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Soil fertility controls soil–atmosphere carbon dioxide and methane fluxes in a tropical landscape converted from lowland forest to rubber and oil palm plantations

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BGD
12, 9163–9207, 2015

Abstract

Expansion of palm oil and rubber production, for which global demand is increasing, causes rapid deforestation in Sumatra, Indonesia and is expected to continue in the next decades. Our study aimed to (1) quantify changes in soil CO_2 and CH_4 fluxes with land-use change, and (2) determine their controlling factors. In Jambi Province, Sumatra, we selected two landscapes on heavily weathered soils that differ mainly in texture: loam and clay Acrisol soils. At each landscape, we investigated the reference land uses: forest and secondary forest with regenerating rubber, and the converted land uses: rubber (7–17 years old) and oil palm plantations (9–16 years old). We measured soil CO_2 and CH_4 fluxes monthly from December 2012 to December 2013. Annual soil CO_2 fluxes from the reference land uses were correlated with soil fertility: low extractable phosphorus (P) coincided with high annual CO_2 fluxes from the loam Acrisol soil that had lower fertility than the clay Acrisol soil ($P < 0.05$). Soil CO_2 fluxes from the oil palm decreased compared to the other land uses ($P < 0.01$). Across land uses, annual CO_2 fluxes were positively correlated with soil organic carbon (C) and negatively correlated with ^{15}N signatures, extractable P and base saturation. This suggests that the reduced soil CO_2 fluxes from oil palm was a result of strongly decomposed soil organic matter due to reduced litter input, and possible reduction in C allocation to roots due to improved soil fertility from liming and P fertilization in these plantations. Soil CH_4 uptake in the reference land uses was negatively correlated with net nitrogen (N) mineralization and soil mineral N, suggesting N limitation of CH_4 uptake, and positively correlated with exchangeable aluminum (Al), indicating decrease in methanotrophic activity at high Al saturation. Reduction in soil CH_4 uptake in the converted land uses compared to the reference land uses ($P < 0.01$) was due to decrease in soil N availability in the converted land uses. Our study shows for the first time that differences in soil fertility control soil–atmosphere exchange of CO_2 and CH_4 in a tropical landscape, a mechanism that we were able to detect by conducting this study at the landscape scale.

BGD
12, 9163–9207, 2015

1 Introduction

Oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*) are two of the fastest expanding tree cash crops in the tropics (Clay, 2013). Global oil palm production has quintupled from 1990 to 2013 and is currently grown on an estimated area of 17 million hectare (Mha) (Food and Agricultural Organization, 2014). Indonesia contributes nearly half of global palm oil production (Food and Agricultural Organization, 2014), and is planning to double its production in the coming decade (Carlson et al., 2013). Similarly, rubber is grown on around 10 Mha globally, whereby Indonesia is the second largest rubber producer (Food and Agricultural Organization, 2014). Most Indonesian oil palm and rubber production are located in Sumatra (Indonesian Ministry of Agriculture, 2014), where conversion of lowland rainforest to plantations has been widespread (Laumonier et al., 2010). It has been estimated that plantation establishment has caused a loss of 7.5 Mha of Sumatran natural forest in the last two decades (1990–2010) (Margono et al., 2012), and future expansion will probably be at the expense of large areas of tropical forest, unless a properly planned and spatially explicit development strategy will be implemented (Koh and Ghazoul, 2010).

Although the majority of remaining lowland tropical forests are located on nutrient poor, heavily weathered soils, these ecosystems are among the most productive worldwide and contain globally significant above- and belowground carbon stocks. The high ecosystem productivity is possible despite the nutrient poor soils because of efficient cycling of rock-derived nutrients (phosphorus (P) and base cations) between vegetation and soil, and also high soil nitrogen (N) availability caused by biological N fixation (Hedin et al., 2009). Conversion of tropical forest to agricultural land-use systems does not only decrease biodiversity and contribute to climate change (Danielsen et al., 2009) but also alters soil fertility and soil physical properties in the newly established land-use systems (Dechert et al., 2004; Klinge et al., 2004). Burning of slashed vegetation is typically part of forest conversion, releasing large amounts of nutrients previously bound in the vegetation. A considerable part of these nutrients ends up in the soil but is sus-

BGD
12, 9163–9207, 2015

ceptible to losses (through leaching and gaseous emission), which are especially high in the earlier years of crop establishment and decrease with time (Klinge et al., 2004). Furthermore, forest conversion is often associated with increases in soil bulk density. These dynamic changes in soil fertility and soil bulk density following forest conversion do not only affect agricultural production but also the soil–atmosphere exchange of trace gases like carbon dioxide (CO_2) and methane (CH_4) since their production, consumption and exchange are directly related to soil fertility and soil bulk density (Keller et al., 1993; Veldkamp et al., 2008).

Globally, soils are the largest natural source of CO_2 (IPCC, 2007), which is released during respiration processes of microbial communities and roots (Raich and Schlesinger, 1992). While the important proximal controllers of soil CO_2 fluxes are soil temperature and moisture, it has been demonstrated that other distal regulators such as vegetation type and soil physical and biochemical properties (e.g. bulk density, texture, pH, carbon stocks) also affect soil CO_2 fluxes (Raich and Schlesinger, 1992). Soils also play a dominant role in the production and consumption of CH_4, a greenhouse gas with a global warming potential of 23 times that of CO_2 over a 100 year time horizon (IPCC, 2007). In soils, CH_4 can be produced during anaerobic decomposition by methanogenic archaea, while CH_4 can also be consumed by methanotrophic bacteria which are able to utilize CH_4 as an energy source. Whether net consumption or net emission of CH_4 occurs at the soil surface depends on the balance between production and consumption in the soil. For soil CH_4 fluxes, the proximal controllers are soil moisture, gas diffusivity and temperature, while other distal regulators include microbial activity, N availability and aluminum toxicity (Verchot et al., 2000; Tamai et al., 2003; Bodelier and Laanbroek, 2004; Veldkamp et al., 2013).

In tropical lowland forest landscapes with heavily weathered soils, much of the spatial variability in trace gas fluxes appears to be related to soil texture (Sotta et al., 2006). In the Brazilian Amazon, lowland forests on Acrisol and Ferralsol soils display high soil CO_2 emissions with large variations among sites that relate to soil texture: soils with sandy loam to sandy clay loam texture had 21–36 % higher CO_2 emissions than soils

BGD
12, 9163–9207, 2015

with clay texture (Keller et al., 2005; Sotta et al., 2006). Moreover, although well-drained soils in tropical lowland forests act generally as a sink for CH_4 (Keller and Reiners, 1994; Verchot et al., 2000; Veldkamp et al., 2013), their differences in CH_4 uptake are explicable by their differences in soil texture. In a review of 16 tropical lowland forests, the only factor correlating annual CH_4 fluxes with site characteristics was a significant positive correlation with clay contents, indicating that the higher the clay content the lower is the CH_4 uptake (Veldkamp et al., 2013).

Since much of the original forest in our study area have been converted to oil palm and rubber plantations, the management practices in these land uses added important factors that influence soil CO_2 and CH_4 fluxes from these converted landscapes. Earlier studies have shown that forest conversion to agricultural land uses in the tropics lead to considerable changes in soil CO_2 fluxes, which were related to changes in belowground C allocation (Davidson et al., 2000; Salimon et al., 2004), carbon quality (Werner et al., 2006), living fine root biomass and litter input (Ishizuka et al., 2002; Sheng et al., 2010). Conversion of tropical forest to agricultural land uses causes a reduction in soil CH_4 uptake or even turns the soil into a source of CH_4. Often this trend is explained by soil compaction, which leads to reduced gas diffusivity and accordingly limits aerobic CH_4 oxidation while enhancing anaerobic CH_4 production (Keller et al., 1993; Veldkamp et al., 2008). Changes in N availability may also play a role since CH_4 uptake may be N limited (Bodelier and Laanbroek, 2004; Veldkamp et al., 2013) and high concentrations of ammonium (NH_4^+, e.g. from fertilization) can inhibit CH_4 oxidation (Veldkamp et al., 2001; Werner et al., 2006). Finally, termites are known to produce CH_4 and their presence may also affect the balance between production and consumption of CH_4 (Seiler et al., 1984).

Although Sumatra, Indonesia represents a hot spot of land-use change, especially for the establishment of rubber and oil palm plantations, how this affects soil CO_2 and CH_4 fluxes remains highly uncertain for the following reasons: (1) most studies relating land-use change to trace gas emissions have been conducted in South and Central America (Keller and Reiners, 1994; Davidson et al., 2000; Verchot et al., 2000; Veld-

BGD
12, 9163–9207, 2015

kamp et al., 2001; Salimon et al., 2004) and only few studies were conducted in Southeast Asia (Ishizuka et al., 2002; Veldkamp et al., 2008), (2) most studies have focused on forest conversion to traditional land uses such as maize, pastures, slash-and-burn agriculture, cacao and coffee, and less on the rapidly expanding tree cash crops such as rubber and oil palm, (3) the few studies that reported CO_2 and CH_4 fluxes from oil palm plantations were conducted on peat soils (Melling et al., 2005a, b) whereas the studies conducted on mineral soils, where most of the rubber and oil palm plantations are located, were either conducted without spatial replication, covered only short periods of measurements (Ishizuka et al., 2002; Adachi et al., 2005; Werner et al., 2006) or measured only once (Ishizuka et al., 2005). It is imperative that better information becomes available on trace gas fluxes from these economically-important and rapidly-expanding rubber and oil palm plantations. Whether palm oil-based biofuel indeed has environmental advantages compared to fossil fuel depend, among many facets, on the greenhouse gas balance during oil palm fruit production.

In the present study, our aims were to (1) quantify changes in soil–atmosphere fluxes of CO_2 and CH_4 with land-use change, and (2) determine their controlling factors in a converted lowland landscape in Sumatra, Indonesia. Soil–atmosphere fluxes of CO_2 and CH_4 were measured in forest and secondary forest with regenerating rubber (hereafter called jungle rubber, which is a more traditional rubber agroforestry system (Gouyon et al., 1993)) as reference land uses and the converted land uses of monoculture rubber and oil palm plantations. Our study was designed to cover these four land-use types in each of the two landscapes on highly weathered soils that differed mainly in texture: clay and loam Acrisol soils. We tested the following hypotheses: (1) soil CO_2 emissions and CH_4 uptake are higher in loam than in clay Acrisol soils, and (2) soil CO_2 fluxes and CH_4 uptake rates are higher in the reference land uses (forest and jungle rubber) than in the converted land uses (rubber and oil palm plantations). Here, we present the first spatially replicated study with a full year of measurements that investigates soil CO_2 and CH_4 fluxes from conversion of forest or jungle rubber to rubber and oil palm plantations on mineral soils. We also evaluate the effect of man-

BGD
12, 9163–9207, 2015

agement intensity since we compare rubber plantations without fertilizer inputs with fertilized oil palm plantations. Our results will be a critical contribution to trace gases life-cycle assessment of rubber and palm oil at the production stage.

2 Material and methods

2.1 Study area and experimental design

The study area is located in the lowlands (35–95 m a.s.l.) of Jambi province, Sumatra, Indonesia. In the past two decades, forest cover in Jambi province decreased by 1.14 Mha, which was about 40 % of the forest cover in 1990 (Margono et al., 2012). The climate is humid tropical with a mean annual air temperature of 26.7 ± 0.1 °C and a mean annual precipitation of 2235 ± 385 mm (1991–2011; data from Jambi–Sultan–Thaha airport of the Indonesian Meteorological, Climatological and Geophysical Agency). The dry season is usually from May to September and the rainy season occurs from October to April. In 2013, during our study period, the wet season lasted slightly longer, while a drier period was detected between mid-June and end-October. During this dry period, rainfall was reduced by 35–57 % compared to the wetter months during which rainfall was 333–362 mm per month.

We selected two landscapes on heavily weathered soils that mainly differed in texture: loam Acrisol soil (36 ± 6 % sand, 32 ± 4 % silt and 32 ± 2 % clay in the top 0.5 m) and clay Acrisol soil (26 ± 6 % sand, 29 ± 3 % silt and 45 ± 4 % clay in the top 0.5 m). This textural difference led to differences in soil fertility: forest sites in the clay Acrisol soil had higher base saturation, Bray-extractable P and lower Al saturation compared to those in the loam Acrisol soil ($P \leq 0.01$ to 0.04; Appendix Table A1; Allen et al., unpublished data). Detailed soil physical and biochemical characteristics from our study sites were measured by Allen et al. (unpublished data) and are summarized in Appendix Table A1. Acrisol soils cover about 50 % of the land area in Sumatra and about one third of Indonesia (FAO et al., 2009). The clay Acrisol landscape was located about

BGD
12, 9163–9207, 2015

160 km southwest of Jambi City between 01.94° S, 102.58° E and 02.14° S, 102.85° E. Forest sites in this landscape were established within the Bukit Duabelas National Park (administered by the Ministry of Forestry, PHKA). The loam Acrisol landscape was located about 80 km southwest of Jambi City between 01.79° S, 103.24° E and 2.19° S, 103.36° E. The forest sites in this landscape were established within the Harapan Forest Reserve and had been partially logged in the past (administered by the Restoration Ecosystem Indonesia Harapan, PT REKI).

In each landscape, we studied four land-use types: lowland forest, jungle rubber, and smallholder monoculture plantations of rubber and oil palm. In Jambi province, the smallholder rubber and oil palm plantations were established after clearing and burning either the forest (often partially logged) or jungle rubber (based on interviews conducted by Euler et al., unpublished data). Thus, in our study the lowland forest and jungle rubber served as the reference land uses, representing the baseline conditions with which we compared the rubber and oil palm plantations.

For each of the four land-use types within each landscape, we selected four replicate plots (50 m × 50 m each with a minimum distance of 200 m between plots), totaling to 32 plots that were all located on relatively flat, well drained positions in the landscape. Additional information on tree species composition, tree density, tree height, basal area, and plantation age of these plots are reported in Appendix Table A2. Within each plot, we established a 10 × 10 grid which was used to select four randomly nested subplots (5 m × 5 m each) that were at least 5 m from the plot's border. In each subplot, we randomly deployed one permanent chamber base to measure soil trace gas fluxes.

This approach of comparing soil CO_2 and CH_4 fluxes from the converted land uses to the reference land use in order to assess the effects of land-cover change has the implicit assumption that before land-use conversion soil characteristics were comparable. We tested this assumption by comparing the land-use independent soil characteristics, i.e. clay content in 0.5–2 m depth, among land uses within each landscape. Since there were no significant differences in clay contents between the reference and converted land uses at these depths (Appendix Table A1; Allen et al., unpublished data), we de-

BGD
12, 9163–9207, 2015

duced that the sites within each landscape had previously similar soil characteristics and that differences in trace gas fluxes can be attributed to the changes in land use and its associated management practices.

Since all the plantations were managed by smallholders, management practices of rubber and oil palm were diverse. The following information on management practices were based from our interviews of the smallholders. In 2013, oil palm and rubber plantations were weeded once or twice a year either manually or using herbicide (most commonly 2–5 L Gramaxone® or Roundup® $ha^{-1}\,year^{-1}$). Oil palm plantations were fertilized whereas rubber plantations were not. Oil palm plantations in the clay Acrisol landscape were fertilized only once during the rainy season, whereas those in the loam Acrisol landscape had a second fertilizer application in the dry season. The most commonly used fertilizers were NPK complete fertilizer (i.e. Phonska, Mahkota), potassium chloride (KCl) and urea. Plantations fertilized once received about 300 kg NPK-fertilizer $ha^{-1}\,year^{-1}$ and plantations fertilized twice received about 550 kg NPK-fertilizer $ha^{-1}\,year^{-1}$. In terms of added nutrient element, these rates were equivalent to 48–88 kg N $ha^{-1}\,year^{-1}$, 21–38 kg P $ha^{-1}\,year^{-1}$ and 40–73 kg K $ha^{-1}\,year^{-1}$. Additionally, three of the smallholders applied 157 kg K-KCl $ha^{-1}\,year^{-1}$ and 143 kg KCl-K $ha^{-1}\,year^{-1}$ and two of the smallholders applied 138 kg urea-N $ha^{-1}\,year^{-1}$. One of the smallholders also applied lime in 2013 at about 200 kg dolomite $ha^{-1}\,year^{-1}$. Smallholders typically applied the fertilizer around the oil palm tree at about 0.8–1 m distance from the tree base. Additionally, senescing fronds were regularly cut and piled on the inter-rows of an oil palm plantation, typically in the middle of the 9 m distance between rows of oil palms. Oil palm fruits were harvested every two weeks, whereas the latex of the rubber and jungle rubber was collected weekly.

2.2 CO_2 and CH_4 flux measurement

Soil CO_2 and CH_4 fluxes were measured monthly from December 2012 to December 2013, using static vented chambers. We are aware that the use of static vented chambers for CO_2 and CH_4 flux measurements could have possible sources of er-

BGD
12, 9163–9207, 2015

ror due to changes in diffusion gradients during chamber closure. We have however adapted the design of our chambers and the flux calculation to minimize, if not avoid, these possible errors (see below). A clear advantage of the static vented chamber method compared to other methods is that it remains the only operational method that can be used to measure trace gas fluxes at a large number of plots (in our case 32) spread over a large area with regular measurements within a year. Furthermore, it also yields information on short-distance spatial variability of trace gas fluxes, which cannot be quantified by more integrative tower-based methods. Our chamber bases were made of polyvinyl chloride (0.05 m^2 area) and inserted ~ 0.03 m into the soil. In each of the four subplots per replicate plot, we randomly placed a permanent chamber base one month before the first measurement started. Since the area occupied by piled fronds or applied with fertilizer in oil palm plantations was relatively small, none of these randomly placed chamber bases (range of distance to the tree base was 1.8–5 m) happened to be located on such area. During sampling, the chamber bases were covered with polyethylene hoods (0.27 m total chamber height, and 12 L total volume) equipped with a Luer-lock sampling port and a vent for pressure equilibrium. Four gas samples (30 mL each) were removed at 1, 11, 21 and 31 min after chamber closure using a plastic syringe connected to the Luer-lock port. Immediately after sampling, gas samples were stored with overpressure into pre-evacuated 12 mL Labco Exetainers® (Labco Limited, Lampeter, UK) with rubber septa that were only used once. Our group has tested these exetainers for extended period of sample storage (e.g. up to 6 months) and airfreight transport by storing and transporting standard gases of known concentrations in overpressure, and these exetainers were proven to be leak proof. Gas samples in exetainers were transported to Germany by airfreight every 3–4 months and were analyzed upon arrival using a gas chromatograph (GC 6000 Vega Series 2, Carlo Erba Instruments, Milan, Italy with an ASPEC autosampler, Gilson SAS, Villiers, Le Bel, France), equipped with a flame ionization detector and an electron capture detector. Three standard gases were used for calibration with concentrations from 350 to 5000 ppm for CO_2 and 1000 to 5000 ppb for CH_4 (Deuste Steininger

BGD
12, 9163–9207, 2015

GmbH, Mühlhausen, Germany). The software Probe66 Version 1.3 (Messwert GmbH, Göttingen, Germany) was used to determine CH_4 and CO_2 sample concentrations by comparing integrated peak areas with those of the standard gases. Fluxes were calculated from the concentration change over time of chamber closure, and adjusted with actual air temperature and pressure measured at the time of sampling. Linearity of increase of CO_2 concentrations with time of chamber closure ($R^2 \geq 0.98$) was checked for each chamber measurement and in a few cases where concentration curved at the last sampling time we excluded the last data points and calculated the fluxes based on the linear increase in concentrations during the first 3 samplings. For CH_4, zero fluxes were included. Assuming constant flux rates per day, annual soil CO_2 and CH_4 fluxes from the monthly sampling and total fluxes during a fertilization event (see below) were calculated by adopting the trapezoidal rule on time intervals between measured flux rates, similar to the method we employed in our earlier studies (e.g. Koehler et al., 2009; Veldkamp et al., 2013).

Since our monthly measurements may have missed the short-term effect of fertilization on soil CO_2 and CH_4 fluxes, we evaluated such effect by simulating a fertilizer application and conducted more frequent (6 to 11 times) measurements during 3–8 weeks following fertilization. We chose 3 plots of oil palm plantations in each of the 2 landscapes, and in each plot we selected 3 trees separated by an inter-row distance of 9 m (in total, 18 oil palm trees). At 0.8 m distance from the base of each tree, we applied manually the fertilizer within a width of 0.2 m around the tree using the same rate that smallholders applied to these oil palm plantations (i.e. equivalent to 2 kg fertilizer per tree, based from 300 kg NPK-fertilizer ha^{-1} divided by 134–140 trees ha^{-1}; Appendix Table A2). We used the same fertilizer forms that smallholders applied, i.e. NPK complete fertilizer in the clay Acrisol landscape and a combination of KCl, ammonium sulfate and NPK complete fertilizer in the loam Acrisol landscape. One chamber base was placed at 0.3 m distance from the tree base (chamber location a); another chamber base was placed at 0.8 m distance from the tree wherein the fertilizer was applied (chamber location b); and a third chamber was placed at 4–4.5 m distance from the tree

BGD
12, 9163–9207, 2015

that served as a reference chamber without direct fertilizer application (chamber location c). In the clay Acrisol landscape, measurements in the 3 oil palm plots were done from mid-October to mid-December 2013, mid-February to mid-March 2014, and mid-February to mid-April 2014. In the loam Acrisol landscape, measurements were done from the end of October 2013 to mid-December 2014, mid-January to mid-March 2014, and mid-March to the start of April 2014. Shorter intervals of sampling days (Appendix Fig. B1) were conducted right after the fertilizer application.

2.3 Auxiliary measurements

Soil temperature, moisture and mineral N content were measured with each trace gas measurement. Soil temperature was determined in the top 0.05 m depth using a GMH 1170 digital thermometer (Greisinger electronic GmbH, Regenstauf, Germany). Soil samples for mineral N content were also taken from the top 0.05 m at approximately 1 m distance from each chamber with 4 soil samples per plot. These 4 soil samples were pooled to represent each replicate plot on each day of measurement, and roots, leaves and twigs were manually removed. For the fertilization experiment, soil samples taken near each chamber location (a, b and c) were processed separately. Since even short storage of disturbed soil samples can affect mineral N concentrations (Arnold et al., 2008), extraction was done in the field immediately following soil sampling. A soil sample was added to a prepared 250 mL plastic bottle containing 150 mL of 0.5 mol L^{-1} K_2SO_4 (approximately 1 : 3 ratio of fresh soil to extractant volume) and transported to the field station. At the field station, samples were shaken for 1 h, filtered through pre-washed (with 0.5 mol L^{-1} K_2SO_4) filter papers (Whatman, GE Healthcare Life Sciences, 4 µm nominal pore size) and the filtrate were immediately stored in a freezer. The remaining field-moist soil samples were stored in plastic bags and gravimetric moisture content was determined at the field station, for which 50–100 g of fresh soil was dried at 105 °C for at least 1 day. The gravimetric moisture content was used to calculate the dry mass of the soil extracted for mineral N. Frozen extracts were transported by airfreight to Germany to ensure that they stayed frozen

BGD
12, 9163–9207, 2015

throughout the transport until analysis. At our laboratory in the University of Göttingen, Germany, NH_4^+ and NO_3^- concentrations in the extracts were analyzed using continuous flow injection colorimetry (SEAL Analytical AA3, SEAL Analytical GmbH, Norderstedt, Germany). NH_4^+ was determined by salicylate and dicloro-isocyanuric acid reaction (Autoanalyzer Method G-102-93), and NO_3^- by cadmium reduction method with NH_4Cl buffer (Autoanalyzer Method G-254-02). Soil water content was expressed as water-filled pore space (WFPS), calculated using a particle density of 2.65 g cm^{-3} for mineral soil and the measured bulk densities in our study sites (Appendix Table A1).

2.4 Statistical analysis

All statistical analyses of the monthly measurements of soil CO_2 and CH_4 fluxes were conducted using the means of the four chambers (or subplots) that represent each replicate plot on a given sampling day. Data were checked for normal distribution (using Shapiro–Wilk's tests), and if necessary a logarithmic or square root transformation was used. For our first objective, we conducted comparisons of the reference land uses between the two landscapes in order to test the first hypothesis. Then we carried out comparisons among land-use types within each landscape to test our second hypotheses. Linear mixed effect models (LME) were applied (Crawley, 2009) with either landscape (i.e. comparing landscapes for each reference land use) or land use (i.e. comparing land-use types within each landscape) as the fixed effect and replicate plots and sampling days as the random effects. For the fertilization experiment, we tested differences in soil CO_2 and CH_4 fluxes between chamber locations within each oil palm plantation plot, using LME with chamber location as the fixed effect and palm trees and sampling days as the random effects. We extended the LME model to include: either (1) a variance function that allows different variances of the fixed effect, (2) a first-order temporal autoregressive process that assumes the correlation between sampling days decreases with increasing time difference, or both if these improved the relative goodness of the model fit based on the Akaike information criterion. Fixed effect was considered significant based on analysis of variance at $P \leq 0.05$, and differences

BGD
12, 9163–9207, 2015

between landscapes or land-use types (or chamber locations for the fertilization experiment) were assessed using Fisher's least significant difference test $P \leq 0.05$. For our second objective, we assess how soil factors influence the seasonal variations of soil CO_2 and CH_4 fluxes, using Pearson's correlation tests with soil temperature, WFPS, NO_3^-, NH_4^+ and total mineral N. This assessment of seasonal controls of trace gas fluxes was conducted for each land use within each landscape using the means of the four replicate plots on each of the 12 monthly measurements. Lastly, we assessed the influence of soil physical and biochemical characteristics (Appendix Table A1) on the spatial variations of soil annual CO_2 and CH_4 fluxes first on the reference land uses across landscapes (16 plots) and second across land-use types within each landscape (16 plots), using Spearman's rank correlation test. The first was to assess the spatial controls of trace gas fluxes from the reference land uses, and the second was to evaluate which soil factors drive the spatial variation of trace gas fluxes across land uses. For all correlation tests, statistical significance was taken at $P \leq 0.05$, except in a few cases for which marginal significance at $P \leq 0.09$ was considered because our experimental design encompassed the inherent spatial variability in the studied landscapes. All statistical analyses were conducted using R 3.0.2 (R Development Core Team, 2013).

3 Results

3.1 Reference land uses (forest and jungle rubber): comparison between landscapes

WFPS in the jungle rubber was higher in the clay than loam Acrisol soils ($P < 0.01$), but in the forest WFPS did not differ between landscapes ($P = 0.56$; Fig. 1a and b). In both landscapes, we detected a distinctly lower WFPS during the drier period (mean WFPS ranged 38–80 % between mid-June and October) compared to the wetter period (mean WFPS ranged 50–96 %; $P < 0.01$; Fig. 1a and b). Soil temperatures in the forest were

BGD
12, 9163–9207, 2015

lower in the clay than loam Acrisol soils ($P = 0.02$; Fig. 1c and d), which was probably due to the difference in the time of the day when measurements were conducted. Soil temperatures in the jungle rubber did not differ between landscapes ($P = 0.17$).

In both landscapes, NH_4^+ was the dominant form of mineral N (Table 1). Soil NH_4^+ contents in the jungle rubber were higher in the clay than loam Acrisol soils ($P = 0.02$), but in the forest soil NH_4^+ contents did not differ between landscapes ($P = 0.90$; Table 1). Soil NO_3^- contents in the forest were higher in the clay than loam Acrisol soils ($P < 0.01$), whereas soil NO_3^- contents in the jungle rubber was higher in the loam than clay Acrisol soils ($P = 0.02$; Table 1). Total mineral N contents in both reference land uses did not differ between landscapes ($P = 0.11$–0.19; Table 1).

We detected no differences in soil CO_2 fluxes between landscapes for the reference land-use types ($P = 0.63$–0.69; Table 2; Fig. 2a and b). Similarly, soil CH_4 fluxes from both reference land uses were also comparable between the two landscapes ($P = 0.26$–0.27; Table 2; Fig. 2c and d). However, in the loam Acrisol soil, two of the four forest sites displayed net CH_4 emissions in 26 % of the measurements, which resulted in its largest variation among plots (as indicated by its largest standard error around the mean; Table 2).

3.2 Converted land uses (rubber and oil palm plantations): comparisons to the reference land uses within each landscape

While in both landscapes WFPS did not differ among land-use types ($P = 0.12$–0.26; Fig. 1a and b), soil temperatures were slightly higher in the plantations (27.2 ± 0.1 °C) compared to the reference land uses (25.9 ± 0.1 °C) in each landscape (both $P < 0.01$; Fig. 1c and d). Soil NH_4^+ contents in rubber were lower than in all other land uses in the clay Acrisol soil ($P = 0.05$), and soil NH_4^+ contents in both rubber and oil palm were also lower than in the reference land uses in the loam Acrisol soil ($P = 0.03$; Table 1). In the clay Acrisol soil, NO_3^- contents in rubber and oil palm were lower than in forest ($P < 0.01$), and in the loam Acrisol soil NO_3^- contents in rubber were lowest

BGD
12, 9163–9207, 2015

whereas these were intermediary in oil palm ($P < 0.01$; Table 1). The latter was related to a fertilizer application by the owner of one of the oil palm plots just a month prior to our measurement. Total mineral N showed similar differences among land-use types in each landscape as those with soil NH_4^+ and NO_3^- contents (both $P < 0.01$; Table 1).

Soil CO_2 fluxes from oil palm were 45 % lower in the clay Acrisol soil and 38 % lower in the loam Acrisol soil compared to the forest (both $P < 0.01$; Table 2; Fig. 2a and b). From the fertilization experiment, soil CO_2 fluxes from within 1 m distance to the oil palm base (chamber locations a and b) were on average 2.3 ± 0.2 times higher than those at 4–4.5 m from the tree base (chamber location c) in both landscapes (all $P <$ 0.01; Appendix Table A3). However, this area within 1 m distance to the tree base is only 3 m^2 $tree^{-1}$ or 4 % on a hectare basis, and so even if we would weight with area coverage the annual soil CO_2 fluxes (Table 2), which were measured from chambers placed randomly between 1.8–5 m from the oil palm base, such high fluxes within 1 m distance to the tree base would still account less than the standard errors (7–9 %) of the mean annual fluxes.

Soil CH_4 uptake in the plantations were 84 % (oil palm) and 93 % (rubber) lower compared to the forest and 69 % (oil palm) and 86 % (rubber) lower compared to the jungle rubber in the clay Acrisol soil ($P < 0.01$; Table 2; Fig. 2c and d). Also in the loam Acrisol soil, CH_4 uptake in the plantations was lower (reduction of 64 % for rubber and 44 % for oil palm) compared to jungle rubber ($P = 0.02$; Table 2; Fig. 2c and d). However, CH_4 uptake in the forest on loam Acrisol soils deviated from the differences detected in the clay Acrisol soils because of the two forest sites that displayed net CH_4 emissions (see above; Table 2; Fig. 2d). From the fertilization experiment, soil CH_4 uptake from the area of fertilizer application (chamber location b) were 2.6 ± 0.2 times lower than the unfertilized chamber locations a and c (respectively at 0.3 m and 4–4.5 m distance from the oil palm base) ($P \leq 0.01$–0.05; Appendix Table A3), with the exception of plot 3 in the clay Acrisol soil ($P = 0.45$; Appendix Table A3). In most cases, CH_4 uptake in chamber location b was reduced immediately following fertilizer application and was restored to pre-fertilization values after about 6 weeks (Appendix

BGD
12, 9163–9207, 2015

Fig. B1). Thus, even if we would weight with the area coverage (~ 1.3 % of the area in a hectare) and time duration (12 % of the time in a year) the annual soil CH_4 fluxes, the effect of this fertilized location would be negligible.

3.3 Seasonal controls of CO_2 and CH_4 fluxes from each land-use type

In the clay Acrisol soil, CH_4 fluxes were positively correlated with WFPS (Table 3) in each of the four land-use types, signifying the higher CH_4 uptake in the dry than wet season ($P \leq 0.01$–0.03; Fig. 2c). Soil CH_4 fluxes correlated negatively with NO_3^- contents in forest and with soil CO_2 fluxes in rubber (Table 3). Across all land-use types, soil CH_4 uptake was negatively correlated with total mineral N content ($R = -0.47$, $P \leq 0.01$, $n = 41$; Fig. 3a) and NO_3^- content ($R = -0.73$, $P \leq 0.01$, $n = 41$). Some correlations in Table 3 were possibly spurious: in oil palm, soil CO_2 fluxes were positively correlated with soil temperatures (Table 3) even if the temperate range was small (25.5–28.8 °C) such that this correlation was likely caused by the differences in sampling time during the day rather by seasonal temperature pattern. In jungle rubber, plotting soil CO_2 fluxes against soil NO_3^- contents showed that their correlation (Table 3) was apparently caused by a group of many low NO_3^- contents against one high NO_3^- value and this correlation became insignificant when the one high value was removed. Also, in rubber, the marginal negative correlation between soil CH_4 fluxes with NO_3^- contents was because of the correlation between WFPS and NO_3^- contents.

In the loam Acrisol soil, seasonal variations of soil CO_2 fluxes were positively correlated with WFPS in jungle rubber and negatively correlated with WFPS in rubber (Table 3). Some correlations in Table 3 were also spurious caused by differences in sampling time during the day rather than by seasonal pattern: correlation between soil CO_2 fluxes and soil temperature in forest and oil palm despite narrow temperate ranges (24.8–27.2 °C in forest and 25.8–29.4 °C in oil palm). The negative correlation between soil CO_2 fluxes and NO_3^- contents in jungle rubber was driven by the negative correlation between WFPS and NO_3^- (Table 3). As was observed in the clay Acrisol

BGD
12, 9163–9207, 2015

soil, seasonal variation in soil CH_4 fluxes from the loam Acrisol soil was positively correlated with WFPS in each of the three land-use types (Table 3) with the exception of the forest which was caused by one extreme CH_4 emission from a single chamber (656.47 $\mu g\,C\,m^{-2}\,h^{-1}$). When this one value was excluded, a positive correlation between soil CH_4 fluxes and WFPS was also detected for forest ($R = 0.60$, $P \leq 0.01$, $n = 12$). Soil CH_4 fluxes correlated also positively with soil CO_2 fluxes in jungle rubber whereas this correlation was negative in rubber (Table 3). In the jungle rubber, soil CH_4 fluxes correlated negatively with soil NO_3^- contents (Table 3). Across land-use types, we also observed negative correlations of soil CH_4 uptake with total mineral N content ($R = -0.52$, $P \leq 0.01$, $n = 38$; Fig. 3b) and NO_3^- content ($R = -0.75$, $P \leq 0.01$, $n = 38$).

3.4 Spatial controls of annual CO_2 and CH_4 fluxes across land-use types within each landscape

For these correlation analyses, all soil physical and biochemical characteristics, which were measured by Allen et al. (unpublished data), are reported in Appendix Table A1. First, analyzing both reference land uses (forest and jungle rubber) across landscapes, the only significant correlation between annual soil CO_2 emissions and soil parameters was with sand content ($R = -0.51$, $P = 0.08$, $n = 16$). However, analyzing for each landscape separately, annual soil CO_2 fluxes from the reference land uses in the loam Acrisol soil correlated with Bray-extractable soil P ($R = -0.74$, $P = 0.04$, $n = 8$). Furthermore, annual soil CH_4 fluxes from both reference land uses across landscapes were correlated with net N mineralization rates ($R = -0.75$, $P < 0.01$, $n = 16$) and, for each landscape separately, with exchangeable Al ($R = 0.74$, $P = 0.04$, $n = 8$ in the clay Acrisol soil, and $R = 0.69$, $P = 0.06$, $n = 8$ in the loam Acrisol soil).

Second, analyzing across four land-use types within each landscape, annual soil CO_2 fluxes correlated only with soil ^{15}N natural abundance signatures in the clay Acrisol soil ($R = -0.49$, $P = 0.05$, $n = 16$). In the loam Acrisol soil, annual soil CO_2 fluxes correlated with soil organic C ($R = 0.49$, $P = 0.06$, $n = 16$), base saturation ($R = -0.53$, $P = 0.04$, $n = 16$), Bray-extractable P ($R = -0.71$, $P < 0.01$, $n = 16$) and soil ^{15}N natural

BGD
12, 9163–9207, 2015

abundance signatures ($R = -0.60$, $P = 0.02$, $n = 16$). Annual soil CH_4 fluxes across all land uses in the clay Acrisol soil correlated with net N mineralization rates ($R = -0.52$, $P = 0.04$, $n = 16$), whereas in the loam Acrisol soil this correlation only showed up after exclusion of one plot in rubber that had an unusually high net N mineralization ($R = -0.51$, $P = 0.07$, $n = 15$). Net N mineralization significantly decreased in rubber that had no fertilization and intermediate in oil palm that had fertilization, particularly in the clay Acrisol soil (Appendix Table A1).

4 Discussion

4.1 CO_2 and CH_4 fluxes from the reference land uses

Mean soil CO_2 fluxes from our forest sites (Table 2) were within the range of reported fluxes (123–228 mg C m^{-2} h^{-1}) from tropical rainforests in Asia (Adachi et al., 2005; Ohashi et al., 2008) and Latin America (Davidson et al., 2000; Schwendenmann et al., 2003; Keller et al., 2005; Sotta et al., 2006; Koehler et al., 2009). Compared to measurements conducted in Indonesia, our lowland forests had higher soil CO_2 fluxes than a montane forest in Sulawesi at 1000 m elevation with similar spatially replicated and temporally intensive measurements (127 mg C m^{-2} h^{-1}; van Straaten et al., 2011) and than the seven partially logged forest sites in Jambi with only one-time measurement (162 mg C m^{-2} h^{-1}; Ishizuka et al., 2005). While the difference with this last study may be caused by their one-time sampling, the only other study that measured CO_2 fluxes from the same region (that conducted nine measurements spread over one year at three plots) reported values that were as low as 33 to 50 % of our measured soil CO_2 fluxes (63–94 mg C m^{-2} h^{-1}; Ishizuka et al., 2002). Such values are hard to reconcile with our and other measurements in tropical lowland forests, including the measurements by Ishizuka et al. (2005).

Seasonal variation of soil CO_2 fluxes from the reference land uses was driven by changes in soil water content, as suggested by the positive correlation with WFPS in

BGD
12, 9163–9207, 2015

jungle rubber on the loam Acrisol soil (Table 3). Other studies conducted in tropical rainforests have shown that seasonal changes in soil CO_2 fluxes are often caused by changes in soil water content (e.g. Sotta et al., 2007; Koehler et al., 2009; van Straaten et al., 2011), and sometimes in combination with reduction in solar irradiation caused by clouds during the wet season (Schwendenmann et al., 2003). In tropical forest soils, the relationship of soil CO_2 flux with soil water content is curvilinear with the highest fluxes typically at field capacity (pF ∼ 2 or WFPS between 50–55 %; Sotta et al., 2007; Koehler et al., 2009; van Straaten et al., 2011), which explains why WFPS did not show correlation in forests in both landscapes where WFPS (mostly ≥ 60–80 %; Fig. 1a and b) fluctuated at the top curve of this curvilinear relationship.

In the reference land uses, the negative correlation of annual soil CO_2 fluxes with the sand contents differed from the results in the Amazon Basin where sandy Ferralsol soil has higher soil CO_2 fluxes than the clay Ferralsol soil (Sotta et al., 2006). Our result suggests that soil texture may not be the proximal factor controlling annual soil CO_2 fluxes, but instead sand content indirectly affects soil fertility (e.g. P) which, in turn, influences soil CO_2 fluxes. In the study by Sotta et al. (2006), annual CO_2 emissions were negatively correlated with total soil P content. In the loam Acrisol soil, which had lower soil fertility (i.e. lower Bray-extractable P and base saturation and higher Al saturation) than the clay Acrisol soil (Appendix Table A1; Allen et al., unpublished data), there may be high competition for P such that trees have to allocate more C to their root or root-mycorrhizal system to obtain this nutrient. From the same study sites, there was also lower P concentration in fine roots in the top 0.2 m soil depth of the reference land uses in the loam than clay Acrisol soils (Sahner et al., unpublished data). This strategy of high below-ground C investment was reflected in the negative correlation of annual soil CO_2 fluxes from the reference land uses with Bray-extractable P contents in the loam Acrisol soil.

Mean soil CH_4 fluxes from our forest sites (Table 2) fall within the range for tropical lowland forests reported by other studies (−6.3–−55.9 $\mu g\, CH_4\text{-}C\, m^{-2}\, h^{-1}$; summarized by Veldkamp et al., 2013); however, our measured CH_4 uptake rates were at the up-

BGD
12, 9163–9207, 2015

per end (towards more negative values) of these reported rates and were also higher than the CH_4 uptake rates reported for old-growth forests in the same region (−21.3–+4.2 $\mu g\, CH_4\text{-}C\, m^{-2}\, h^{-1}$; Ishizuka et al., 2002).

Seasonal variation of soil CH_4 fluxes was strongly controlled by soil water content with higher uptake in the dry season (Fig. 1a and b), as shown by the strong positive correlations with WFPS in all land uses in both landscapes (Table 3). Such seasonal changes reflect diffusional limitation on the supply of CH_4 to methanotrophs at high WFPS (Keller and Reiners, 1994) and the possible occurrence of anaerobic decomposition, producing CH_4, which may partially offsets CH_4 consumption (Keller and Reiners, 1994; Verchot et al., 2000). Since we measured occasional net CH_4 emissions from some reference land uses (Fig. 2d), we cannot exclude this anaerobic CH_4 production. High microbial and root activity consume oxygen in the soil, which may contribute to the creation of anaerobic microsites where CH_4 can be produced. This may have occurred in the jungle rubber on the loam Acrisol soil, where we detected a positive correlation of soil CO_2 fluxes with soil CH_4 fluxes (Table 3). Positive correlations of soil CO_2 fluxes and CH_4 fluxes have been reported also for tropical forests (Verchot et al., 2000). In addition to WFPS, soil mineral N dynamics also influenced the seasonal variation of soil CH_4 fluxes. The negative correlations of soil CH_4 fluxes with soil NO_3^- contents in the forest on the clay Acrisol soil and in the jungle rubber on the loam Acrisol soil (Table 3) imply that some of the observed seasonal variability may have been caused by temporal N limitation of CH_4 oxidation (Bodelier and Laanbroek, 2004; Veldkamp et al., 2013).

The negative correlations of annual soil CH_4 fluxes from the reference land uses with net N mineralization rates (see Sect. 3.4) across landscapes indicate further that CH_4 uptake was probably N limited. Indications of N-limited CH_4 uptake have been reported for tropical forests in Panama (Veldkamp et al., 2013) and Ecuador (Wolf et al., 2012), but this is the first time it has been shown on a landscape scale in the tropics. Furthermore, the positive correlations of annual soil CH_4 fluxes from the reference land uses with exchangeable Al within each landscape signified the lower CH_4 uptake

BGD
12, 9163–9207, 2015

measured in sites with more exchangeable Al in the soil. The soil Al saturation in our reference land uses was high (mean values ranged from 61 to 80 %; Appendix Table A1). High Al^{3+} concentrations in the soil solution and higher exchangeable Al in the soil are known to be toxic for plants which root growth may be inhibited (Ma et al., 2001). Dissolved Al^{3+} can also be toxic for soil microorganisms and it has been shown that high dissolved Al concentrations in the soil inhibited CH_4 uptake in a temperate forest soil in Japan (Tamai et al., 2003). We are not aware of any study reporting such a relationship for tropical ecosystems, which is not surprising since in most trace gas studies exchangeable Al in the soil is either not measured or does not reach such high levels as in our sites.

In summary, seasonal variation of soil CO_2 fluxes from the reference land uses were related to soil water content (i.e. jungle rubber in loam Acrisol soil), while spatial control of annual soil CO_2 fluxes across landscapes were related to soil fertility: low Bray-extractable P concentrations coincided with high annual soil CO_2 fluxes from the loam Acrisol soil, which had lower soil fertility than the clay Acrisol soil. Seasonal variation of CH_4 fluxes from the reference land uses were mainly explained by soil water content, although we found indications that also temporal N limitation may have played a role. Spatial controls of annual soil CH_4 fluxes across landscapes were also related to soil fertility, as shown by their negative correlation with soil N availability, suggesting N limitation on CH_4 uptake, and positive correlation with exchangeable Al, suggesting Al toxicity on methanotrophs, which has not yet been reported for tropical ecosystems. These results are in contrast to our first hypothesis – soil texture was not the proximal factor controlling soil CO_2 and CH_4 fluxes but only indirectly through its influence on soil fertility that, in turn, controlled the spatial variations of these trace gases across our studied landscapes.

4.2 Effects of land-use change on CO_2 and CH_4 fluxes

Mean soil CO_2 fluxes from our rubber plantations (Table 2) were in the same order of magnitude as those reported for seven rubber plantations in Jambi (Indonesia)

BGD
12, 9163–9207, 2015

measured once (171 mg C m^{-2} h^{-1}; Ishizuka et al., 2005), while soil CO_2 fluxes from a rubber plantation in a sandy clay loam Nitisol soil in Malaysia with one measurement were lower (123 mg C m^{-2} h^{-1}; Adachi et al., 2005). Some other studies reported soil CO_2 fluxes that are much lower than our measured fluxes: a rubber plantation on a heavily weathered silty clay soil in China (35 mg C m^{-2} h^{-1}; Werner et al., 2006) and a rubber plantation in Jambi (Indonesia) with nine measurements (75 mg C m^{-2} h^{-1}; Ishizuka et al., 2002). Since this last study also reported 33–50 % lower soil CO_2 fluxes from forests (see Sect. 4.1) as well as 50 % lower soil CO_2 fluxes from oil palm (51 mg C m^{-2} h^{-1}; Ishizuka et al., 2002) than our measured fluxes from the same region (Table 2), we suspect some methodological issues in this study. Mean soil CO_2 fluxes from our oil palm sites were comparable with other reported fluxes from five oil palm plantations in Jambi (Indonesia) that were measured once (98 mg C m^{-2} h^{-1}; Ishizuka et al., 2005). Lastly, soil CO_2 fluxes from an oil palm plantation that were more than double of our measured fluxes were reported from a one-time measurement in a sandy clay loam Nitisol soil in Malaysia (222 mg C m^{-2} h^{-1}; Adachi et al., 2005).

Seasonal variation of soil CO_2 fluxes from oil palm was not as pronounced as that of rubber (Fig. 2a and b). In rubber plantations in loam Acrisol soil, where WFPS were all above 55 % (Fig. 1b), the seasonal variation of soil CO_2 fluxes reflected the curvilinear relationship of soil CO_2 fluxes with WFPS, whereby soil CO_2 fluxes typically decline at WFPS larger than about 55 % (e.g. Sotta et al., 2007; Koehler et al., 2009), and hence the negative correlation with WFPS (Table 3). The spatial variation of annual soil CO_2 fluxes across land uses, as reflected by their negative correlations with soil ^{15}N natural abundance signatures (see Sect. 3.4), illustrates the effect of changes in soil organic matter quality with changes in land use. The soil ^{15}N signatures in our oil palm plantations were significantly higher than the reference land uses (i.e. loam Acrisol soil; Appendix Table A1; Allen et al., unpublished data), which we interpreted as an indication of the extent of decomposition of soil organic matter. The more decomposed the soil organic matter, the higher is the soil ^{15}N signature, as illustrated by increasing soil ^{15}N signatures with increasing depth of tropical forest soils (Sotta et al.,

BGD
12, 9163–9207, 2015

2008; Baldos et al., 2015). The more decomposed soil organic matter in the oil palm plantations was probably due to their lower input from litterfall and fine root production than inputs in forests (measured from the same sites by Kotowska et al., 2015). Similar causes were attributed to the decreases in CO_2 fluxes from forest conversion to tree plantations on Acrisol soil in subtropical southern China that had decreases in annual litterfall and root biomass (Sheng et al., 2010). In our oil palm sites, management practices by smallholders also included pruning of senescing fronds and piling them on inter-rows to reduce the risk of snake bites when walking through plantations. This practice reduced the input of fresh litter to a large area of the plantations, which may have further contributed to the low annual soil CO_2 fluxes.

Furthermore, spatial variation of annual soil CO_2 fluxes across land uses in the loam Acrisol soil was also controlled by changes in soil fertility with changes in land use, as shown by their positive correlation with soil organic C and negative correlations with base saturation and Bray-extractable P (see Sect. 3.4). The control of soil organic C on annual soil CO_2 fluxes was probably related to the extent of organic matter decomposition, as shown by the slight decrease (although not statistically significant) of soil organic C stocks in the converted land uses in this landscape (Appendix Table A1; Allen et al., unpublished data). Conversion of forest or jungle rubber to rubber and oil palm plantations was accompanied by burning of slashed vegetation, whereby considerable amounts of bases and P could be released from the plant biomass to ashes (Klinge et al., 2004). Input of these nutrients to the soil from the ashes, combined with P fertilization and liming (particularly in the oil palm plantations), significantly increased soil pH in both rubber and oil palm as well as base saturation and Bray-extractable P in oil palm (Appendix Table A1; Allen et al., unpublished data). The negative correlations of annual soil CO_2 fluxes with base saturation and Bray-extractable P across land uses suggest that the decrease in soil CO_2 fluxes from oil palm compared to the other land uses (Table 2) could also be due to lower C allocation to its root or root-mycorrhizal system with the increase in base cations and P availability. On the other hand, Ishizuka et al. (2005) speculated that low soil CO_2 fluxes from oil palm plantations could be

BGD
12, 9163–9207, 2015

explained by higher soil bulk densities related to intensive management practices. We did not find evidence for this explanation, since soil bulk densities were comparable to the reference land uses (Appendix Table A1; Allen et al., unpublished data).

Mean soil CH_4 fluxes from rubber plantations (Table 2) were comparable with those reported for a rubber plantation in southwest China ($-5.7\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$; Werner et al., 2006) and for seven rubber plantations in Jambi (Indonesia) measured only once ($-5.8\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$; Ishizuka et al., 2005). From the oil palm plantations, mean soil CH_4 fluxes (Table 2) were comparable with those reported for five oil palm plantations in Jambi (Indonesia) measured only once ($-20.1\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$; Ishizuka et al., 2005) but larger (or more CH_4 uptake rate) than that reported for an oil palm plantation in Jambi with nine measurements ($-6.2\,\mu g\,CH_4\text{-}C\,m^{-2}\,h^{-1}$; Ishizuka et al., 2002).

Seasonal variation of soil CH_4 fluxes from the converted land uses were also controlled by WFPS (Table 3), and the possible mechanisms were the same as those discussed for the reference land uses (see Sect. 4.1). Moreover, strong negative correlations of soil CH_4 uptake with total mineral N (Fig. 3) and NO_3^- contents across all land uses (see Sect. 3.3), of which total mineral N was lowest in the converted land uses (Table 1), also suggest a temporal N limitation on methanotrophic activity (Veldkamp et al., 2013) that may have contributed to the decrease in CH_4 uptake in the converted land uses (Fig. 2c and d; Table 2).

The negative correlations of annual soil CH_4 fluxes with net N mineralization rates across land uses further suggest a N limitation on CH_4 uptake, as indicated by the lowest CH_4 uptake in the converted land uses (Table 2) that had the lowest (i.e. rubber with no N fertilization) to intermediate (i.e. oil palm with N fertilization) net N mineralization rates (see Sect. 3.4). The results from the fertilization experiment in the oil palm sites that showed inhibition of CH_4 uptake in the fertilized spot (chamber location b; Appendix Table A3) within 6 weeks following fertilizer application (Appendix Fig. B1) was probably caused by salt effect, as has been observed in a fertilization experiment in tropical pastures (Veldkamp et al., 2001). However, this CH_4 inhibition following fertilizer application did not influence our annual flux estimates because of the negligible

BGD
12, 9163–9207, 2015

area coverage of the fertilized spots (~ 1.3 % of the area in a hectare) and its short-term effect (less than 6 weeks or 12 % of the time in a year).

In summary, soil CO_2 fluxes decreased only in oil palm and not in rubber, which partly supports our second hypothesis. These converted land uses showed decrease in soil CH_4 uptake, which supports our second hypothesis. Seasonality of soil CO_2 and CH_4 fluxes in the converted land uses appeared to be controlled by the same factors as those in the reference land uses. The strong decrease in soil CO_2 fluxes from the oil palm was probably caused by a combination of strongly decomposed soil organic matter (caused by the low input of litterfall as senescing fronds were typically piled on the inter-rows and not spread over the whole area), low fine root production (Kotowska et al., 2015), and possibly low C allocation to root or root-mycorrhizal system (due to the improved base cations and P availability from liming and P fertilization). Reduction in annual CH_4 uptake in the converted land uses were primarily caused by the decrease in soil N availability in these converted land uses.

5 Consequences of land-use change on soil trace gas fluxes

Our study shows that land-use change had a profound effect on the soil–atmosphere fluxes of the trace gases CO_2 and CH_4, with reduced soil CO_2 fluxes from oil palm plantations and reduced soil CH_4 uptake in both rubber and oil palm plantations. The reduced soil CO_2 fluxes in the oil palm should not be interpreted as reduced net ecosystem emissions because we did not measure the net CO_2 uptake by the vegetation and the changes in soil and vegetation carbon stocks. Rather the strong decrease in soil CO_2 fluxes from oil palm is a reflection of the present belowground carbon dynamics in this land use, and this decrease allows us to speculate on the net soil carbon change in these oil palm plantations. Due to decreases in litterfall and fine root production (Kotowska et al., 2015) as well as frond management practice (stacking them on inter-rows) that reduced fresh litter input on the whole area, which together caused reduction in CO_2 emissions from oil palm, it is likely that soil organic C stock in these plantations

BGD
12, 9163–9207, 2015

are decreasing over time. Whether this decrease is detectable in these mid-age plantations (9–16 years old) depends on the size of this change relative to the inherent spatial variability of the soil organic C stocks in these studied landscapes.

Our estimate of decrease in CH_4 uptake from conversion of forest or jungle rubber to rubber and oil palm in these landscapes was about 2 kg CH_4-C ha^{-1} $year^{-1}$ (based on average of values in Table 2). If we multiply this with 0.52 Mha, the increase in areal coverage of oil palm and rubber plantations in Jambi from 1996 to 2011 (BPS, 2012), this suggests that the capacity of the province of Jambi to remove this potent greenhouse gas from the atmosphere has decreased by about 1040 Mg CH_4-C $year^{-1}$ as a result of this land-use conversion. This calculation does not take into account land-use changes that occurred in the peatlands. Finally, we detected important soil fertility controls on trace gas exchange in this converted tropical landscape on highly weathered Acrisol soils, including the controls of base cation and P availability on annual soil CO_2 fluxes and N availability and Al toxicity on annual soil CH_4 fluxes. Such controls at the landscape scale have not yet been reported, and thus we stress the importance of conducting landscape-scale studies as field studies on a few small plots or laboratory-based studies may not be able to detect such important controls.

Appendix: Soil sampling and analysis

Soil samples were taken from randomly selected ten subplots per plot that were at least 5 m distance from the plot's border. Soil characteristics for each replicate plot were the average of the ten subplots. Soil sampling was conducted between June and December 2013. Soil samples were taken at various depth intervals down to 2 m, and we report here the values from the top depth interval (0–0.1 m), except for soil texture, which we report for the entire 2 m. Soil texture was analyzed using the wet sieving and pipette methods. Soil bulk density was measured using the core method. Soil pH (H_2O) was analyzed in a 1 : 4 soil-to-water ratio. Soil organic C and total N concentrations were analyzed from air-dried, sieved (2 mm) and ground samples using a CN analyzer (Vario

BGD
12, 9163–9207, 2015

EL Cube, Elementar Analysis Systems GmbH, Hanau, Germany). Air-dried and sieved soils were used to determine effective cation exchange capacity (ECEC) by percolating with unbuffered 1 mol L^{-1} NH_4Cl and cations (Ca, Mg, K, Na, Al, Fe, and Mn) were measured in percolate using an inductively coupled plasma-atomic emission spectrometer (iCAP 6300 Duo VIEW ICP Spectrometer, Thermo Fischer Scientific GmbH, Dreieich, Germany). Base and aluminum saturation were calculated as percent exchangeable base cations and aluminun of the ECEC. Extractable P was determined using the Bray 2 method, which is typically used for acidic tropical soils. For soil ^{15}N natural abundance signatures, ground soil samples were analyzed using isotope ratio mass spectrometry (IRMS; Delta Plus, Finnigan MAT, Bremen, Germany). Net N mineralization rate was measured in two subplots per plot that were at least 10 m from the plot's border, using the buried bag method on intact soil cores incubated in situ for 7 days. This was conducted between January and May 2013 during the rainy season. The same field extraction of the soil with 0.5 M K_2SO_4, analysis of NH_4^+ and NO_3^- concentrations, and calculation of rate are used as described in our earlier work (Arnold et al., 2008). Net N mineralization rate for each plot was the average of two subplots.

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BGD
12, 9163–9207, 2015

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BGD
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BGD
12, 9163–9207, 2015

Table 1. Mean (±SE, $n = 4$) soil extractable mineral nitrogen in the top 0.05 m depth for different land-use types within each soil landscape in Jambi, Sumatra, Indonesia, measured monthly from December 2012 to December 2013. Means followed by different lowercase letter indicate significant differences among land-use types within a soil landscape and different capital letter indicate significant differences between soil landscapes within a land-use type (Linear mixed effects models with Fisher's LSD test at $P \leq 0.05$).

Land-use type	NH_4^+ ($mg\,N\,kg^{-1}$)	NO_3^- ($mg\,N\,kg^{-1}$)	mineral N ($mg\,N\,kg^{-1}$)
clay Acrisol soil			
Forest	$6.99 \pm 1.03^{a,A}$	$2.15 \pm 0.36^{a,A}$	$9.14 \pm 1.34^{a,A}$
Jungle Rubber	$7.33 \pm 0.21^{a,A}$	$0.23 \pm 0.06^{b,B}$	$7.56 \pm 0.26^{b,A}$
Rubber	$4.25 \pm 0.23^{b,A}$	$0.05 \pm 0.01^{b,B}$	$4.30 \pm 0.23^{c,A}$
Oil Palm	$5.80 \pm 0.64^{a,A}$	$0.81 \pm 0.49^{b,A}$	$6.60 \pm 0.42^{b,A}$
loam Acrisol soil			
Forest	$5.94 \pm 0.40^{a,A}$	$0.61 \pm 0.15^{ab,B}$	$6.55 \pm 0.28^{a,A}$
Jungle Rubber	$5.64 \pm 0.28^{a,B}$	$1.25 \pm 0.63^{a,A}$	$6.89 \pm 0.59^{a,A}$
Rubber	$4.14 \pm 0.57^{b,A}$	$0.12 \pm 0.02^{b,A}$	$4.26 \pm 0.58^{b,A}$
Oil Palm	$4.20 \pm 1.10^{b,B}$	$0.60 \pm 0.36^{ab,B}$	$4.81 \pm 1.44^{b,B}$

BGD
12, 9163–9207, 2015

Table 2. Mean (±SE, $n = 4$) soil CO_2 and CH_4 fluxes and annual soil CO_2 and CH_4 fluxes from different land-use types within each soil landscape in Jambi, Sumatra, Indonesia, measured monthly from December 2012 to December 2013. Means followed by different lowercase letter indicate significant differences among land-use types within a soil landscape and different capital letter indicate significant differences between soil landscapes within a land-use type (Linear mixed effects models with Fisher's LSD test at $P \leq 0.05$). Annual soil CO_2 and CH_4 fluxes were not statistically tested for differences between landscapes or land-use types since these annual values are trapezoidal extrapolations. For the loam Acrisol soil, CH_4 fluxes in parenthesis included only the two forest sites that had dominantly net CH_4 uptake, and comparison among land-use types was conducted between jungle rubber, rubber and oil palm that all showed net CH_4 uptake.

Land-use type	CO_2 fluxes ($mg\,C\,m^{-2}\,h^{-1}$)	Annual CO_2 fluxes ($Mg\,C\,ha^{-1}\,year^{-1}$)	CH_4 fluxes ($\mu g\,C\,m^{-2}\,h^{-1}$)	Annual CH_4 fluxes ($kg\,C\,ha^{-1}\,year^{-1}$)
clay Acrisol soil				
Forest	$195.93 \pm 13.51^{a,A}$	16.93 ± 1.19	$-40.3 \pm 10.25^{c,A}$	-3.63 ± 0.89
Jungle Rubber	$185.25 \pm 9.40^{a,A}$	16.11 ± 0.72	$-20.79 \pm 7.24^{b,A}$	-1.85 ± 0.59
Rubber	$182.77 \pm 16.22^{a,A}$	16.09 ± 1.40	$-3.00 \pm 1.26^{a,A}$	-0.29 ± 0.12
Oil Palm	$107.24 \pm 7.23^{b,A}$	9.22 ± 0.61	$-6.37 \pm 3.06^{a,A}$	-0.52 ± 0.26
loam Acrisol soil				
Forest	$186.64 \pm 13.72^{a,A}$	16.21 ± 1.17	-1.56 ± 17.07^{A} (-29.45 ± 11.92)	-0.18 ± 1.55
Jungle Rubber	$178.69 \pm 11.17^{a,A}$	15.55 ± 0.94	$-26.92 \pm 3.85^{b,A}$	-2.42 ± 0.34
Rubber	$182.86 \pm 14.47^{a,A}$	16.52 ± 1.32	$-9.73 \pm 3.79^{a,A}$	-0.93 ± 0.35
Oil Palm	$115.74 \pm 10.99^{b,A}$	10.29 ± 0.88	$-14.94 \pm 3.14^{a,A}$	-1.38 ± 0.31

BGD
12, 9163–9207, 2015

Table 3. Pearson correlation coefficients ($n = 12$) between soil CO_2 flux ($mg\,C\,m^{-2}\,h^{-1}$), soil CH_4 flux ($\mu g\,C\,m^{-2}\,h^{-1}$), soil temperature (°C, top 0.05 m depth), water-filled pore space (WFPS) (%, top 0.05 m depth) and extractable mineral nitrogen ($mg\,N\,kg^{-1}$, top 0.05 m depth), using the means of the four replicate plots per land-use type on monthly measurement between December 2012–December 2013.

Land use	Variable	Soil CH_4 flux	Soil temp.	WFPS	NH_4^+	NO_3^-	Min. N
clay Acrisol soil							
Forest	Soil CO_2 flux	0.19	0.42	0.49	−0.17	0.37	−0.01
	Soil CH_4 flux		0.25	0.68[b]	0.18	−0.59[b]	−0.09
	Soil temperature			0.34	0.63[b]	−0.32	0.54[a]
	WFPS				0.25	−0.18	0.18
Jungle Rubber	Soil CO_2 flux	−0.03	0.38	0.21	−0.39	0.61[b]	0.27
	Soil CH_4 flux		0.49	0.74[c]	0.33	−0.19	0.34
	Soil temperature			0.78[c]	0.34	0.19	0.39
	WFPS				0.25	0.07	0.28
Rubber	Soil CO_2 flux	−0.51[a]	0.49	−0.39	0.05	0.14	0.06
	Soil CH_4 flux		−0.14	0.84[c]	−0.06	−0.52[a]	−0.1
	Soil temperature			−0.24	0.3	0.16	0.31
	WFPS				−0.06	−0.53[a]	−0.1
Oil Palm	Soil CO_2 flux	−0.29	0.82[c]	−0.37	0.31	0.24	0.41
	Soil CH_4 flux		−0.09	0.69[c]	0.19	0.13	0.25
	Soil temperature			−0.19	0.32	0.32	0.52[a]
	WFPS				0.16	0.08	0.16
loam Acrisol soil							
Forest	Soil CO_2 flux	0.12	0.58[b]	0.05	−0.12	0.23	−0.01
	Soil CH_4 flux		0.19	0.32	0.09	−0.24	−0.24
	Soil temperature			0.42	0.41	−0.03	0.37
	WFPS				0.4	−0.33	0.23
Jungle Rubber	Soil CO_2 flux	0.74[c]	0.21	0.59[b]	−0.05	−0.60[b]	−0.41
	Soil CH_4 flux		0.35	0.74[c]	0.35	−0.58[b]	0.11
	Soil temperature			0.42	0.47	−0.22	0.38
	WFPS				0.32	−0.67[b]	0.05
Rubber	Soil CO_2 flux	−0.74[c]	0.16	−0.54[a]	0.06	−0.07	0.05
	Soil CH_4 flux		−0.07	0.84[c]	0.33	−0.11	0.32
	Soil temperature			0.07	0.57[b]	−0.42	0.54[a]
	WFPS				0.23	−0.24	0.2
Oil Palm	Soil CO_2 flux	−0.05	0.57[a]	−0.29	0.25	0.36	−0.05
	Soil CH_4 flux		0.16	0.86[c]	0.06	0.17	0.1
	Soil temperature			0.08	0.13	−0.19	0.16
	WFPS				−0.08	−0.05	−0.07

[a] $P \leq 0.09$, [b] $P \leq 0.05$, [c] $P \leq 0.01$.

BGD
12, 9163–9207, 2015

Table A1. Mean (±SE, $n = 4$) soil physical and biochemical characteristics in the top 0.10 m depth (except for the clay content, 0–2 m depth with $n = 3$) for different land-use types within each soil landscape in Jambi, Sumatra, Indonesia. Means followed by different lowercase letter indicate significant differences among land-use types within each soil landscape and different capital letter indicate significant differences between soil landscapes within a land-use type (Linear mixed effects models with Fisher's LSD test at $P \leq 0.05$ and marginally significant at $^{*}P \leq 0.09$). Soil characteristics were measured by Allen et al. (unpublished data). Soil sampling and analysis are described in Appendix A.

Soil characteristics	Land use			
	Forest	Jungle Rubber	Rubber	Oil Palm
clay Acrisol soil				
Clay (0–0.5 m) (%)	31.4 ± 5.4^{a}	47.2 ± 12.40^{a}	42.4 ± 3.1^{a}	$59.7 \pm 5.2^{a,A}$
Clay (0.5–1.0 m) (%)	$34.9 \pm 9.0^{b*}$	$51.4 \pm 12.6^{ab*}$	$36.8 \pm 8.00^{b*}$	$69.7 \pm 4.8^{a*A}$
Clay (1.0–1.5 m) (%)	39.0 ± 13.0^{a}	62.8 ± 12.6^{a}	40.8 ± 10.3^{a}	$62.8 \pm 3.6^{a,A}$
Clay (1.5–2.0 m) (%)	41.3 ± 11.2^{a}	46.6 ± 16.2^{a}	36.5 ± 10.8^{a}	$63.3 \pm 6.1^{a,A}$
Sand (0–0.10 m) (%)	36 ± 11^{a}	27 ± 20^{a}	35 ± 7^{a}	$11 \pm 2^{a,B*}$
Bulk density ($g\,cm^{-3}$)	1.0 ± 0.1^{a}	0.8 ± 0.1^{a}	0.9 ± 0.1^{a}	$0.9 \pm 0.1^{a,B}$
pH (1 : 4 H_2O)	4.2 ± 0.4^{b}	$4.5 \pm 0.0^{a,A}$	4.5 ± 0.1^{a}	4.4 ± 0.1^{a}
Soil organic C ($kg\,C\,m^{-2}$)	3.3 ± 0.5^{a}	$4.3 \pm 0.4^{a,A}$	2.8 ± 0.4^{a}	$3.5 \pm 0.2^{a,A}$
Total N ($g\,N\,m^{-2}$)	263.4 ± 67.1^{a}	$331.4 \pm 34.1^{a,A}$	198.4 ± 32.5^{a}	$260.2 \pm 22.6^{a,A}$
C : N ratio	13.1 ± 1.3^{a}	13.0 ± 0.3^{a}	$14.3 \pm 0.6^{a,A}$	13.5 ± 0.2^{a}
Effective cation exchange capacity ($cmol_3\,kg^{-1}$)	9.4 ± 4.1^{a}	$12.4 \pm 2.6^{a,A}$	7.1 ± 2.2^{a}	$7.8 \pm 0.8^{a,A}$
Base saturation (%)	$23 \pm 6^{a,A}$	23 ± 6^{a}	20 ± 3^{a}	38 ± 7^{a}
Aluminum saturation (%)	$61 \pm 3^{ab,B}$	71 ± 6^{a}	73 ± 4^{a}	53 ± 7^{b}
Bray-extractable phosphorus ($g\,P\,m^{-2}$)	$1.4 \pm 0.1^{a,b,A}$	0.8 ± 0.1^{bc}	0.4 ± 0.0^{c}	$4.7 \pm 1.5^{a,A*}$
^{15}N natural abundance (‰)	4.5 ± 0.0^{a}	4.0 ± 0.3^{a}	4.6 ± 0.4^{a}	5.2 ± 0.4^{a}
Net N mineralization ($mg\,N\,kg^{-1}\,d^{-1}$)	1.2 ± 0.3^{a}	0.5 ± 0.0^{b}	0.5 ± 0.2^{b}	0.9 ± 0.2^{ab}
loam Acrisol soil				
Clay (0–0.5 m) (%)	26.0 ± 2.6^{a}	30.6 ± 4.6^{a}	37.3 ± 10.3^{a}	$33.4 \pm 2.2^{a,B}$
Clay (0.5–1.0 m) (%)	28.7 ± 4.8^{a}	38.8 ± 9.0^{a}	45.1 ± 11.3^{a}	$41.0 \pm 3.1^{a,B}$
Clay (1.0–1.5 m) (%)	33.3 ± 7.56^{a}	42.4 ± 9.9^{a}	46.1 ± 9.9^{a}	$43.3 \pm 2.8^{a,B}$
Clay (1.5–2.0 m) (%)	37.3 ± 8.7^{a}	44.5 ± 10.0^{a}	43.4 ± 6.5^{a}	$47.6 \pm 4.5^{a,B}$
Sand (0–0.10 m) (%)	39 ± 8^{a}	42 ± 19^{a}	26 ± 13^{a}	$43 \pm 14^{1,A*}$
Bulk density ($g\,cm^{-3}$)	1.0 ± 0.0^{ab}	0.9 ± 0.0^{b}	1.1 ± 0.1^{a}	$1.1 \pm 0.1^{a,A}$
pH (1 : 4 H_2O)	$4.3 \pm 0.0^{b*}$	$4.3 \pm 0.0^{b*,B}$	$4.5 \pm 0.1^{ab*}$	$4.5 \pm 0.1^{a*}$
Soil organic C ($kg\,C\,m^{-2}$)	2.6 ± 0.2^{a}	$2.7 \pm 0.3^{a,B}$	2.0 ± 0.3^{a}	$1.8 \pm 0.2^{a,B}$
Total N ($g\,m^{-2}$)	182.9 ± 10.8^{a}	$186.19 \pm 11.0^{a,B}$	172.6 ± 23.8^{a}	$145.0 \pm 13.5^{a,B}$
C : N ratio	14.3 ± 0.2^{a}	13.7 ± 0.8^{a}	$11.7 \pm 0.7^{b,B}$	12.5 ± 0.5^{ab}
Effective cation exchange capacity ($mmol_3\,kg^{-1}$)	4.5 ± 0.5^{a}	$4.1 \pm 0.8^{a,B}$	4.6 ± 0.5^{a}	$4.0 \pm 0.8^{a,B}$
Base saturation (%)	$11 \pm 1^{b*B}$	$16 \pm 2^{ab*}$	$21 \pm 8^{ab*}$	$28 \pm 5^{a*}$
Aluminum saturation (%)	$80 \pm 1^{a,A}$	78 ± 2^{a}	73 ± 8^{a}	67 ± 5^{a}
Bray-extractable phosphorus ($g\,P\,m^{-2}$)	0.5 ± 0.1^{aB}	0.7 ± 0.1^{a}	0.5 ± 0.1^{a}	$0.8 \pm 0.1^{aB*}$
^{15}N natural abundance (‰)	4.3 ± 0.2^{b}	4.5 ± 0.1^{b}	5.0 ± 0.4^{ab}	5.4 ± 0.3^{a}
Net N mineralization ($mg\,N\,kg^{-1}\,d^{-1}$)	0.8 ± 0.2^{a}	0.7 ± 0.1^{a}	0.7 ± 0.3^{a}	0.5 ± 0.2^{a}

BGD
12, 9163–9207, 2015

Table A2. Plantation age and mean (±SE, $n = 4$) tree density, tree height, basal area, diameter at breast height (DBH) of trees with ≥ 0.10 m BDH and the most common tree species for different land-use types within each soil landscape in Jambi, Sumatra, Indonesia.

Land-use type	Age range (years)	Tree density ($n\,ha^{-1}$)[a]	Tree height (m)[a]	Basal area ($m^2\,ha^{-1}$)[a]	DBH (cm)[a]	Most common tree species[b]
clay Acrisol soil						
Forest	not deter-mined (ND)	471 ± 31	17.0 ± 0.5	29.4 ± 1.7	23.0 ± 0.4	*Archidendron* sp., *Baccaurea* spp., *Ochanostachys* sp.
Jungle rubber	ND	685 ± 72	15.2 ± 0.3	21.1 ± 1.4	17.3 ± 0.6	*Artocarpus* spp., *Endospermum* sp., *Hevea* sp., *Macaranga* spp.
Rubber	7–16	497 ± 15	13.4 ± 0.1	10.0 ± 1.4	15.2 ± 0.7	*Hevea brasiliensis*
Oil Palm	9–13	134 ± 6	4.0 ± 0.3	n/a	n/a	*Elaeis guineensis*
loam Acrisol soil						
Forest	ND	658 ± 26	20.0 ± 0.6	30.7 ± 1.0	21.0 ± 0.5	*Aporosa* spp., *Burseraceae* spp., *Dipterocarpaceae* spp., *Fabaceae* spp., *Gironniera* spp., *Myrtaceae* spp., *Plaquium* spp., *Porterandia* sp., *Shorea* spp.
Jungle Rubber	ND	525 ± 60	14.0 ± 0.2	16.6 ± 0.4	16.8 ± 0.5	*Alstonia* spp., *Artocarpus* spp., *Fabaceae* sp., *Hevea* sp., *Macaranga* spp., *Porterandia* sp., *Sloetia* sp.
Rubber	14–17	440 ± 81	13.4 ± 0.5	12.2 ± 1.6	17.8 ± 1.2	*Hevea brasiliensis*
Oil Palm	12–16	140 ± 4	4.9 ± 0.6	n/a	n/a	*Elaeis guineensis*

[a] Kotowska et al. (2015). [b] Rembold et al. (unpublished data), based on trees found in five subplots (5 m × 5 m) of each replicate plot (50 m × 50 m) which had ≥ 20 individuals, except *Fabaceae* spp. which had ≤ 20 individuals.

BGD
12, 9163–9207, 2015

Table A3. Mean (±SE, n = 3 oil palm trees) soil CO_2 and CH_4 fluxes from three different chamber locations during a fertilization in three oil palm plantations within each soil landscape, measured 6 to 11 times during 3–8.5 weeks following fertilization. Means followed by different letter indicate significant differences among chamber locations within each oil palm plantation site (Linear mixed effects models with Fisher's LSD test at $P \leq 0.05$). Chamber locations a, b and c were placed at 0.3, 0.8, and 4–4.5 m, respectively, from each of the three trees in each oil palm plantation site. Smallholders fertilized around the base of each tree at about 0.8–1 m from the tree base, and thus chamber location b was on this fertilized area and chamber location c serves as the reference chamber not receiving any fertilizer. The same fertilization rate and form were used as the smallholders applied in these studied oil palm plantations, described in Sect. 2.2 CO_2 and CH_4 flux measurement.

Oil palm plantation site	Chamber location	CO_2 fluxes ($mg\,C\,m^{-2}\,h^{-1}$)	CH_4 fluxes ($\mu g\,C\,m^{-2}\,h^{-1}$)
clay Acrisol soil			
1	a	272.83 ± 36.68^{a}	-23.66 ± 2.56^{b}
	b	218.25 ± 25.91^{b}	-12.61 ± 5.12^{a}
	c	103.56 ± 11.72^{c}	-16.66 ± 8.68^{ab}
2	a	226.16 ± 38.17^{a}	-28.44 ± 1.48^{b}
	b	246.39 ± 42.80^{a}	-6.64 ± 2.07^{a}
	c	86.04 ± 7.83^{b}	-10.60 ± 5.29^{a}
3	a	222.56 ± 72.49^{b}	-8.13 ± 4.77^{a}
	b	311.63 ± 89.87^{a}	-10.38 ± 3.61^{a}
	c	105.49 ± 12.06^{c}	-14.49 ± 2.03^{a}

BGD
12, 9163–9207, 2015

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Oil palm plantation site	Chamber location	CO_2 fluxes ($mg\,C\,m^{-2}\,h^{-1}$)	CH_4 fluxes ($\mu g\,C\,m^{-2}\,h^{-1}$)
loam Acrisol soil			
1	a	334.67 ± 32.12^{a}	-14.00 ± 3.31^{b}
	b	378.47 ± 50.97^{a}	-4.12 ± 2.24^{a}
	c	160.35 ± 20.48^{b}	-18.53 ± 1.32^{b}
2	a	271.35 ± 17.31^{a}	-13.18 ± 1.22^{a}
	b	233.27 ± 18.98^{b}	-8.63 ± 0.52^{a}
	c	127.66 ± 17.13^{c}	-19.47 ± 5.08^{b}
3	a	240.81 ± 23.12^{a}	-28.13 ± 3.40^{b}
	b	243.92 ± 24.23^{a}	-10.34 ± 2.70^{a}
	c	136.55 ± 19.08^{b}	-29.41 ± 2.39^{b}

BGD
12, 9163–9207, 2015

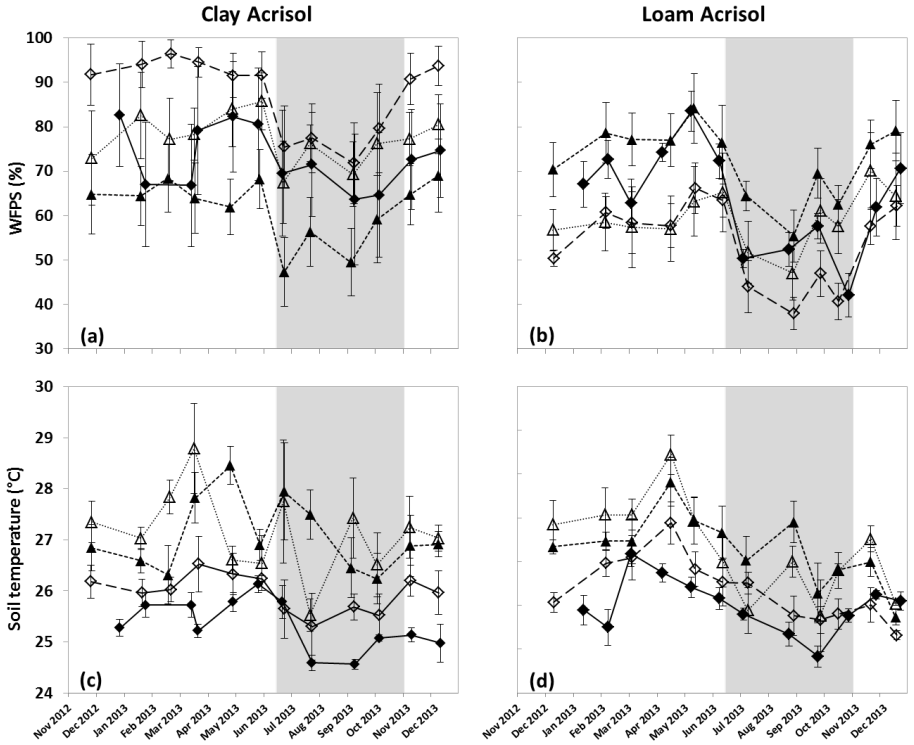

Figure 1. Mean (±SE, n = 4) soil water-filled pore space (WFPS) and soil temperature in the top 0.05 m depth under forest (♦), jungle rubber (⋄), rubber (▲) and oil palm (△) on the clay Acrisol soil (**a** and **c**) and the loam Acrisol soil (**b** and **d**) in Jambi, Sumatra, Indonesia, measured monthly from December 2012 to December 2013. Grey shadings mark the dry season.

BGD
12, 9163–9207, 2015

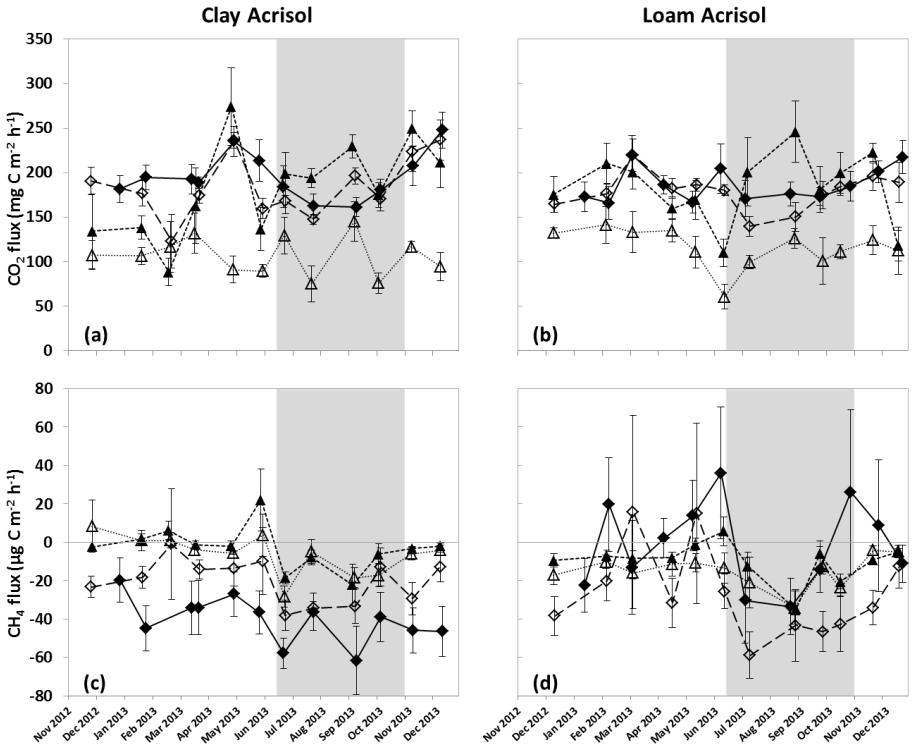

Figure 2. Mean (±SE, $n = 4$) soil CO_2 fluxes and soil CH_4 fluxes from forest (♦), jungle rubber (⋄), rubber (▲) and oil palm (△) on the clay Acrisol soil (**a** and **c**) and the loam Acrisol soil (**b** and **d**) in Jambi, Sumatra, Indonesia, measured monthly from December 2012 to December 2013. Grey shadings mark the dry season.

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12, 9163–9207, 2015

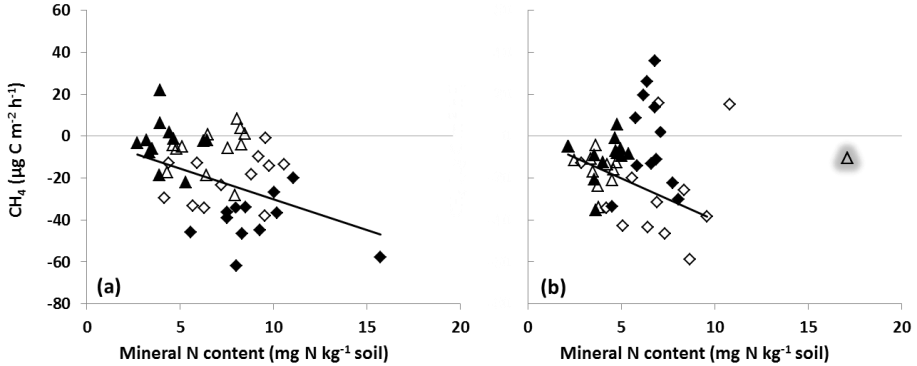

Figure 3. Relationship between soil CH_4 uptake and soil mineral N content, using the means of four replicate plots per land-use type on monthly measurement between December 2012–December 2013: forest (♦), jungle rubber (⋄), rubber (▲) and oil palm (Δ) on the clay Acrisol soil (Pearson correlation: $R = -0.47$, $P = 0.01$, $n = 41$) **(a)** and the loam Acrisol soil (Pearson correlation: $R = -0.52$, $P < 0.01$, $n = 38$) **(b)**. Correlations exclude net CH_4 emissions (fluxes above 0) in both landscapes and an outlier plot of oil palm on the loam Acrisol soil (shaded grey).

BGD
12, 9163–9207, 2015

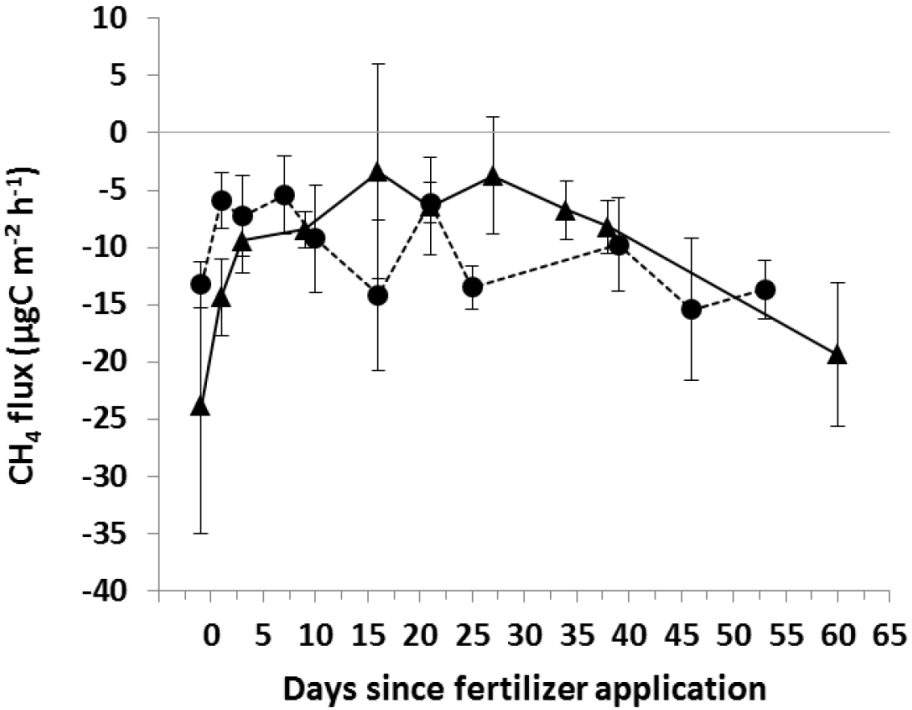

Figure B1. Mean (±SE, n = 3 oil palm trees) soil CH_4 fluxes during a fertilization in one oil palm plantation site in the clay Acrisol soil (▲) and loam Acrisol soil (•). Smallholders fertilized around the base of each tree at about 0.8–1 m from the tree base, and these fluxes were measured on this fertilized location (chamber location b) with the same rate and form that smallholders applied in these oil palm plantations (described in Sect. 2.2 CO_2 and CH_4 flux measurement).

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12, 9163–9207, 2015