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Spatial variations in heterotrophic respiration from oil palm plantations on tropical peat soils

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Oil palm plantations growing on peat soil are associated with high soil CO_2 emissions. Oil palm plantations are set up with regular spatial patterns consisting of different surface management microforms: bare soil harvest paths, frond piles, cover plants and drainage ditches. Currently, there is limited understanding about the extent that this spatial variation impacts soil carbon losses, in part due to the challenges of partitioning peat oxidation from total soil respiration. We explored this spatial variation by measuring total soil respiration (R_{tot}), root density and environmental variables at 210 locations. Measurements were taken along transects going from the base of oil palms into the different microforms. R_{tot} was partitioned into root respiration (R_a) and heterotrophic respiration (R_h) using two different methods: (i) a “distance from palm” method (which utilizes the fluxes taken from soil with minimal root density) and (ii) a “linear regression” method (which models root density and R_{tot}, using the regression intercept for R_h). Here, the distance from palm partitioning method gave higher R_h estimates than the linear regression method. R_h varied significantly between the different palms used in the assessment but did not show significant spatial variation aside from this. R_{tot} and R_a were highest next to the palm and decreased with increasing distance from the palm. R_{tot} and R_a also showed significant spatial variation between the different surface management microforms, with each giving significantly higher fluxes below the frond piles near the drainage ditches than from below the frond piles near the cover plants. Area-weighted upscaling gave plantation best estimates of R_{tot}, R_h, R_a of 0.158 ± 0.016, and 0.130 ± 0.036 and 0.029 ± 0.030 g CO_2-C m^{-2} h^{-1}, respectively. We conclude that spatial patterns impact root density, R_a and R_{tot} fluxes but not R_h fluxes.

KEYWORDS

oil palm, peat, peat oxidation, heterotrophic respiration, autotrophic respiration

1 Introduction

Oil palm (*Elaeis guineensis*) plantations have been estimated to produce 146 Tg C from plantations annually, accounting for 95% of total emissions from tropical agriculture (Carlson et al., 2017). A large proportion of these emissions can be attributed to oil palm plantations growing on drained tropical peat soils – these agroecosystems have been estimated to have high rates of peat oxidation by heterotrophic respiration (R_h) (Carlson et al., 2017). However, current estimates of oil palm plantation R_h have a wide range from 0.047 to 0.307 g CO_2-C m^{-2} h^{-1} (mean: 0.152 g CO_2-C m^{-2} h^{-1}; 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; Manning et al., 2019; Cooper et al., 2020). The underlying basis for this extensive range of R_h values is poorly established.

Agricultural systems growing on peat soils often have high CO_2 emissions due to lowering the naturally occurring water table to prevent waterlogging the crop's roots (Philipson and Coutts, 1978; Corley and Tinker, 2008; Melling et al., 2009; McCalmont et al., 2021). This soil drainage accelerates the activity of heterotrophic bacteria, which break down labile components of peat leading to enhanced atmospheric CO_2 fluxes (Hoojier et al., 2012). Oil palm (*Elaeis guineensis*) plantations are no exception (Carlson et al., 2015). South East (SE) Asia has 24.7 Mha of peatlands, of which 4.3 Mha of peatlands have been cultivated for industrial oil palm or *Acacia* sp. plantations (Page et al., 2011; Miettinen et al., 2016).

Understanding R_h in oil palm plantations is complicated by within plantation spatial variation caused by microsite-level (i.e., <10 m) plant and soil management practices (Manning et al., 2019). Oil palm plantations have a regular, repeating pattern of surface management microforms, consisting of: bare soil harvest paths, piles of decomposing fronds, cover plants and bare soil around the palm where the roots grow – referred to as the palm circle or rhizosphere. Furthermore, oil palm plantations growing on peat soil have drainage ditches at regular intervals (Cook et al., 2018; Manning et al., 2019). These different surface management microforms have different microclimatic and environmental conditions, leading to differences in soil C flux from the microforms (Manning et al., 2019). These spatial patterns complicate estimation of plantation-scale R_h as it has to take into account high variability and potentially increases the sample size needed to constrain plantation-scale flux estimates.

Existing sampling methodologies may not adequately quantify natural variability in soil respiration and therefore the estimation of plantation-scale R_h (Subke et al., 2006). To estimate R_h, total soil respiration (R_{tot}) must be partitioned into R_h and autotrophic respiration (R_a). A common method to partition R_{tot} into R_h in oil palm plantations is to take an R_{tot} measurement at the furthest distance between two or more palms (referred to as the "*distance from palm method*"), in areas of soil where root density is assumed to be insignificant or so low that it has a negligible effect on total soil respiration (Dariah et al., 2014; Matysek et al., 2018). The *distance from palm* method produces estimates of R_h that avoids artificially changing the environmental conditions, but may still contain some contribution from R_a. Another method to partition R_h from R_{tot} is the "*linear regression*" method (Baggs, 2006; Farmer, 2013). The *linear regression* method uses linear regression to quantify the correlation between R_{tot} and root density. R_{tot} is assumed to be equal to R_h at the point where root density approaches zero. The *linear regression* method assumes that spatial variations in R_{tot} within the plantation are due to variation in R_a and that R_h is constant. A third commonly used method is the "*physical partitioning method*" (Subke et al., 2006). In *physical partitioning* methods, root-excluding mesh or trenching techniques are used to create root-free areas of soil (Melling et al., 2013; Hergoualc'h et al., 2017). In these *physical partitioning* methods, R_h is measured directly, but the environmental conditions under which R_h was measured may have been significantly altered by the root exclusion meshes or trenches (Manning, 2019). Finally, "*isotopic*" methods allow for the quantification of the proportion of R_h in an R_{tot} measurement, however, these methods are expensive and complex to implement.

This study explores the spatial variations and uncertainties in estimates of R_h from oil palm plantations on tropical peat soils. Sampling was carried out at increasing distances from the base of the palm along transects extending toward different surface management microforms. These surface management microforms are: the bare soil harvest path, beneath frond piles next to the cover plants (frond pile-C), beneath the frond piles next to the drainage ditches (frond pile-D), into cover plants and toward the field drains. R_{tot} was partitioned into R_h and R_a using two methods: the distance from palm method and the linear regression method. These methods were chosen because they do not alter the soil environment physically, while also being practical and economical to employ. Statistical analyses were used to consider how R_{tot} varies with environmental variation and variations in surface management practices. R_{tot}, R_h and R_a were scaled up to plantation level and estimated using two methods: straight mean averaging and area-weighted upscaling. This paper aims to answer the following research questions:

- Do measured R_{tot} and partitioned R_h and R_a vary significantly between surface management microforms?
- What are plantation-scale estimates of R_{tot} and the partitioned R_h and R_a?
- What are the errors in R_{tot}, R_h and R_a if spatial variation is not adequately taken into account?

2 Methods

2.1 Site description

The data were collected during August and September 2014 from the Sebungan oil palm plantation in Sarawak, Malaysia (latitude 003°09' N, longitude 113°21' E). Sebungan Estate has been established on 4.0 m deep peat soils broadly classified as histosols (FAO, 2006). The plantation has a tropical climate; the mean annual temperature was 26°C and the mean annual precipitation was approximately 3,000 mm (Cook et al., 2018; McCalmont et al., 2021). The northeast monsoon from October to January has the most rainfall, with a slightly drier southwest monsoon between May and August (Cook et al., 2018).

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 7 years old when measurements began. The plantation was laid out systematically with ~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, leading to 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):

- Palm (fertilizer) circle – the ring of soil around the palm where the majority of oil palm roots grow and the fertilizer is applied. In this paper we refer to this area as the rhizosphere due to the distribution of the roots in this plantation.
- 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. The analysis in this paper differentiated the frond piles next to the cover plants (frond pile-C) from the frond piles next to the drainage ditches (frond pile-D).
- 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 centre of the plantation blocks.

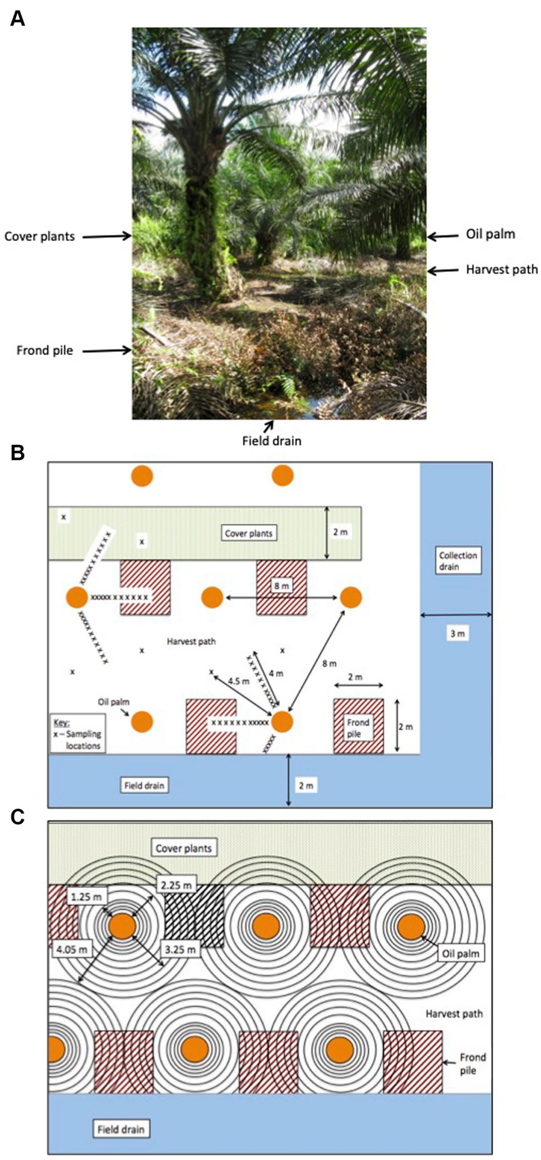

FIGURE 1
(A) An image of the palm oil plantation **(B)** the measurement sampling design and **(C)** a visualisation of the areal rings used for the flux upscaling methodology.

2.2 Experimental design

Six palms were selected within a 1 ha plot for this experiment. Three palms were located in rows next to the field drains and three palms were located in rows next to the rows of cover plants. At each palm, three sampling transects were set up, with each transect going across a different surface management microform (Figure 1). These transects within each management microform enabled us to determine if the effect of management microform interacted with root density to influence R_{tot}, R_h and R_a.

2.3 R_{tot} measurements

R_{tot} measurements were collected on the 30th and 31st August 2014. Samples were collected at 0, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5, 4 m from the base of each palm. A further sample was taken at a point equidistant from the three nearest palms (i.e., 4.5 m from the palm bases). Flux measurements were performed with a static chamber approach, using 10 cm diameter flux chambers (Livingston and Hutchinson, 1995). Chamber bases were installed in the soil to a depth of 5 cm 4 weeks prior to the commencement of sampling in order to avoid disturbance effects associated with base installation. R_{tot} measurements were made in triplicate using a PP Systems EGM-4 and SRC-1 chamber (Hansatech Instruments Ltd., Norfolk, UK). For each replicate measurement, CO_2 concentrations were measured over a 2 minute enclosure period, with concentrations recorded at 3 second intervals, or until an increase of 50 ppm CO_2 had been observed.

2.4 Environmental measurements

Ambient air temperature was measured at the same time as the R_{tot} measurement using a thermometer (LCD Digital Thermometer, ATP Instrumentation, Leicestershire, UK; precision ±1°C). Soil temperature and soil moisture measurements were taken following the completion of R_{tot} measurement, adjacent to the collar as in Marthews et al. (2012) and Manning et al. (2019). Soil moisture was measured using an ML3 probe and HH2 moisture meter (Delta-T, Cambridge, UK; precision 1%). Following the chamber measurements for each palm, water table depth (WTD) was determined by digging a hole in the peat in the harvest path to the water table, 2 m away from the palm.

2.5 Root density measurements

After the flux measurements, a 10 cm diameter, 30 cm deep, soil core was collected from each collar. Root dry mass was determined in

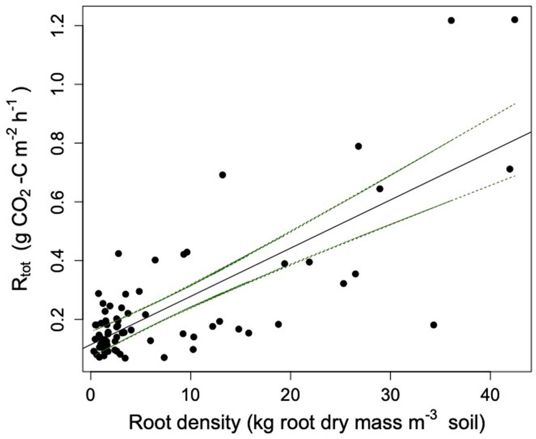

FIGURE 2
R_{tot} plotted against root density. The equation for the regression line is: R_{tot} = 0.016 x root density + 0.114 ($r^2 = 0.57$, $p < 0.0001$). Confidence intervals are represented by the green dashed line.

each soil core using the method developed by Metcalfe et al. (2008), sampling up to 50 min for each soil core. The roots were washed and dried at 70°C to constant weight (Metcalfe et al., 2008). Root density was calculated as mass of dry roots over total volume of core extracted.

2.6 Soil characteristics

Following the extraction of roots, soil samples were dried and sieved to 2 mm. Chemical analyses were performed at the Malaysian Palm Oil Board headquarters in Kuala Lumpur, where soil C and N were measured in a CNS analyzer (Elementar Vario MACRO Cube, Germany), and soil pH was determined (Thermo Orion pH/ORP/cond model 555A, Thermo Fisher Scientific, Chelmsford, MA, USA).

Bulk density was estimated by finding the dry mass of soil with known volumes, sampled from the top 10 cm in the harvest path, frond piles and cover plants with bulk density rings. Soil C and N content were estimated by multiplying the bulk density by the soil C and N for the top 10 cm by 1 m of soil.

2.7 Calculating R_{tot} chamber fluxes

R_{tot} fluxes were calculated using R version 2.15.1 GUI 1.52[1]. Here linear regressions were fitted and flux estimates determined (Equation 1) using the method in Marthews et al. (2012):

$$Rate\ of\ flux = \frac{\Delta CPVMY}{\Delta tTAR} \quad (1)$$

where ΔC is the change in CO_2 over the measurement period (ppm), P is pressure (mb), V is volume (m^3), M is the relative molecular mass of CO_2, Y is the conversion to upscale the flux to annual emissions, Δt is the duration of the measurement period (s), T is temperature (K), A is surface area (m^2) and R is the Universal Gas Constant 8.31432 J mol^{-1} K^{-1}.

1 http://www.R-project.org

2.8 Estimating R_h and R_a

R_{tot} was partitioned into R_h and R_a using Equation 2:

$$R_{tot} = R_h + R_a \quad (2)$$

Two different methodological approaches were used to estimate the partitioning of R_{tot} into R_h and R_a:

- Distance from palm – This method considered the pattern of R_{tot} and root density with distance from the palm on this plantation and assumed R_{tot} and R_h were equivalent for distances >1 m from the palm, where root density was shown to be minimal and not to vary statistically between datapoints. This method was based on Dariah et al. (2014) and Matysek et al. (2018) who each used a different distance as their R_h estimation due to the root growth in their respective plantations. R_a was estimated using Equation 2.
- Linear regression – This method linearly regressed root density and R_{tot}. R_h was assumed to be root-free respiration, i.e., at the intercept (Figure 2; Kucera and Kirkham, 1971; Baggs, 2006). R_a was estimated using Equation 2.

For the analysis, the aggregated mean R_{tot} per distance class per palm and aggregated mean root density per distance class per palm were used, reducing the maximum $n = 210$ to $n = 72$. This was done because it had been estimated that the proportional representation of each microform within each distance class ring was equal by creating a spatial model of the oil palm plantation and determining the size of each land cover type.

2.9 Estimating R_h and R_a at individual points

Estimating R_h and R_a at each individual measurement points was modeled using the linear regression in section 2.8. Here, measured root density was substituted into the linear regression equation in order to model R_a. Equation 2 was used to model R_h for each collar.

2.10 Upscaling $R_{tot,}$ R_h and R_a to plantation scale

R_{tot}, R_h and R_a fluxes were upscaled to plantation-scale estimates using two different approaches: straight mean averaging and area-weighted upscaling.

2.10.1 Straight mean averaging

Here, plantation mean R_{tot} was calculated using aggregated means. Firstly, the mean R_{tot} per distance class per palm was calculated. Secondly the overall mean of these means was estimated. Plantation scale R_h and R_a were calculated using the methods in section 2.8. To keep straight mean averaging results from this study

TABLE 1 The proportional areas for the area-weighted upscaling.

Land area	Proportion when palm location is not differentiated	If split - proportion for palms by cover crop	If split - proportion for palms by drainage ditch
Palm area (radius 0.49 m)	0.0120	0.0060	0.0060
Triangles	0.0112	0.0056	0.0056
Drain area	0.0750	0.0375	0.0375
Distance from palm:			
0–0.15 m	0.0069	0.00345	0.00345
0.16–0.375 m	0.0186	0.0093	0.0093
0.376–0.625 m	0.0248	0.0124	0.0124
0.626–0.875 m	0.0311	0.01555	0.01555
0.876–1.25 m	0.0572	0.0292	0.0280
1.26–1.75 m	0.0927	0.0500	0.0427
1.76–2.25 m	0.1117	0.0625	0.0492
2.26–2.75 m	0.1306	0.0751	0.0555
2.76–3.25 m	0.1496	0.0877	0.0619
3.26–3.75 m	0.1684	0.1002	0.0682
3.76–4.05 m	0.1101	0.0662	0.0439

comparable to other studies, it was assumed that the proportional area the drainage ditches took up did not impact the overall plantation results (Table 1).

2.10.2 Area-weighted upscaling

Spatial area-weighted estimates of R_{tot} were performed to derive more accurate plantation-level estimates of soil CO_2 fluxes. Here, areal fractions were estimated for each distance class surrounding the palm (0, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 3, 3.5 and 4 m from the palm; Figure 1; Table 1). Mean R_{tot} was estimated for each fraction and then multiplied by the values in Table 1, which have been calculated to correct for the spatial area of the drainage ditches. The different microforms were also given equal weighting within each ring, due to them taking up equal areal space in this plantation. The scaled R_{tot} values were then summed to get plantation level fluxes.

Slightly different approaches were used for R_h and R_a:

- Distance from palm – The straight mean averaging R_h estimate was multiplied by 0.91, to take into account the area of the drainage ditches and the area beneath the palms (it was assumed that the gasses produced beneath the palms were either transported to the atmosphere through the surrounding bare soil or through the palm roots as shown with CH_4 in Manning et al., 2019). R_a was estimated by subtracting this R_h from the area-weighted upscaling R_{tot}.
- Linear regression method – The method in section 2.9 was first used to get individual estimates of R_h and R_a by collar. Mean R_h and mean R_a were estimated at each difference distance class. Finally R_h and R_a were spatially weighted, by multiplying the values by the proportions in Table 1, to get the area-weighted upscaling estimates.

2.11 Bootstrapping confidence intervals

The standard deviation was used to determine the confidence intervals (CIs) for the straight mean averaging estimate of R_{tot} and the straight mean averaging estimate of R_h and R_a calculated using the distance from palm method. It was possible to scale these CI for the distance from palm area-weighted upscaling estimate. Confidence intervals for R_h calculated using the linear regression method were found by estimating confidence intervals for the linear regression line and the estimates at the intercept were used for the R_h estimate. CIs for R_a using the linear regression method were found using the combination of errors technique.

These methods of determining CIs could not be applied to area-weighted upscaling estimates of R_{tot} or R_h and R_a estimated using the linear regression method. In these instances, CIs were determined by resampling the data in R 10,000 times, repeating the upscaling analysis and determining the 5th and 95th percentile mean estimate. CIs for the distance from palm area-weighted upscaling R_a were found using the combination of errors technique.

2.12 Statistical analyses

All statistical analyses were performed using R version 2.15.1 (see footnote 1). The estimates of R_h and R_a used for statistical analysis were taken from the method described in section 2.9 in order to obtain individual points.

Linear models were used to determine how R_{tot}, R_a and root density varied with distance from palm and with sampling transect. Tukey HSD tests were used for *post hoc* analyses, using the ANOVA function in R. Kruskal-Wallis tests were used for R_h. Nemenyi tests using Tukey HSD were used for Kruskal-Wallis *post hoc* analyses (R package: PMCMR v4.3; Pohlert, 2018). Following each statistical model, the fixed effect (and where necessary also random effect) residuals were considered for normality using Shapiro–Wilk normality tests, heteroscedasticity and equal variance.

Linear models were used to determine whether environmental variables were significantly different between distance from palm or the different surface management microforms. A log transformation was used for soil moisture and Box Cox transformations were used for soil carbon (lambda = 3.9), soil nitrogen (lambda = −2.05), soil C:N (lambda = 1.55) and soil pH (lambda = 3) to achieve normality with the model residuals.

The effects of environmental variation on R_{tot} were considered using a linear mixed effect model using the nlme package in R

(Pinheiro et al., 2017). The fixed effects in the model included soil moisture, soil temperature, air temperature, root density and an interacting fixed effect factor between soil pH and soil surface microform transect. Distance from palm was included as a random effect.

2.13 Quantifying the implications of sampling strategy and effort on estimating soil carbon dynamics

Variation in the plantation-scale estimates of R_{tot}, R_h and R_a were assessed based on:

1) Partitioning methodology
2) Sample size
3) Sampling design
4) Including and excluding the rhizosphere
5) Including or excluding microforms

In order to assess variation in R_h due to partitioning methodology, the variation in R_h estimates produced in this study was considered. To assess sample size, subsets of the data were resampled from the dataset at sample sizes 5, 10, 20, 35 and the entire dataset. R_{tot}, R_h and R_a were then estimated using straight mean averaging. Furthermore, a power analysis was applied to the dataset to determine the number of samples needed to accurately estimate R_{tot}, using the method in Metcalfe et al. (2008). Here Equation 3 was applied to the dataset:

$$Sample\ size = \frac{t\alpha^2\, CV^2}{D^2} \quad (3)$$

where t_α is the statistical significance wanted for the power analysis (here 0.05), CV is the sample coefficient of variation, and D is the specified confidence interval (here 10; Hammond and McCullagh, 1978).

With the intention of assessing variation in R_{tot}, R_h and R_a due to sampling design, random sampling with straight mean averaging and spatial sampling with area-weighted upscaling were compared. To show the variation in R_{tot}, R_h and R_a whether the rhizosphere was included or not, plantation-scale estimates of R_{tot}, R_h and R_a were estimated with and without rhizosphere data. Similarly, to consider whether including or excluding the different surface microform data, plantation-scale estimates of R_{tot}, R_h and R_a were considered for the different sampling scenarios with the harvest path data only or with the full dataset (Supplementary Tables S1, S2).

3 Results

3.1 Within plantation spatial variability in R_{tot}, R_h, R_a and root density

3.1.1 R_{tot}

Mean R_{tot} was 0.245 ± 0.017 g CO_2-C m^{-2} h^{-1} (Table 2). R_{tot} showed significant spatial variation within the oil palm plantation, with measurements ranging from 0.025 to 1.79 g CO_2-C m^{-2} h^{-1}. R_{tot} varied significantly between the six different palm subplots within the plantation (ANOVA: $F = 8.61$; d.f. = 5, 169; $p < 0.0001$).

In each subplot, the highest R_{tot} fluxes were measured next to the palm (Figure 3). R_{tot} decreased significantly as distance from palm increased (ANOVA: $F = 38.36$; d.f. = 1, 169; $p < 0.0001$) until 0.75 m. Thereafter, there was no significant difference in mean R_{tot} as the distance from palm increased (Figure 3).

R_{tot} varied significantly among the different surface management microforms (ANOVA: $F = 2.56$; d.f. = 4, 169; $p = 0.04$; Figure 4). R_{tot} fluxes were highest measured from the transects going towards the drainage ditches and the frond piles next to the drainage ditches, and lowest from the frond piles next to the cover plants and the cover plants.

Within each surface management microform, R_{tot} varied significantly with increasing distance from the palm (ANOVA: $F = 5.90$; d.f. = 4, 169; $p = 0.0002$; Figure 5). In the harvest path transect, R_{tot} decreased significantly as distance from palm increased to 1 m, and then R_{tot} did not vary significantly. In the other transects, R_{tot} showed decreasing trends with distance from palm until set distances, and then did not vary. These trends were not statistically significant. The distance where R_{tot} stopped decreasing was 0.75 m distance from the palm in both the transect going towards the frond pile next to the cover plants and the transect going towards the drainage ditch, and 3 m distance from the palm in the transect going towards the frond pile next to the drainage ditch.

3.1.2 Root density

Sampled oil palm root density varied between 0.119 and 79.03 kg roots m^{-3} soil with a mean root density of 7.843 ± 0.544 kg roots m^{-3} soil (Table 2). Root density varied significantly between the six different palms or subplots (ANOVA: $F = 6.85$, d.f. = 5, 164; $p < 0.0001$). Root density was greatest next to the palm, with a mean of 33.49 ± 7.36 kg roots m^{-3} soil measured up to 1 m distance from the palm (Figure 3). Root density decreased with increasing distance from the palm, with significantly less root density at each 0.25 m increment up to 1 m away from a palm (ANOVA: $F = 364$; d.f. = 1, 164; $p < 0.0001$). After 1 m, root density did not vary significantly with increasing distance from the palm, giving an average of 1.82 ± 0.30 kg roots m^{-3} soil from samples taken more than 1 m away from the palm.

Root density varied significantly between the different surface management microforms (ANOVA: $F = 6.83$; d.f. = 4, 164; $p < 0.0001$; Figure 4). Root density was highest when sampled from beneath the frond piles next to the drainage ditches. Root density was the lowest when sampled from the frond piles next to the cover plants. In the five different microform transects, root density showed different variation

TABLE 2 Summaries of the mean, minimum, maximum and number of R_{tot}, R_h, R_a and root biomass measured (R_{tot} and root biomass) or modeled (R_h and R_a) in this study.

	Mean ± S.E.	Minimum	Maximum	*n*
R_{tot}	0.245 ± 0.017	0.025	1.79	208
R_h	0.115 ± 0.008	−0.831	1.38	206
R_a	0.129 ± 0.009	0.002	1.30	208
Root density	7.843 ± 0.544	0.119	79.03	208

Fluxes are in g CO_2-C m^{-2} h^{-1} and standard errors of the mean are included. Here the linear regression method was used to partition R_{tot} into R_h and R_a (Section 2.9).

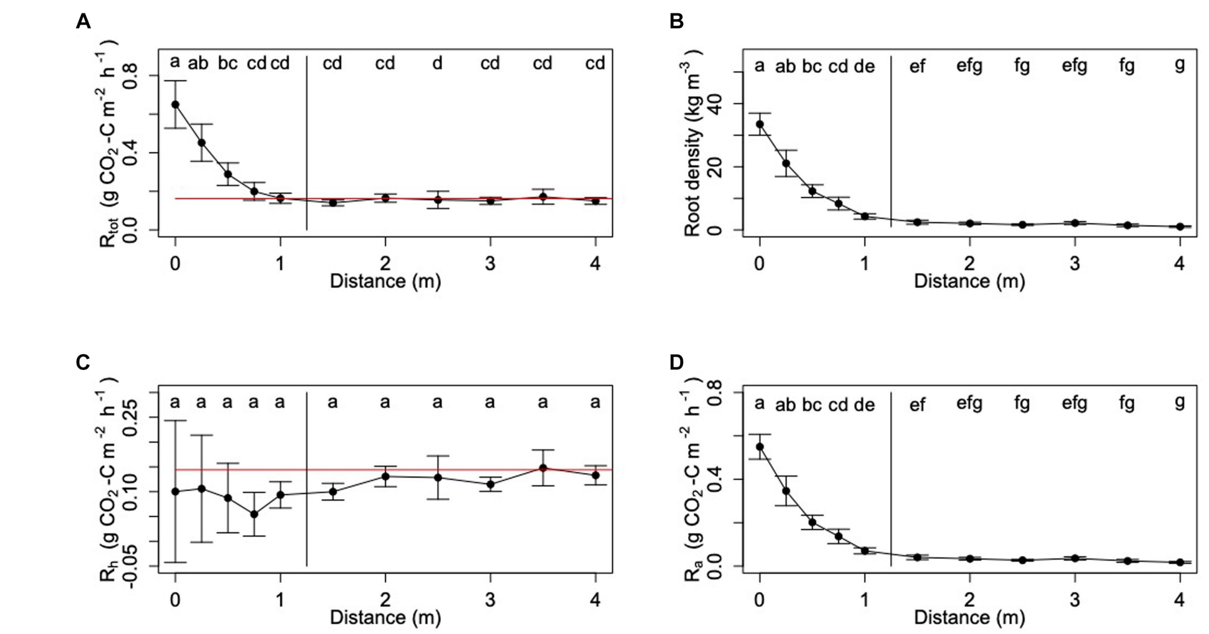

FIGURE 3
Trends in **(A)** R_{tot}, **(B)** root density, **(C)** R_h and **(D)** R_a as a function of distance from palm. For panels **(C)** and **(D)**, R_a and R_h are estimated using the linear regression equation substitution method. Lower case letters indicate statistically significant differences between means (Tukey-Kramer HSD: $p < 0.05$).

with increasing distance from palm (Figure 6). In each transect, root density was highest at 0 m next to the palm. Comparing the transects, root density was highest at 0 m in the harvest path, drainage ditch and frond pile next to the drainage ditch transects. The frond pile next to the cover plants and cover plants transects had the lowest root density next to the palm. The cover plants transect saw the steepest decline in root density as distance from palm increased, with a slight increase in root density at 4 m distance from the palm.

3.1.3 Heterotrophic respiration (R_h)

R_h estimated using the distance from palm method ranged between 0.147 ± 0.020 g CO_2-C m^{-2} h^{-1} and 0.162 ± 0.022 g CO_2-C m^{-2} h^{-1} (Table 3). R_h estimated from the linear regression method ranged between 0.112 ± 0.016 g CO_2-C m^{-2} h^{-1} and 0.114 ± 0.058 g CO_2-C m^{-2} h^{-1} (Table 3). Modeling individual R_h using the linear regression gave estimates ranging from −0.831 to 1.380 g CO_2-C m^{-2} h^{-1}, with a mean R_h of 0.115 ± 0.008 g CO_2-C m^{-2} h^{-1} (Table 2).

Modeled estimates of R_h showed limited spatial variation within the oil palm plantation. R_h varied significantly between the different palm subplots sampled in the oil palm plantation (Kruskal-Wallis: chi-squared = 28.21; d.f. = 5; $p < 0.0001$). R_h did not vary significantly with distance from palm or between the microforms (Figures 3, 7).

3.1.4 Autotrophic respiration (R_a)

R_a estimated using the distance from palm method ranged between 0.011 ± 0.026 g CO_2-C m^{-2} h^{-1} and 0.079 ± 0.057 g CO_2-C m^{-2} h^{-1} (Table 3). R_a estimated from the linear regression method ranged between 0.046 ± 0.004 g CO_2-C m^{-2} h^{-1} and 0.127 ± 0.079 g CO_2-C m^{-2} h^{-1} (Table 3). Using the linear regression to model individual R_h and estimating R_a through Equation 2 gave estimates of R_h that varied between 0.002 and 1.297 g CO_2-C m^{-2} h^{-1} with a mean R_a of 0.129 ± 0.009 g CO_2-C m^{-2} h^{-1} (Table 2).

Significant spatial variation was seen in R_a measurements. R_a did not vary significantly between the different palm subplots. The highest R_a measurements were taken next to the palm (Figures 3). There were significant reductions in R_a with increasing distance from the palm; the highest R_a fluxes were measured next to the palm and the lowest R_a fluxes were measured after 1 m distance from the palm (ANOVA: $F = 364.15$; d.f. = 1, 164; $p < 0.0001$). R_a showed significant variation between the different surface management microform transects (ANOVA: $F = 6.84$; d.f. = 4, 164; $p < 0.0001$; Figure 4), with the highest measurements in the frond pile next to the drainage ditch and the drainage ditch transects, and the lowest measurements from the cover plants and the frond pile next to the cover plants transects (Figure 8). R_a was highest next to the palm in the harvest path, frond pile next to the drainage ditch and drainage ditch transects. These transects saw the steepest decline in R_a as distance from palm increased. R_a did vary significantly between the transects outside of the palm rhizosphere (i.e., more than 1 m distance from the palm; ANOVA: $F = 8.03$; d.f. = 6, 71; $p < 0.0001$). Here, R_a in the cover plants and the frond pile next to the drainage ditch transects were significantly higher than R_a in the frond pile next to the cover plants transects.

3.2 Effects of environmental variables on R_{tot}

3.2.1 Variation in environmental variables

WTD ranged from −0.25 m to −0.45 m at the time of the study, with a mean of −0.35 ± 0.03 m. Air temperature ranged from 25.4 °C to 35.9 °C whilst the flux measurements were being taken, with a

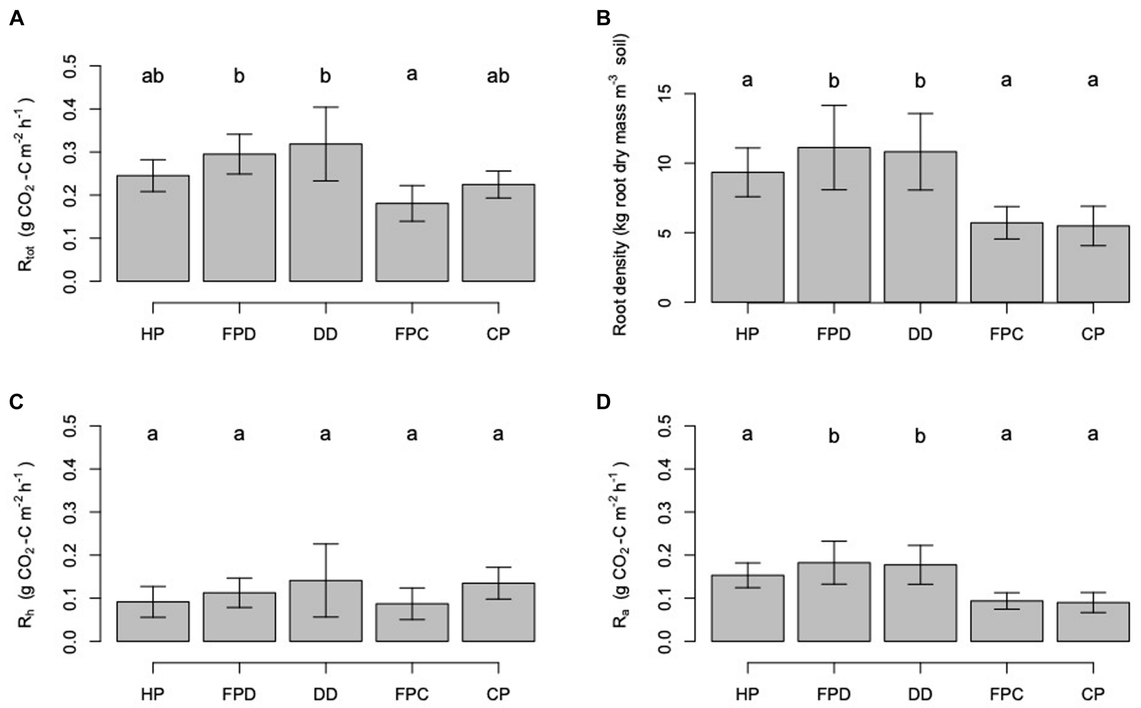

FIGURE 4
Trends in mean **(A)** R_{tot}, **(B)** root density, **(C)** R_h and **(D)** R_a as a function surface microform transect. HP stands for harvest path, FPD stands for frond pile next to the drainage ditch, FPC stands for frond pile next to the cover plants, CP stands for cover plants and DD stands for towards the drainage ditch. Letters signify significant difference between the results. Error bars show the standard errors of the mean.

mean air temperature of 30.0 ± 0.16 °C. Bulk density, soil C, soil N, soil C:N, soil pH, soil moisture and soil temperature are summarized in Table 4. Spatial variation was seen between the different palm subplots for soil temperature, air temperature, soil C, soil C:N, soil N and soil pH (soil temperature: ANOVA: $F = 20.00$; d.f. 1,163; $p < 0.001$; air temperature: ANOVA: $F = 16.99$; d.f. 1,173; $p < 0.001$; soil C: ANOVA: $F = 3.85$; d.f. 1,173; $p = 0.05$; soil N: ANOVA: $F = 20.46$; d.f. 1,172; $p < 0.001$; soil C:N: ANOVA: $F = 11.65$; d.f. 1,176; $p < 0.001$; soil pH: ANOVA: $F = 23.56$; d.f. 1,177; $p < 0.001$). Soil moisture and water table depth did not vary significantly between the different palms.

Significant differences were seen between measurements in the rhizosphere and outside the rhizosphere for soil temperature, soil moisture and soil N (Figure 9; Supplementary Table S2; soil temperature: ANOVA: $F = 10.39$; d.f. 1,163; $p = 0.002$; soil moisture: ANOVA: $F = 131.10$; d.f. 1,173; $p < 0.001$; soil N: ANOVA: $F = 5.34$; d.f. 1,172; $p = 0.002$). Soil C, soil C:N and soil pH did not vary significantly between the rhizosphere and outside the rhizosphere.

Significant differences were seen between measurements in the different surface microforms for soil temperature, soil moisture, soil N, soil C:N, soil pH and bulk density (Figure 9; Supplementary Table S2; soil temperature: ANOVA: $F = 4.72$; d.f. 4,163; $p = 0.001$; soil moisture: ANOVA: $F = 4.58$; d.f. 4,173; $p = 0.002$; soil N: ANOVA: $F = 4.33$; d.f. 4,172; $p = 0.002$; soil C.N: ANOVA: $F = 6.74$; d.f. 4,176; $p < 0.001$; soil pH: ANOVA: $F = 7.10$; d.f. 4,177; $p < 0.001$; bulk density: ANOVA: $F = 9.22$; d.f. = 2, 72; $p < 0.001$). Soil C did not vary significantly between the different surface microforms. Significant differences were seen between measurements in different surface microforms and between measurements in the rhizosphere and outside the rhizosphere for soil moisture only, with the harvest path having much higher soil moisture than the other surface microforms from 2.5 m distance from the palm (Figure 9; Supplementary Table S2; ANOVA: $F = 2.87$; d.f. 4,173; $p = 0.02$).

3.2.2 Relationship between environmental variables and R_{tot}

Variation in R_{tot} within the plantation was explained by variation in soil pH, soil temperature, root density, air temperature and soil moisture (Supplementary Tables S3, S4). R_{tot} was positively related to soil temperature but inversely related to air temperature. The effect size of soil temperature was 10 times greater than that of air temperature, indicating that soil temperature was a stronger driver of R_{tot}. R_{tot} increased as soil moisture decreased. R_{tot} increased as root density increased. There was a significant relationship between R_{tot} and soil pH and the interaction between soil pH and soil microform. R_{tot} increased as soil pH increased in all microforms apart from in measurements taken next to the drainage ditches. The largest pH effect was seen in the cover plants, followed by the harvest path, frond pile next to the cover plants, drainage ditch and frond pile next to the drainage ditch transects.

3.3 Plantation-scale estimates of R_{tot}, R_h and R_a

Best estimates of plantation R_{tot}, R_h and R_a are presented in Table 3. Straight mean averaging results were higher than estimates based on area-weighted upscaling. Distance from palm gave higher R_h estimates

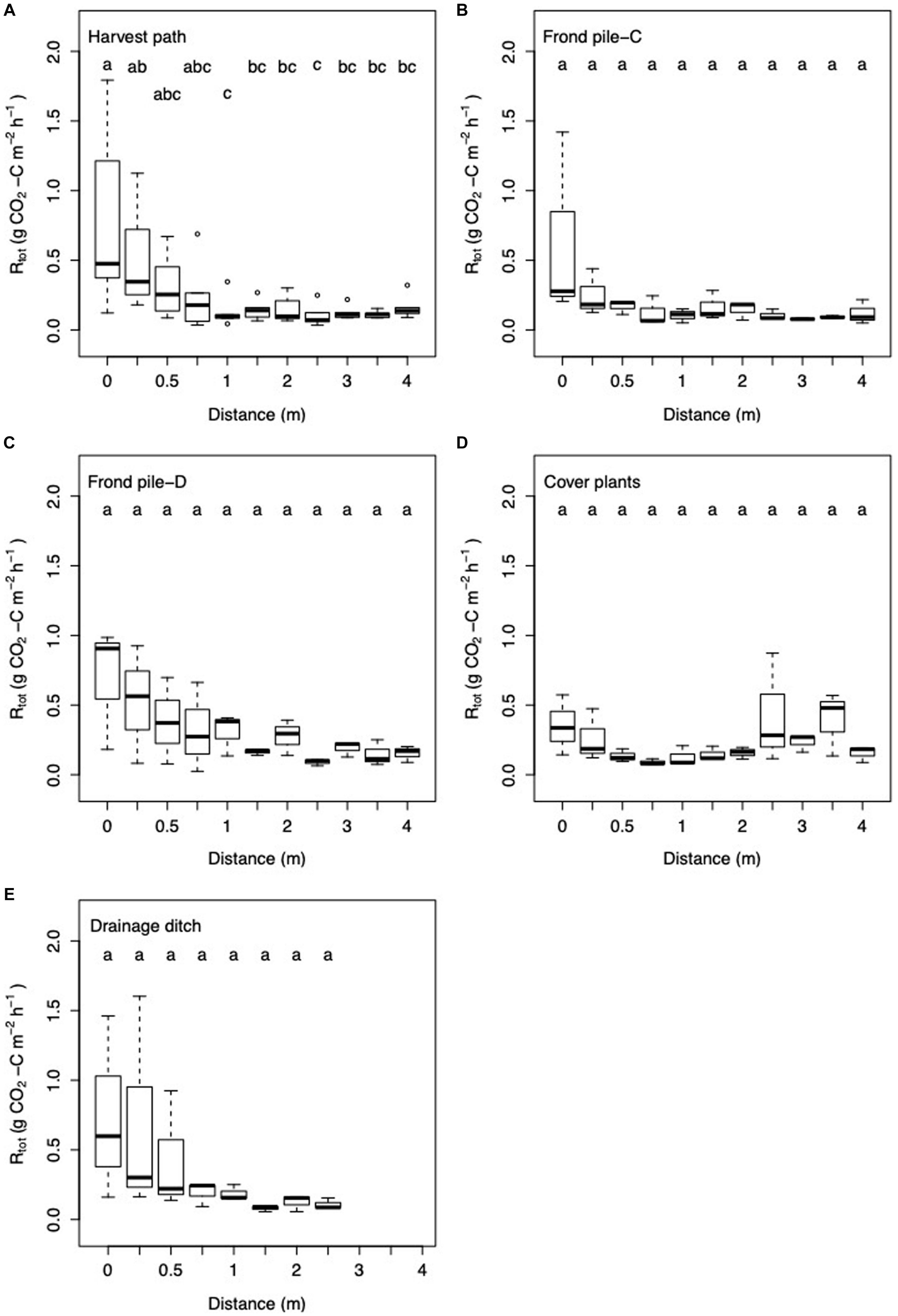

FIGURE 5
Box and whisker plot of R_{tot} with increasing distance from palm in the **(A)** harvest path (n = 64); **(B)** frond pile next to the cover plants, Frond pile-C (n = 33); **(C)** frond pile next to the drainage ditch, Frond pile-D (n = 33); **(D)** cover plants (n = 33); and **(E)** towards the drainage ditch (n = 24). Letters signify significant difference between the results.

TABLE 3 Plantation R_{tot}, R_h and R_a estimates.

Method	R_x	Straight mean averaging estimate	Area-weighted upscaling estimate	Area-weighted upscaling estimate with drainage ditch area taken into account
	R_{tot}	0.241 ± 0.053	0.174 ± 0.016	0.158 ± 0.016
Distance from palm	R_h	0.162 ± 0.022	0.162 ± 0.020	0.147 ± 0.020
	R_a	0.079 ± 0.057	0.012 ± 0.004	0.011 ± 0.026
Linear regression	R_h	0.114 ± 0.058	0.123 ± 0.016	0.112 ± 0.016
	R_a	0.127 ± 0.079	0.051 ± 0.026	0.046 ± 0.004
Average	R_h		0.143 ± 0.036	0.130 ± 0.036
Average	R_a		0.032 ± 0.030	0.029 ± 0.030

Results are presented in g CO_2-C m^{-2} h^{-1} and standard errors of the mean are included. Straight mean averaging results do not include the area for the drainage ditches. Area-weighted upscaling results have been presented that do and do not take the drainage ditch area into account (8% of the surface area). Average estimates of R_h and R_a have been proposed.

and lower R_a estimates than the linear regression method. Estimates of R_a gave greater changes with upscaling method than R_h estimates.

3.4 Partitioning methodologies, sample size and sampling design influence plantation-scale R_h estimates

Methodological decisions influenced the estimates of R_{tot}, R_h and R_a. The sample size of data points impacted the final R_{tot}, R_h and R_a estimated from oil palm plantations on peat soil. A power analysis showed that 35 samples are needed to accurately capture the within-plantation spatial variation in R_{tot}. Modeling for a reduced sample size gave broader confidence intervals surrounding the R_{tot}, R_h and R_a estimates (Figure 10). Estimates of plantation R_{tot}, R_h and R_a were higher in the random sampling designs than in spatially stratified sampling designs. R_{tot} and R_a gave higher plantation mean estimates and R_h gave lower plantation mean estimates when rhizosphere data were included in plantation means. Plantation R_{tot}, and R_a were lower and plantation R_h was higher when samples were taken from the harvest path only (Figure 10; Supplementary Tables S1, S2).

4 Discussion

4.1 R_h was not impacted by surface management microform or root distribution

Different spatial patterns were seen in the oil palm plantation for R_{tot}, R_h, R_a and root density. R_h varied significantly between the different subplots, but R_{tot} and R_a did not. R_{tot} and R_a showed significant spatial variation based on the experimental design within the subplots but R_h did not. Manning et al. (2019) took monthly repeated measurements from the different microforms at this site over a year and also found no significant difference in R_h between the different microforms, with variation in water table driving R_h dynamics in the plantation. A neighboring plantation did show significant variation in rates of R_h with surface management microform – this second plantation had an open canopy, unlike the study site here, and the frond piles provided shade that reduced the rates of R_h.

4.2 R_{tot} and R_a showed significant within plantation spatial variation, driven by patterns in root density

First and foremost, root density was highest next to the palm and decreased as distance from the palm increased. R_{tot} followed the same pattern as root density, with the highest fluxes measured next to the palm. R_{tot} fluxes also decreased as distance from palm increased. Similar trends have been seen clearly in other studies (Farmer, 2013; Dariah et al., 2014; Matysek et al., 2018). In this study, there was no significant difference in R_{tot} with increasing distance from palm after 0.75 m. This was slightly different to root density, which had no significant difference with increasing distance from the palm after 1 m distance from the palm. This study therefore defined the rhizosphere in this plantation as ≤1 m distance from the palm. Modeled estimates of R_a followed the same pattern seen by root density. Modeled estimates of R_h showed no significant variation with distance from palm, remaining relatively constant.

R_{tot}, R_a and root density varied significantly between the different microforms, suggesting that the spatial patterns in respiration fluxes and root density were at least partially determined by the microforms themselves. There was a clear divide in R_{tot}, R_a and root density depending on whether the measurements were taken nearer the drainage ditch or the cover plants, with consistently higher measurements nearer the drainage ditches than nearer the cover plants. These trends were also seen in the corresponding frond piles, with higher R_{tot}, R_a and root density in the frond pile next to the drainage ditch (frond pile-D) and lower R_{tot}, R_a and root density in the frond pile next to the cover plants (frond pile-C). Furthermore, measurements of R_{tot}, R_a and root density varied next to the palm in the same transects, showing that the change in root density around the palm began at the palm base.

We propose that the uneven distribution of oil palm roots in space was affected by competition between oil palm and cover plant roots. Competition between oil palm roots and other plants has been shown in a greenhouse experiment in Indonesia (Rahmadhani et al., 2020). Here, oil palm saplings were grown in polybags with herbaceous plants (one plant and one sapling per bag) and root growth was inhibited compared to the polybags that had only an oil palm sapling. Oil palm roots themselves compete for space in mineral soil, when palms are planted 8 m apart (Jourdan and Rey, 1997). In this study,

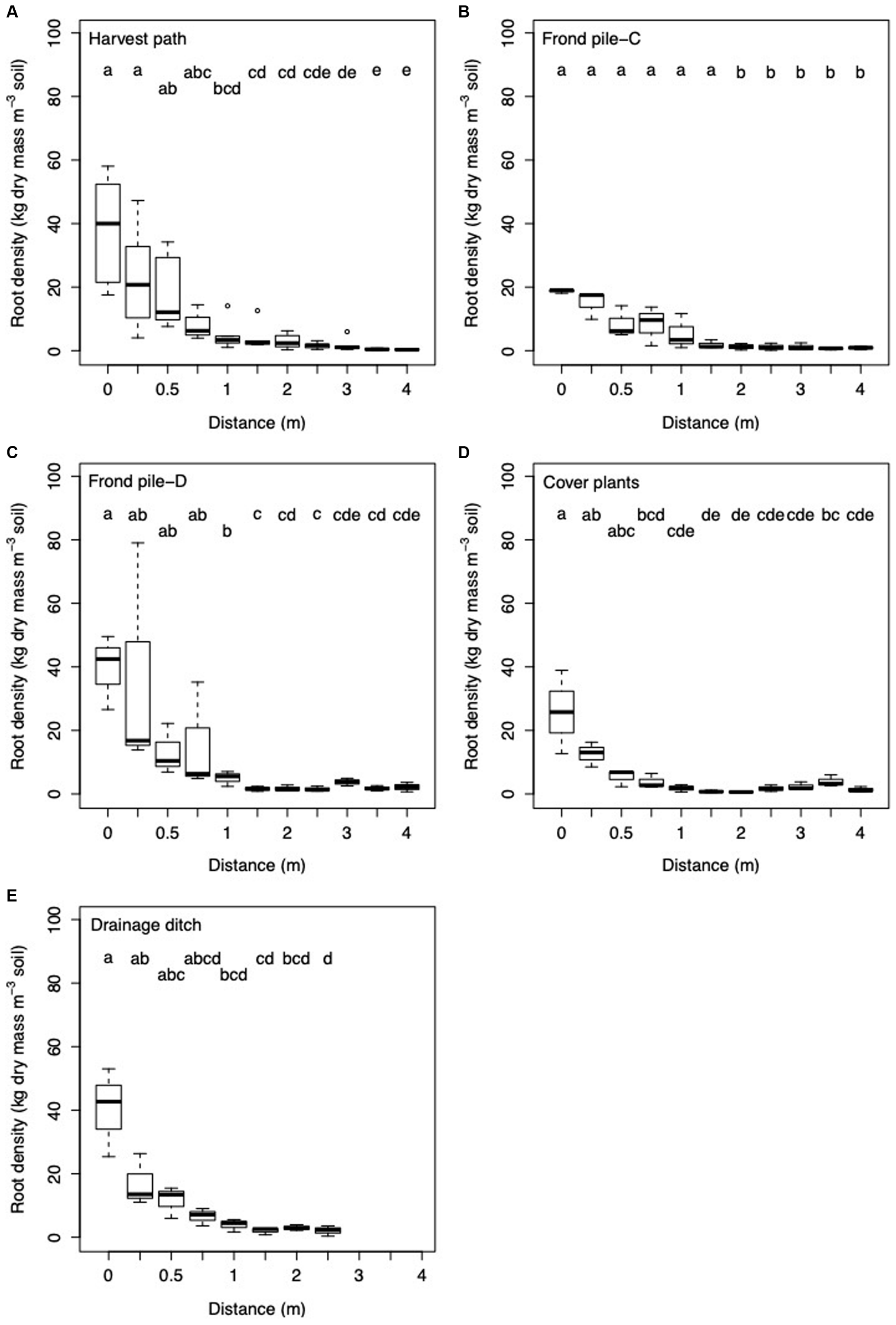

FIGURE 6
Box and whisker plot of root density with increasing distance from palm in the **(A)** harvest path (n = 64); **(B)** frond pile next to the cover plants, Frond pile-C (n = 33); **(C)** frond pile next to the drainage ditch, Frond pile-D (n = 33); **(D)** cover plants (n = 33); and **(E)** towards the drainage ditch (n = 24). Letters signify significant difference between the results.

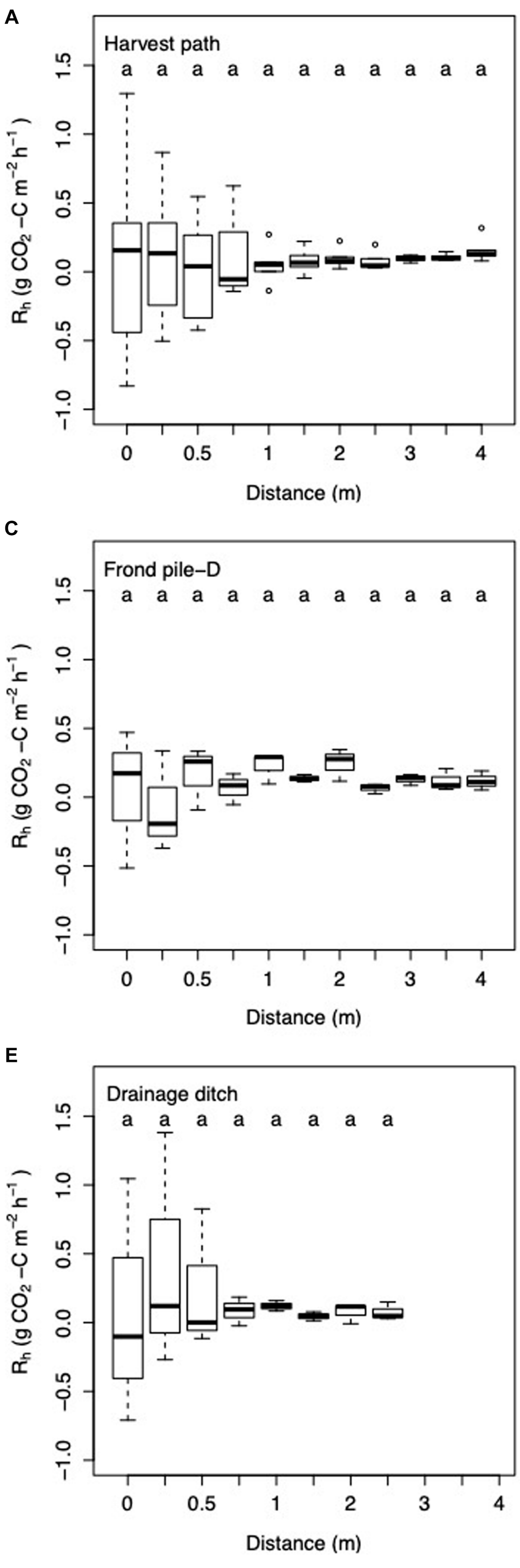

FIGURE 7
Box and whisker plot of R_h with increasing distance from palm in the **(A)** harvest path (*n* = 64); **(B)** frond pile next to the cover plants, Frond pile-C (*n* = 33); **(C)** frond pile next to the drainage ditch, Frond pile-D (*n* = 33); **(D)** cover plants (*n* = 33); and **(E)** towards the drainage ditch (*n* = 24). Here the linear regression equation substitution method was used to partition R_{tot} into R_h and R_a. Letters signify significant difference between the results.

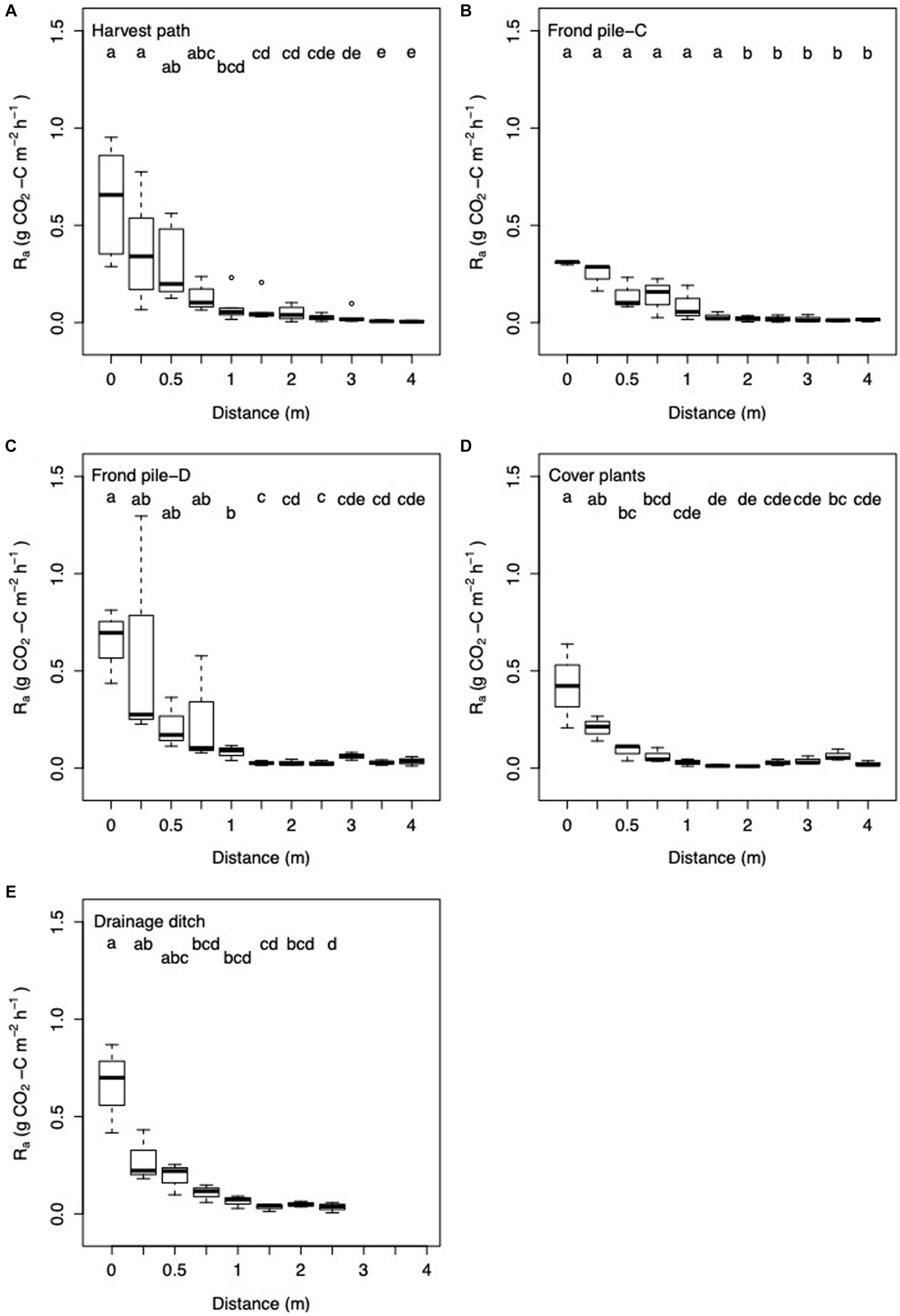

FIGURE 8
Box and whisker plot of R_a with increasing distance from palm in the **(A)** harvest path (*n* = 64); **(B)** frond pile next to the cover plants, Frond pile-C (*n* = 33); **(C)** frond pile next to the drainage ditch, Frond pile-D (n = 33); **(D)** cover plants (*n* = 33); and **(E)** towards the drainage ditch (*n* = 24). Here the linear regression equation substitution method was used to partition R_{tot} into R_h and R_a. Letters signify significant difference between the results.

TABLE 4 Plantation R_{tot}, R_h and R_a estimates. Results are presented in g CO_2-C m^{-2} h^{-1} and standard errors of the mean are included. Straight mean averaging results have not been corrected to take the drainage ditch area into account. Area-weighted upscaling results have been presented that do not and do take the proportional area of the oil palm drainage ditches and soil under the palm into account (aka 9 % of the plantation surface area). Average estimates of R_h and R_a have been proposed.

Environmental variable	Plantation means	Means within the different surface microforms					
		Rhizosphere (≤ 1 m distance from the palm)	Away from palm (> 1 m distance from the palm)				
			Harvest path	Frond pile by the cover plants	Frond pile by the drainage ditches	Cover plants	Drainage ditches
Physical variables							
Bulk density* (g cm^{-3})	0.15 (±0.008)	–	0.14^a (±0.008)	0.14^a (±0.008)		0.17^b (±0.005)	–
Chemical variables							
Soil C* (%)	48.72 (±0.61)	49.08^a (±0.46)	48.80^{ab} (±0.60)	49.44^{ab} (±0.79)	50.19^a (±0.78)	46.16^b (±0.69)	50.17^{ab} (±0.98)
Soil C content to 10 cm*** (g C m^{-2})		–	6832^a (±83.93)	6921.6^a (±111.07)	7026.6^a (±109.29)	7847.2^b (±121.43)	7023.8^a (±137.5)
Soil N** (%)	1.95 (±0.046)	1.91^a (±0.043)	1.92^{ab} (±0.033)	2.52^b (±0.32)	1.93^{ab} (±0.061)	2.02^{ab} (±0.038)	1.93^{ab} (±0.079)
Soil N content to 10 cm*** (g N m^{-2})		–	268.8^a (±4.64)	352.8^{bc} (±45)	270.2^{ab} (±8.57)	343.4^c (±6.51)	270.2^{ab} (±11.07)
Soil C:N*** (%)	25.54 (±0.62)	26.25^a (±0.41)	25.77^{ab} (±0.59)	22.60^a (±1.41)	26.49^a (±1.03)	23.00^b (±0.61)	26.24^{ab} (±1.30)
Soil C:N content to 10 cm** (%)	25.13 (±0.22)		25.42^{ab} (±0.13)	19.62^b (±2.33)	26.01^a (±0.42)	22.85^b (±0.087)	25.99^{ab} (±0.56)
Soil pH**	3.50 (±0.028)	3.52^{ab} (±0.020)	3.48^a (±0.023)	3.57^{ab} (±0.064)	3.49^{ab} (±0.054)	3.66^b (±0.064)	3.37^a (±0.056)
Environmental variables							
Soil moisture*** (%)	63.11 (±3.06)	24.52^a (±1.90)	68.48^b (±2.98)	49.27^{bc} (±4.28)	43.22^{bc} (±2.70)	36.71^c (±4.54)	45.29^{bc} (±4.97)
Soil temperature** (°C)	27.69 (±0.094)	27.81^a (±0.099)	27.70^a (±0.097)	27.70^a (±0.089)	27.08^b (±0.21)	27.76^a (±0.12)	27.26^{ab} (±0.42)

Standard errors of the mean are included. Stars denote whether the environmental variable varied significantly between the different surface microforms.

there was minimal root density halfway between two palms, suggesting that roots do not grow as far from the palm in peat soil as they do in mineral soil.

4.3 Variation in R_{tot} is influenced by environmental drivers, as well as root density and distance from palm

R_{tot} showed significant spatial variation driven by environmental drivers, as well as driven by distance from palm and surface management microform, which may better explain variation in R_h. Soil pH, soil temperature, air temperature and soil moisture all significantly explained variation in R_{tot}. Soil pH significantly explained variation in R_{tot}, with different relationships seen in the different surface microforms. Soil pH varied within the plantation (from 3.08 to 4.45), with pH in soil beneath cover plants being higher than elsewhere. The cover crops consisted of leguminous cover crops, such as *Mucuna bracteate*. These are planted in oil palm plantations on peat for nitrogen fixation and to preserve soil moisture, in order to minimize the risk of peat subsidence and fires (Othman et al., 2012). In this study, total nitrogen was higher in the cover plant microform than in the other surface microforms, suggesting that some of the nitrogen produced by the cover plants entered the peat soil system and increased the pH locally. Nitrogen fertilization with urea has been shown to increase rates of R_h (Comeau et al., 2016). The increase in R_{tot} in the cover plants may therefore be caused by the increase in ammonium from nitrogen fixation in the legumes increasing rates of R_h, with soil pH acting as an indicator of the process.

R_{tot} increased significantly as soil temperature increased. Temperature has been shown to increase the rate of respiration due to an increase in activation energy for biochemical reactions (Lloyd and Taylor, 1994). This can be used as a management strategy - shading tropical peat by 90% has been shown to reduce rates of R_h by 30% (Jauhiainen et al., 2014). The relationship between R_{tot} and soil temperature did not vary with microform in this study, despite the frond pile and cover plants offering shade. Manning et al. (2019) found that soil temperature and R_h varied between soil management microforms when measured over a year. In longer-term studies at other sites, soil temperature has consistently had a significant effect increasing rates of respiration from peat soil, both when roots were present (Farmer, 2013; Sakata et al., 2015) and absent (Comeau, 2016; Hergoualc'h et al., 2017; Ishikura et al., 2018).

R_{tot} increased significantly as soil moisture decreased. Soil moisture inhibits R_h by preventing heterotrophic micro-organisms from decomposing the peat, due to the absence of oxygen (Hirano et al., 2012; Mishra et al., 2014; Tonks et al., 2017). Longitudinal data from this site showed that all of the surface microforms had higher R_h

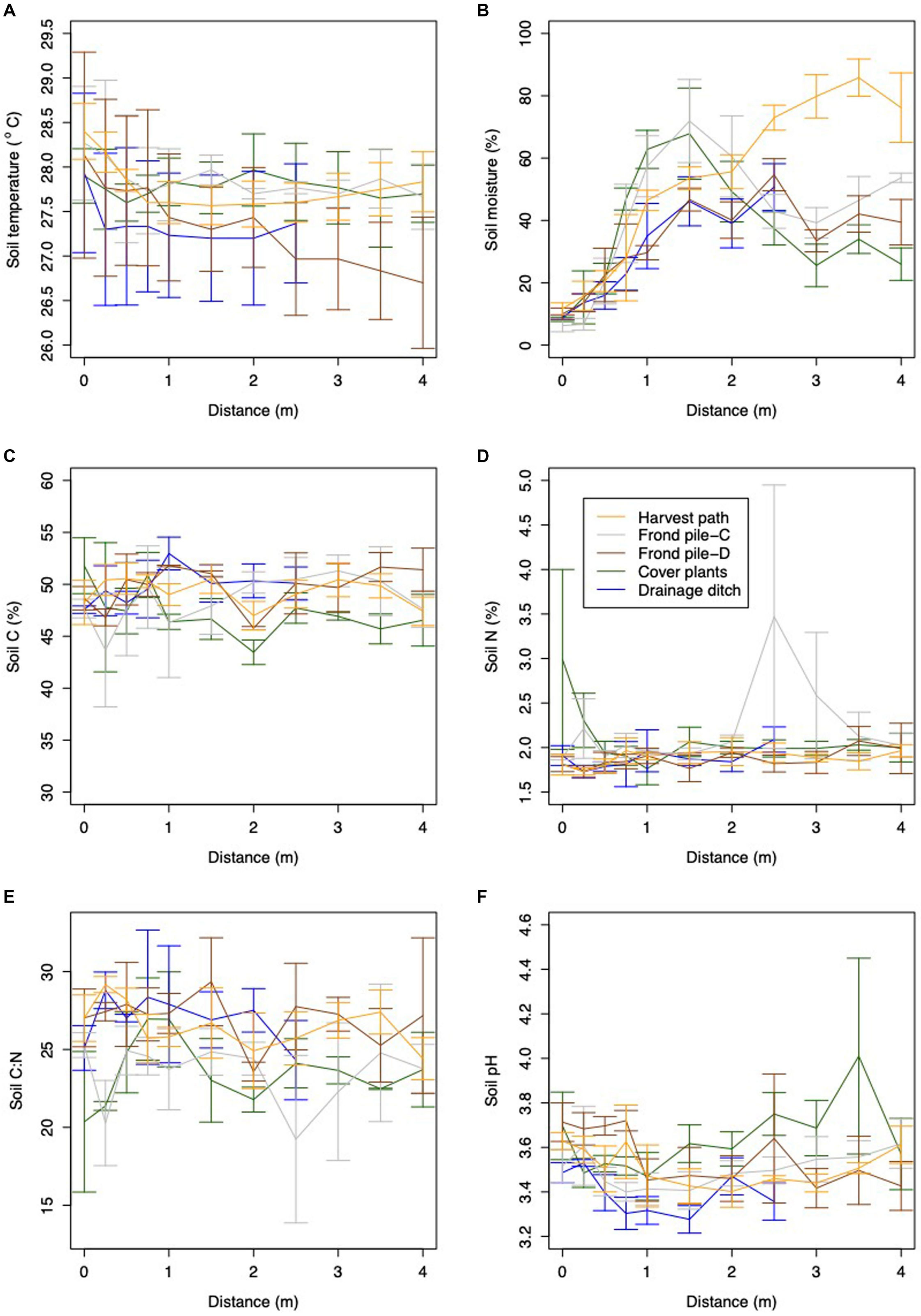

FIGURE 9
Variation in environmental variables with distance in the different transects, including: **(A)** soil temperature, **(B)** soil moisture, **(C)** soil C, **(D)** soil N, **(E)** soil C:N and **(F)** soil pH. Error bars show the standard error of the mean.

rates at lower soil moisture levels, with the frond piles having the strongest effects (Manning et al., 2019). Similar trends have been seen at other oil palm plantations on peat soil (Hergoualc'h et al., 2017; Ishikura et al., 2018; Matysek et al., 2018).

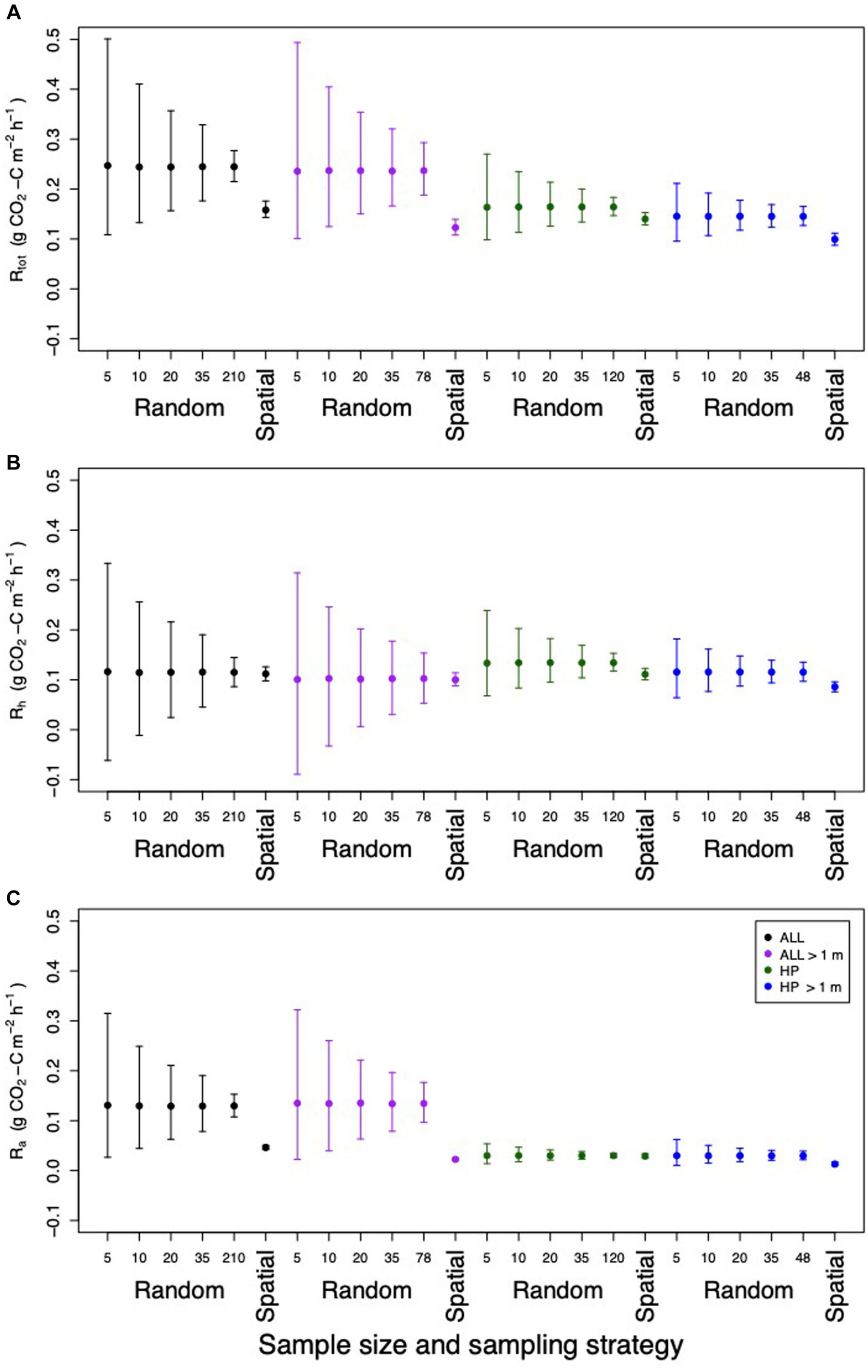

FIGURE 10
Estimated plantation mean and 95% confidence intervals for **(A)** R_{tot}, **(B)** R_h and **(C)** R_a when different sample sizes and sampling strategies are used. Results were bootstrapped 10,000 times and then random sampling was applied to 5, 10, 20 and 35 randomly selected samples or the entire dataset. The entire dataset was used in the spatial sampling. This analysis was repeated on all samples (black), samples taken >1 m from the palm (purple), samples taken from the harvest path (green) and samples taken >1 m from the palm in the harvest path (blue).

Bulk density was significantly higher in the cover plants than in the harvest path or frond piles. Bulk density was not included in the environmental linear mixed effect model in this plantation due to the bulk density being taken, necessarily (because it disturbs the soils), from slightly different locations to the respiration and root measurements. Melling et al. (2013) found higher R_{tot} measurements when bulk densities were higher. In this plantation, soil bulk density was significantly higher in the cover plants than from the harvest path or frond piles due to compaction of the harvest path by machinery (Melling et al., 2009). It would be expected that there would therefore be an increase in rates of R_{tot} and R_h in the cover plants at this plantation due to the increase in bulk density.

4.4 Plantation-scale estimates of R_{tot}, R_h and R_a

The plantation-scale estimates calculated using area-weighted upscaling were decided to give the best estimates of plantation R_{tot}, R_h and R_a. The best estimate of plantation R_{tot} in this study was 0.158 ± 0.016 g CO_2-C m^{-2} h^{-1}, the best estimates of R_h ranged from 0.112 ± 0.016 to 0.147 ± 0.020 g CO_2-C m^{-2} h^{-1}, and the best estimates of R_a ranged from 0.011 ± 0.004 to 0.046 ± 0.026 g CO_2-C m^{-2} h^{-1}. These estimates take into account the spatial variation within the oil palm plantation, including scaling to include the proportional area of the drainage ditches. None of these values should be used as annual estimates of R_{tot}, R_a and R_h fluxes because they were not taken over the year and R_{tot} and R_a have been shown to have significant temporal variation (Manning et al., 2019).

Two methods were used to partition R_{tot} into R_h and R_a in order to get these estimates. The lower result comes from the linear regression method, which assumes that the only variation in R_{tot} is due to variation in R_h and that R_a is fixed. The higher result comes from the distance from palm method, which assumes that the only variation in R_{tot} is due to variation in R_a and that R_h is fixed. This study has shown that R_{tot}, root density, R_h and R_a all vary spatially within the plantation. Therefore, the best estimate will lie between these values, with these values providing the upper and lower boundary. We propose that the real value of R_h falls between these two values, i.e., 0.130 ± 0.046 g CO_2-C m^{-2} h^{-1}. The best estimate of R_a therefore lies between the estimates of 0.011 ± 0.026 and 0.046 ± 0.004 g CO_2-C m^{-2} h^{-1}, i.e., 0.029 ± 0.030 g CO_2-C m^{-2} h^{-1}.

Estimates of R_{tot}, R_h and R_a are similar to other reported estimates of these fluxes in the literature. Published results from chamber measurements of R_{tot} have a mean of 0.207 ± 0.016 g CO_2-C m^{-2} h^{-1} and range between 0.085 and 0.365 g CO_2-C m^{-2} h^{-1} (Murayama and Bakar, 1996; Melling et al., 2005; Farmer, 2013; Melling et al., 2013; Dariah et al., 2014; Husnain et al., 2014; Sakata et al., 2015; Comeau, 2016; Comeau et al., 2016; Hergoualc'h et al., 2017; Ishikura et al., 2018; Matysek et al., 2018; Manning et al., 2019; Cooper et al., 2020).

Published results from chamber measurements of R_h have a mean of 0.152 ± 0.014 g CO_2-C m^{-2} h^{-1} and range from 0.047 to 0.307 g CO_2-C m^{-2} h^{-1} and published results from chamber measurements of R_a have a mean of 0.088 ± 0.018 g CO_2-C m^{-2} h^{-1} and range from 0.001 to 0.290 g CO_2-C m^{-2} h^{-1} (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; Manning et al., 2019; Cooper et al., 2020).

4.5 Partitioning methodology and sample size can bias plantation-scale flux estimates

Obtaining accurate estimates of R_{tot}, R_h and R_a is essential in order to create precise flux estimates for climate modeling and for local to global policy decision-making. Published estimates of R_{tot}, R_h and R_a vary by factors of 4.3, 6.5 and 290.0, respectively. Five reasons why this range is so large include: (1) different partitioning methodologies, (2) different sample sizes, (3) within plantation spatial variations, (4) within plantation micro-climates and (5) variation in temporal dynamics and seasonality. Here we address some of the errors that can be brought in by not taking the first four reasons into account. The fifth reason is explored in more detail in Manning et al. (2019), where significant variation between R_{tot} and R_a was driven by temporal changes in environmental drivers at this site.

Firstly, this study considered how two different partitioning methodologies gave different results. Estimates of R_h and R_a measured in this study varied by 30 and 61% respectively, considering the straight mean averaging results, and between 24 and 318% for the area-weighted upscaling results. This is important because R_h is often compared between studies without different partitioning methodologies being considered. We recommend using multiple methods to partition R_{tot} into R_h and R_a where possible, to reduce experimental bias being interpreted as between site variations. We also recommend that modeling studies take partitioning method into account as a covariate.

Secondly, sample size was explored in this research. Sample sizes for R_{tot} in the literature range from 3 to 72, with an average of 24 samples (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; Manning et al., 2019; Cooper et al., 2020). This study showed that changing the sample size of the dataset gave different results for R_{tot}, R_h and R_a. Using resampling techniques to model the sample size of random sampling from 5 to 10, 20 and 35 samples reduced the confidence intervals of the estimate of R_{tot}, R_h and R_a, making sure that it was more accurate. A power analysis on the dataset in this study suggested that 35 samples were sufficient to give a precise estimate of plantation-scale R_{tot}, when the samples were stratified based on distance from palm and surface management microform. This suggests that future sampling designs could have more accuracy with larger sample sizes than the average found in the literature.

Thirdly, within-plantation spatial variation was shown to give significant variation in R_{tot}, R_h and R_a in this study. Therefore, estimates of R_{tot}, R_h and R_a could be inaccurate if spatial variation is not taken into account. The high root density around the palm and high R_a fluxes in the rhizosphere had a large influence on plantation-scale estimates of respiration. Modeling the difference in R_{tot}, R_h and R_a in this study when the rhizosphere was excluded, gave 22, 11 and 50% lower estimates of R_{tot}, R_h and R_a, respectively. Furthermore, estimates of plantation-scale R_{tot} reduced by 34% when results were scaled up using area-weighted upscaling as opposed to straight mean averaging. This was due to the large contribution from R_a next to the palm that was overrepresented without weighting. Estimates of R_a reduced by 81 and 64% between straight mean averaging and area-weighted upscaling for the results calculated using the distance from palm method and linear regression method, respectively. Similarly, estimates of R_h reduced by 9 and 2% between straight mean averaging and area-weighted upscaling for the results calculated using the distance from palm method and linear regression method. Taken collectively, these results highlight the importance of the spatial variation caused by the rhizosphere in plantation-scale estimates, particularly for accurate estimates of R_{tot} and R_a.

Fourthly, within plantation micro-climates (aka the surface management microforms) were investigated in this study and one of the key results from this paper was that R_{tot} and R_a varied between the different surface management microforms outside of the rhizosphere. Here and in Manning et al. (2019) we show different dynamics in soil organic matter mineralization in the different surface management microforms, highlighting the importance of representing these microforms in the plantation-scale respiration estimates. Our sensitivity analysis shows a reduction in plantation-scale R_{tot} and R_a and an increase in R_h if samples were taken from the harvest path transect only. Other studies measuring R_{tot}, R_h and R_a from oil palm plantations have focused on measurements in the harvest path, with the exception of Manning et al. (2019), which may lead to an overestimation in plantation R_h.

5 Conclusion

R_h did not show significant spatial variation in the oil palm plantation but varied significantly between the subplots. This suggested that oil palm root patterns and soil management microforms do not substantially affect variation in R_h. Environmental drivers, including soil temperature and soil moisture, had significant effects on variation in R_{tot} and may better explain variation in R_h. This snapshot study has not investigated the spatial and temporal trends in environmental drivers and whether this influences the microclimates in the different surface microforms differently, with corresponding impacts on R_h.

Spatial variation in root density drove the variation in R_{tot} and R_a in an oil palm plantation on peat soil. R_{tot}, R_a and root density were highest next to the palm and decreased with increasing distance from the palm. Root density showed competition dynamics between oil palm and cover plant roots, with greater root density measured in the rhizosphere in the transects that were growing in directions away from the cover plants. R_a and root density were highest from the drainage ditch and frond pile next to the drainage ditch transects.

Plantation best estimates of R_{tot}, R_h, R_a were 0.158 ± 0.016, 0.130 ± 0.036 and 0.029 ± 0.030 g CO_2-C m^{-2} h^{-1}, respectively. Area-weighted upscaling gave better estimates of R_{tot}, R_h and R_a due to weighting the high R_{tot} and R_a fluxes next to the palm. Not using area-weighted upscaling changed estimates of R_{tot}, R_h and R_a by 34, 6 and 75%, respectively.

Two different methods were used to partition R_{tot} into R_h and R_a, the distance from palm method and the linear regression method. R_h measurements were higher from the distance from palm method. Both methods have value and the best estimate will be between the two.

Overall, we show that root competition appears to impact oil palm root growth, which may have implications for productivity and nutrient cycling in agroforestry, intercropping or cover cropping systems. We also show that with plantation spatial dynamics need to be taken into account for the calculation of reliable estimates of R_{tot} and R_a. We propose that temporal variation in water table, soil moisture and temperature may be more important for variation in R_h than within plantation spatial variation from surface management microforms.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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 manuscript. LK was involved in the study design, data collection, field support, and data interpretation. TN and ER were involved in the data collection and field support. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1236566/full#supplementary-material

References

Baggs, E. M. (2006). Partitioning the components of soil respiration: a research challenge. *Plant Soil* 284, 1–5. doi: 10.1007/s11104-006-0047-7

Carlson, K. M., Gerber, J. S., Mueller, N. D., Herrero, M., MacDonald, G. K., Brauman, K. A., et al. (2017). Greenhouse gas emissions intensity of global croplands. *Nat. Clim. Chang.* 7, 63–68. doi: 10.1038/nclimate3158

Carlson, K. M., Goodman, L. K., and May-Tobin, C. C. (2015). Modeling relationships between water table depth and peat soil carbon loss in southeast Asian plantations. *Environ. Res. Lett.* 10:074006. doi: 10.1088/1748-9326/10/7/074006

Comeau, L. P. (2016) *Carbon dioxide fluxes and soil organic matter characteristics on an intact peat swamp forest, a drained and logged forest on peat, and a peatland oil palm plantation*. Indonesia: University of Aberdeen

Comeau, L. P., Hergoualc'h, K., Hartill, J., Smith, J., Verchot, L. V., Peak, D., et al. (2016). How do the heterotrophic and the total soil respiration of an oil palm plantation on peat respond to nitrogen fertilizer application? *Geoderma* 268, 41–51. doi: 10.1016/j.geoderma.2016.01.016

Cook, S., Whelan, M. J., Evans, C. D., Gauci, V., Peacock, M., Garnett, M. H., et al. (2018). Fluvial organic carbon fluxes from oil palm plantations on tropical peatland. *Biogeosciences* 15, 7435–7450. doi: 10.5194/bg-15-7435-2018

Cooper, H. V., Evers, S., Aplin, P., Crout, N., Dahalan, M. P. B., and Sjogersten, S. (2020). Greenhouse gas emissions resulting from conversion of peat swamp forest to oil palm plantation. *Nat. Commun.* 11, 1–8. doi: 10.1038/s41467-020-14298-w

Corley, R. H., and Tinker, P. B. (2008) *The oil palm*. Hoboken, NJ: John Wiley & Sons.

Dariah, A., Setiari Marwanto, S., and Agus, F. (2014). Root-and peat-based CO2 emissions from oil palm plantations. *Mitig. Adapt. Strateg. Glob. Chang.* 19, 831–843. doi: 10.1007/s11027-013-9515-6

FAO (2006) *World Reference Base for soil resources 2006: a framework for international classification*, Correlation and Communication. Rome

Farmer, J. (2013) *Measuring and modeling soil carbon and carbon dioxide emissions from Indonesian peatlands under land use change*. University of Aberdeen. United Kingdom

Hammond, R., and McCullagh, P. S. (1978) *Quantitative techniques in geography: an introduction*. Clarendon Press. Oxford

Hergoualc'h, K., Hendry, D. T., Murdiyarso, D., and Verchot, L. V. (2017). Total and heterotrophic soil respiration in a swamp forest and oil palm plantations on peat in Central Kalimantan, Indonesia. *Biogeochemistry* 135, 203–220. doi: 10.1007/s10533-017-0363-4

Hirano, T., Segah, H., Kusin, K., Limin, S., Takahashi, H., and Osaki, M. (2012). Effects of disturbances on the carbon balance of tropical peat swamp forests. *Glob. Chang. Biol.* 18, 3410–3422. doi: 10.1111/j.1365-2486.2012.02793.x

Hoojier, A., Page, S., Jauhiainen, J., Lee, W. A., Lu, X. X., Idris, A., et al. (2012). Subsidence and carbon loss in drained tropical peatlands. *Biogeosciences.* 9, 1053–1071.

Husnain, H., Wigena, I. G. P., Dariah, A., Marwanto, S., Setyanto, P., and Agus, F. (2014). CO2 emissions from tropical drained peat in Sumatra, Indonesia. *Mitig. Adapt. Strateg. Glob. Chang.* 19, 845–862. doi: 10.1007/s11027-014-9550-y

Ishikura, K., Hirano, T., Okimoto, Y., Hirata, R., Kiew, F., Melling, L., et al. (2018). Soil carbon dioxide emissions due to oxidative peat decomposition in an oil palm plantation on tropical peat. *Agric. Ecosyst. Environ.* 254, 202–212. doi: 10.1016/j.agee.2017.11.025

Jauhiainen, J., Kerojoki, O., Silvennoinen, H., Limin, S., and Vasander, H. (2014). Heterotrophic respiration in drained tropical peat is greatly affected by temperature-a passive ecosystem cooling experiment. *Environ. Res. Lett.* 9:105013. doi: 10.1088/1748-9326/9/10/105013

Jourdan, C., and Rey, H. (1997). Modelling and simulation of the architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. *Plant Soil* 190, 235–246. doi: 10.1023/A:1004270014678

Kucera, C., and Kirkham, D. R. (1971). Soil respiration studies in tallgrass prairie in Missouri. *Ecology* 52, 912–915. doi: 10.2307/1936043

Livingston, G. P., and Hutchinson, G. L. (1995). "Enclosure-based measurement of trace gas exchange: applications and sources of error" in *Methods in ecology. Biogenic trace gases: measuring emissions from soil and water*. eds. P. A. Matson and R. C. Harriss (Malden, Mass: Blackwell Science), 14–51.

Lloyd, J., and Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323. doi: 10.2307/2389824

Manning, FC (2019) *Carbon dynamics in oil palm agro-ecosystems*. University of Aberdeen, United Kingdom.

Manning, F. C., Kho, L. K., Hill, T. C., Cornulier, T., and Teh, Y. A. (2019). Carbon emissions from oil palm plantations on peat soil. *Front. For. Glob.* 2:37. doi: 10.3389/ffgc.2019.00037

Marthews, T. R., Metcalfe, D., Malhi, Y., Phillips, O., Huaraca Huasco, W., Riutta, T., et al (2012) Measuring tropical forest carbon allocation and cycling: a RAINFOR-GEM field manual for intensive census clots (v2.2). Available at:http://gem.tropicalforests.ox.ac.uk/.

Matysek, M., Evers, S., Samuel, M. K., and Sjogersten, S. (2018). High heterotrophic CO2 emissions from a Malaysian oil palm plantations during dry-season. *Wetl. Ecol. Manag.* 26, 415–424. doi: 10.1007/s11273-017-9583-6

McCalmont, J., Kho, L. K., Teh, Y. A., Lewis, K., Chocholek, M., Rumpang, E., et al. (2021). Short-and long-term carbon emissions from oil palm plantations converted from logged tropical peat swamp forest. *Glob. Chang. Biol.* 27, 2361–2376. doi: 10.1111/gcb.15544

Melling, L., Chaddy, A., Goh, K. J., and Hatano, R. (2013). Soil CO2 fluxes from different ages of oil palm in tropical peatland of Sarawak, Malaysia as influenced by environmental and soil properties. *Acta Hortic.* 982, 25–35. doi: 10.17660/ActaHortic.2013.982.2

Melling, L., Chua, K., and Lim, K. (2009) *Managing peat soils under oil palm*. Available at: http://tropicalpeat.sarawak.gov.my/modules/web/pages.php?mod=download&sub=download_show&id=16

Melling, L., Hatano, R., and Goh, K. J. (2005). Methane fluxes from three ecosystems in tropical peatland of Sarawak, Malaysia. *Soil Biol. Biochem.* 37, 1445–1453. doi: 10.1016/j.soilbio.2005.01.001

Metcalfe, D., Meir, P., Aragão, L. E. O. C., da Costa, A., Almeida, S., Braga, A., et al. (2008). Sample sizes for estimating key ecosystem characteristics in a tropical terra firme rainforest. *For. Ecol. Manag.* 255, 558–566. doi: 10.1016/j.foreco.2007.09.026

Miettinen, J., Shi, C., and Liew, S. C. (2016). Land cover distribution in the peatlands of peninsular Malaysia, Sumatra and Borneo in 2015 with changes since 1990. *Glob. Ecol. Conserv.* 6, 67–78. doi: 10.1016/j.gecco.2016.02.004

Mishra, S., Lee, W. A., Reuben, S., Sudiana, I. M., Idris, A., and Swarup, S. (2014). Microbial and metabolic profiling reveal strong influence of water table and land-use patterns on classification of degraded tropical peatlands. *Biogeosciences* 11, 1727–1741. doi: 10.5194/bg-11-1727-2014

Murayama, S., and Bakar, Z. A. (1996). Decomposition of tropical peat soils. *Jpn. Agric. Res. Q.* 30, 145–151.

Othman, H., Darus, F. M., and Hashim, Z. (2012) Best management practices for oil palm cultivation on peat: Mucuna bracteata as ground cover crop. Available at: (http://palmoilis.mpob.gov.my/publications/TOT/TT-501.pdf).

Page, S. E., Rieley, J. O., and Banks, C. J. (2011). Global and regional importance of the tropical peatland carbon pool. *Glob. Chang. Biol.* 17, 798–818. doi: 10.1111/j.1365-2486.2010.02279.x

Philipson, J. J., and Coutts, M. P. (1978). The tolerance of tree roots to waterlogging: III. Oxygen transport in lodgepole pine and Sitka spruce roots of primary structure. *New Phytol.* 80, 341–349. doi: 10.1111/j.1469-8137.1978.tb01567.x

Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D.R Core Team (2017) Nlme: linear and nonlinear mixed effect models. Available at: https://CRAN.R-project.org/package=nlme.

Pohlert, T (2018) Package 'PMCMR'. Available at: https://cran.r-project.org/web/packages/PMCMR/index.html.

Rahmadhani, T. P., Suwandi, S., and Suparman, S. (2020). Growth responses of oil palm seedling inoculated with Ganoderma boninense under competition with edible herbaceous plants. *J. Sci. Agric.* 35, 45–49. doi: 10.25081/jsa.2020.v4.6231

Sakata, R., Shimada, S., Arai, H., Yoshioka, N., Yoshioka, R., Aoki, H., et al. (2015). Effect of soil types and nitrogen fertilizer on nitrous oxide and carbon dioxide emissions in oil palm plantations. *Soil Sci. Plant Nutr.* 61, 48–60. doi: 10.1080/00380768.2014.960355

Subke, J. A., Inglima, I., and Cotrufo, M. F. (2006). Trends and methodological impacts in soil CO2 efflux partitioning: a metaanalytical review. *Glob. Chang. Biol.* 12, 921–943. doi: 10.1111/j.1365-2486.2006.01117.x

Tonks, A. J., Aplin, P., Beriro, D. J., Cooper, H., Evers, S., Vane, C. H., et al. (2017). Impacts of conversion of tropical peat swamp forest to oil palm plantation on peat organic chemistry, physical properties and carbon stocks. *Geoderma* 289, 36–45. doi: 10.1016/j.geoderma.2016.11.018