

AGROECOSYSTEMS

How does replacing natural forests with rubber and oil palm plantations affect soil respiration and methane fluxes?

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Citation: Aini, F. K., K. Hergoualc'h, J. U. Smith, L. Verchot, and C. Martius. 2020. How does replacing natural forests with rubber and oil palm plantations affect soil respiration and methane fluxes? *Ecosphere* 11(11):e03284. 10.1002/ecs2.3284

Abstract. Replacement of forest by agricultural systems is a major factor accelerating the emissions of greenhouse gases; however, related field studies in the tropics are very scarce. To evaluate the impact of forest transition to plantations on soil methane (CH₄) and respiration (CO₂) fluxes, we conducted measurements in an undisturbed forest, a disturbed forest, young and old rubber plantations, and an oil palm plantation on mineral soil in Jambi, Sumatra, Indonesia. Methane fluxes and their controlling variables were monitored monthly over fourteen months; soil respiration was measured less frequently. All of the plantations were managed by smallholders and had never been fertilized. To assess the effect of common management practices in oil palm plantations, we added urea at a rate of 33.3 kg N/ha and thereafter monitored intensively soil CH₄ fluxes. The soil acted as a sink for CH₄ (kg CH₄-C·ha⁻¹·yr⁻¹) in the undisturbed forest (-1.4 ± 1.0) and young rubber plantation (-1.7 ± 0.7). This was not the case in the other land-use systems which had fluxes similar to fluxes in the undisturbed forest, with 0.4 ± 0.9, -0.2 ± 0.3, and 0.2 ± 0.7 kg·ha⁻¹·yr⁻¹ in the disturbed forest, old rubber plantation, and oil palm plantation, respectively. In the oil palm plantation, there was no inhibitory effect of nitrogenous fertilizer on methanotrophy. Annual soil respiration (Mg CO₂-C·ha⁻¹·yr⁻¹) was higher in the oil palm plantation (17.1 ± 1.9) than in the undisturbed forest (13.9 ± 1.2) while other land-use systems respired at a similar level to the undisturbed forest (13.1 ± 1.4, 15.9 ± 1.7, and 14.1 ± 1.0 in the disturbed forest, young, and old rubber plantations, respectively). Substrate (litterfall and soil) availability and quality exerted a strong control over annual fluxes of both gases along the land-use gradient. Temporal variation in CH₄ was extremely high and in respiration fluxes was moderate, but was not specifically linked to seasonal variation. Further comprehensive and long-term research is critically needed to determine more thoroughly the direction and magnitude of changes in soil trace gas emissions as affected by forest-to-plantation conversion in the tropics.

Key words: CH₄; CO₂; fertilizer; forest conversion; land-use change; smallholder.

Received 17 April 2020; **accepted** 20 April 2020; **final version received** 14 September 2020. **Corresponding Editor:** Debra P. C. Peters.

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INTRODUCTION

Human activities greatly increase greenhouse gas emissions (Hütsch 2001), in particular those of methane (CH₄) and carbon dioxide (CO₂; Muñoz et al. 2010). In the atmosphere, methane has a short residence time (~9 yr; Montzka et al. 2011) but absorbs 32 times more long-wave radiation than CO₂ and has the second highest contribution to radiative forcing after CO₂, contributing approximately 20% to climate change (Hütsch 2001). Ciais et al. (2013) reported that atmospheric CH₄ concentrations reached 1803 ppb in 2011, an increase of 250% over the pre-industrial period (722 ppb). From 1750 to 2016, atmospheric CO₂ concentrations increased by 44% from 278 to 400 ppm as a result of cement production and fossil fuel combustion (together contributing 68% of global CO₂ emissions) and land-use change (which contributes 32% of global CO₂ emissions; Ciais et al. 2013, Le Quéré et al. 2016). The latest observation at the Mauna Loa Observatory in Hawaii in March 2019 indicates a high record level of CO₂ (411 ppm) in the atmosphere (<https://www.esrl.noaa.gov/gmd/ccgg/trends/monthly.html>).

Land-use change is a key contributor to greenhouse gas emissions in the tropics (DeFries et al. 2006). Gibbs et al. (2010) reported that agriculture has contributed to more than 70% of forest loss across the tropics. Maintaining the forest cover is a low-cost method to mitigate climate change but remains difficult to achieve with the rising demand for agricultural products due to the continued population growth (DeFries et al. 2010). Between 2000 and 2012, Indonesia lost primary forest, at a rapid rate of 0.84 Mha yr⁻¹, due to conversion to agricultural lands (Margono et al. 2014). However, the moratorium policy on new land concessions that was put in place in 2011 has successfully slowed the rate of conversion to plantations (Chen et al. 2019). Rubber is the second most important agricultural commodity in the country, and a key driver of deforestation. In 2013, the rate of rubber plantation expansion was 1.42% with the majority of plantations belonging to smallholders (85%; Kurniawan et al. 2014). Oil palm plantations in Indonesia expanded rapidly at rates of 3.3% and 11.3% yr⁻¹ in 2009 and 2013 (Ulum and Hariyanto 2014), with 52% of them being managed

by private companies, 42% by smallholders, and 8% by state companies. The region of Jambi in Sumatra is an important production area for rubber and palm oil by supplying, respectively, 10% and 6% of the national production in 2013 (Kurniawan et al. 2014, Ulum and Hariyanto 2014). Despite continued forest replacement by plantations, uncertainties of greenhouse gas emissions associated with oil palm and rubber expansion remain high. In particular, CH₄ and CO₂ emission factors characterizing the impact of forest degradation and conversion to oil palm and rubber plantations are critically lacking.

The soil is a net sink for CH₄, globally taking up CH₄ at a rate of around 21 Tg C yr⁻¹ (Ciais et al. 2013). Methane is emitted or taken up by the soil depending on the balance between methanotrophy and methanogenesis. Methanogenesis is favored by anaerobic conditions (Dutaur and Verchot 2007, Naser et al. 2007) but also occurs as the result of termite activity or in aerobic soils within anaerobic microsites (Eggleton et al. 1999, Jamali et al. 2011). Aerated and dry soils favor methanotrophy (CH₄ oxidation) and usually act as sinks for CH₄ (Hütsch 2001). Soil respiration (R_S) is a general term referring to CO₂ production by both heterotrophic respiration by microbes and fauna such as termites (R_H) and autotrophic respiration by vegetation (R_A; Subke et al. 2006, Risch et al. 2012). In forests, the contribution of R_A and R_H to R_S is estimated to be equally important (46% for R_A, 54% for R_H) while in non-forest ecosystems (oil palm plantations, pastures, grasslands, croplands), R_A contributes on average 61% to R_S (Hanson et al. 2000). The estimation of annual global R_S rates was in the range between 93.8 and 94.8 Pg C yr⁻¹ in 2001–2009 (Adachi et al. 2017). Important factors reported to affect rates of both soil CH₄ and respiration fluxes include temperature, moisture, substrate quantity and quality, edaphic characteristics, and flora and fauna activity (Verchot et al. 2000, Ryan and Law 2005). In well-drained soils, CH₄ and respiration fluxes are favored by increased precipitation and soil moisture (Hassler et al. 2015, Wanyama et al. 2019). The change in soil moisture generates a curvilinear model of soil respiration in forest systems with the highest rate typically occurring at field capacity (Koehler et al. 2009, van Straaten et al. 2011). High levels of nitrogen (N) availability, as an example through fertilization, reduce

methanotrophy while high inputs of C substrate (e.g., via litterfall) raise soil respiration (Le Mer and Roger 2001, Acton and Baggs 2011). Soil texture influences gas diffusion, and fine and medium-textured soils generate lower CH₄ uptake than coarse-textured soils (Dutaur and Verchot 2007). Furthermore, acidic soils tend to exhibit lower soil CH₄ emission and respiration rates than alkaline soils (Oertel et al. 2016). Finally, termite activity was postulated to increase CH₄ production in tropical soils (Cattânio et al. 2002, Ishizuka et al. 2002) and contribute on average 7% to soil respiration through emissions from nests that exhibit around five times the efflux observed in the surrounding soil (Lopes de Gerenyu et al. 2015, Ohashi et al. 2017). Land-use change, by modifying one or several of the above-mentioned abiotic and biotic factors controlling the fluxes, has the potential to impact significantly soil CH₄ and respiration exchanges. Nevertheless, studies examining the effect of forest degradation and conversion to plantations in the tropics remain extremely limited.

The purpose of this work is to build knowledge on soil CH₄ and respiration flux rates after forest conversion to oil palm and rubber plantations. We conducted measurements of soil CH₄ fluxes and controlling factors for fourteen months and monitored soil respiration for five months in natural and degraded forests, young and old rubber, and oil palm plantations. The study had the specific objectives of (1) exploring the temporal variability of the fluxes, (2) assessing the timing and magnitude of the response of CH₄ fluxes to N fertilizer application in the oil palm plantation, and (3) evaluating the key biogeochemical controls of CH₄ and respiration fluxes. We hypothesized that soil CH₄ uptake would decrease, while respiration rates would increase following forest degradation and conversion due to vegetation changes and induced changes in soil properties and environmental variables. We also hypothesized that N fertilizer application, density of termite nests, and increased rainfall would promote soil CH₄ emission and respiration rates.

MATERIALS AND METHODS

Our experimental design aimed to investigate spatio-temporal variability of the fluxes and their

controls along a forest-plantation gradient. It comprised five sites presenting different land uses (forest, rubber plantation, oil palm plantation) in different stages (undisturbed or disturbed for the forest, and different ages for the rubber plantation). Sites were not replicated; instead, the design focused on capturing site-specific spatial variability by including an adequate sample size per site with a disaggregation between fertilized and non-fertilized area in the oil palm plantation which received amendment. It also monitored the fluxes and their controls monthly but more intensively following N application in the oil palm plantation.

Site description

The work was conducted in the humid tropical lowland area of Pasir Mayang, Jambi Province, Sumatra, in an undisturbed forest (FR), a disturbed forest (DF), a one-year-old rubber plantation (RB1), a twenty-year-old rubber plantation (RB20), and an eight-year-old oil palm plantation (OP). The FR was a Dipterocarp forest harboring a high density of trees (669 stems/ha) and a large biomass stock of around 325 Mg dry matter/ha (Rutishauser et al. 2013). The DF which was adjacent to the FR had been selectively logged before 1997 (Ishizuka et al. 2002) and illegally logged in 2002. It was in a recovery state when this study took a place with a floor densely covered by shrubs. All of the plantations belonged to smallholders and were managed extensively with no application of fertilizers. Rubber trees and oil palms were planted with a 3 × 4 m distance and 9 m between palms in a triangular pattern, respectively (Aini et al. 2015).

The average annual air temperature was 29°C (Aini et al. 2015). The annual rainfall of 2,646 mm during the measurement period (July 2010–August 2011, 14 months) was within the range of long-term records (2030–2986 mm between 2007 and 2010; Tujuh Koto Ilir weather station, BMKG Jambi 2011, *unpublished data*). The area did not exhibit a clear seasonal pattern with distinctive wet and dry seasons. Therefore, months were classified as wet when rainfall was >100 mm/month (nine months; July, September, November, December 2010 and January, March, April, June, July 2011), or as dry when rainfall was <100 mm month⁻¹ (five months; August, October 2010, February, May and August 2011); following the approach of Oldeman (1980).

Soils were Oxisols (FR, DF, RB1, and RB20) and Inceptisols (OP; Table 1). The research area displayed an undulating landscape (Wasrin et al. 1999) with a very steep slope in the forests, a moderate slope in the young rubber plantation, and a gentle slope in the old rubber and oil palm plantations.

Flux measurement

The static chamber method was used to measure soil CH₄ fluxes (Verchot et al. 2000, Hergoualc'h et al. 2008) while soil respiration was

monitored using dynamic closed chambers connected to an Infrared Gas Analyser (IRGA; Norman et al. 1997). Both fluxes were measured consecutively in the same chamber. Round-based polyvinyl chloride chambers (0.045 m² in area, 0.15 m in height) were permanently installed in each land-use system (LUS) during the 14-month monitoring period. The chambers were manually fanned for 2–3 minutes to bring soil surface gas concentration close to the ambient value and then covered with a lid before gas sample collection (van Straaten et al. 2010). For the

Table 1. Average of soil (0–10 cm[†]) and environmental properties in the forest (FR), disturbed forest (DF), one-year-old rubber plantation (RB1), twenty-year-old rubber plantation (RB20), and eight-year-old oil palm plantation (OP) at Pasir Mayang, Jambi, Sumatra, Indonesia.

Variable	FR	DF	RB1	RB20	OP
Coordinates‡	102°6'03.6" E, 1°4'36.3" S	102°6'00.6" E, 1°4'45.1" S	102°6'36.5" E, 1°5'04.0" S	102°6'58.4" E, 1°5'27.1" S	102°6'58.4" E, 1°5'27.1" S
Soil type‡	Xanthic Kandiudox (Oxisol)	Xanthic Kandiudox (Oxisol)	Xanthic Kandiudox (Oxisol)	Typic Hapludox (Oxisol)	Typic Dystrudept (Inceptisol)
Sand/silt/clay (%)‡, ¶	63/12/25	63/8/29	68/9/23	12/15/73	60/12/28
pH _{H2O} ¶	3.8	4	4	4.2	4.9
Cation exchange capacity (cmol(+) kg ⁻¹)¶	5.5	4.7	3.5	5.7	7.1
Base saturation (%)¶	14.6	11.5	12.2	7.0	44.8
Bulk density (g d.m. cm ⁻³)‡	1.16 ^B (0.04, 9)	1.23 ^{BC} (0.04, 9)	1.32 ^C (0.04, 9)	0.86 ^A (0.03, 9)	1.34 ^C (0.04, 9)
Particle density (g d.m. cm ⁻³)‡	2.42 ^A (0.03, 2)	2.30 ^A (0.02, 2)	2.57 ^A (0.02, 2)	2.56 ^A (0.02, 2)	2.39 ^A (0.09, 2)
Porosity (%)‡	52 ^B (0.02, 9)	47 ^{AB} (0.02, 9)	49 ^{AB} (0.02, 9)	66 ^C (0.02, 9)	44 ^A (0.02, 9)
P (mg 100 g ⁻¹)‡	0.23 ^B (0.03, 9)	0.21 ^A (0.03, 9)	0.20 ^A (0.01, 9)	0.13 ^A (0.01, 9)	0.47 ^B (0.15, 12)
Total C (%)‡	1.9 ^A (0.2, 9)	1.9 ^A (0.4, 9)	1.8 ^A (0.2, 9)	2.6 ^B (0.2, 9)	1.9 ^A (0.1, 9)
Total N (%)‡	0.11 ^A (0.01, 9)	0.11 ^A (0.01, 9)	0.13 ^A (0.01, 9)	0.19 ^B (0.01, 9)	0.17 ^B (0.01, 9)
Soil C:N‡	16.9 ^B (1.4, 9)	16.0 ^B (1.7, 9)	13.6 ^B (0.8, 9)	14.3 ^B (0.5, 9)	11.0 ^A (0.7, 9)
Termite nest density (nest ha ⁻¹)	254 (79, 2)	257 (77, 2)	161 (83, 2)	259 (130, 2)	32 (10, 2)
Soil moisture (%)§	39.1 ^{BC} (3.9, 14)	31.4 ^{AB} (3.0, 14)	28.9 ^A (3.6, 14)	43.0 ^C (3.9, 14)	29.7 ^{AB} (2.5, 14)
Soil moisture at field capacity (%)§	18.0 (0.6, 2)	17.7 (0.3, 2)	17.3 (1.0, 2)	43.3 (0.8, 2)	28.6 (1.4, 2)
Air temperature (°C)‡	26.4 ^A (0.3, 14)	27.9 ^{AB} (0.3, 14)	31.6 ^C (0.8, 14)	29.3 ^{BC} (0.7, 14)	28.4 ^{AB} (0.5, 14)
Soil temperature (°C)‡	25.6 ^A (0.2, 14)	25.8 ^{AB} (0.3, 14)	27.3 ^C (0.2, 14)	26.5 ^B (0.2, 14)	26.3 ^{AB} (0.3, 14)
Soil NH ₄ ⁺ content (mg N kg ⁻¹)‡	14.4 ^{AB} (1.9, 9)	13.2 ^{AB} (2.8, 6)	9.4 ^A (1.5, 6)	30.7 ^C (6.5, 6)	17.5 ^{BC} (12, 3)
Annual litterfall DM mass (Mg d.m.·ha ⁻¹ ·yr ⁻¹)‡	8.4 ^C (0.3, 13)	4.5 ^B (0.4, 13)	0.1 ^A (0.0, 13)	5.1 ^{BC} (0.3, 13)	NA
Annual litterfall C:N‡	34.7 (3.1, 30)	37.1 (5.1, 30)	34.2 (4.8, 6)	36.2 (3.9, 31)	NA
Annual litterfall N mass (kg N·ha ⁻¹ ·yr ⁻¹)‡	138.6 ^C (15.9, 13)	73.2 ^B (17.7, 13)	2.3 ^A (1.0, 13)	80.9 ^B (18.8, 13)	NA
Annual litterfall C mass (Mg C·ha ⁻¹ ·yr ⁻¹)	4.0 ^C (0.5, 13)	2.1 ^B (0.5, 13)	0.1 ^A (0.0, 13)	2.5 ^B (0.6, 13)	NA

† Except for soil temperature which was measured in the top 5 cm. Numbers in parentheses are SE, *n*. Means for the land-use systems followed by different letters (A, B, C) are significantly different from each other. In the absence of significant differences, no letters are displayed.

‡ From Aini et al. (2015).

§ Gravimetric soil moisture.

¶ No replicate.

measurement of CH₄ fluxes, the lid of the chamber was equipped with a vent (2 mm in diameter, 25 mm in length) for pressure equilibration and a port gas sample collection. The samples were taken 0, 10, 20, and 30 min after closure, transferred to pre-evacuated glass vials, transported by road to the laboratory in Jambi city, and analyzed, within a month, with a gas chromatograph (Shimadzu 14 A) equipped with a flame ionization detector (Loftfield et al. 1997). Prior to each sequence of gas analysis, the chromatograph was calibrated using ultrahigh-purity standard gases with a concentration of 1,500, 2,000, 10,000, and 40,000 ppb CH₄. The analytical precision of the chromatographic measurement of CH₄ at ambient concentration was assessed by computing the average, standard deviation, and coefficient of variation from 35 samples, following the method by Parkin et al. (2012). The average ambient CH₄ concentration determined by chromatography was 1616 ppb with a standard deviation of 198 and a coefficient of variation of 12.3%. For the soil respiration measurements, the chambers were closed using a lid equipped with a small vent (1 mm in diameter, 25 mm in length) and two 2-mm-diameter ports through which air was circulated between the chamber headspace and the IRGA. The IRGA (Li 800; Li-Cor, Lincoln, Nebraska, USA) was operated by a pump calibrated to circulate the air at 0.8 dm³/min and connected to a data logger (Campbell CR 800), which recorded the CO₂ concentration in the headspace every 5 s. The fluxes were usually measured for a period of 5 min. Prior to each field data collection campaign, the IRGA was calibrated in the laboratory using standard gases with a CO₂ concentration of 350 and 700 ppm. The analytical precision of the IRGA measurement of CO₂ at ambient concentration was determined by computing the average, standard deviation, and coefficient of variation from 44 concentrations measured at the onset of IRGA recording in the field. The average ambient CO₂ concentration was 430 ppm with a standard deviation of 56 and a coefficient of variation of 13.1%. The CH₄ and soil respiration fluxes were calculated by linear regression over time of gas concentration in the headspace which is the most precise, least biased and computationally simplest method available (Venterea et al. 2015). Negative CH₄ flux values represent consumption; positive values represent

emissions to the atmosphere. Due to a technical problem with the IRGA, soil respiration was monitored over five months (July–November 2010) only, comprising three wet months and two dry months. All measurements were done during daytime (06.00 AM–17.00 PM). To avoid potential diurnal fluctuation interference, the sequence of plot measurement was randomized.

The fluxes were measured from nine replicate chambers in non-OP systems, and twelve replicates in the OP. In non-OP systems, the chambers were distributed along a 5 × 5 m grid in a 400-m² plot. In the OP, the chambers were deployed over a 1,000-m² surface, with six chambers positioned close to a palm in the fertilized zone (FZ) and six others located at mid-distance between two palms in the non-fertilized zone (NFZ; Aini et al. 2015). The chambers in the FZ and NFZ were about 3.5 m distant. The experiment was designed to capture site-specific spatial variation of fluxes while avoiding spatial dependency between chambers. A number of six to eight replicated chambers are recommended to achieve robust spatial representation in emission rates and to provide adequate power for statistical analysis (Rochette et al. 2015). The minimum distance required between chambers to avoid spatial autocorrelation in CH₄ fluxes and soil respiration, respectively, is 3 m (Ishizuka et al. 2005) and 5–10 m (Savage and Davidson 2003, Ishizuka et al. 2005). In addition, the spatial stratification between the FZ and NFZ in the OP has proved to be effective in capturing the effects of fertilizer application on soil trace gas emissions and avoiding under or over-estimation of fertilization effects (Aini et al. 2015, Oktarita et al. 2017). To translate the results to the plot scale, the flux data from the FZ and NFZ were weighted by the percentage occupied by the FZ and NFZ areas (10% and 90%, respectively) in the OP-plot and summed. Soil CH₄ and respiration fluxes were interpolated linearly between measurement dates to calculate annual emissions.

The monitoring of CH₄ fluxes was separated into two modes: (1) monthly measurements and (2) intensive measurements following fertilizer application when emissions can be expected to be changing rapidly. The monthly measurements were conducted between July 2010 and August 2011 in all LUS. The intensive measurement in

the OP site took place in April 2011, starting 2 d before fertilization, and then on days 0, 1, 2, 3, 4, 5, 6, 7, 10, 14, 17, 21, and 28 after fertilizer application. Urea, triple super phosphate, and potassium chloride equivalent to rates of 33.3 kg N ha⁻¹, 33.3 kg P ha⁻¹, and 46.4 kg K ha⁻¹ were applied on day 0 in the FZ, following typical practices by local farmers. The mass of fertilizer spread within each chamber of the FZ was calculated from the surface ratio between the chamber and FZ areas multiplied by the fertilizer application rate (Aini et al. 2015).

Ancillary data

Vegetation N and C inputs to the soil were assessed by monitoring the monthly litterfall during the 14-month experimental period. Litterfall collection was done in three litter traps of 2 × 1 m² installed randomly in each of the FR, DF, and RB20 sites. In the RB1 site, six 1 × 1 m² traps were installed under six young rubber trees that were selected at random. No litter traps were placed in the OP site because the fronds are usually pruned by the farmers at harvesting time and left to decompose on the ground. Upon monthly collection, the litter from the traps was oven-dried for three days at 70°C and weighed. Finally, three replicates of litter per LUS were analyzed for C following the Walkley-Black method and N content following the Kjeldahl method.

The rainfall and air temperature in the research area were measured hourly using a weather station (Delta Ohm type HD2013-D) installed permanently in a nearby village located about 1–2 km from the sites. Air temperature in the shade together with temperature in the top 5 cm of the soil was monitored concomitantly with soil respiration and CH₄ fluxes, at each chamber (Aini et al. 2015). Air temperature was measured approximately 1 m above the ground. The soil gravimetric moisture content from the top 10 cm was measured from nine replicates per plot in non-OP LUS and twelve replicates per plot in the OP (six from the FZ and six from the NFZ). Samples were taken about 20–30 cm away from the chambers to avoid creating disturbance. Samples were oven-dried at 105°C for 24 h, and their water content was determined on a dry mass basis.

Soil properties were analyzed on one, two, or nine replicate samples per LUS depending on the variable (n values are presented in Table 1),

taken from the top 10 cm of soil in September 2010. The pH was measured in water (1:5 soil: water ratio) using a standard pH electrode while available P content was extracted in Bray 1 reagent and analyzed by spectrophotometry following Bray and Kurtz (1945). The availability of base cations (Ca²⁺, Mg²⁺, K⁺, Na⁺) and the cation exchange capacity (CEC) were determined using the ammonium acetate (1N) method at pH 7 (Pansu and Gautheyrou 2006), and the base saturation was calculated as the sum of available base cations divided by the CEC. The particle size distribution, particle density, and bulk density were measured following the methods provided by Henríquez and Cabalceta (1999), Grimaldi et al. (2003), and Pansu and Gautheyrou (2006), respectively. The dry combustion method was used to analyze total C and N contents (Flash EA 1112 Series Elemental Analyser, Thermo Finnigan, Bremen, Germany). Soil moisture at field capacity, the amount of water that a soil retains against gravitational forces after a rain or irrigation, was determined using a pressure plate apparatus at a 2.5 suction potential (pF; Lavelle 2012, Cutillas et al. 2015). To assess N availability, the NH₄⁺ content in the top 10 cm of soil was measured in May 2010, June 2010, and August 2010 by extraction using 100 mL of 2 mol/L KCl to a 10 g fresh soil subsample. After shaking for 1 h and filtering, the supernatant was analyzed by spectrophotometry using an autoanalyzer (Bran and Luebbe, Norderstedt, Germany). Due to sample contamination, all NO₃⁻ content results and NH₄⁺ content results from May 2010 in the DF, RB1, and RB20 had to be discarded. Three replicates were used in non-OP LUS, four in the OP with two of them sampled in the FZ and the two others in the NFZ at each measurement time. The extrapolation of NH₄⁺ concentrations to the plot scale in the OP was achieved in a similar fashion as for gas fluxes by using the surface-area weight of the FZ and NFZ areas (10% and 90%, respectively).

The termite nest density was monitored twice in a year; once in April 2011 during a wet month and again in August 2011 during a dry month. It was measured by counting all of above-ground termite nests (epigeal, arboreal, and wood nests) within one ha in all LUS except in the RB1 (0.6 ha) where a fire took place and prevented the survey being done over one ha. Hypogean

nests (underground nests) were not counted because of the difficulty to locate them. While quantifying the potential contribution of termites to soil fluxes would require a detailed assessment of emissions from nests, our objective here was to test whether the density of nests could serve as an indicator of flux change along the LUS gradient. This used the hypothesis that the influence of termites might extend beyond the position where the nests are located. More methodological details on ancillary data collection are provided by Aini et al. (2015).

Statistical analysis

The statistical analysis was conducted using the SPSS 20 (IBM 2011) and Infostat (Di Rienzo et al. 2011) softwares with probability level of 0.05 to test the significance of effects. Kolmogorov-Smirnov and Shapiro-Wilk tests were applied to verify the normality of the residual data distribution (Park 2008). The Box-Cox procedure (Box and Cox 1964) was used to evaluate the appropriate transformation to normalize the residual data when required (Elío et al. 2013). The residuals of CH₄ and soil respiration fluxes in individual chambers were not normally distributed but those of monthly averages were. Hence, the LUS comparison of monthly averages was analyzed by analysis of variance (ANOVA). The LUS comparison in wet and dry months was performed using either the ANOVA or Kruskal-Wallis test depending on the distribution of the residuals. The temporal variability of the fluxes was assessed by averaging the coefficients of variation (CV) calculated for each chamber in each LUS. The spatial uncertainty associated with monthly CH₄, soil respiration, and litterfall fluxes was included in annual fluxes by Gaussian error propagation (Lo 2005, Malhi et al. 2009). Annual cumulative fluxes \pm SE which did not overlap were considered significantly different between LUS. Linear and non-linear models were used to test relationships between environmental variables, soil properties and soil CH₄ and respiration fluxes. A stepwise linear multiple regression analysis was used to identify the best predictors of CH₄ and soil respiration fluxes. The procedure combined backwards elimination and forwards selection as described by Ghani and Ahmad (2010). Whenever more than one independent variable controlled the fluxes, a

collinearity test was applied to discard correlated factors. Only relationships with significant coefficients and an $R^2 > 0.25$ are displayed. All results are presented as mean/cumulative value \pm SE.

We used boxplots to summarize soil CH₄ and respiration annual fluxes from other studies conducted in comparable land-use systems on mineral soils. The boxplots present maximum, first quartile, median, third quartile, and minimum values. The studies carried out at an altitude >1000 m above sea level and not covering temporal dynamics (i.e., short-term experiments with <4 measurements over a year and studies that did not distinguish between wet and dry months/seasons) were not considered. The age of rubber plantations could not be included in the analysis because of the limited number of studies, and comparison was made to averaged fluxes in the RB1 and RB20. The annual rate of soil CH₄ and soil respiration rates from this study were categorized as high or low if they fell above the third quartile or below the first quartile of the summarized fluxes from the literature.

RESULTS

Soil, environmental, and vegetation properties

Soil and environmental properties at the sites are presented in Table 1. All soils had a sandy clay loam texture except in the RB20 where the texture was clay. The soil was strongly acidic (<5), but less so in the OP than in other LUS. The CEC was smaller, and the base saturation was larger in the OP plantation than in other LUS. Furthermore, the bulk density was lower, and the porosity was higher in the RB20 than in other LUS. All soils were limited in P (<50%; Holford and Cullis 1985) and N (<0.2%; Sulaeman and Eviati 2005). Soils had a medium C content (around 2%), higher in the RB20 than elsewhere. Soil C:N ratios were significantly lower in the plantations than in the forests ($P = 0.0036$). The termite nest density ranged between 32 ± 10 and 259 ± 130 nests ha⁻¹ and was similar across all LUS but lower in the OP than in non-OP systems ($P = 0.04$).

The soil was moist, with a range between 29 and 43% (Table 1, Fig. 1C). The average soil moisture content was much higher than field capacity in the FR, DF, and RB1 sites, whereas in the RB20 and OP plantations, it was close to field

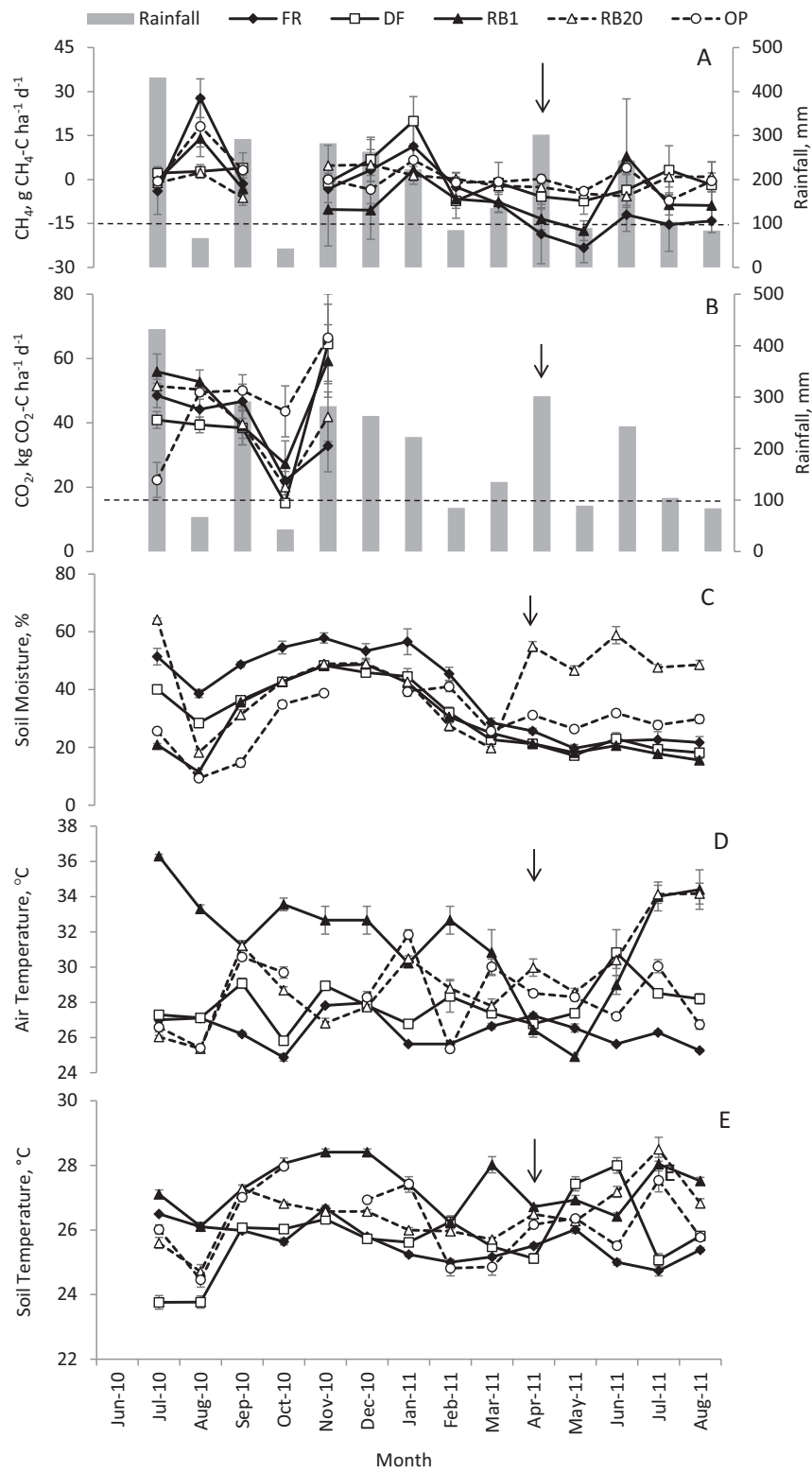


Fig. 1. Average and SE of monthly soil CH₄ fluxes (A), respiration rates (B), gravimetric soil moisture (C), air

(Fig. 1. *Continued*)

temperature (D), and soil temperature (E) in the forest (FR), disturbed forest (DF), one-year-old rubber plantation (RB1), 20-yr-old rubber plantation (RB20), and eight-year-old oil palm plantation (OP) at Pasir Mayang, Jambi, Sumatra, Indonesia. The arrow indicates the fertilization in the OP. Subfigures D and E were taken from the paper by Aini et al. (2015). The horizontal dashed line in panels A and B delimits dry months from wet months.

capacity. The soil moisture in the RB20 was greater ($P < 0.01$) than in all other LUS except for the FR. Overall, it was higher ($P < 0.01$) during wet months ($34.9 \pm 0.1\%$) than during dry months ($30.2 \pm 0.8\%$); however, such a difference was not apparent in individual LUS (Table 2). In the OP, soil moisture was higher in the NFZ—in between palms ($32.5 \pm 1.4\%$) than in the FZ—underneath the palms ($28.0 \pm 1.3\%$) over the year but not within dry and wet months (Table 2) and it was similar before, during, and after fertilizer application (Table 3). High rainfall events (>30 mm/d) took place on the day of fertilizer application and 6, 17, and 21 d thereafter (Fig. 2A); soil moisture was significantly higher over the 28-d period after fertilizer application

than two days before fertilizing ($P = 0.0004$; Fig. 2B); the former result was significant only at the $P = 0.06$ level in the FZ.

The annual average of air temperature in the LUS ranged from 26° to 32°C . Forest conversion to agriculture, especially to the young rubber plantation, increased air temperature (Table 1). The air temperature changed significantly over time ($P < 0.01$) but displayed similar averages in wet and dry months ($29.0^\circ \pm 0.8^\circ\text{C}$ and $28.3^\circ \pm 1.0^\circ\text{C}$, respectively). Only in the NFZ area of the OP was the air temperature higher during wet than during dry months (Table 2). Average soil temperature in the LUS ranged between 26° and 27°C and displayed a similar temporal and land-use trend as air temperature

Table 2. Average of soil CH_4 and respiration fluxes, soil gravimetric moisture, air and soil temperature, and soil ammonium concentration during dry and wet months in the forest (FR), disturbed forest (DF), one-year-old rubber plantation (RB1), twenty-year-old rubber plantation (RB20), and eight-year-old oil palm plantation (OP).

Characteristic	FR	DF	RB1	RB20	OP-plot	OP-FZ	OP-NFZ
Dry months							
CH_4	-3.1 (11.2, 4)	-3.4 (2.4, 4)	-4.8 (6.7, 4)	-0.4 (1.6, 4)	3.2 (5.0, 4)	1.3 (2.8, 4)	3.4 (5.3, 4)
Soil respiration	33.1 (11.1, 2)	27.2 (12.1, 2)	40.0 (12.7, 2)	35.2 (15.1, 2)	46.6 (3.0, 2)	43.1 (4.4, 2)	46.9 (2.8, 2)
Soil moisture	35.1 (6.5, 5)	27.4 (4.7, 5)	24.1 (6.0, 5)	37.5 (6.3, 5)	28.4 (5.3, 5)	26.5 (4.9, 5)	30.3 (5.8, 5)
Air Temp.	25.9 ^A (0.4, 5)	27.4 ^{AB} (0.5, 5)	31.8 ^B (1.7, 5)	29.1 ^{AB} (1.4, 5)	27.1 ^{AB} (0.8, 5)	27.1 (0.8, 5)	27.1 ^a (0.9, 5)
Soil Temp.	25.6 (0.2, 5)	25.9 (0.6, 5)	27.0 (0.4, 5)	26.1 (0.4, 5)	25.9 (0.6, 5)	25.8 (0.7, 5)	26.0 (0.6, 5)
NH_4^+	14.2 (3.0, 2)	16.4 (NA, 1)	7.5 (NA, 1)	23.4 (NA, 1)	18.8 (1.3, 2)	32.2 (12.7, 2)	17.2 (0.1, 2)
Wet months							
CH_4	-5.4 (3.1, 9)	2.7 (2.5, 9)	-4.5 (2.3, 9)	-0.7 (1.4, 9)	-0.2 (1.2, 9)	4.3 (3.5, 9)	-0.7 (1.8, 9)
Soil respiration	42.7 (4.9, 3)	48.0 (8.3, 3)	51.4 (6.3, 3)	44.3 (3.6, 3)	46.3 (12.9, 3)	42.2 (7.8, 3)	46.7 (13.5, 3)
Soil moisture	41.4 (4.9, 9)	33.6 (3.9, 9)	31.5 (4.6, 9)	45.9 (4.9, 9)	30.4 (2.7, 9)	28.9 (2.6, 9)	32.0 (2.8, 9)
Air temp	26.7 ^A (0.3, 9)	28.2 ^{AB} (0.4, 9)	31.5 ^C (1.0, 9)	29.4 ^{BC} (0.9, 9)	29.0 ^{ABC} (0.6, 9)	28.9 (0.6, 9)	29.2 ^B (0.6, 9)
Soil temp	25.6 ^A (0.2, 9)	25.7 ^{AB} (0.4, 9)	27.5 ^C (0.2, 9)	26.7 ^{BC} (0.3, 9)	26.5 ^{ABC} (0.3, 9)	26.5 (0.4, 9)	26.5 (0.3, 9)
NH_4^+	15.0 (NA, 1)	9.9 (NA, 1)	11.3 (NA, 1)	38.0 (NA, 1)	15.0 (NA, 1)	23.6 (NA, 1)	13.9 (NA, 1)

Notes: In the OP, the averages are presented in the fertilized (FZ) and non-fertilized (NFZ) zones. Plot-scale values (OP-plot) for soil CH_4 and respiration fluxes and NH_4^+ content were calculated as 10% OP-FZ + 90% OP-NFZ. For the other variables, the OP-plot value was computed as the average of the values measured in the FZ and NFZ zones.

Values are presented as mean (SE, n months). There were five dry months (August 2010, October 2010, February 2011, May 2011, and August 2011) and nine wet months over the monitoring period. Means of CH_4 ($\text{g C}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$) and soil respiration ($\text{kg C}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$) fluxes, soil moisture (%), air and soil temperature ($^\circ\text{C}$), and NH_4^+ content (mg N/kg) followed by different letters (A, B, C) are significantly different between land-use systems within dry and wet months. Means followed by Greek symbols (α , β) are significantly different between dry and wet months within a land use. Means in the FZ and NFZ of the OP within dry and wet months were not significantly different from each other. In the absence of significant differences, no letters or symbols are displayed.

Table 3. Average of CH₄ fluxes (g C·ha⁻¹·d⁻¹), soil moisture (%), air and soil temperatures (°C) in the fertilized (FZ) and non-fertilized (NFZ) zones in the oil palm plantation before, during and after fertilizer application.

Characteristic	Before fertilizer application (Jul 2010–April 2011)	During fertilizer application (April–May 2011)	After fertilizer application (May–Aug 2011)
CH ₄ , OP-plot	1.2 (2.6, 9)	0.5 (1.7, 13)	–2.0 (2.4, 4)
OP-FZ	4.7 (3.7, 9)	–1.1 (0.6, 13)	–0.9 (1.0, 4)
OP-NFZ	0.8 (2.8, 9)	0.7 (1.9, 13)	–2.1 (2.7, 4)
Soil moisture, OP-plot	28.7 (3.9, 9)	31.3 (0.6, 13)	28.8 (1.3, 4)
OP-FZ	27.5 (3.6, 9)	28.3 ^a (0.8, 13)	26.5 (1.5, 4)
OP-NFZ	29.9 (4.1, 9)	34.3 ^b (0.6, 13)	31.1 (1.2, 4)
Air Temp., OP-plot	28.5 (0.8, 9)	28.5 (0.4, 13)	27.9 (0.7, 4)
Soil Temp., OP-plot	26.1 (0.4, 9)	26.2 (0.1, 13)	26.3 (0.5, 4)

Notes: The CH₄ fluxes at the plot scale were calculated as 10% OP-FZ + 90% OP-NFZ. For the other variables, the OP-plot value was computed as the average of the values measured in the FZ and NFZ zones. Values are expressed as mean (S.E., n: number of sampling dates). No letters or symbols are displayed because all values were not significantly different from each other.

(Fig. 1E). The soil and air temperature in the OP were on average similar before, during, and after fertilizer application (Table 3). Both reached their maximum 14 d after N application and were similar in the FZ and NFZ areas following the fertilization (Fig. 2C; Table 2).

The average of soil NH₄⁺ concentration in the LUS was between 9.4 and 30.7 mg N/kg. It was highest in the RB20 and lowest in the RB1 ($P < 0.01$, Table 1). At the OP site, the soil NH₄⁺ content was, on average, higher in the FZ (29.3 ± 8.2 mg N/kg) than in the NFZ (16.1 ± 0.7 mg N/kg; $P < 0.05$) mainly as the result of the fertilizer application in April 2011. In all LUS, the NH₄⁺ concentration was similar during wet and dry months (Table 2). Within dry and wet months, it was similar among LUS or among the FZ and NFZ areas in the OP (Table 2). The annual litterfall rate expressed either in dry matter or C mass was the highest in the FR, followed by the RB20, the DF, and the RB1, with a production rate ranging between 0.1 and 4 Mg C·ha⁻¹·yr⁻¹.

Soil methane fluxes

Between July 2010 and August 2011, individual chamber fluxes of CH₄ varied between –95 and 148 g C·ha⁻¹·d⁻¹. Most CH₄ fluxes were negative (62%); only 28% of the positive fluxes were generated during wet months, and 12% exhibited a high average flux rate over 10 g C·ha⁻¹·d⁻¹. The temporal variability of CH₄ fluxes was extremely high but lower in the forests (average CVs of 821% and 599% in the undisturbed and disturbed forest) than in the plantations (1073–3222%).

It was particularly high in the FZ of the OP site. The fluxes were significantly lower ($P < 0.01$) in the wet month of April and the dry month of May 2011 (-8 ± 3 , -11.3 ± 3 g C·ha⁻¹·d⁻¹, respectively) than in the dry month of August 2010 and the wet month of January 2011 (2.5 ± 3 , 8.3 ± 3 g C·ha⁻¹·d⁻¹, respectively; Fig. 1A). There was no significant difference in the average CH₄ fluxes between the dry and wet months in any of the LUS (Table 2). The average fluxes were also similar between LUS within dry and wet months.

In the OP, the range of CH₄ fluxes from individual chambers during the intensive measurements after fertilizer application was between –28 and 97.0 g C·ha⁻¹·d⁻¹. Most CH₄ flux values (66%) were negative, 32% were between 0 and 10 g C·ha⁻¹·d⁻¹, and 2% were over 10 g C·ha⁻¹·d⁻¹. The average fluxes in the fertilized (FZ) and non-fertilized (NFZ) zones were similar to each other (Table 3, middle column). The fluxes fluctuated over time in both FZ and NFZ areas (Fig. 2A). The maximum CH₄ emission rate in the FZ was reached ten days after fertilizer application (4.3 ± 3.0 g C·ha⁻¹·d⁻¹, $P < 0.05$). In this zone, the average soil flux of CH₄ up to ten days after N fertilizer application (-0.6 ± 0.7 g C·ha⁻¹·d⁻¹) was significantly higher than two days before application (-7.1 ± 1.9 g C·ha⁻¹·d⁻¹) and between 14 and 28 d after application (-2.3 ± 0.7 g C·ha⁻¹·d⁻¹; $P = 0.0003$). The same was observed in the NFZ with flux averages of 2.4 ± 2.3 , -8.3 ± 1.1 , and -3.1 ± 0.9 g C·ha⁻¹·d⁻¹ for the same periods ($P < 0.0001$). Similar temporal trends, combined with similar average rates in the area where the fertilizer was applied

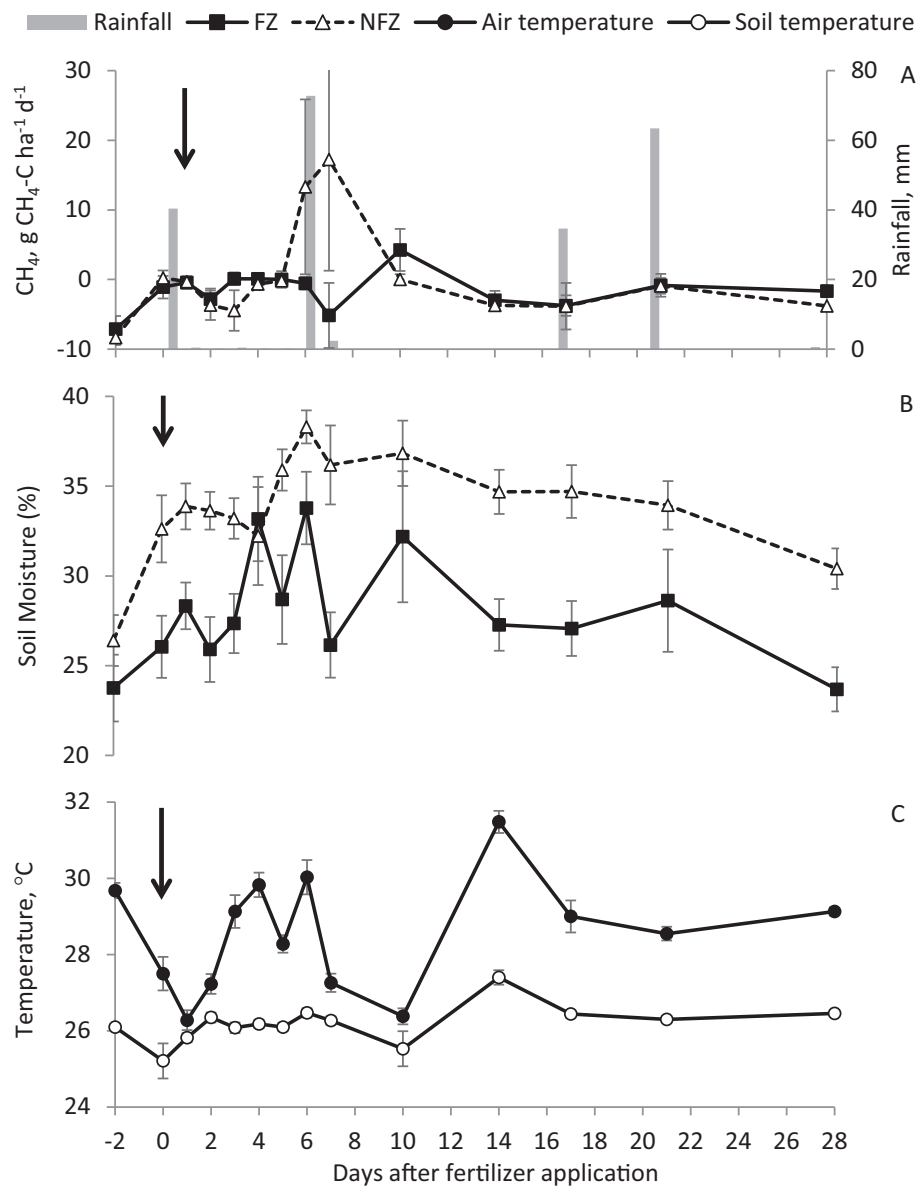


Fig. 2. Daily rainfall together with soil CH_4 fluxes (A) and soil gravimetric moisture (B) in the fertilized and non-fertilized zones of the oil palm plantation following fertilizer application. Air and soil temperatures (C) are the average values in the FZ and NFZ. The arrow indicates the fertilization date.

(FZ) and in the area where no fertilizer was applied (NFZ), suggest that the temporary increase in CH_4 flux in the two zones over the period following N fertilization was likely to be due to factors other than N addition (see section 3.4). Over the 14 months of measurements, the average fluxes were similar before, during, and after fertilizer application in both FZ and NFZ

areas denoting no fertilization impact in the long term (Table 3).

On an annual scale, only the FR and RB1 were significant CH_4 sinks of similar magnitude (-1.4 ± 1.0 and $-1.7 \pm 0.7 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ C, respectively). The annual fluxes in the DF, RB20, and OP (0.4 ± 0.9 , -0.2 ± 0.3 , $0.2 \pm 0.7 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively) were not significantly

different from the fluxes in the undisturbed forest. Annual fluxes in the FZ and NFZ in the OP (1.4 ± 1.2 and 0.1 ± 0.8 kg C·ha⁻¹·yr⁻¹, respectively) were also not different from each other.

Soil respiration fluxes

Individual chamber CO₂-C fluxes varied between 10 and 140 kg C·ha⁻¹·d⁻¹ between July 2010 and August 2011. About half of the chambers (56%) exhibited a high average CO₂ flux rate over 33 kg C·ha⁻¹·d⁻¹. The temporal variability of soil respiration was much less pronounced than that of CH₄ fluxes with average CVs amounting to from 38% ± 4% in the FZ of the OP to 58% ± 8% in the NFZ of the OP. The variability was intermediate in the other LUS and similar across all LUS. Soil respiration was lower in the dry month of October 2010 (25.6 ± 4.9 kg C/ha) than in the dry month of August 2010 (47.2 ± 2.4 kg C/ha) and the wet month of November 2010 (53.0 ± 6.6 kg C/ha; $P < 0.01$; Fig. 1B). In the OP, soil respiration remained steady in the FZ area but in the NFZ area it was significantly lower in July 2010 (21.7 ± 6.0 kg C/ha) than in November 2010 (68.0 ± 15.0 kg C/ha; $P < 0.05$). In none of the LUS did the average soil respiration exhibit a significant difference between wet and dry months (Table 2). It was also similar between LUS within wet and dry months, and between the FZ and NFZ areas in the OP.

Given the low CV values of the respiration measurements and the lack of a clear seasonal trends, we extrapolated the five-month measurement time to estimate the annual flux. The annual soil respiration was significantly higher in the OP (17.1 ± 1.9 Mg C·ha⁻¹·yr⁻¹) than in the undisturbed forest (13.9 ± 1.2 Mg C·ha⁻¹·yr⁻¹). The rate in the disturbed forest, young, and old rubber plantations (13.1 ± 1.4 , 15.9 ± 1.7 , and 14.1 ± 1.0 Mg·Cha⁻¹·yr⁻¹, respectively) was similar to the rate in the FR. As for soil CH₄ fluxes, the annual rate of soil respiration rate in the OP was not significantly different between the FZ and NFZ areas (16.9 ± 4.0 and 19.4 ± 3.5 Mg C·ha⁻¹·yr⁻¹, respectively).

Determinants of soil methane and respiration fluxes

Soil CH₄ fluxes were driven by different variables depending on the LUS. In the forests, monthly fluxes increased logarithmically with

increasing soil moisture while in the OP plantation, they increased linearly with increasing soil NH₄⁺ content (Table 4). From the day of the fertilizer application until 28 d after application, the CH₄ fluxes in the OP responded positively to soil moisture rises and rainfall on the day before measurement, suggesting that moisture rather than N availability induced the increase in CH₄ fluxes observed in both fertilized and unfertilized areas after fertilizing (Fig. 2A). Along the LUS gradient, annual cumulative CH₄ flux rates increased as litterfall C:N ratio increased. The relationship excluded the OP plantation where the litterfall rate or frond pruning was not monitored. We found no relationship between termite nest density and CH₄ fluxes across these sites.

Soil respiration was not driven by any specific variable within a given LUS. Across LUS, the variation in monthly soil respiration rate was only partially explained by changes in rainfall. On the other hand, the annual soil respiration rate was strongly related to differences in soil properties, density of termite nests, and litterfall rates along the LUS gradient. The annual cumulative soil respiration rate increased linearly with the decrease in termite nest density and the decrease in soil C:N ratio. The average annual soil respiration rate increased with total soil N content, annual litterfall dry matter, and N mass rate increased along the LUS gradient.

DISCUSSION

Annual fluxes and flux changes associated with conversion: Magnitude and controls

Aerobic forest soils in the tropics are known to be CH₄ sinks, and forest conversion is suspected to weaken the sink or turn this sink into a source (Verchot et al. 2000). The annual uptake rate of CH₄ in the FR site (-1.4 ± 1.0 kg C·ha⁻¹·yr⁻¹) was within the range of values from the literature in the tropics (Fig. 3A). Our results demonstrate no significant change in soil CH₄ fluxes following natural forest conversion but show that the soil in the DF, RB20, and OP sites did not act as significant net CH₄ sinks. Notwithstanding, the average rate in the RB1 and RB20 sites (-1.0 ± 0.7 kg C·ha⁻¹·yr⁻¹) indicates a CH₄ sink for the rubber plantation LUS category, which is in agreement with previous work (Fig. 3A). Annual CH₄ fluxes in the DF and OP sites were

Table 4. Relationships between soil CH₄ flux rate, soil respiration flux rate, and environmental parameters within a land-use system (LUS) or across them.

Parameter by dependent variable	LUS	<i>n</i>	<i>R</i> ²	Equation
Monthly soil CH ₄ flux				
<i>x</i> = soil moisture	FR	13	0.44	$Y = -81.7 (26.1, *) + 21.6 (7.3, *) \log x$
	DF	13	0.32	$Y = -35.8 (16.2, NS) + 10.9 (4.8, *) \log x$
<i>x</i> = soil NH ₄ ⁺ content	OP	3	1.00	$Y = 27.0 (1.4, *) - 1.6 (0.1, *) x$
<i>x</i> ₁ = rainfall a day before flux measurement	OP during fertilization	13	0.67	$Y = -45.3 (15.2, *) + 0.18 (0.05, ***) x_1 + 1.4 (0.5, *) x_2$
<i>x</i> ₂ = soil moisture				
Annual cumulative soil CH ₄ flux				
<i>x</i> = litterfall C:N ratio	All except OP	4	1.00	$Y = -27.6 (0.6, ***) + 0.8 (0.0, ***) x$
Monthly soil respiration flux				
<i>x</i> = monthly rainfall	All	25	0.26	$Y = 50.2 (3.6, ***) - 817.5 (286.9, ***)/ x$
Annual cumulative soil respiration flux				
<i>x</i> = termite nest density	All	5	0.91	$Y = 17.9 (0.6, ***) - 0.02 (0.0, *) x$
<i>x</i> = soil C:N ratio	All	5	0.82	$Y = 24.2 (1.4, **) - 0.7 (0.2, *) x$
Annual average soil respiration flux				
<i>x</i> = soil total N content	All	5	0.99	$Y = 78.5 (10.8, *) + 1684.4 (152.2, **) x - 5571.1 (512.8, **) x^2$
<i>x</i> = litterfall dry mass	All except OP	4	0.98	$Y = 42.8 (0.3, ***) - 1.87 (0.2, *) \log x$
<i>x</i> = litterfall N mass	All except OP	4	0.98	$Y = 48.3 (0.78, ***) - 1.9 (0.2, ***) \log x$

Notes: Abbreviations are FR, undisturbed forest; DF, disturbed forest; OP, oil palm plantation. Values for the variables in OP are plot-scale results. Numbers in parentheses are SE, *P* value (**P* < 0.05, ***P* < 0.01, ****P* < 0.001). Only relationships with an *R*² ≥ 0.25 are displayed. Monthly and annual average soil CH₄ and respiration flux rates are expressed in g CH₄-C·ha⁻¹·d⁻¹ and kg CO₂-C·ha⁻¹·d⁻¹, respectively. Annual cumulative soil CH₄ and respiration flux rates are expressed in kg CH₄-C·ha⁻¹·yr⁻¹ and Mg CO₂-C·ha⁻¹·yr⁻¹, respectively. Independent variables include soil gravimetric moisture (%); soil NH₄⁺ content (mg N/kg), rainfall a day before flux measurement (mm/d), litterfall C:N ratio, monthly rainfall (mm/month), termite nest density (nest/ha), soil C:N ratio, soil total N content (%), annual litterfall dry mass (Mg d.m. ha⁻¹·yr⁻¹), and N mass (kg N·ha⁻¹·yr⁻¹). In the OP, plot-scale results for soil CH₄ flux and NH₄⁺ content were calculated as 10% OP-FZ + 90% OP-NFZ, where OP-FZ and OP-NFZ designate values measured in the fertilized and non-fertilized zones. For the other variables, the OP-plot value was computed as the average of the values measured in the FZ and NFZ zones. OP during fertilization refers to the period from the day of N application until 28 d after application.

higher than the median rates obtained from other studies. The difference from the literature for disturbed forests may be due to the extent of soil drying and compaction that occur during different forest disturbance processes. For instance, selective logging has been reported to compact the soil surface, impede water drainage, reduce gas diffusion into the soil profile, and augment soil CH₄ fluxes (Keller et al. 2005). The higher CH₄ flux in the OP plantation as compared to fluxes measured by Hassler et al. (2015) may result from higher soil bulk density, water-filled pore space (93%; Aini et al. 2015), base saturation, and NH₄⁺ content at our site than at the sites investigated by Hassler et al. (2015) (bulk density of 1 g cm⁻³, water-filled pore space of 68%, base saturation of 33%, and NH₄⁺ content of 5 mg N/kg). The impact of forest conversion to either rubber or oil palm plantation on soil CH₄ uptake

remains unclear. While Hassler et al. (2015) found a decrease in uptake following forest conversion on a clay Acrisol, the study by Ishizuka et al. (2002) and the one by Hassler et al. (2015) on a loam Acrisol detected no change in uptake. Despite no significant difference among LUS at our site, there was a strong trend toward lower annual uptake of CH₄ when the C:N ratio of litter inputs increased (Table 4). Methanogenesis is commonly correlated with plant productivity because the organic matter from senescent vegetation is a main source of C to soil microbes (Bridgham et al. 2013), and significant methanogenesis stimulates methanotrophy (Le Mer and Roger 2001). Moreover, the quality of the organic matter is also considered to be a determining factor for CH₄ production (Le Mer and Roger 2001). The reduction in CH₄ uptake in converted plantations observed by Hassler et al. (2015) was

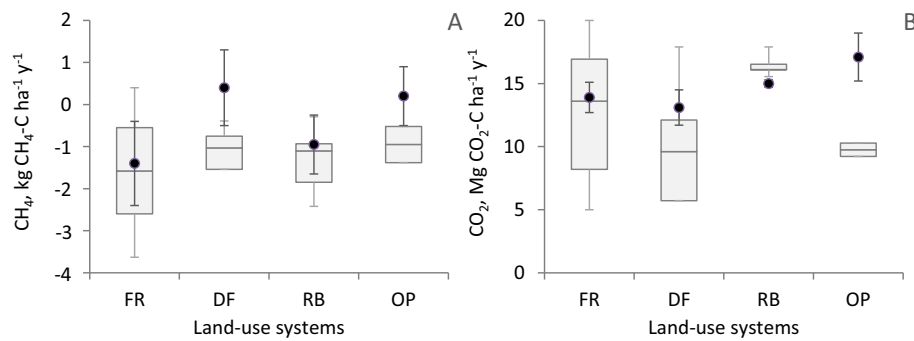


Fig. 3. Boxplot summary of annual soil CH₄ (A) and respiration (B) fluxes in tropical intact forests (FR), disturbed forests (DF), rubber plantations (RB), and oil palm plantations (OP). Black circles with error bars indicate the annual cumulative fluxes from this study and their standard error. The review in FR included nine cases for both CH₄ and respiration fluxes from sources a, b, c, d, e, f. The review in DF included four cases for both soil CH₄ and respiration fluxes from sources a, c, e. In RB, five cases were considered for both CH₄ and respiration from sources c, f. In OP, two cases were considered for both CH₄ and respiration from source f. Study sources are a, Verchot et al. (2000), Brazil; b, Fernandes et al. (2002), Brazil; c, Ishizuka et al. (2002), Indonesia; d, Keller et al. (2005), Brazil; e, Yashiro et al. (2008), Malaysia; f, Hassler et al. (2015), Indonesia.

attributed to decreased soil N availability. Thus, the existing limited research on tropical forest conversion to plantation points toward a stronger control of substrate availability and quality over changes in CH₄ uptake than that of soil climatic or physical parameters.

The annual cumulative soil respiration in the FR (13.9 ± 1.2 Mg C·ha⁻¹·yr⁻¹) and DF (13.1 ± 1.4 Mg C·ha⁻¹·yr⁻¹) was very similar to each other and in the range of previous studies carried out in tropical forests (Fig. 3B). The soil respiration in the rubber plantation category (15.0 ± 0.3 Mg C·ha⁻¹·yr⁻¹) and in the OP (17.1 ± 1.9 Mg C·ha⁻¹·yr⁻¹) were, respectively, slightly lower and higher than literature values. Our results concur with the findings by Ishizuka et al. (2002) and Hassler et al. (2015) that denote no change in the soil respiration rate following primary forest conversion to rubber plantation. By contrast, while Hassler et al. (2015) found a decrease in soil respiration from forest conversion to oil palm, we detected the opposite trend. Hassler et al. (2015) attributed the decrease to reduced soil C stocks and strongly decomposed soil organic matter following conversion to oil palm. Here, soil respiration along the conversion gradient increased with decreasing soil C:N ratio (Table 4), and so the higher respiration in the OP as compared to the result by Hassler et al. (2015) may be linked to the smaller C:N ratio of our soil

as compared to that of the soils inspected by Hassler et al. (C:N of 13). Higher rates of soil organic C decomposition with decreasing soil C:N ratio are consistent with findings by, for example, Swails et al. (2018) for peat soils of Indonesia. Soil respiration along the LUS transition was also markedly linked to changes in soil N content and litterfall quantity and quality. Both autotrophic activity and heterotrophic activity in the soil are controlled by substrate availability, and soil respiration is often related to litterfall (Ryan and Law 2005). While at global scales, soil respiration and litterfall are typically positively correlated, their relationship at our site displayed an opposite tendency. According to Raich and Tufekcioglu (2000), at local scales soil respiration varies less among nearby stands than do rates of plant production and local factors such as soil properties or species composition may obscure correlations that are obvious at broader scales. Lastly, we found a negative relationship between soil respiration and the density of termite nests which is contrary to our hypothesis. Termites can contribute 4–10% to forest floor respiration in the tropics (Lopes de Gerenyu et al. 2015, Ohashi et al. 2017), so a reduced population resulting from land-use change as observed in this study would be expected to diminish the influence of termites on the fluxes in and outside of the nests. While the study by Aini et al. (2015) showed that

the distance to the nearest termite nest could serve as a qualitative indicator to assess the influence of termites on soil N₂O emissions, results from the current research suggest that parameters additional to the density of termite nests would be necessary for evaluating potential impacts of termites on soil respiration. Similarly, the lack of a relationship between density of termite nests and CH₄ fluxes indicates that a better characterization of nests including their species or feeding group assemblage (Sugimoto et al. 1998, Eggleton et al. 1999) would be required to test termite nests as an indicator of the influence of termites on greenhouse gas fluxes.

Temporal variation of the fluxes and controlling factors

The coefficients of variation (CV) of soil CH₄ fluxes over the measurement period were extremely high (around 1,400%) while the CVs of soil respiration were moderate (38%). Studies using the CV for evaluating the temporal variability of soil CH₄ fluxes in tropical systems found values in the range 20–200% (Butterbach-Bahl et al. 2004, Werner et al. 2007, Rowlings et al. 2012), although in a Kenyan rainforest, Werner et al. (2007) obtained a CV of ~1900% for one chamber switching between being a sink and a source for atmospheric CH₄, potentially due to the influence of termite activity. The CV of soil CH₄ fluxes was lower for forests than for plantations, which concurs with the results by Werner et al. (2006) in rainforests and a rubber plantation in China. Temporal variation of soil respiration was within the ranges found in the tropics with CV between 20% and 80% (Butterbach-Bahl et al. 2004, Werner et al. 2006) and was homogeneous among land uses.

The environmental variables affecting temporal variation in CH₄ and respiration fluxes were essentially soil moisture and rainfall, both of them known to influence gas diffusion in the soil (Davidson et al. 2000, Verchot et al. 2000). According to Del Grosso et al. (2000), methanotrophic activity responds positively to increasing soil moisture when moisture is below field capacity and responds negatively when moisture is above field capacity. The increase in CH₄ fluxes (potentially corresponding to decreased methanotrophy) with increasing soil moisture in the forests, where the average soil moisture was far

above field capacity (Table 1), is therefore consistent with the models by Del Grosso et al. (2000). In the RB20 and OP, on the other hand, the average of soil moisture was very close to field capacity, so methanotrophy was likely not influenced by soil moisture variation explaining the absence of a significant response of CH₄ fluxes to soil moisture in these LUS over the year. Notwithstanding, during the fertilization experiment in the OP plantation, the average soil moisture (31.2%) was above field capacity and soil CH₄ fluxes responded positively when soil moisture was raised. In the RB1 plantation, the absence of a significant response may have resulted from the simultaneous interaction of multiple parameters controlling soil fluxes of CH₄. Monthly CO₂ respiration across land uses was inversely related to monthly precipitation with increasing rates of precipitation having sequentially lesser impacts on fluxes, as found by Raich and Potter (1995) using published field fluxes of soil CO₂ efflux. The relationship in our study was poor, with precipitation explaining only 26% of temporal variability in soil respiration. The weakness of the relationship may be related to the limited data given that soil respiration was monitored over only five months, but also to the lesser impact of rainfall on soil respiration in wet tropical forests as compared for instance to dry forests (Waring and Hawkes 2015, Waring and Powers 2016).

Despite the relationships between CH₄ and soil respiration fluxes and soil moisture or rainfall discussed above, we did not observe significant seasonal variations of the fluxes (Table 2). Moreover, soil moisture displayed overall higher values in wet than in dry months, but not in each individual land use. Several studies reported CH₄ uptake during dry months and emission during wet months (Verchot et al. 2000, Fernandes et al. 2002) or observed a decline in soil respiration in the dry season as compared to the wet season (Davidson et al. 2000, Fernandes et al. 2002, Ishizuka et al. 2002). By contrast and similar to our results, the research by Veldkamp et al. (2008) conducted in Sulawesi, Indonesia, found no seasonality in trace gas emissions. The general high climatic variability in the study area with an inconsistent and limited dry season likely explains the lack of seasonality in fluxes.

In addition to soil moisture, temporal variation in soil CH₄ fluxes was also influenced by soil mineral N dynamics in the OP plantation (Table 4). The negative correlation between CH₄ fluxes and NH₄⁺ content denotes N limitation of CH₄ consumption, in agreement with observations by Hassler et al. (2015). Ammonium can either inhibit or stimulate CH₄ oxidation, but most studies have focused on the inhibitory effect of nitrogenous fertilizer on methanotrophy (Bodelier and Laanbroek 2004). We expected N fertilizer application to promote soil CH₄ emission on the short-term but did not observe such an effect potentially because the amount of fertilizer applied was too small to inhibit CH₄ monooxygenase.

CONCLUSION

Degrading natural forests and converting them to plantations altered soil–atmosphere fluxes of CH₄ without turning the CH₄ sink into a source but weakening the sink in most land uses. Forest degradation and conversion to rubber plantation did not alter soil–atmosphere fluxes of CO₂ but conversion to oil palm plantation increased soil respiration. There was a strong control of substrate availability and quality over changes in soil CH₄ and respiration fluxes along the conversion gradient. The density of termite nests did not serve as good qualitative indicator to evaluate termite impact on soil CH₄ or respiration fluxes. Furthermore, the temporal variability of soil CH₄ fluxes was extremely high and markedly influenced by soil moisture variations in the forests and N dynamics in the oil palm plantation. Considering the high rate of forest conversion to rubber and oil palm plantations, there is a critical need for expanding the limited research on soil–atmosphere trace gas exchanges to reduce uncertainties and generate conclusions applicable at broader scales.

ACKNOWLEDGMENTS

This research was conducted under the Redd-Alert Project (Grant Agreement # 226310) with financial support from the European Commission Seventh Framework Programme [Fp7/2007-2013]. It was also generously funded by the Australian Agency for International Development (Ausaid) (Grant Agreement # 46167) and the Norwegian Agency for Development

Cooperation (Norad) (Grant Agreement #Qza-10/0468). This work is part of the Consultative Group on International Agricultural Research (Cgiar) Programs on Trees, Forests and Agroforestry (Fta) and Climate Change, Agriculture and Food Security (Ccafs). The authors extend their gratitude to staff from Brawijaya University in Malang, the Indonesian Soil Research Institute (Isri) in Bogor, and Balai Lingkungan Pertanian in Jakenan for laboratory support. We also thank Robbin Matthews and John Hillier, whose insights, feedbacks, and recommendations contributed to improve the quality of the manuscript and to the modeling team of the School of Biological and Environmental Science from the University of Aberdeen for Constructive Discussions. Furthermore, we are very thankful to all assistants and to the Redd-Alert Indonesia Team who supported fieldwork in Jambi. Finally, we are very grateful to the two anonymous reviewers for their constructive comments which contributed to improve this manuscript.

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DATA AVAILABILITY

Raw and summary replicate data of soil CH₄ and respiration fluxes and environmental variables together with soil N₂O emissions from the study by Aini et al. (2015) are available at <https://doi.org/10.17528/CIFOR/DATA.00204>