 m away from trees/palms to avoid root presence and the two sampling positions inside them were chosen at random. The trenched plots did not receive fertilizers. At all sites, the distance between subplots both in control and trenched plots was around 8 m; which is the average palm spacing in the plantations.

To minimize soil disturbance boardwalks were placed to access each measurement point. All equipment was installed at least a month before the measurements started.

#### Soil CO<sub>2</sub> respiration measurement

Soil respiration was monitored monthly from June 2013 to June 2014 (over 13 months) using a portable infra-red analyzer (EGM-4 Environmental Gas Monitor) connected to a soil respiration chamber (SRC-1) (PP System, Amesbury, USA). The chamber was placed on top of a PVC collar (inner diameter of 10 cm, height of 5 cm) that was permanently inserted into the ground to a 5 cm depth at each sampling point. Concentrations of CO<sub>2</sub> were recorded automatically at 4.5 s intervals for 1.5–2 min until reaching a constant flux rate. Since the EGM-4 connected to a SRC-1 can overestimate the flux (Pumpanen et al. 2004), the measurement was repeated three times whenever a flux rate >65 kg C

$\text{ha}^{-1} \text{ day}^{-1}$  was read. The latest of the 3 records, usually the one with the lowest flux rate, was the value considered. The  $\text{CO}_2$  flux was calculated by the EGM from the linear increase of  $\text{CO}_2$  concentration in the headspace with time. The EGM-computed fluxes were in agreement with the fluxes regularly recomputed manually from  $\text{CO}_2$  concentration readings. Before each measurement the collars were manually fanned in order to remove any accumulated  $\text{CO}_2$ . Sampling was performed between 7:00 and 13:00 over a 2.5–4 h duration per site. Complementary experiments indicated no significant diurnal variation in soil respiration rate at the research sites. Soil respiration was also monitored more intensively following re-trenching at the forest and OP2012 sites. Measurements were conducted on days +1, +3/+5 (forest/OP2012), +7 and +14 after trenching.

Mean monthly soil respiration rates were calculated for each spatial position (in the control plots only) in each treatment (control and trenched) at each site. Annual total and heterotrophic soil respiration rates were computed by integration of monthly flux rates using a linear interpolation between measurement dates for a 365 day year (Aini et al. 2015). Plot-scale total soil respiration rate was calculated as the average of the rates from the two spatial positions (FT, CT) in the forest. Field observation indicated an equal share of hummocks and hollows at the forest site. In the plantations, the proportion allocated to each position was based on the radius of fertilizer application (defined by the farmer) that likely coincides with the active rooting zone of the palms. In the OP2012 and OP2007 the fertilizer was usually applied inside a 1 and 2 m radius circle around the palms, respectively. Using the palm density we calculated that in the OP2012 the close to and far from palm areas represented, respectively, 9 and 91% of the plot surface. In the OP2007 these two areas represented, respectively 35 and 65% of the plot surface. We conducted a sensitivity analysis testing how changes in our estimates of the proportion that the CT area occupies in the plot impact upon annual total soil respiration and the contribution of heterotrophic respiration to total respiration. The contribution of heterotrophic to total soil respiration was computed from cumulative values before re-trenching, after re-trenching and for the whole monitoring period.

## Environmental parameters and soil properties

Rainfall was monitored daily using a weather station (Delta Ohm HD2013R, Padova, Italy) installed in the OP2012. Soil temperature was measured at a 10 cm depth using a soil thermometer probe (Reotemp Digital TM99-A, USA) and air temperature was manually recorded using a digital thermometer placed in the shade at about 1 m from the ground. The water table depth was measured in PVC wells (2.5 cm in diameter, 2 m in length) inserted permanently into the peat. A measuring stick was lowered into the well until its end touched the water surface. The water table depth was computed by subtracting the depth of the measuring point above ground surface from the depth recorded between the water surface to the measuring point on top of the well. Each of these parameters was measured at each respiration collar and concomitantly with  $\text{CO}_2$  fluxes. The soil gravimetric water content, bulk density and water-filled pore space (WFPS) were also determined monthly by collecting six soil samples using a metallic ring (8.15 cm in diameter  $\times$  6 cm in height). Three replicates were collected at each spatial position (CT, FT) from outside of the soil respiration subplots to minimize disturbance. Soil moisture was therefore not monitored inside trenched subplots. Soil moisture was calculated from the fresh mass measured in the field and the dry mass after oven-drying at 60° for 2–3 days. Bulk density was calculated from the dry mass of soil and the ring volume. The WFPS was computed using the formula by Linn and Doran (1984) using a default particle density of  $1.4 \text{ g cm}^{-3}$ , representative for Indonesian ombrogenous peats (Driesen and Rochimah 1976).

Litterfall was collected monthly in the forest using twelve permanent litter baskets (area =  $0.28 \text{ m}^2$ ) randomly positioned on trees. The litter was subsequently oven-dried at 60 °C for two days and weighted. Annual litterfall rate was calculated by summing monthly litterfall over the thirteen month monitoring period and annualizing to twelve months. Annual litterfall was converted to a carbon rate using a C fraction of 48% (Aalde et al. 2006). At the end of the experiment the density of roots was measured in the control plots from six replicates per spatial position (CT and FT) by using the above described ring inserted to a 6 cm depth. Root samples were washed, sorted into dead and live roots and oven-dried at 60°

for 2–3 days to determine the dry mass. Their density was calculated from their dry mass and the corer area. Finally at each site, we collected three composite soil samples (CT and FT confounded) at 0–6 cm depth for soil chemical analysis at the forestry faculty of Bogor agricultural institute (IPB). The pH was determined in water and 1 M KCl (1:1 ratio) (Thomas 1996). Exchangeable cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^{+}$  and  $\text{K}^{+}$ ), Cation Exchange Capacity (CEC) and base saturation were determined by displacement from the soil colloids with ammonium acetate adjusted to pH 7 (Pansu et al. 2001). Concentrations of C and N of dried peat samples were analyzed using an induction furnace C/N analyzer (LECO Corporation, St. Joseph MI, USA) from 9 to 17 replicates per site taken from the top 15 cm of the soil profile.

### Statistical analysis

Statistical analysis was performed using the software Infostat (Di Rienzo et al. 2014). A probability threshold of 0.05 was used to determine the significance of the effects. All of the measured variables were tested for normality of distribution of residuals using the Shapiro–Wilks test. Averages of environmental parameters and soil respiration rates were compared across trenched plots, CT and FT positions in control plots within a site. They were also compared across sites within trenched plots, CT and FT positions in control plots. The difference in average of the variables between dry and wet months was tested considering a month as dry when its cumulative rainfall rate was <100 mm. For multiple comparisons, ANOVA and the non-parametric Kruskal–Wallis test were applied for normally and non-normally distributed data, respectively. For single comparisons, the *t* test or non-parametric Mann–Whitney test were applied for normal and non-normally distributed data, respectively. Annual cumulative soil respiration  $\pm$  standard error which did not overlap were considered significantly different between trenched plots, CT and FT positions in control plots within a site; or between sites within trenched plots, CT and FT positions in control plots. The same assumption was made for the contribution of SR<sub>h</sub> to SR<sub>t</sub> within a site before re-trenching, after re-trenching and for the whole monitoring period.

Relationships between soil respiration and environmental variables or between environmental

variables themselves were analyzed using simple and multiple linear or non-linear regression models. Only significant relationships with an  $R^2 > 0.35$  are presented.

## Results

### Soil properties

The peat depth differed between sites following the order: forest > OP2007 > OP2012 (Table 1). As typically reported for ombrotrophic peats, the soil exhibited low pH and high CEC values. The sites did not display a significant difference in soil C content; however, the plantations had a lower N content ( $P = 0.0001$ ) and higher C/N ratio ( $P = 0.0006$ ) than the forest. The bulk densities were low as the result of a high pore space volume. These were significantly ( $P < 0.0001$ ) increased by the conversion to plantation, at both spatial positions (CT and FT), as the result of drainage and compaction during land preparation. Root density was higher in the OP2012 than in the OP2007 at the CT position ( $P = 0.0043$ ). At the FT position it was higher in the OP2012 and forest than in the OP2007 ( $P = 0.0136$ ). The root density was higher CT than FT at the OP2012 site only ( $P = 0.026$ ).

### Environmental parameters

Air temperature was the highest at the OP2012 plantation, whereas the OP2007 and forest exhibited similar temperatures ( $P < 0.0001$ ) (Table 1). The two CT and FT spatial positions had a same temperature at all sites while the trenched plots (T) in the forest and OP2012 were significantly warmer than the control plots ( $P < 0.0001$ ). The air temperature remained relatively stable throughout the year in the forest and OP2007, with average values between 28–32 °C and 26–34 °C, respectively (Fig. 3a). Abrupt increases in temperature with values >40 °C were recorded at the OP2012 in September, October and December 2013. Mean peat temperature was the highest in the OP2012, followed by the OP2007 and the forest ( $P < 0.0001$ ). In the OP2012 the temperature was significantly warmer at the FT position than at the CT one ( $P < 0.0001$ ). The peat temperature in the trenched plots of the forest and OP2012 displayed higher values

**Table 1** Top 6–15 cm edaphic physical, chemical and climatic properties in the forest, 1 (OP2012) and 6 (OP2007) year old oil palm plantations in Central Kalimantan, Indonesia

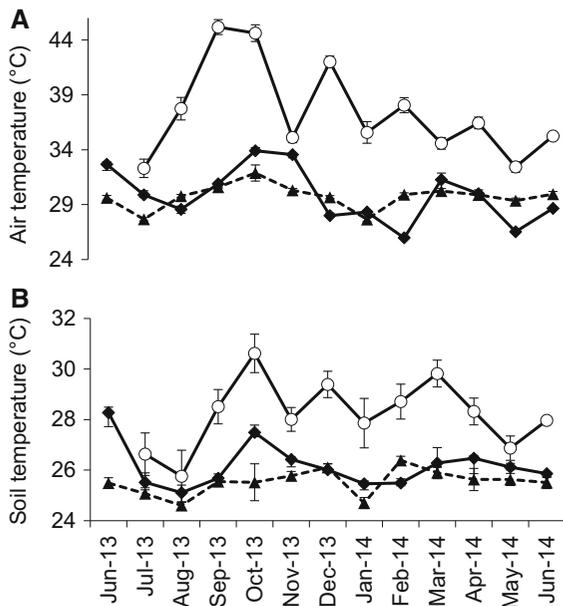
Parameter	Forest	OP2012	OP2007
Peat depth (cm)	155.3 ± 5.9 (18) <sup>c</sup>	29.6 ± 3.6 (9) <sup>a</sup>	46.0 ± 3.6 (9) <sup>b</sup>
pHH <sub>2</sub> O	3.9 ± 0.0 (3)	3.7 ± 0.1 (3)	3.8 ± 0.0 (3)
pH <sub>KCL</sub>	2.9 ± 0.1 (3)	2.9 ± 0.0 (3)	2.9 ± 0.1 (3)
Base saturation (%)	7.9 ± 0.1 (3)	7.2 ± 1.7 (3)	6.3 ± 0.1 (3)
CEC (cmolc kg <sup>-1</sup> )	98.3 ± 0.4 (3)	80.7 ± 12.1 (3)	96.0 ± 0.9 (3)
Total C (%)	48.5 ± 1.2 (17)	45.1 ± 1.9 (12)	47.4 ± 5.3 (9)
Total N (%)	1.6 ± 0.1 (17) <sup>b</sup>	1.2 ± 0.1 (12) <sup>a</sup>	0.9 ± 0.1 (9) <sup>a</sup>
C/N	31.5 ± 2.3 (17) <sup>a</sup>	39.9 ± 2.6 (12) <sup>b</sup>	57.1 ± 9.6 (9) <sup>b</sup>
Bulk density (g dm cm <sup>-3</sup> )			
CT	0.15 ± 0.01 (39) <sup>a</sup>	0.32 ± 0.03 (36) <sup>b</sup>	0.27 ± 0.01 (39) <sup>b</sup>
FT	0.18 ± 0.02 (39) <sup>a</sup>	0.34 ± 0.02 (36) <sup>b</sup>	0.34 ± 0.02 (39) <sup>b</sup>
Roots (Mg dm ha <sup>-1</sup> )			
CT	3.6 ± 0.5 (6) <sup>ab</sup>	4.9 ± 0.3 (6) <sup>b</sup> <sup>β</sup>	2.2 ± 0.5 (6) <sup>a</sup>
FT	3.5 ± 0.7 (4) <sup>b</sup>	3.7 ± 0.2 (6) <sup>b</sup> <sup>α</sup>	1.8 ± 0.4 (6) <sup>a</sup>
Air temperature (°C)			
CT	29.4 ± 0.2 (131) <sup>a</sup> <sup>α</sup>	35.6 ± 0.4 (142) <sup>b</sup> <sup>α</sup>	29.8 ± 0.3 (149) <sup>a</sup>
FT	29.4 ± 0.1 (130) <sup>a</sup> <sup>α</sup>	35.3 ± 0.4 (144) <sup>b</sup> <sup>α</sup>	29.5 ± 0.3 (148) <sup>a</sup>
T	30.0 ± 0.2 (285) <sup>a</sup> <sup>β</sup>	39.6 ± 0.4 (272) <sup>b</sup> <sup>β</sup>	29.9 ± 0.2 (228) <sup>a</sup>
Peat temperature (°C)			
CT	25.3 ± 0.2 (131) <sup>a</sup> <sup>α</sup>	26.9 ± 0.1 (142) <sup>c</sup> <sup>α</sup>	6.2 ± 0.1 (149) <sup>b</sup>
FT	25.5 ± 0.1 (132) <sup>a</sup> <sup>α</sup>	27.4 ± 0.1 (144) <sup>c</sup> <sup>β</sup>	26.1 ± 0.1 (148) <sup>b</sup>
T	25.7 ± 0.0 (267) <sup>a</sup> <sup>β</sup>	29.3 ± 0.1 (283) <sup>c</sup> <sup>γ</sup>	26 ± 0.1 (239) <sup>b</sup>
Water table level (cm)			
CT	-25.3 ± 1.5 (136) <sup>b</sup> <sup>γ</sup>	-27.2 ± 1.7 (156) <sup>b</sup>	-37.9 ± 2.6 (151) <sup>a</sup> <sup>α</sup>
FT	-13.8 ± 1.4 (105) <sup>c</sup> <sup>β</sup>	-24.2 ± 1.9 (120) <sup>b</sup>	-34.0 ± 2.6 (135) <sup>a</sup> <sup>α</sup>
T	-4.7 ± 0.9 (249) <sup>c</sup> <sup>α</sup>	-25.8 ± 1.5 (262) <sup>b</sup>	-44.7 ± 1.8 (153) <sup>a</sup> <sup>β</sup>
Water filled pore space (%)			
CT	40.0 ± 2.8 (39) <sup>α</sup>	46.9 ± 3.1 (36)	44.8 ± 2.4 (39) <sup>α</sup>
FT	60.7 ± 3.1 (39) <sup>b</sup> <sup>β</sup>	50.5 ± 2.9 (36) <sup>a</sup>	60.1 ± 4.0 (39) <sup>b</sup> <sup>β</sup>

CT designates the close to tree position and FT the far from tree position in the control plots; T designates the trenched plots. Data are presented as mean ± SE (n). Letters a, b, c indicate a significant difference between sites within trenched plots, CT and FT positions in control plots;  $\alpha$ ,  $\beta$ ,  $\gamma$  a significant difference between trenched plots, CT and FT in control plots within a site. No letters are displayed in the absence of a significant difference  
CEC: cation exchange capacity

than their respective control plots ( $P = 0.0079$  and  $P < 0.0001$ ); following the same trend as air temperature. The peat temperature was stable in the forest over the monitoring period whilst more fluctuation was observed in the plantations (Fig. 3b). A high average peat temperature was recorded at both plantations in October.

The rainfall during the monitoring period of 2658 mm year<sup>-1</sup> was above long-term records. Dry months (rainfall <100 mm month<sup>-1</sup>) occurred in June, September and October 2013 (Fig. 4). The water table was significantly deeper in the OP2007 than in the forest in control and trenched plots ( $P < 0.001$ ) while the OP2012 displayed intermediary values except at the CP position where the level was similar

to that in the forest. The observed difference in water table level between the two plantations reflects their difference in drainage canal depth (57 and 100 cm in the OP2012 and OP 2007, respectively). The water table was significantly influenced by the spatial position in the forest only, with a lower level in hollows (FT) than in hummocks (CT) ( $P < 0.0001$ ). In the OP2007 the water table was deeper in the trenched than in the control plots whereas the opposite was true in the forest ( $P < 0.0001$ ). Over the experimental period the average water table level fluctuated between -39 and 8 cm in the forest, -68 and 1 cm in the OP2012 and -99 and 0 cm in the OP2007 (Fig. 4, left). The water table level was on average lower during dry months than during wetter months



**Fig. 3** Monthly air (A) and soil temperature (B) (mean  $\pm$  SE,  $n = 48$ ) in the forest (dashed line, solid triangle), OP2012 (solid line, open circle) and OP2007 (solid line, solid diamond) plantations on peat in Central Kalimantan, Indonesia

( $P < 0.003$ ) at all sites, in trenched and control plots. At the plantations it decreased linearly with decreasing rainfall ( $R^2 = 0.56$  and  $0.46$  in the OP2012 and OP2007, respectively;  $P < 0.0001$ ). The WFPS was similar across sites at the CT position but at the FT position it was significantly lower in the OP2012 than at the two other sites indicating drier conditions ( $P = 0.039$ ). In the forest and OP2007 the WFPS was significantly higher FT than CT ( $P < 0.001$  and  $P = 0.001$ , respectively). Throughout the year the WFPS oscillated in a similar fashion at the CT and FT positions in the OP2012 (Fig. 4b, right). On the contrary in the forest and OP2007 the WFPS remained relatively stable close to tree but fluctuated substantially far from tree (Fig. 4a, c). The WFPS was on average lower in dry than in wet months, at both spatial positions in the plantations ( $P < 0.03$ ). Monthly WFPS and rainfall were significantly but very poorly related ( $R^2 = 0.02$ ).

Annual litterfall production in the forest amounted to  $8.7 \pm 0.4$  Mg dm ha<sup>-1</sup> year<sup>-1</sup> or  $4.2 \pm 0.2$  Mg C ha<sup>-1</sup> year<sup>-1</sup>. Litterfall shifted from low rates in November–December 2013 to high rates in January–

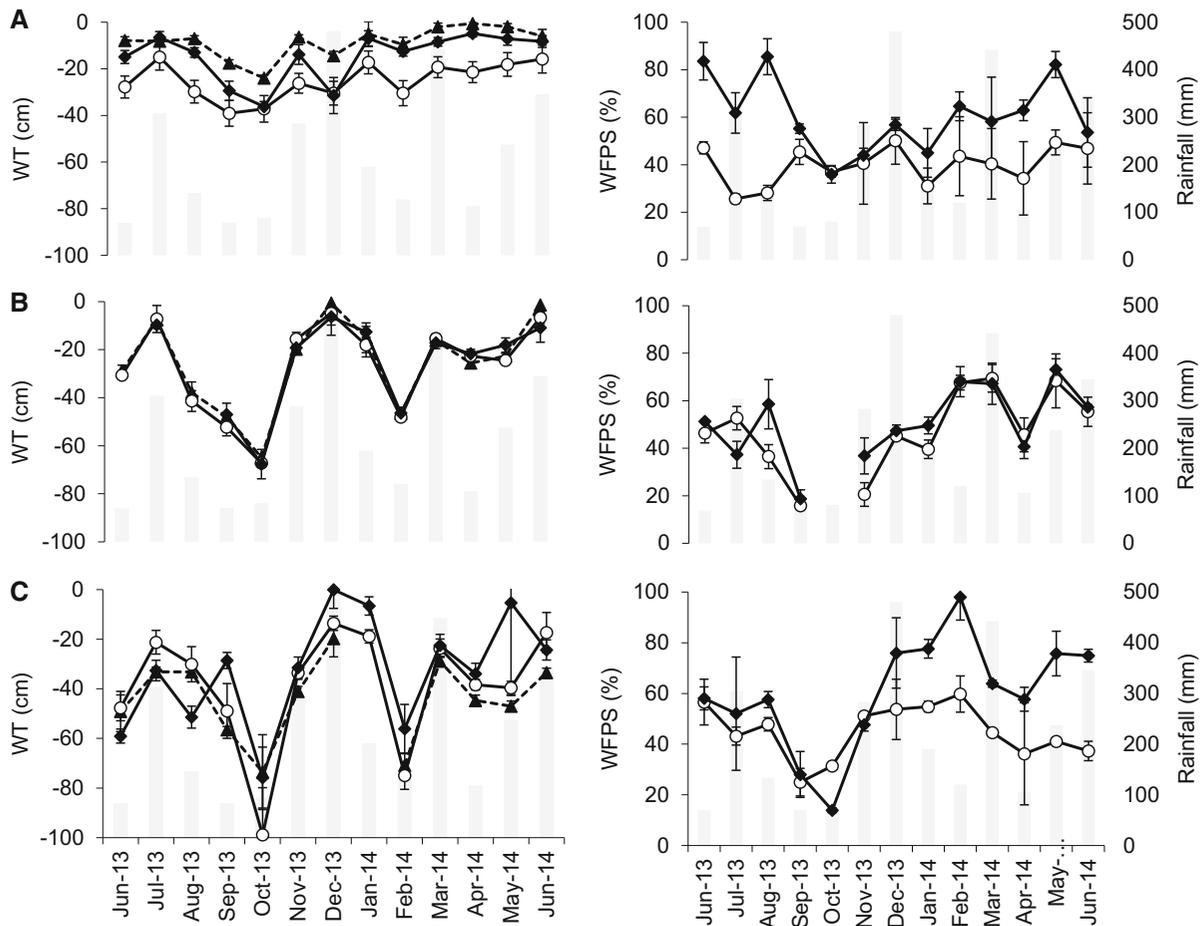
February 2014 (Fig. 5). The litterfall rate was on average lower in months following a dry month than in months following a wet month ( $P = 0.018$ ).

### Soil respiration

The average total soil respiration rate (SRt) was significantly higher in the OP2007 than at the two other sites at the CT position ( $P < 0.0001$ ) but higher in the forest than in the plantations at the FT position ( $P = 0.0042$ ) (Table 2). In both plantations SRt was higher at the CT than at the FT position ( $P \leq 0.0024$ ). The soil heterotrophic respiration rate (SRh) was significantly higher in the OP2012 than at the other sites ( $P = 0.0001$ ). It was lower than SRt at both spatial positions in the forest and OP2007 ( $P < 0.0001$ ); in the OP2012 it was lower than SRt at the CT position only ( $P = 0.0153$ ).

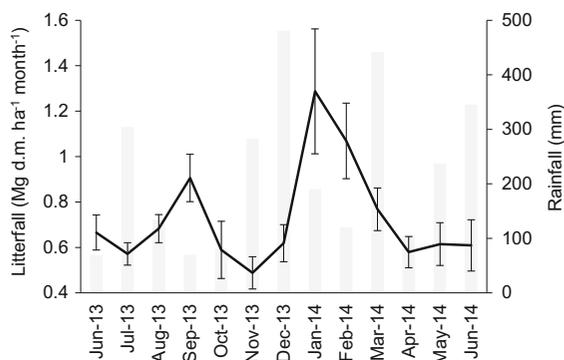
High emission rates in SRt at the FT position were observed in the forest and OP2012 in September and October (Fig. 6A, B) whereas such a pattern was not apparent in the OP2007. In the latest SRt at the CT position was uneven with high rates recorded in August, January, February and April. Heterotrophic respiration remained relatively stable throughout the monitoring period but increased in the two months following re-trenching in the forest and OP2012, suggesting a potential exacerbation of SRh induced by the disturbance. SRh was significantly lower before re-trenching in December than during the two months following re-trenching ( $P = 0.0046$  and  $0.0055$  in the forest and OP2012, respectively). The contribution of SRh to SRt increased following re-trenching at both sites (Fig. 7). This increase is very apparent in the days following the trenching event until a month afterwards. The contribution of SRh to SRt went back to pre-re-trenching levels after April in the OP2012 whereas in the forest it remained higher than pre-re-trenching levels until the end of the experiment.

Annual cumulative SRt rate at the plot scale was the highest in the OP2007 followed by the forest and OP2012 (Table 2) while annual cumulative SRh rate followed the order OP2012 > forest > OP2007. From these results the contribution of SRh to SRt was the lowest in the OP2007 and forest; the highest in the OP2012. Nevertheless, given the apparent increase in SRh and in the contribution of SRh to SRt (%SRh) following re-trenching, we assume the %SRh before re-trenching to be more accurately representative of



**Fig. 4** Monthly water table level (WT) (*left*) and water-filled pore space (WFPS, *right*) in the forest (**A**), OP2012 (**B**) and OP2007 (**C**) plantations; close to tree (CT, *solid line, open circle*), far from tree (FT, *solid line, solid diamond*) and in the trampled plots (*dashed line, solid triangle*). WT and WFPS

values are mean  $\pm$  SE. For the WT,  $n = 12$  at the CT and FT positions,  $n = 24$  in the trampled plots. For the WFPS,  $n = 3$  at the CT and FT positions. The WFPS was not measured in the trampled plots to avoid disturbance. Grey bars are monthly rainfall rates



**Fig. 5** Monthly litterfall rate (*solid line*) in the forest at Tanjung Puting, Central Kalimantan, Indonesia. Error bars are standard error of the mean ( $n = 12$ ). Grey bars are monthly rainfall rates

actual values in the forest and OP2012. These contributions applied to annual SR<sub>t</sub> rate indicate that annual SR<sub>h,adjusted</sub> rate was the highest at the OP2012 youngest plantation ( $9.6 \pm 0.8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ), followed by the OP2007 plantation ( $8.4 \pm 0.3 \text{ Mg C ha}^{-1}$ ), and the forest ( $7.1 \pm 0.4 \text{ Mg C ha}^{-1}$ ).

In the OP2012 neither plot-scale annual SR<sub>t</sub> nor the %SR<sub>h</sub> were significantly affected by varying the proportion that the CT area occupies in the plot (Fig. 8A). Contrastingly, given the large difference in soil respiration rate between the CT and FT positions in the OP2007, the share of the CT area had a substantial impact on both annual SR<sub>t</sub> rate and the %SR<sub>h</sub> (Fig. 8B). Varying the CT proportion from 5 to 50% implied a 43% increase and a 30% decrease

**Table 2** Annual average, cumulative soil respiration rates and contributions of heterotrophic to total soil respiration (%SRh) in the forest, 1 (OP2012), and 6 (OP2007) year old oil palm plantations. Total respiration rates (SRt) are presented at the close to tree (CT), far from tree (FT) positions and at the plot scale\*. Heterotrophic respiration rates (SRh) are presented at the plot scale only since no trees were present in the subplots.

Land use	Soil respi. component	Spatial position	CO <sub>2</sub> (kg C ha <sup>-1</sup> day <sup>-1</sup> )	CO <sub>2</sub> (Mg C ha <sup>-1</sup> year <sup>-1</sup> )	%SRh	%SRh <sub>Before re-trenching</sub>	SRh <sub>adjusted</sub> (Mg C ha <sup>-1</sup> year <sup>-1</sup> )
Forest	SRt	CT	36.1 ± 2.0 (182) <sup>a β</sup>	13.1 ± 0.5			
		FT	34.2 ± 1.6 (183) <sup>b β</sup>	12.6 ± 0.4			
		Plot	35.1 ± 1.3 (365)	<b>12.9 ± 0.3<sup>b</sup></b>			
OP2012	SRt	CT	33.7 ± 1.5 (210) <sup>a β</sup>	12.0 ± 0.4			
		FT	30.3 ± 1.7 (212) <sup>a α</sup>	11.6 ± 0.5			
		Plot	30.6 ± 1.6 (422)	<b>11.7 ± 0.4<sup>a</sup></b>			
OP2007	SRt	CT	54.5 ± 2.4 (155) <sup>b γ</sup>	20.5 ± 0.6			
		FT	28.1 ± 1.3 (153) <sup>a β</sup>	10.2 ± 0.3			
		Plot	37.3 ± 1.2 (138)	<b>13.8 ± 0.3<sup>c</sup></b>			
Forest	SRh	CT	25.5 ± 1.0 (405) <sup>a α</sup>	9.5 ± 0.3 <sup>b</sup>	73.9 ± 3.2 <sup>b</sup>	<b>55.1 ± 2.8</b>	<b>7.1 ± 0.4<sup>a</sup></b>
		FT	29.8 ± 1.1 (405) <sup>b α</sup>	11.7 ± 0.3 <sup>c</sup>	100.0 ± 4.7 <sup>c</sup>	<b>82.5 ± 5.7</b>	<b>9.6 ± 0.8<sup>c</sup></b>
		Plot	24.2 ± 1.0 (287) <sup>a α</sup>	<b>8.4 ± 0.3<sup>a (b***)</sup></b>	<b>61.0 ± 2.3<sup>a</sup></b>	— <sup>**</sup>	— <sup>**</sup>

\* In the forest  $SRt_{plot} = 50\% SRt_{CT} + 50\% SRt_{FT}$ ; in the OP2012  $SRt_{plot} = 9\% SRt_{CT} + 91\% SRt_{FT}$ ; in the OP2007  $SRt_{plot} = 35\% SRt_{CT} + 65\% SRt_{FT}$ . Letters a, b, c indicate a significant difference between sites within trenched plots, CT and FT in control plots;  $\alpha$ ,  $\beta$ ,  $\gamma$  a significant difference between SRh,  $SRt_{CT}$  and  $SRt_{FT}$  within a site

\*\* The OP2007 site was not re-trenched

\*\*\* Statistic comparing SRh in the OP2007 to SRh adjusted in the forest and OP2012. Bold values highlight annual plot-scale SRt rates, SRh rates and %SRh considering the most reliable estimates for the forest and OP2012

in SRt and %SRh, respectively; for a range in SRt and %SRh of  $[10.8 \pm 0.3; 15.4 \pm 0.4]$  Mg C ha<sup>-1</sup> year<sup>-1</sup> and  $[54.9 \pm 2.1; 78.4 \pm 3.4]\%$ , respectively.

### Relationships between soil respiration and environmental parameters

At the forest site, monthly SRt rate at both microtopographies presented a positive relationship with air temperature; a negative one with water table level (Table 3, Eq. 1–4). At the OP2012, monthly SRt rate at the FT position increased exponentially as the result of water table draw down (Eq. 5) whereas at the OP2007 the relationship was, as in the forest, linear (Eq. 6). The response of SRt to water table draw down was much less pronounced in the plantations than in the forest. At the OP2007, SRt at the FT position increased linearly with increasing peat temperature (Eq. 7), with a response less marked than that of  $SRt_{FT}$  to increasing air temperature in the forest (Eq. 1). The relationship between monthly SRt rate at the FT

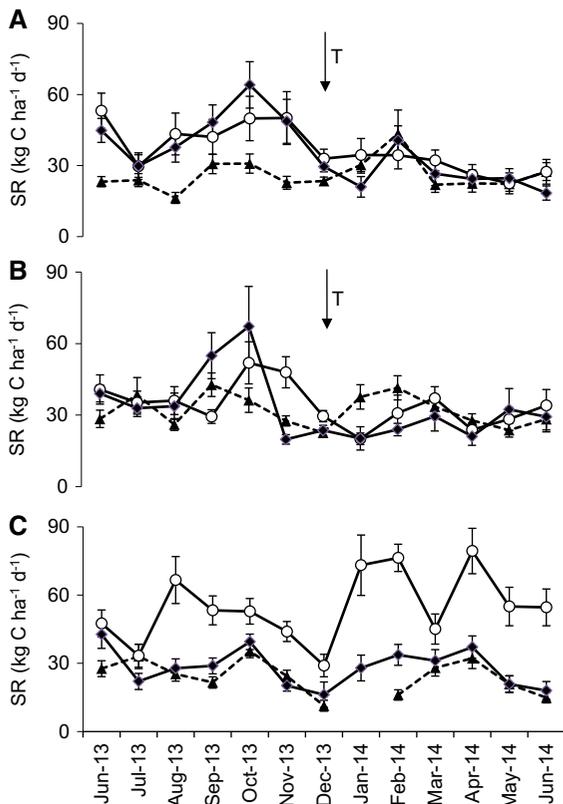
The %SRh was computed for the whole observation period and for the period before re-trenching in the forest and OP2012 ( $\%SRh_{Before\ re-trenching}$ ). Annual cumulative  $SRh_{adjusted}$  rates were calculated as  $\%SRh_{Before\ re-trenching}$  multiplied with the annual  $SRt_{plot}$  rate. Data are mean or cumulative values ± SE (n). N = 12 for annual values

position and rainfall in the OP2007 (Eq. 9) was more predictive than that with the water table level (Eq. 6). Monthly SRh rate did not exhibit significant relationships with environmental parameters except for the litterfall rate in the forest (Eq. 10–11). Notwithstanding, these relationships should be regarded with caution given that the high litterfall rates of January and February coincide with the two months following re-trenching when the contribution of SRh to SRt peaked (Fig. 7A).

### Discussion

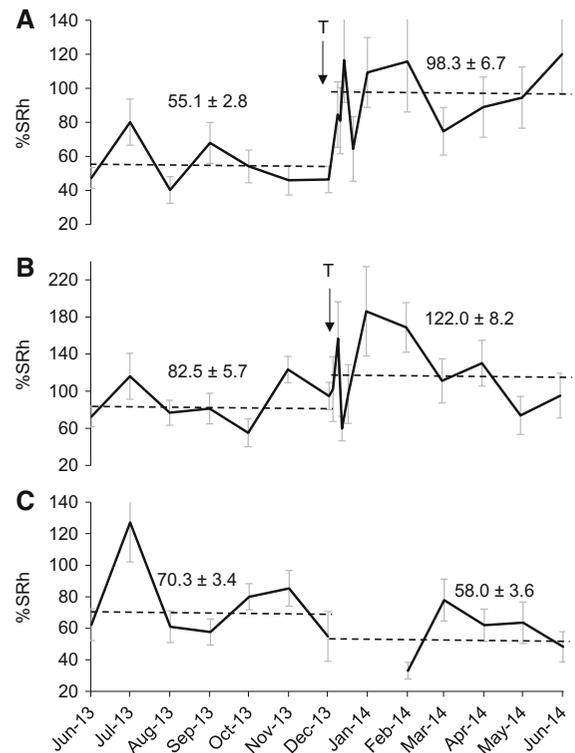
Efficiency of the trenching method in evaluating heterotrophic respiration and its contribution to total soil respiration

Most techniques used to separate SRh from SRt are associated with disturbance of the soil and inevitably introduce a bias (Subke et al. 2006). Concerns with the



**Fig. 6** Monthly soil CO<sub>2</sub> emissions in the forest (A), OP2012 (B) and OP2007 (C) plantations. The figure presents heterotrophic respiration (SRh, *dashed line, solid triangle*;  $n = 24$ ), total soil respiration close to tree (SRt-CT, *solid line, open circle*;  $n = 12$ ), and total soil respiration far from tree (SRt-FT, *solid line, solid diamond*;  $n = 12$ ). Values are mean  $\pm$  SE. The *arrows with a T* indicate the re-trenching event

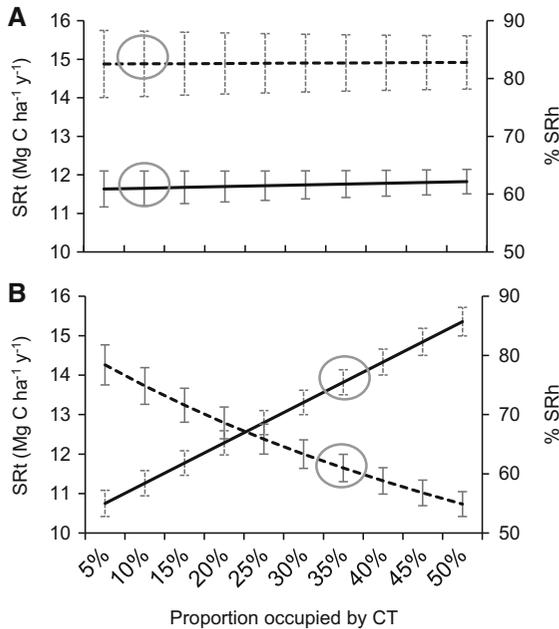
trenching method of root exclusion include disturbance effect due to trenching, influence of excised decomposing roots and differences in abiotic environment (soil moisture, temperature, presence/absence of canopy interception of precipitation, litterfall rate) between trenched and control plots (Jassal and Black 2006; Subke et al. 2006). Trenching commonly occasions an initial flush of CO<sub>2</sub> efflux and prolonged increased CO<sub>2</sub> flux rates resulting from the decomposition of the severed roots (Hanson et al. 2000). The timing and magnitude of SRh exacerbation are site-specific and dependent on ecosystem type, root decay rate, climate, etc. (Subke et al. 2006). Sayer and Tanner (2010) estimated that the decomposition of residual roots dominated SRh over 7 months after trenching in a tropical moist forest of Panama. Given that organic matter decay rates are lower in peat



**Fig. 7** Monthly contribution of heterotrophic respiration to total soil respiration (%SRh) in the forest (A), OP2012 (B) and OP2007 (C) plantations. The *arrow* indicates the re-trenching event. Daily contributions following re-trenching are displayed in (A, B). The *dashed lines* indicate %SRh calculated from cumulative values of SRh and SRt before ( $n = 7$ ) and after re-trenching ( $n = 9$ ). For comparison purposes, these are also displayed for the oldest plantation where re-trenching was not performed

swamp forests than in other types of tropical rainforests (Yule and Gomez 2009) we allowed 1 year to pass after trenching before starting collecting CO<sub>2</sub> efflux data and assume that residual root decomposition contributed little to belowground respiration at the beginning of the experiment. Following re-trenching at two of the sites, the contribution of SRh to SRt increased drastically and more pronouncedly in magnitude and timing at the waterlogged forest than at the drained OP2012 plantation (Fig. 7). Both disturbance of microbial activity and decomposition of trenched roots may be at the origin of this increase and the difference in response between the two ecosystems is likely linked to differences in environmental conditions (soil moisture and temperature), root decomposition rates, and microbial communities.

In order to minimize disturbance we didn't collect samples inside trenched plots for soil moisture determination and are therefore unable to evaluate whether



**Fig. 8** Sensitivity analysis testing how the portion that the close to palm (CT) area occupies in the plot impact upon plot-scale annual total soil respiration (SRT, solid line) and the contribution of heterotrophic respiration to plot-scale annual total soil respiration (%SRh, dashed line) in the OP2012 (A) and OP2007 (B). Bars are SE, grey circles indicate results obtained at the CT proportions selected in this study

**Table 3** Relationships between average monthly total (SRT) or heterotrophic (SRh) soil respiration rate and environmental parameters in the forest (F), 1 (OP2012) and 6 (OP2007) year old oil palm plantations. CT designates the close to tree

Model	R <sup>2</sup>	n	Eq.
$SRT_{F FT} = 10.34^{***} (2.24) \times AirTemp - 268.82^{**} (67.36)$	0.65	13	1
$SRT_{F CT} = 6.30^* (2.08) \times AirTemp - 148.49^* (61.33)$	0.45	13	2
$SRT_{F FT} = -0.82^* (0.28) \times WT + 16.20^* (7.44)$	0.43	13	3
$SRT_{F CT} = -0.90^{**} (0.27) \times WT + 21.88^{**} (4.90)$	0.50	13	4
$SRT_{OP2012 FT} = 23.46^{***} (3.42) \times \exp [-0.01^{**} (0.0035) \times WT]$	0.64	11	5
$SRT_{OP2007 FT} = -0.28^{**} (0.09) \times WT + 18.54^{***} (3.57)$	0.47	13	6
$SRT_{OP2007 FT} = 6.27^* (2.15) \times SoilTemp - 135.62^* (56.3)$	0.44	13	7
$SRT_{OP2007 CT} = -0.07^* (0.03) \times Rainfall + 69.57^{***} (6.81)$	0.38	13	8
$SRT_{OP2007 FT} = 40.61^{***} (4.08) \times \exp [-0.002^{**} (0.001) \times Rainfall]$	0.56	13	9
$SRh_F = 15.77^{***} (3.03) \times \exp [0.04^* (0.01) \times Litterfall_{previous\ month}]$	0.43	12	10
$SRh_F = 1.10^* (0.44) \times Litterfall + 13.28^* (5.31)$	0.37	13	11

\* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001. Soil respiration is expressed in kg C ha<sup>-1</sup> day<sup>-1</sup>, water table level (WT) in cm with a negative value indicating a level below ground, air (AirTemp) and soil (SoilTemp) temperature in °C; and litterfall rate (Litterfall) in kg C ha<sup>-1</sup> day<sup>-1</sup>

root severance may have increased soil moisture. Nonetheless the lack of significant relationship between SRT and soil moisture (Table 3) suggests that a potential difference in moisture due to root removal would not have induced CO<sub>2</sub> flux change in a particular direction. At the forest site the average water table level was higher in the trenched than in the control plots as the result of site topographic variations. Also, temperatures were higher in trenched than in control plots. SRh rates in the forest did not exhibit a significant trend of variation with WT level or temperature changes but SRT did (Table 3). A WT level closer to the surface would decrease SRT rates while a higher temperature would have the opposite effect. Combining the over- and underestimation of SRT with respect to SRh due to, respectively, WT level and temperature differences cancels out the two effects so we consider the contribution of SRh to SRT at the forest site to be reasonably unbiased. At the OP2007, trenched plots were on average more deeply drained than control plots (due to a closer proximity to drainage canals) and at the OP2012 soil temperature was higher in trenched than in control plots. On the basis of the relationships established between SRT and the above-mentioned variables (Table 3), the contribution of SRh to SRT at the OP2007 and OP2012 plantations may therefore be slightly overestimated.

We evaluated SRh in trenched plots established away from trees to minimize root intrusion. Therefore

position and FT the far from tree position. The models are presented with slope (SE), intercept (SE) and level of significance

in the oil palm plantations where SRt was spatially stratified with lower SRt rates far from palms than close to palms (Table 2), SRh is not truly representative of plot-scale SRt. Notwithstanding the bias can be considered minimal and moderate in the OP2012 and OP2007, respectively, since the proportion that SRt close to tree represents at the plot scale is 9 and 35%, respectively.

#### Spatial trends, temporal patterns and biochemical controls

Contrary to observations by Comeau et al. (2013) and Jauhiainen et al. (2005), hummocks and hollows in the forest respired at a similar average rate throughout the monitoring period (Fig. 6). Jauhiainen et al. (2005) indicated that high water table conditions in hollows led to reduced cumulative soil respiration. Hollows were also wetter on average than hummocks at our site and respiration was partially driven by the WT level at each of the two microtopographic positions but other parameters such as root activity seemed to be predominant in governing SRt over the WT level. In the plantations, SRt was significantly higher close to palm than at mid-distance between palms. A higher SRt rate near trunk than in the harvest path is in agreement with observations by Comeau et al. (2016) and Dariah et al. (2014) in mature plantations established on peat soils and by Nelson et al. (2014) in mature plantations on mineral soil. Nelson et al. (2014) attributed elevated respiration near trunk to inputs of organic matter in stemflow, root respiration and decomposition of root-derived organic matter since root density was higher there than elsewhere in the studied plantation. Root density in the 6 cm top soil was higher at the CT than at the FT position in the OP2012 but not in the OP2007. Oil palm root biomass often exhibits a radial pattern (Dariah et al. 2014; Haron et al. 1998; Nelson et al. 2014) yet this is not always the case (Oktarita et al. 2017; Ruer 1967). The difference in spatial allocation of roots between the plantations as well their difference in root density may originate from their development stage. The architecture of the oil palm root system evolves progressively from the juvenile to the adult stage towards deeper horizons and towards the periphery of the system (Jourdan and Rey 1997). We found no relationship between root density and SRt. According to Nelson et al. (2006) and Wang et al. (2008) root density does

not accurately reflect root respiration and exudation activities since old coarse roots are usually less active than young fine roots. In addition regression between root density and SRt in Indonesian oil palm plantations on peat performed poorly ( $0.003 < R^2 < 0.29$ ) (Dariah et al. 2014) suggesting a weak contribution of root density to spatial variation of SRt. Based on the observation that SRt decreased linearly with increasing distance from the palm trunk up a distance of 2.5 m and reached a plateau afterwards, Dariah et al. (2014) proposed the use of soil CO<sub>2</sub> efflux measured at a distance of  $\geq 3$  m from the palm to represent SRh. Likewise Carlson et al. (2015) assigned total respiration rates measured far from tree in plantations to SRh rates. Our results indicate that the use of SRt rates measured at the FT position would overestimate SRh rates by 21% on average.

The sensitivity analysis testing how the share of the CT area impacted annual total soil respiration rate and the contribution of heterotrophic to total respiration highlighted the critical need for improved knowledge on spatial patterns of soil respiration in mature oil palm plantations. The thorough grid approach undertaken by Nelson et al. (2014) in a mature plantation on mineral soil showed a patchy distribution of soil respiration with highest rates observed near trunks, in the frond pile and where empty fruit bunches had been placed. These areas all together accounted for about 40% of plot-scale soil respiration. Given the existing trade-off between spatial and temporal variability, our design was limited to two spatial positions for assessing SRt. We tested it by computing plot-scale SRt from the respiration rates measured by Nelson et al. (2014) near trunks and at mid-distance between palms and the 35:65 ratio we computed for the CT:FT share in the OP2007. We obtained a result of  $7.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  very close to the  $7.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  flux calculated by Nelson et al. (2014), which suggests that our design and assumptions can capture reasonably well the spatial variability in SRt inherent to mature plantations.

Temporal variations in SRt were closely related to climatic variations whereas fluctuations in SRh rates were not (Table 3). This suggests that climatic changes exerted a control on root respiration via photosynthate allocation to roots rather than on soil organic matter and litter decomposition. In the forest, changes over time in SRh rates were linked to litter C inputs corroborating that soil organic matter and litter

respiration is affected by the supply of substrate from above-ground vegetation (Metcalf et al. 2007). The air or peat temperature response of SRt followed a linear model instead of an exponential one as found by Hirano et al. (2009) in undrained and drained peat swamp forests in Central Kalimantan. In addition our models explained <65% of the variability of SRt versus >92% in the study by Hirano et al. (2009). It seems therefore that the sensitivity of SRt to temperature varies substantially across peatland sites and land uses in the region. The water table level response of SRt in the forest was very similar to that measured in a Sumatran peat swamp forest (Comeau et al. 2013) but much different from the results by Hirano et al. (2009) that indicate no change in SRt when the WT was below-ground and a sharp decrease when the WT raised above-ground. In the OP plantations, SRt was linked to the WT level only at the FT position, where root water uptakes are the lowest (Nelson et al. 2006). Other studies conducted in OP plantations on peat did not find a control of WT level over SRt.

#### Magnitude of the emissions and land-use change implications

Annual rates of total and heterotrophic soil respiration as well as the contribution of SRh to SRt in the forest were remarkably close to the literature averages for Southeast Asian peatlands of  $12.9 \pm 2.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  ( $n = 13$ ),  $6.9 \pm 1.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  ( $n = 14$ ) and 53.5% ( $n = 1$ ), respectively (Hergoualc'h and Verchot 2014). On the other hand, annual SRt in the plantations were about 20–30% lower than the literature average ( $16.9 \pm 1.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ,  $n = 7$ ). Combining our values with up-to-date literature annual rates (Database available at <http://hdl.handle.net/1902.1/22351> updated with the results by Sakata et al. (2015)) brings the average soil respiration in OP plantations on peat down to  $14.2 \pm 1.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  ( $n = 13$ ). The range of SRt rates in OP plantations on peat is wide (10.9–28.4  $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ,  $n = 13$ ) presumably owing to differences in inherent peat properties, land use history (e.g. fire history) and management practices. Melling et al. (2013) found an increase in SRt along a chronosequence of plantations aged one, five and seven year old and attributed the rise to higher root respiration rates when the palms grow. Such an increase was also apparent in our results. Across all OP

sites on peat, the correlations between SRt and either the plantation age or indicators of oxygen availability (WFPS, WT level) or soil organic matter quality (peat C/N ratio) were not significant and very poor ( $R^2 < 0.15$ ). A linear relationship with soil CEC was promising ( $R^2 = 0.54$ ,  $n = 6$ ) but significant only at the  $P = 0.1$  level. The only soil property significantly linked to SRt in OP plantations on peat across sites was the base saturation, as already found over a wide range of land uses on peat (Hergoualc'h and Verchot 2014). The rate of SRt decreases linearly with increasing CEC ( $R^2 = 0.78$ ,  $n = 6$ ) that is with increasing decomposition state of the peat. Indeed the large amount of lignin-derivates formed upon decomposition provide many exchange sites (Andriess 1988). Conversely the rate of SRt increases linearly with base saturation increase ( $R^2 = 0.91$ ,  $n = 6$ ), as the result of CEC decrease but also potentially of increase in pH and eutrophy (Andriess 1988). These relationships explain the lower SRt rates at our plantations as compared to SRt rates measured in Malaysia by Melling et al. (2005, 2013). Smaller SRt rates than observed elsewhere in Southeast Asia may also be associated with the intense land clearing fire history at our sites. Repeated fires lead to increased recalcitrance of the peat (Könönen et al. 2016). These fires may also explain the lower soil N content in the plantations than in the forest (Wan et al. 2001).

Annual total soil respiration was on average similar in the forest and in the plantations. A meta-analysis conducted by Hergoualc'h and Verchot (2014) indicated no consistent and overall effect of intact peat swamp forest conversion on total soil respiration, on the account of a simultaneous enhanced peat decomposition and reduced or increased root density and activity in the land covers replacing the forest. As expected annual soil heterotrophic respiration as well as the contribution of heterotrophic respiration to total soil respiration were significantly higher in the OP plantations than in the forest. The updated OP plantation average of %SRh and heterotrophic soil respiration from the literature including this study amount to  $72.4 \pm 6.9\%$  ( $n = 4$ ) and  $10.4 \pm 1.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  ( $n = 20$ ), respectively; close to the previously reported  $73 \pm 13\%$  ( $n = 2$ ) and  $12.3 \pm 2.7 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  ( $n = 9$ ). A preliminary C budget combining the heterotrophic soil respiration rates measured at our site with literature averages for most other peat C in- and outputs suggests that the peat

**Table 4** Peat C budget calculated as the difference of annual C inputs from litterfall and root mortality and C outputs from heterotrophic soil respiration (SRh) and dissolved organic C (DOC) in the forest (F) and oil palm plantations (OP)

Land use	Soil C inputs			Soil C outputs			C budget
	Litterfall	Roots	Total	SRh	DOC	Total	
F	<b>4.2 ± 0.2</b>	<i>1.5 ± 0.8</i>	<i>5.7 ± 0.8</i>	<b>7.1 ± 0.4</b>	<i>0.6 ± 0.0</i>	<i>7.7 ± 0.4</i>	2.0 ± 0.9
OP <sup>a</sup>	<i>1.5 ± 0.1</i>	<i>3.6 ± 1.1</i>	<i>5.0 ± 1.0</i>	<b>9.0 ± 0.6</b>	<i>0.9 ± 0.1</i>	<i>9.9 ± 0.6</i>	4.9 ± 1.2

Values are mean ± standard error expressed in Mg C ha<sup>-1</sup> year<sup>-1</sup>. Values in bold are from this study, values in italic are from the literature review of Hergoualc'h and Verchot (2014)

<sup>a</sup> OP values from this study are the average of results measured in the OP2012 and OP2007

in the forest was a net source of C emitting at a rate of 2 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Table 4). This loss rate is very similar to the mean annual net ecosystem exchange of 1.74 Mg C ha<sup>-1</sup> year<sup>-1</sup> monitored by Hirano et al. (2012) in an intact peat swamp forest of Central Kalimantan. Average peat net C losses in the plantations are more than twice as large as the losses in the forest. They are within the range of the average net loss rate of 8.2 ± 2.9 Mg C ha<sup>-1</sup> year<sup>-1</sup> computed by Hergoualc'h and Verchot (2014) or the default IPCC emission factor for OP plantations on peat of 11.8 [6.2; 18.1] Mg C ha<sup>-1</sup> year<sup>-1</sup>, that integrates net decomposition loss (11 [5.6; 17] Mg C ha<sup>-1</sup> year<sup>-1</sup>) and dissolved organic C loss (0.8 [0.6; 1.1] Mg C ha<sup>-1</sup> year<sup>-1</sup>) (Drösler et al. 2014).

## Conclusion

Agriculture in peatlands as currently practiced in Southeast Asia by either smallholders or the industry has devastating consequences on the environment (Wijedasa et al. 2017). Peatland-rich countries such as Indonesia need to refine their greenhouse gas emission inventories in this area as a priority. However peat net CO<sub>2</sub> emission estimates resulting from forest to oil palm plantation conversion are based on limited data. Peat C mass balance calculation requires knowledge on rates of C entering and leaving the peat such as, respectively, litterfall and soil heterotrophic respiration rates. We found a 20% higher heterotrophic soil respiration in oil palm plantations than in the forest, a result in agreement with, but lower than literature estimates. Separating the components of soil respiration is difficult and simplistic approaches should be

regarded cautiously. These include the assumption that total soil respiration measured far from trees is representative of heterotrophic soil respiration. Ideally several methods should be tested simultaneously. Our preliminary C budget suggests that the peat in the forest was a small source of C during the observation period. Since climatic variations exert influence on soil respiration, long-term monitoring is required to determine whether the peat continues to be a C sink or not in this forest. The budget in the plantations underlines C losses more than twice as high as the losses in the forest, reinforcing current conclusions on the negative impacts on the atmosphere of oil palm cultivation on peat.

## Supplementary material

The database of field measurements of soil respiration and environmental variables is available at <http://dx.doi.org/10.17528/CIFOR/DATA.00061>.

**Acknowledgements** This research was conducted under the Sustainable Wetlands Adaptation and Mitigation Program (SWAMP) and was generously supported by the governments of the United States of America (Grant MTO-069018) and Norway (Grant agreement # QZA-12/0882). It was undertaken as part of the CGIAR research program on Climate Change, Agriculture and Food Security (CCAFS). The authors are grateful to the staff of Tanjung Puting National Park for facilitating the study and providing lodging. We would also like to thank all assistants and villagers for their continuous help in the field. We are extremely thankful to Nisa Novita for contributing to site selection and supporting diligently field work as part of her Ph D research activities conducted in the same area. Two referees did their utmost to improve this manuscript; their contribution is much appreciated.

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