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Soil carbon dioxide and methane fluxes from forests and other land use types in an African tropical montane region

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Abstract In the last 40 years, large areas of the Mau forest, the largest contiguous tropical montane forest in East Africa, have been cleared for agriculture. To date, there are no empirical data on how this land use change affects carbon dioxide (CO_2) fluxes from soil respiration and soil methane (CH_4) fluxes. This study reports measured annual soil CO_2 and CH_4 fluxes from the native Mau forest and previously forested lands converted to smallholder grazing land, smallholder and commercial tea plantations and eucalyptus plantations. Fluxes were measured weekly from August 2015 to August 2016 using the static chamber method. Grazing lands had the highest ($p = 0.028$) cumulative respiratory CO_2 fluxes (25.6 ± 2.9 Mg CO_2–C ha^{-1} $year^{-1}$), whereas lowest fluxes were observed in commercial tea plantations (5.6 ± 0.5 Mg CO_2–C ha^{-1} $year^{-1}$). Soil respiratory CO_2 fluxes were positively correlated with soil pH, but negatively correlated with soil C:N ratio. Annual soil fluxes were explained by soil pH, bulk density and the interaction between soil pH and C:N ratio. Most soils were sinks for atmospheric CH_4 across all land use types. Methane uptake was highest for native forest sites (-3.08 ± 0.35 to -5.84 ± 0.61 kg CH_4–C ha^{-1} $year^{-1}$) and for eucalyptus plantations (-3.43 ± 0.19 kg CH_4–C ha^{-1} $year^{-1}$). Uptake decreased significantly with increasing land use intensity (smallholder tea plantations: -1.42 ± 0.09 kg CH_4–C ha^{-1} $year^{-1}$, commercial tea plantations: -1.44 ± 0.29 kg CH_4–C ha^{-1} $year^{-1}$). Soils of smallholder grazing lands had the lowest CH_4 uptake rates (-0.36 ± 0.25 kg CH_4–C ha^{-1} $year^{-1}$). Annual CH_4 uptake was negatively correlated with mean annual soil water-filled pore space ($p < 0.01$) and bulk density ($p = 0.003$) and decreased with increasing soil inorganic NH_4^+

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concentrations (p = 0.03). Annual soil CH_4 can be explained by mainly soil water content and bulk density and these factors are related to gas diffusion. Our study shows that converting tropical montane forests to managed land use types affects soil CO_2 and CH_4 fluxes. Specifically, the CH_4 sink strength in managed land use types of these montane tropical soils was reduced to less than half of the sink strength in the native forest. Soil respiratory CO_2 fluxes were also altered by land use with grazing lands emitting 3–4 times more CO_2 than the other land use types.

Keywords Deforestation · Kenya · GHG emissions · Fertilisers · Livestock

Introduction

Soil respiration is one of the dominant fluxes in the global carbon cycle (Adachi et al. 2017). Hashimoto et al. (2015) estimated that the mean annual CO_2 fluxes from soils to the atmosphere between 1965 and 2012 were 91 Pg C year^{-1}, of which 64% originate from tropical regions. Soil respiration can be broken down into two processes: organic matter mineralisation by soil microbes (heterotrophic respiration) and root respiration (autotrophic respiration) (Bond-Lamberty et al. 2004). The relative contribution of autotrophic and heterotrophic soil respiration varies between land use types and seasons (Arevalo et al. 2010; Hanson et al. 2000). Soil respiration typically increases with increasing temperature as long as soil moisture, aeration and supply of easily degradable soil carbon compounds are not limiting (Davidson and Jansen 2006).

Soils are also the largest terrestrial sink of atmospheric methane (CH_4) (Dutaur and Verchot 2007). Global CH_4 uptake by upland soils has been estimated to range from 9 to 51 Tg CH_4 year^{-1} (Dutaur and Verchot 2007; Ghosh et al. 2015; Kirschke et al. 2013), with tropical forest and grassland soils contributing approximately 58% to this uptake (Yu et al. 2017). CH_4 fluxes of upland soils are the result of two processes: methanogenesis (production) under anaerobic conditions and methanotrophy (consumption/oxidation) in aerobic soils (Trotsenko and Khmelenina 2002). Depending on soil aeration, upland soils can act as a sink or source of CH_4. Gas diffusion into the soil is affected by soil water content and soil texture and these two factors have been regarded as primary controls of CH_4 uptake in upland soil ecosystems (Verchot et al. 2000). In upland forest soils, soil conditions favour the activity and growth of methanotrophs and therefore the methane oxidation process is dominant compared to production (Kravchenko 2017), as a result forests soils usually act as methane sinks. Soil tillage or animal trampling, typically associated with agriculture, can affect soil properties such as bulk density (Owuor et al. 2018), which in turn reduces soil pore size and connectivity (Dexter 2004) and thus, gas diffusivity. This reduction in diffusivity can then cause lower CH_4 uptake compared to soils of natural ecosystems (Jacinthe et al. 2014). It has often been reported that the conversion of natural forests to managed land use types reduces soil methane uptake (Oertel et al. 2016).

Another factor affecting methanotrophic activity in soils is the availability of inorganic nitrogen (N). For instance, Wolf et al. (2012) reported that in a tropical montane forest in southern Ecuador, CH_4 uptake was limited by ammonium (NH_4^+) and nitrate (NO_3^-) availability. Comparable results were also found for methanotrophic activity in soils of tropical lowland forests in Indonesia and Panama, where methane uptake also increased with increasing NH_4^+ and NO_3^- availability (Veldkamp et al. 2013; Hassler et al. 2015). These studies indicate that CH_4 uptake in tropical soils can be limited by N availability. In contrast, other studies show a reduction in CH_4 uptake capacity with increasing soil NH_4^+ concentrations at temperate forest sites affected by high rates of atmospheric N deposition (Bédard and Knowles 1989; Butterbach-Bahl and Papen 2002). This can be explained by osmotic stress by NH_4^+ salts and by competitive inhibition of the methane mono-oxygenase due to its capability to also oxidise NH_4^+ to nitrite. Moreover, intermediate and end products of the latter process, hydroxylamine and nitrite, are toxic for methanotrophs, which also leads to a reduction of CH_4 oxidation in soils (Bodelier and Laanbroek 2004).

In Sub-Saharan Africa, measurements of soil CO_2 and CH_4 fluxes remain limited to approximately 30 studies in natural ecosystems (forests and grassland) and about 26 studies in agricultural lands (Kim et al. 2016). Moreover, only one study (Pelster et al. 2017), measured fluxes from a number of land use types that are typical of the heterogeneous landscape of the East

African highlands, while none of these studies compared CO_2 and CH_4 fluxes from different land use types to the native forests. This hampers our ability to understand how changes in land use in tropical African highlands affect soil CO_2 and CH_4 fluxes. Thus this area needs to be explored to improve our understanding of the CO_2 and CH_4 dynamics accompanying these changes. The Mau-forest complex is the largest closed-canopy montane forest in East Africa, and provides several ecological services such as provision of water for a number of lakes in Kenya, and acting as a biodiversity reserve. However, large areas of forest have been cleared for arable land, grasslands, tea and tree plantations (Baldyga et al. 2008; Blackie 1972; Kinyanjui 2009; Olang et al. 2014). As a result, the forest area decreased by approximately 34% between 1986 and 2009 (Hesslerova and Pokorny 2010). Land use change from natural forest to managed land use results in changes in vegetation type (litter quality), soil microbial community structure, and soil physicochemical properties (Chiti et al. 2018). These factors interact in complex ways to influence soil GHG fluxes through moderation of plant and soil microbial activity and these effects may vary from site to site (Smith et al. 2018). The Mau Forest presents an excellent landscape to explore how changes associated with land use affect soil CO_2 and CH_4 fluxes and to understand the underlying mechanisms that result in these changes. Therefore, the objectives of this study were to (1) quantify the annual soil respiratory CO_2 and CH_4 fluxes from natural forest and compare them to managed land use types (tea, grazing land, and tree plantations), and (2) assess the factors affecting spatial and temporal variability of soil respiration and CH_4 fluxes from forests and managed land. We hypothesized that the highest rates of soil respiration and oxidation of atmospheric CH_4 would be found at the natural forest, and that grassland and tea plantation soils would have the lowest CH_4 uptake rates as a result of the changes in soil properties, vegetation, and management. We evaluated hypotheses related to the effects of temperature and soil water content on these fluxes and assessed the importance of soil pH and nitrogen availability on soil CO_2 and CH_4 fluxes.

Materials and methods

Study area and experimental design

The study area was located in the southwest Mau Forest in Western Kenya at approximately 2200 m above sea level. During the study period (August 2015 to August 2016) annual rainfall was 2050 mm, while the mean annual air temperature was 16.6 ± 3.9 °C (Wanyama et al. 2018). The rainfall pattern at the study site is bimodal. The first rainy season is typically between April and July, and the second from October to December. During the study period there were sporadic rains during the dry seasons, and dry periods during the rainy seasons.

The study was carried out at two separate agricultural sites with adjacent natural forests. A smallholder site at Chepsir (0°17′41″S, 35°25′4″E) with the major agricultural land use types being pasture *(Pennisetum clandestinum* Hochst. ex Chiov*)* and tea plantations smaller than 0.5 ha. The second site was a commercial tea estate at Kapkatugor (0°19′01″S, 35°23″E), with land use dominated by large scale (> 10 ha) tea and eucalyptus plantations. We selected three blocks at each site; each block comprised one replicate of each of the major land use types at each respective site (Fig. 1). The major land use types at the tea estate site were forest (TEF1, TEF2 and TEF3), tea plantations (TET1, TET2 and TET3) and eucalyptus plantations (TEP1, TEP2 and TEP3). At the smallholder site, forest (SHF1, SHF2, and SHF3), grazing land (SHG1, SHG2 and SHG3) and tea plantations (SHT1, SHT2 and SHT3) were the major land use types. Detailed information was reported by Wanyama et al. (2018) and is also presented in Table 7 in Appendix. The landscape of the study site is undulating and can be divided into lower, mid and crest slope positions: the forest sites were on one side of a valley while the converted land use types were on the other side. We established the plots at the same slope position where the gradient was uniform and used a high precision GPS to measure elevation. Therefore slope position and gradient, and elevation of the replicates were kept consistent within each site. Soils were also uniform as observed from the consistent red colour and texture of subsoil; these are classified as Andic Humic Nitisols (IUSS Working Group WRB 2015).

We carried out an inventory of the tree species and biomass in the forest plots at our sites. We used a 20 m

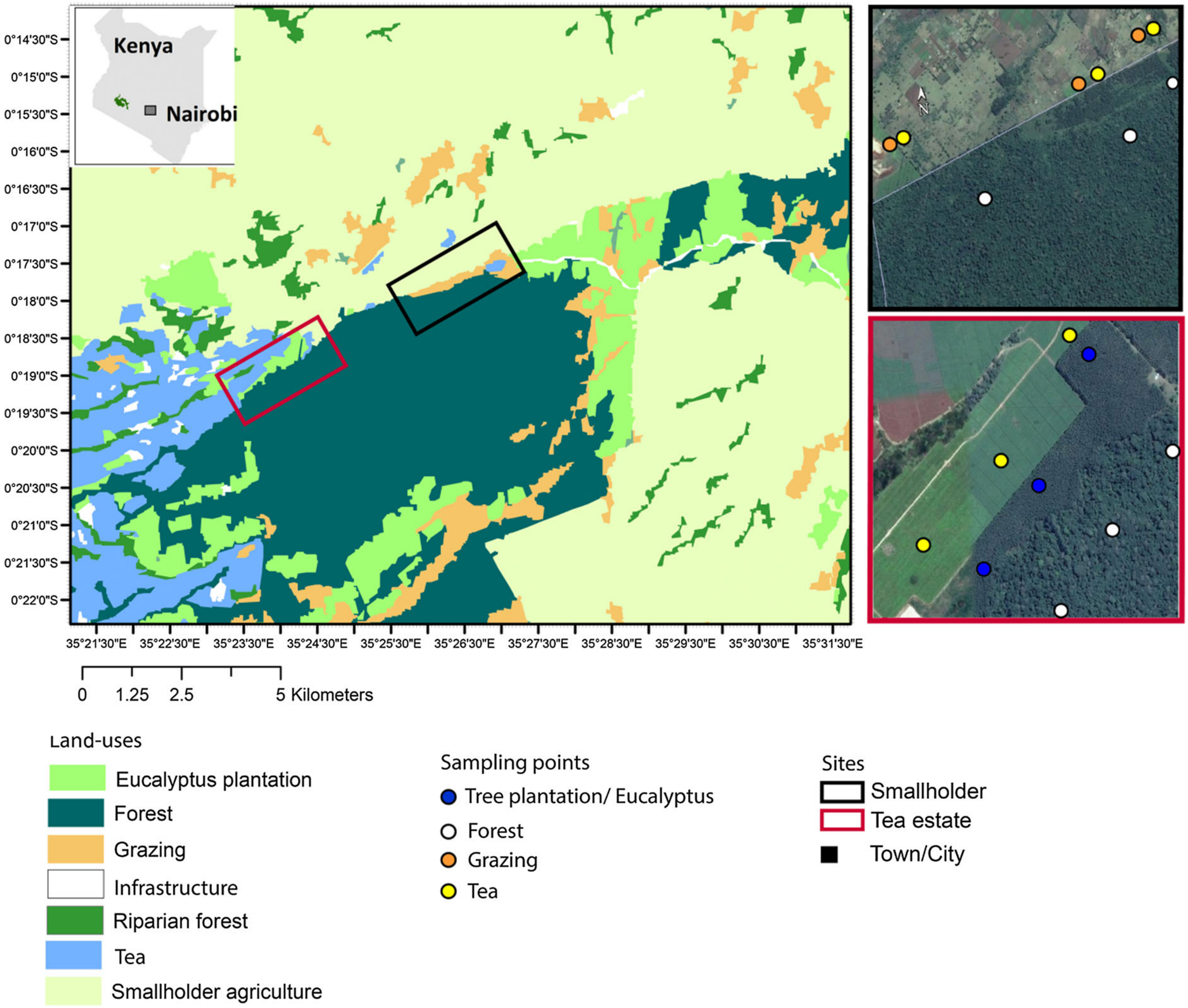

Fig. 1 Map of the study area in SW Mau forest of Kenya, area showing the two sites, smallholder area and tea estate, and the land use types where gas sampling was conducted. The two images showing sampled plots were extracted from Google Earth map©

circular plot and took inventory of all trees with a diameter at breast height (DBH = 1.3 m) > 5 cm including the species name, DBH and tree height (using a Suunto clinometer). To measure the 20 m radius, we used the center of the plots where gas sampling was done as reference point. Tree biomass was estimated using an allometric equation developed for western Kenya tree species by Bradley (1988).The forest was disturbed due to removal of tree species of high commercial value and the setting of forest fires that increased the presence of fire-tolerant species (Kinyanjui et al. 2014). The forest plots at the tea estate site contained greater amounts of above ground biomass compared to the forest plots at the smallholder site (Table 1). The dominant tree species of the forest at the tea estate site were *Croton macrostachyus* Hochst. ex Ferret et Galinier and *Cassipourea malosana* (Bak.) Alston (90%), while the dominant tree species at forest at the smallholder site was *Neoboutonia macrocalyx* Pax with scattered *Syzygium guineense* (Willd) DC and *Syzygium cordatum* Hochst. ex Krauss.

Management of the tea plantations differed between smallholders and the tea estate during the study period. For the smallholder tea plots, two of the three plots received fertilizer (NPK: 26% N, 5% P_2O_5, and 5% K_2O) (SHT1; 125 kg N ha^{-1} and SHT2; 40 kg N ha^{-1} $year^{-1}$) (Fig. 2) that was applied by

Table 1 Inventory of tree species abundance (# ha^{-1}) and aboveground biomass (AGB) from a 20 m radius from the center of the forest plots (extrapolated to one hectare, n = 6) sampled for CO_2 and CH_4 at the smallholder and tea estate sites, in the Mau forest region of, Kenya

Species	Smallholder			Tea Estate		
	SHF1 (#ha^{-1})	SHF2 (#ha^{-1})	SHF3 (#ha^{-1})	TEF1 (#ha^{-1})	TEF2 (#ha^{-1})	TEF3 (#ha^{-1})
Neoboutonia macrocalyx Pax	63	589	621	71	31	40
Syzygium cordatum Hochst ex Krauss	72	–	–	32	–	–
Syzygium guineense (Willd) DC.	72	56	–	–	–	–
Prunus africana (Hook.f.) Kalkman	151	–	23	–	–	–
Cassipourea malosana (Bak.) Alston	–	127	–	215	406	446
Podocarpus falcatus (Thunb.) R. Br. ex Mirb.	–	24	103	–	–	16
Euphorbia tirucalli L.	–	–	48	104	–	–
Croton macrostachyus Hochst. ex Ferret et Galinier	–	–	–	374	326	215
Zanthoxylumus ambarense (Engl.) J.O. Kokwaro	–	–	–	–	16	–
Celtis africana N.L. Burm.	–	–	–	–	16	10
Tree density (# ha^{-1})	358	796	795	796	795	727
Above ground biomass (AGB) (Mg ha^{-1})	102	269	204	337	409	298
Mean AGB	192b			348a		

Different letters next to AGB indicate significant difference between sites ($p < 0.05$). SH-Smallholder site, TE-Tea estate site, F 1-3 are forest plots

placing fertilizer granules around the tea plants. At the tea estate, fertilizer (NPK) was broadcasted at the onset of the rainy season to all three replicate plots at rate of 150 kg N ha^{-1} $year^{-1}$ (plots TET1 and TET3) and 250 kg N ha^{-1} $year^{-1}$ (plot TET2) (Fig. 3). For the smallholder grazing plots, stocking densities were highly variable, ranging from 66 head ha^{-1} (SHG2), to 26 head ha^{-1} (SHG1) to 1.3 head ha^{-1} (SHG3), this high variability is typical in smallholder farming around the Mau forest (Brandt et al. 2018). Management of livestock in these grazing plots was also quite variable: in SHG1 and SHG2 cattle were kept in the paddocks for approximately 12 h per day for 4–5 months of the year. These cattle were grazed in communal lands off the farms and returned to the paddocks in the evening. In contrast, plot SHG3 consisted of a large area (39 ha) where 41 cattle grazed continuously through the year. Further information on plot history is reported by Wanyama et al. (2018).

Soil sampling and analysis

Soil samples were taken from depths 0–0.05 m, 0.05–0.2 m and 0.2–0.3 m at five randomly selected points within each plot using a core sampler (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). The samples were air dried at 30 °C and passed through a 2 mm sieve, and then analysed for soil texture, pH, and total C and N concentration. Soil textural analyses were carried out following the hydrometer method as described by Gee and Bauder (1986). A 1:2.5 soil to deionized water slurry was used to measure soil pH following Jackson (1958). Total C and N (TC and TN) analyses were carried out on powdered soils (Retsch ball mill, Haan, Germany) using an elemental combustion system (ECS 4010, Costech Instruments, Italy). Soil organic carbon and nitrogen stocks (SOC and SON) were calculated using methods described by Baustista et al. (2016). Soil bulk density was determined on separate samples collected with Eijkelkamp rings by drying the known volume of soil at 105 °C to constant weight.

Inorganic N concentrations were determined on samples collected bi-weekly during the gas sampling campaign. Within each sampled plot, a fresh composite soil sample was collected, comprised of three subsamples (0 to 0.05 m depth) from three points near the chamber frames using a sharpened-edge PVC cylinder (0.05 m height and inner diameter). Plant litter was removed, and the fresh sample was mixed thoroughly.

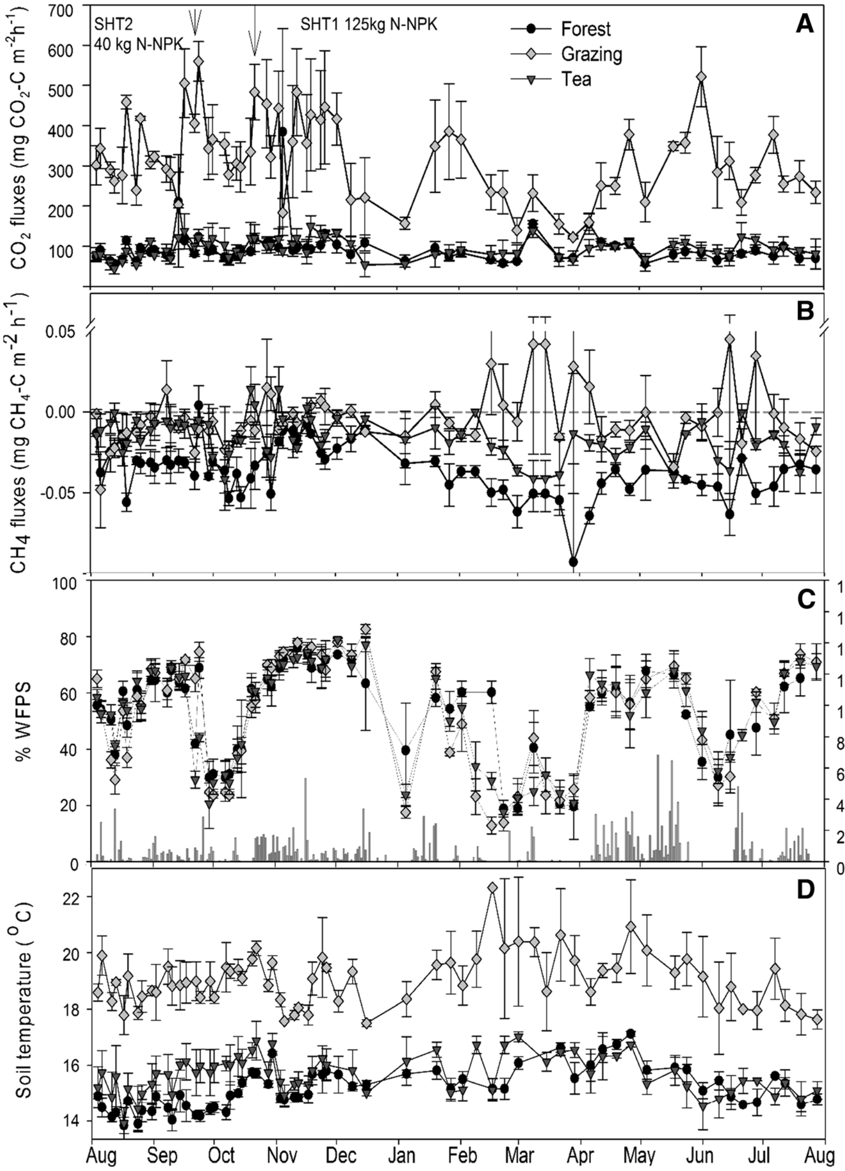

Fig. 2 Mean (± SE, n = 3) soil carbon dioxide (**a**), soil methane fluxes (**b**) measured bi-weekly (August 2015 to December 2015) and weekly (December 2016 to August 2016), and quantity and timing of fertilization (kg N ha^{-1}) applied to two tea plots (SHT1 and SH2), water filled pore space (%WFPS) and precipitation (grey bars) (**c**) and soil temperature (**d**) from forest, grazing and tea land use types at the smallholder site (SH) in the South West Mau forest area, Kenya

Inorganic N extractions were carried out on approximately 10 g of the homogenous fresh soil sample using 50 ml of 0.5 M K_2SO_4, in a plastic bottle. The slurry was shaken for 1 h on a reciprocating shaker and then filtered through 110 mm Whatman™ number 1 filter paper enhanced with a vacuum pump to speed the process. Further filtering was done using a 0.45 µm syringe filter (Minisart®, Sartorius Stedim Biotech Gmbh, Goettingen, Germany) to remove finer particles. Blank samples were also prepared and used for correction during calculations. The extracts were frozen immediately until analysis. Analyses for NH_4^+–N and NO_3^-–N were done using an Epoch™ micro-plate spectrophotometer (BioTek® Instruments, Inc., Winooski, USA). The remaining composite fresh soil sample was oven dried at 105 °C until constant soil weight to determine soil water content, thereafter inorganic N (IN) was calculated on dry soil mass basis. Annual cumulative NH_4^+ and NO_3^- was calculated by integrating the area under respective curves and herein referred to as NH_4^+–N intensity and NO_3^-–N intensity, respectively (Burton et al. 2008; Wanyama et al. 2018).

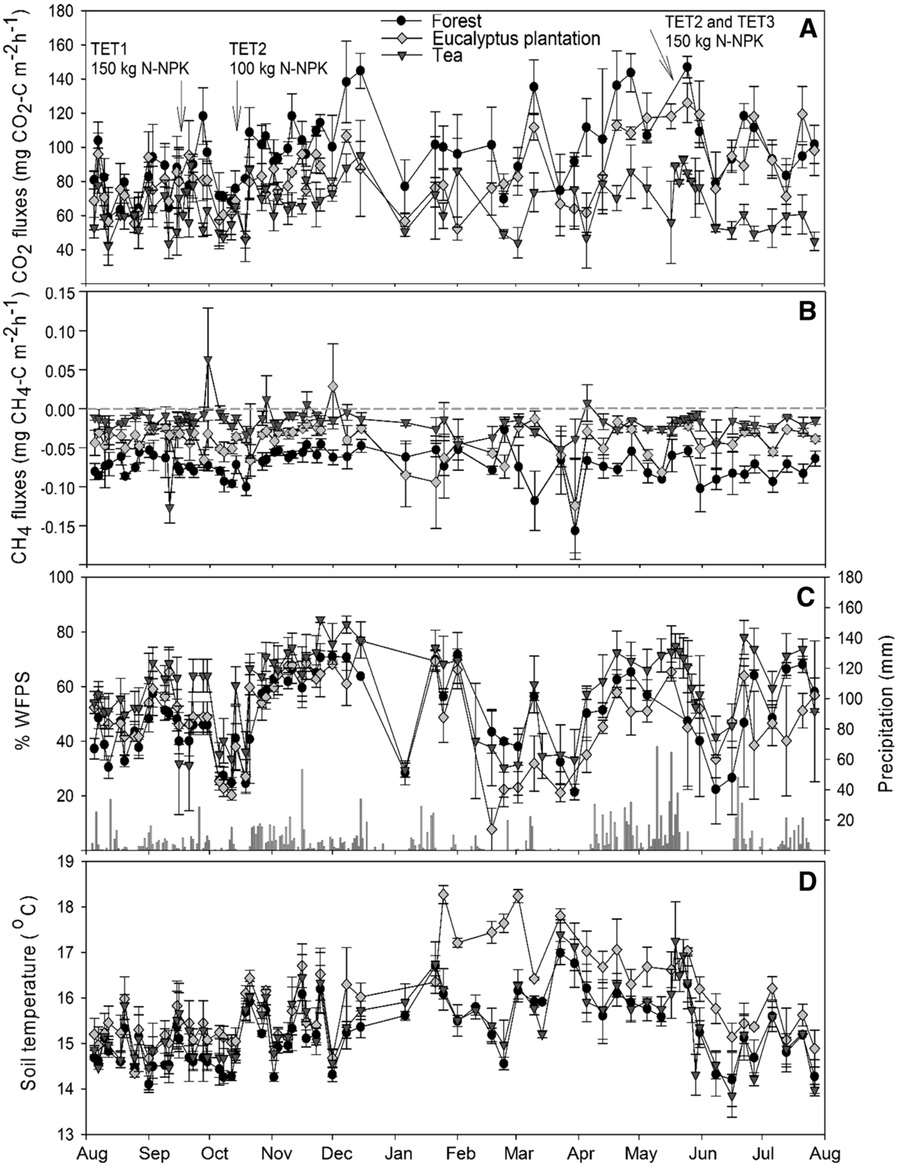

Fig. 3 Mean (± SE, n = 3) soil carbon dioxide (**a**), soil methane fluxes (**b**) measured bi-weekly (August 2015 to December 2015) and weekly (December 2016 to August 2016), and quantity and timing of fertilization (kg N ha^{-1}) applied to three tea plantations (TET1, TET2 and TET3), water filled pore space (%WFPS) and precipitation (grey bars) (**c**) and soil temperature (**d**) from forest, grazing and tea land use types at the Tea Estate site (TE) in the South West Mau forest area, Kenya

Gas sampling and analysis

We collected CO_2 and CH_4 gas samples for a period of 1 year using static (non-flow-through, non-steady state) opaque chambers. For each of the selected plots, five PVC frames with a basal area of 0.0875 m^2 were inserted in the soil (approximately 0.07 m deep) a month prior to gas sampling. A ventilated PVC chamber fitted with a fan, a non-forced vent and a sampling port were attached to the PVC frame by metal clamps during sampling. Closed-foam between frame and chamber ensured airtight sealing. Gas sampling campaigns were usually run between 08h00 and 11h30. During chamber closure we took gas samples immediately and at 15, 30, and 45 min after closing. We used the composite sampling procedure of Arias-Navarro et al. (2013) for each plot. These authors found a marginal deviation of 2–8% for CO_2 and 3–4% for N_2O of pooled gas fluxes compared to individually analyzed samples. This difference between sampling procedures is small and together with the reduced costs of analyses and reduced requirements for sampling justify pooling gas samples from different chambers within a plot. During gas sampling using the pooling approach, 10 ml of gas was drawn from each chamber with a 60 ml syringe at each sampling time to attain a 50 ml composite gas sample (from the five chambers in each selected plot). Twenty-five ml of the 50 ml were used to flush a 10 ml standard glass vial (closed with a rubber septum), while the remaining 25 ml was forced into the flushed vial. Samples were then sent to the Mazingira Centre at the International Livestock Research Institute (ILRI) for analysis. Gas samples were analyzed within a week of sampling using a gas chromatograph equipped with a flame ionization detector (GC, SRI 8610C) for analysis of CO_2 (after passage through a methanizer) and CH_4, as described by Schindlbacher et al. (2004). In the GC, CO_2 is first converted to CH_4 by a methanizer before detection by the FID. Fluxes were calculated using linear regression between the time of chamber deployment and the change in gas concentrations. Fluxes were corrected for actual air temperature and pressure measured at the time of sampling using the ideal gas law. There were a few cases where concentration of CO_2 at the last sampling time was lower than the previous time ($< 2\%$ of the data). In these cases, we excluded the last data point and calculated the fluxes based on the linear increase in concentration during the first three samplings. Daily fluxes were calculated by multiplying the measured hourly flux by 24, given that fluxes measured between 08:30 and 11:20 were found to be representative of the mean daily flux (Yang et al. 2017). Sampling in the morning hours has been shown to minimise the effect of soil temperature in soil respiration (Jian et al. 2018). Research in forests and in rangelands in Kenya showed a negligible effect of soil temperature on CH_4 fluxes (Werner et al. 2007; Zhu et al. 2018). Fluxes were calculated using linear regression between the time of chamber deployment and the change in gas concentrations. In all cases, measurements were inspected, and data flagged when the measurements were not stable or unreliable: a) we excluded data with a negative CO_2 flux, b) we set logical bounds for CH_4 uptake (e.g. $-$ 200 µg CH_4–C m^{-2} h^{-1}) and for emissions ($<$ 1 mg CH_4–C m^{-2} h^{-1}). Annual fluxes were calculated by linear interpolation of daily fluxes and integrating area under the curve. Linear interpolation between sampling dates is a commonly used approach in estimation of cumulative annual GHG fluxes (Parkin and Kaspar 2004; Rowlings et al. 2012), which given the weekly sampling and the low coefficient of variation of the mean daily flux rates should provide an estimate of the cumulative flux rates that is ± 10% of the true value (Barton et al. 2015).

Statistical analysis

Repeated measures analysis of variance using generalized least square (GLS) ANOVA (Pékar and Brabec 2016) was used to assess the effect of land use and time (fixed factors) on soil CO_2 and CH_4 fluxes. The GLS model included an autoregressive structure, accommodated for unequal time of sampling and a variance function that allows for unequal variance in the fixed factors, this structure was the best fit in all cases. The effect of land use and soil properties on annual CO_2 and CH_4 fluxes were tested using a fixed factor linear model with nlme R package (R Core Team 2016). In the models, land use and block were the fixed factors. Residual distributions for the models were examined and data were log or Johnson-transformed where necessary. Dry and wet seasons were defined by a threshold in soil moisture (40% WFPS), comparisons of CO_2 and CH_4 fluxes between dry and wet periods (season) were done using the nlme package with season as the fixed factor for each of the land uses at the two sites. Simple linear regression was used to assess how the spatial and temporal variation of CO_2 and CH_4 were influenced by soil temperature and soil water content for each site and within each land use, as well as variation of annual CO_2 and CH_4 fluxes and soil properties (Total nitrogen (TN), Total carbon (TC), C:N ratio, clay content and bulk density (BD), pH).

Stepwise multiple regression analyses were carried out using annual CO_2 and CH_4 fluxes as response variables and soil temperature, WFPS, soil pH, BD, C:N ratio, inorganic N intensities and significant ($p < 0.05$) interactions as response variables. For soil pH, C:N ratio and BD we used weighed averages for the three depths (0–0.05 m, 0.05–0.2 m and 0.2–0.3 m). We tested for multicolinearity between the independent variables and interaction terms using the variance inflation factor (VIF) in the car R package. VIF values between 1 and 5 implied that the correlation between the variables was low and did not warrant correction. In case of multicollinearity between independent variables (VIF $>$ 5), standardization of the variables by subtracting means from the values of the independent variables was carried out and models re-run using the standardized sets. The normality, linearity and homogeneity of the model's residuals plots was also tested. In this analysis we did not include CO_2 fluxes from grazing land use. In all the other land use types we report soil respiration, however in the grazing lands we did not remove the grass inside the chambers and therefore the CO_2 fluxes include soil respiration and plant respiration.

Results

Soil properties, temperature and soil moisture

Soil properties varied among the land use types from the sampled soil depths (0–0.05, 0.05–0.2 and 0.2–0.3 m) and at both sites (Table 2). All land use types across both sites had clay-textured soils (0–0.3 m depth). The C:N ratio was highest for the tea plantations while the forest C:N ratio was lowest for all soil depths. Soil pH ranged from 3.8 to 6.6, with the lowest pH observed in the tea plots at the tea estate site. Soil BD was highest under grazing land and lowest under forest at all soil depths. NH_4^+–N intensities were higher in the tea than the forest ($p = 0.016$) and eucalyptus ($p < 0.001$) land use types at the tea estate site. However, variation in NH_4^+-N intensities within land use types, especially for the tea plots at the smallholder site, was high as indicated by a coefficient of variation (CV) of 99% (Table 3). The high CV % corresponded with the high variability in management (fertilizer application) between the three smallholder tea plots (Table 7 in Appendix).

At the smallholder site, topsoil temperatures were highest in the grazing plots (18.8 °C), higher than in the tea (15.7 °C) and forest plots (15.2 °C) ($p < 0.001$ for both). At the tea estate site, topsoil temperatures under eucalyptus were highest (Figs. 2d; 3d), and mean annual topsoil temperature in the eucalyptus plots (15.9 °C) was greater ($p = 0.01$) than in the forest soils (15.2 °C). Temporal variation in soil temperature within a land use was small with standard deviations ranging between 0.65 and 0.99 °C. Soil moisture in the topsoil (0–0.05 m) ranged from about 20% WFPS during the dry season to about 80% WFPS during periods with heavy rains. Mean annual WFPS was higher in grazing land at the smallholder site and in the tea plantations at the tea estate site (Figs. 2c; 3c).

Carbon dioxide fluxes

Across all sites and plots, CO_2 fluxes from soil varied between 42 and 559 mg CO_2–C m^{-2} h^{-1} (Figs. 2b, 3c). In most treatments, the highest CO_2 fluxes were observed during the wet period (Table 4), with the largest difference between periods observed for tea (27%), followed by eucalyptus plantations (25%) and forest (20%) at the tea estate site. At the smallholder site the differences between land use types were smaller (18–20%). Annual CO_2 fluxes ranged from 6.0 to 31.4 Mg CO_2–C ha^{-1} $year^{-1}$ and 5.0–9.3 Mg CO_2–C ha^{-1} $year^{-1}$ at the smallholder and tea estate sites, respectively (Table 3). Mean annual CO_2 fluxes at the smallholder site were highest ($p = 0.028$) for grazing land (25.6 ± 2.9 Mg CO_2–C ha^{-1} $year^{-1}$), while the mean annual soil CO_2 fluxes from tea and forest plots ranged between 6.0 and 9.0 Mg CO_2–C ha^{-1} $year^{-1}$ and were similar ($p = 0.875$). At the tea estate, annual CO_2 fluxes were highest ($p < 0.001$) for the forest followed by eucalyptus plantations with the lowest fluxes coming from the tea plots.

Methane fluxes

Methane fluxes ranged between − 0.16 and 0.06 mg CH_4–C m^{-2} h^{-1} at both sites. Forest soils at both sites acted predominantly as sinks for atmospheric CH_4, with approximately 92% of the measurements indicating net CH_4 uptake (Figs. 2a, 3a). Eucalyptus plantations (91% of measurements) and tea plantations (73% of measurements) were also predominantly CH_4 sinks, whereas only 47% of the measurements in grazing lands showed CH_4 uptake. For all land use types except for the smallholder grazing site, CH_4 uptake was significantly higher during the dry than during the wet periods: 43% higher for tea, and 30% higher for forest at the smallholder site, and 64, 35, and 27% higher for the tea, eucalyptus and native forest, respectively, at the tea estate site (Table 4).

Annual cumulative CH_4 fluxes ranged between − 6.61 and 0.08 kg CH_4–C ha^{-1} $year^{-1}$ and apart from one grazing plot (SHG1), soils at all plots acted as net sinks for atmospheric CH_4 (Table 3). The highest CH_4 uptakes at both sites occurred in the forest soils, which were 41–88% higher than the uptake at

Table 2 Mean (± SE) soil chemical and physical properties in 0–0.05, 0.05–0.2 and 0.2–0.3 m soil depth for different land use types at the smallholder and tea estate sites in the SW Mau forest area, Kenya

Soil depth (m)	Site	Land use	Plot code	Total Nitrogen (%)	Total Carbon (%)	SOC (Mg ha^{-1})	SON (Mg ha^{-1})	C:N ratio	pH	Bulk density (g cm^{-3})	Clay (%)	Sand (%)
0–0.05	Smallholder	Forest	SHF 1-3	1.24 ± 0.05a	13.4 ± 0.7a	47.0 ± 2.3a	4.3 ± 0.2a	10.8 ± 0.1b	6.6 ± 0.1a	0.65 ± 0.03b	22 ± 0.1c	46 ± 2.0a
	Smallholder	Grazing	SHG 1-3	0.74 ± 0.03b	7.9 ± 0.3b	37.6 ± 1.2b	3.7 ± 0.1b	10.9 ± 0.1b	6.0 ± 0.1b	0.94 ± 0.02a	33 ± 1.8b	39 ± 2.4b
	Smallholder	Tea	SHT 1-3	0.69 ± 0.03b	8.4 ± 0.5b	29.7 ± 1.8c	2.5 ± 0.1c	11.9 ± 0.2a	5.4 ± 0.21b	0.72 ± 0.05b	45 ± 1.0c	24 ± 2.0c
	Tea estate	Forest	TEF 1-3	0.94 ± 0.04a	9.5 ± 0.5a	28.6 ± 1.5b	2.8 ± 0.1a	10.1 ± 0.1b	5.1 ± 0.01a	0.60 ± 0.03b	49 ± 1.5b	21 ± 1.3a
	Tea estate	Eucalyptus	TEP 1-3	0.61 ± 0.02b	7.0 ± 0.3b	25.9 ± 1.0b	2.3 ± 0.1b	11.3 ± 0.7a	5.4 ± 0.11a	0.74 ± 0.03a	61 ± 1.8a	18 ± 0.3a
	Tea estate	Tea	TET 1-3	0.91 ± 0.10a	10.6 ± 1.3a	36.0 ± 4.4a	3.0 ± 0.4a	12.0 ± 0.1a	3.8 ± 0.06b	0.67 ± 0.04b	65 ± 4.8a	19 ± 2.9a
0.05–0.2	Smallholder	Forest	SHF 1-3	0.58 ± 0.02a	5.3 ± 0.12b	63.9 ± 1.5b	6.9 ± 0.2b	9.3 ± 0.2b	6.1 ± 0.09a	0.80 ± 0.03b	49 ± 1.3a	21 ± 0.7b
	Smallholder	Grazing	SHG 1-3	0.64 ± 0.03a	6.7 ± 0.3a	91.9 ± 3.7a	8.8 ± 0.5a	10.6 ± 0.2b	6.0 ± 0.07ab	0.93 ± 0.02a	40 ± 4.2b	30 ± 3.1a
	Smallholder	Tea	SHT 1-3	0.46 ± 0.01b	5.1 ± 0.1b	64.1 ± 1.0b	5.8 ± 0.2c	11.2 ± 0.3b	5.7 ± 0.1b	0.84 ± 0.03b	49 ± 1.0a	22 ± 0.0b
	Tea estate	Forest	TEF 1-3	0.44 ± 0.02a	4.3 ± 0.2b	40.1 ± 3.6c	4.5 ± 0.2b	9.7 ± 0.2b	4.8 ± 0.1b	0.68 ± 0.04b	48 ± 1.2a	24 ± 3.4a
	Tea estate	Eucalyptus	TEP 1-3	0.42 ± 0.02a	4.6 ± 0.2b	54.3 ± 2.1b	5.2 ± 0.2a	10.7 ± 0.2b	5.5 ± 0.1a	0.79 ± 0.03a	57 ± 0.7a	18 ± 1.2b
	Tea estate	Tea	TET 1-3	0.46 ± 0.01a	5.7 ± 0.2a	62.4 ± 3.2a	5.1 ± 0.2a	12.8 ± 0.3a	4.1 ± 0.05c	0.74 ± 0.02a	53 ± 1.8a	21 ± 2.9ab
0.2–0.3	Smallholder	Forest	SHF 1-3	0.47 ± 0.03a	4.5 ± 0.21b	35.4 ± 1.7c	3.7 ± 0.3b	9.7 ± 0.30b	5.7 ± 0.10b	0.79 ± 0.02b	51 ± 3.7ab	21 ± 1.8a
	Smallholder	Grazing	SHG 1-3	0.49 ± 0.02a	5.4 ± 0.16a	51.7 ± 1.5a	4.7 ± 0.2a	11.2 ± 0.29a	6.0 ± 0.04a	0.96 ± 0.02a	47 ± 5.1b	25 ± 2.1a
	Smallholder	Tea	SHT 1-3	0.47 ± 0.04a	5.3 ± 033a	44.9 ± 2.8b	4.0 ± 0.4a	11.5 ± 0.38a	5.9 ± 0.07ab	0.85 ± 0.03b	59 ± 5.0a	16 ± 2.0b
	Tea estate	Forest	TEF 1-3	0.43 ± 0.01a	4.3 ± 0.15b	30.6 ± 1.1b	3.1 ± 0.1a	9.9 ± 0.18c	4.8 ± 0.09b	0.71 ± 0.04b	53 ± 0.7b	20 ± 0.1b
	Tea estate	Eucalyptus	TEP 1-3	0.37 ± 0.02b	3.9 ± 0.16b	32.5 ± 1.3b	3.0 ± 0.1a	11.0 ± 0.18b	5.5 ± 0.05a	0.82 ± 0.03a	59 ± 0.7a	19 ± 0.7b
	Tea estate	Tea	TET 1-3	0.45 ± 0.01a	5.6 ± 0.18a	41.4 ± 1.3a	3.3 ± 0.1a	12.5 ± 0.16a	4.1 ± 0.05c	0.74 ± 0.02b	52 ± 0.1b	26 ± 1.2c

Same letters following means indicate no significant different among the land use types within the soil depth and site ($p > 0.05$)

Table 3 Mean (± SE) annual CH_4 and CO_2 fluxes, coefficients of variation (CV), NH_4^+ intensity, NO_3^- intensity, annual water-filled pore space and soil temperature for different land use types at the smallholder and tea estate sites, from the SW Mau forest, Kenya

Land use	Plot code	Annual CH_4 (kg CH_4–C ha^{-1} $year^{-1}$)	CV (%)	Annual CO_2 (Mg CO_2–C ha^{-1} $year^{-1}$)	CV (%)	NH_4^+ intensity (g N kg^{-1})	NO_3^- intensity (g N kg^{-1})	Annual WFPS (%)	CV (%)	Annual T (°C)	CV (%)
Smallholdersite											
Forest	SHF1	− 3.16		8.71		4.3	5.7	46		15.2	
Forest	SHF2	− 3.64		8.21		3.5	3.3	46		15.5	
Forest	SHF3	− 2.42		6.54		2.6	3.1	56		14.9	
	Mean	*− 3.08 ± 0.35a*	*20*	*7.8 ± 0.7b*	*4.9*	*3.5 ± 0.5a*	*4.0 ± 0.8a*	*49 ± 5b*	*11.5*	*15.2 ± 0.2b*	*1.9*
Grazing	SHG1	0.08		22.58		5.8	1.0	58		19.6	
Grazing	SHG2	− 0.40		31.36		4	2.1	53		18.5	
Grazing	SHG3	− 0.77		22.92		3.9	1.1	61		18.2	
	Mean	*− 0.36 ± 0.25b*	*119*	*25.6 ± 2.9a*	*19.4*	*4.6 ± 0.6a*	*1.4 ± 0.4a*	*57 ± 2a*	*6.5*	*18.8 ± 0.4a*	*3.8*
Tea	SHT1	− 1.60		6.01		9.2	4.9	52		14.8	
Tea	SHT2	− 1.36		8.53		3.1	2.3	48		15.8	
Tea	SHT3	− 1.29		9.05		0.8	0.9	53		16.4	
	Mean	*− 1.44 ± 0.12b*	*14*	*7.9 ± 0.9b*	*20.6*	*4.4 ± 2.5a*	*2.7 ± 1.2a*	*51 ± 2b*	*5.5*	*15.7 ± 0.5b*	*5.1*
Tea estatesite											
Forest	TEF1	− 6.27		9.26		2.6	3.6	43		15.1	
Forest	TEF2	− 6.61		8.81		2.2	3.8	41		15.3	
Forest	TEF3	− 4.64		8.23		1.7	5.3	45		15.3	
	Mean	*− 5.84 ± 0.61a*	*18*	*8.8 ± 0.3a*	*5.9*	*2.2 ± 0.3b*	*4.2 ± 0.5a*	*43 ± 1b*	*4.4*	*15.2 ± 0.1b*	*0.8*
Tea	TET1	− 0.87		5.13		4.4	8.4	56		15.0	
Tea	TET2	− 1.60		6.59		4.2	4.3	55		15.6	
Tea	TET3	− 1.87		5.01		4.8	3.8	49		15.9	
	Mean	*− 1.44 ± 0.29c*	*10*	*5.6 ± 0.5c*	*15.8*	*4.5 ± 0.2a*	*5.5 ± 1.5a*	*54 ± 2a*	*13.8*	*15.5 ± 0.3ab*	*2.9*
Eucalyptus	TEP1	− 3.51		7.18		1.2	1.7	52		16.0	
Eucalyptus	TEP2	− 3.07		7.26		2.2	3.2	41		16.0	
Eucalyptus	TEP3	− 3.71		7.04		2.0	2.6	42		15.8	
	Mean	*− 3.43 ± 0.19b*	*36*	*7.2 ± 0.1b*	*1.6*	*1.8 ± 0.3b*	*2.5 ± 0.4a*	*45 ± 4b*	*6.9*	*15.9 ± 0.1a*	*0.6*

Table 4 Average daily CH_4 and CO_2 fluxes for three different land use types in the two study sites (smallholders and tea estate) calculated for the wet and dry periods

Site	Land use	Plot code	Daily CH_4 fluxes (mg CH_4–C m^{-2} h^{-1})		*p* value	Daily CO_2 fluxes (mg CO_2–C m^{-2} h^{-1})		p-value
			Wet	Dry		Wet	Dry	
Smallholder	Forest	SHF 1–3	− 0.029 ± 0.001	− 0.042 ± 0.004	< 0.001	98.9 ± 5.4	79.5 ± 3.8	< 0.001
Smallholder	Grazing	SHG 1–3	− 0.006 ± 0.002	0.001 ± 0.007	0.20	335.9 ± 11.9	271.9 ± 17.8	< 0.001
Smallholder	Tea	SHT 1–3	− 0.013 ± 0.001	− 0.023 ± 0.003	< 0.001	97.8 ± 3.2	79.9 ± 5.9	0.002
Tea estate	Forest	TEF 1–3	− 0.058 ± 0.005	− 0.079 ± 0.004	< 0.001	104.1 ± 2.7	82.7 ± 2.7	< 0.001
Tea estate	Eucalyptus	TEP 1–3	− 0.028 ± 0.006	− 0.043 ± 0.003	< 0.001	90.7 ± 2.2	67.4 ± 3.1	< 0.001
Tea estate	Tea	TET 1–3	− 0.009 ± 0.003	− 0.025 ± 0.003	< 0.001	71.7 ± 1.6	52.2 ± 2.7	< 0.001

Water filled pore space (WFPS) of 40% was used to define the seasons

other land use types (p = 0.007 for smallholder and p = 0.008 for tea estate). There was high variability of annual CH_4 fluxes in the grazing plots (CV = 119%), where annual CH_4 fluxes ranged between − 0.77 kg CH_4–C ha^{-1} $year^{-1}$ and 0.08 kg CH_4–C ha^{-1} $year^{-1}$. Plots with high grazing densities tended to be sources of CH_4, while the plot with low grazing density (SHG3) exhibited greater CH_4 uptake. At the tea estate, cumulative CH_4 uptake among the land use types decreased (p = 0.008) in the following order; forest > eucalyptus plantation > tea plantation.

Effect of environmental variables on CO_2 and CH_4 fluxes

Variation of soil CO_2 fluxes with instantaneous WFPS was low, with instantaneous WFPS explaining at most 22% of the variation among the land use types at both sites. As there was little variability in instantaneous soil temperatures within plots, we found that the soil temperature influence on CO_2 fluxes was also weak (R^2 values ranging between 0.01 and 0.31). As with the CO_2 fluxes, the contribution of soil temperature to the instantaneous variation of soil CH_4 fluxes was small, ranging between 0.3 and 9% (Table 5). The strongest relationship (R^2 = 0.25) between instantaneous WFPS and CH_4 was observed in soils of forest plots at the smallholder site; the other land use types exhibited weaker relationship with R^2 values ranging between 0.02 and 0.11. Our measurements of annual log transformed CO_2 fluxes were positively correlated with soil pH (0–0.3 m soil depth) (p = 0.03, R^2 = 0.52) and negatively correlated with the soil C:N ratio (p = < 0.001, R^2 = 0.28). Stepwise linear regression showed that (Log_{10}) soil CO_2 fluxes were influenced by soil pH (pH), weighted bulk density (BD), and that this relationship explained 60.6% of the variation. Addition of the interaction between soil pH and soil C:N ratio (Eq. 1) to the model significantly (p = 0.005) improved the relationship to 83.4% (p = < 0.001) (Table 6).

$$\begin{aligned}\mathrm{Log}_{10}(\mathrm{CO}_2) = {} & 1.49 + 0.06 \times \mathrm{pH} - 0.79 \times \mathrm{BD} \\ & - 0.005 \times \mathrm{C{:}N} + 0.04 \\ & \times (\mathrm{pH} \times \mathrm{C{:}N})\end{aligned} \quad (1)$$

Annual CH_4 uptake from all the land use types decreased with increases in mean annual WFPS (R^2 = 0.60) (Fig. 4a), NH_4^+ intensity (R^2 = 0.30) (Fig. 4b), C:N ratio (R^2 = 0.30) (Fig. 4c) and bulk density (R^2 = 0.43) at all soil depths (Fig. 4d). Results from stepwise regression (Eq. 2) show that CH_4 was driven by ammonium intensity (NH_4^+-N), log WFPS, BD and soil C:N ratio and these factors explained 79.5% ($p \leq 0.001$) of the total variation, the contribution of each variable to the variation is shown in Table 6.

$$\begin{aligned}\mathrm{CH}_4 = {} & -37.9 + 0.27 \times \mathrm{NH}_4^+ - \mathrm{N} + 13.7 \\ & \times \log_{10}(\mathrm{WFPS}) + 0.48 \times \mathrm{C{:}N} + 7.7 \times \mathrm{BD}\end{aligned} \quad (2)$$

Discussion

The mean annual soil respiratory CO_2 fluxes from the forests in this study (7.5 ± 0.2 and 8.8 ± 3.3 Mg CO_2–C ha^{-1} $year^{-1}$, for smallholder and tea estate sites, respectively) were similar to soil fluxes from a

Table 5 Model statistics for the linear relationships (y = a+bx) between daily CH_4, CO_2 and environmental variables: soil temperature and water filled pore space (WFPS) for land use types at two sites in the Mau forest area, Kenya

Site	GHG Gas	Variable	Land use	Plot code	Slope (b)	Intercept (a)	R^2	n	p-value
Smallholder	CH_4	Temperature	Forest	SHF 1–3	− 0.008	0.09	0.31	166	< 0.001
			Grazing	SHG 1–3	0.003	− 0.070	0.02	164	0.08
			Tea	SHT 1–3	− 0.001	0.002	0.005	163	0.38
Tea estate			Forest	TEF 1–3	− 0.0033	− 0.019	0.004	180	0.43
			Plantation	TEP 1–3	− 0.0088	0.107	0.03	168	0.04
			Tea	TET 1–3	− 0.009	0.128	0.03	177	0.02
Smallholder		WFPS	Forest	SHF 1–3	0.0008	− 0.007	0.25	175	< 0.001
			Grazing	SHG 1–3	− 0.0001	0.002	0.008	189	0.24
			Tea	SHT 1–3	0.0002	− 0.028	0.04	180	0.006
Tea estate			Forest	TEF 1–3	0.0007	− 0.010	0.11	186	< 0.001
			Plantation	TEP 1–3	0.0009	− 0.074	0.06	178	0.001
			Tea	TET 1–3	0.0005	− 0.034	0.02	182	0.05
Smallholder	CO_2	Temperature	Forest	SHF 1–3	10.18	− 66.5	0.09	171	< 0.001
			Grazing	SHG 1–3	− 11.1	527.8	0.01	172	0.143
			Tea	SHT 1–3	14.27	− 131.4	0.15	176	< 0.001
Tea estate			Forest	TEF 1–3	13.3	− 104.8	0.13	166	< 0.001
			Plantation	TEP 1–3	6.05	− 11.6	0.05	165	0.003
			Tea	TET 1–3	5.2	− 11.8	0.06	245	< 0.001
Smallholder		WFPS	Forest	SHF 1–3	0.224	77.9	0.01	185	0.120
			Grazing	SHG 1–3	1.563	231.6	0.05	188	< 0.001
			Tea	SHT 1–3	0.74	56.9	0.08	185	< 0.001
Tea estate			Forest	TEF 1–3	1.01	52.0	0.22	174	< 0.001
			Plantation	TEP 1–3	0.63	54.9	0.12	184	< 0.001
			Tea	TET 1–3	0.46	44.1	0.08	182	< 0.001

Table 6 Summary results from multiple regression between annual gas fluxes (CO_2 and CH_4) and soil properties: *pH* soil pH, *BD* bulk density, *C:N* soil C:N ratio, *pH*C:N* interaction term soil pH and soil C:N ratio; NH_4^+ soil ammonium concentration, log_{10} *(WFPS)* water filled pore space

Gas flux	Variables	Coefficients	F value	p-value	% of total variance
Log CO_2	Intercept	1.49		< 0.001	
	pH	0.060	18.3	0.002	30.3
	BD	− 0.79	18.3	0.002	30.3
	C:N	− 0.005	0.58	0.463	1.0
	pH*C:N	0.04	13.3	0.005	21.9
CH_4	Intercept	− 37.9		0.001	
	NH_4^+	0.27	16.4	0.002	28.1
	Log_{10} (WFPS)	13.7	23.1	< 0.001	39.5
	C:N	0.48	1.4	0.256	2.4
	BD	7.7	5.5	0.036	9.5

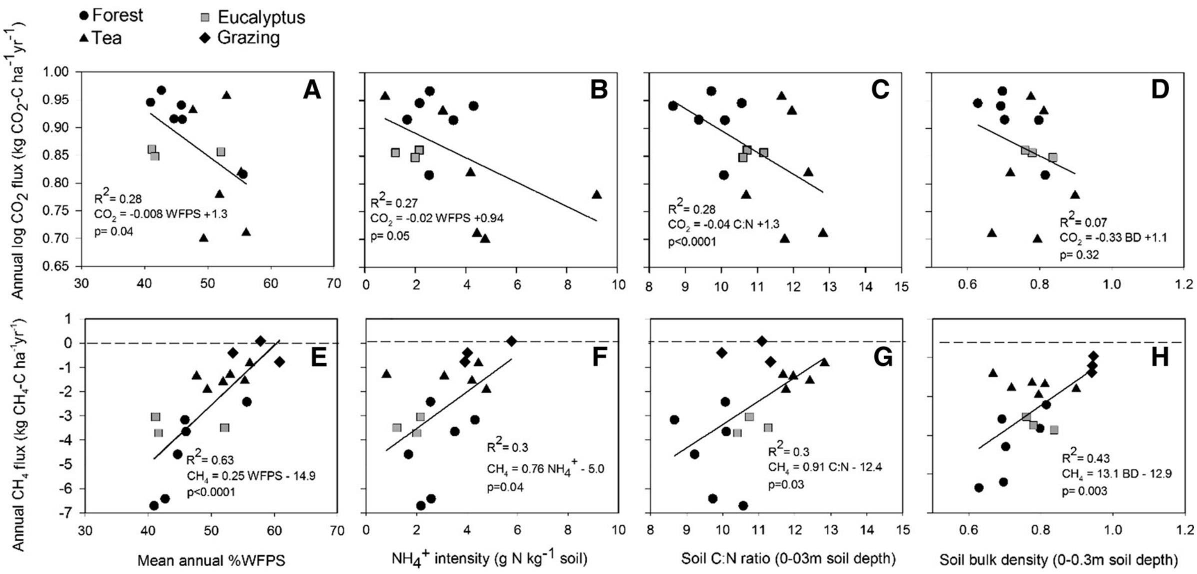

Fig. 4 Linear relationship between annual log transformed CO_2 (Mg CO_2–C ha^{-1} $year^{-1}$) and CH_4 fluxes (kg CH_4–C ha^{-1} $year^{-1}$) fluxes with (**a**, **e**) mean annual water filled pore space (%WFPS), (**b**, **f**) ammonium (NH_4^+) intensity, (**c**, **g**) weighted (0–30 cm depth) C:N ratio and (**d**, **h**) weighted (0–30 cm depth) soil bulk density (**b**) from soils of forest, tea, grazing and eucalyptus plantations land use types at the smallholder and tea estate sites, in the SW Mau forest area of Kenya

tropical montane forest in China (6.85 ± 3.4 Mg CO_2–C ha^{-1} $year^{-1}$; Jiang et al. 2016) but lower than those from soils of a grazed Afromontane forest (15.7 to 19.4 Mg CO_2–C ha^{-1} $year^{-1}$) in Ethiopia (Yohannes et al. 2011). The annual soil respiratory CO_2 fluxes from the grazing lands of our study (25.6 Mg CO_2–C ha^{-1} $year^{-1}$) were higher than those measured in other tropical grazing lands; with previous studies measuring soil annual CO_2 fluxes that ranged from 5.2 to 11.2 Mg CO_2–C ha^{-1} $year^{-1}$ for western Kenya (Pelster et al. 2017), 13.4 to 15.0 Mg CO_2–C ha^{-1-} yr^{-1} for grazing lands in the Kenyan highlands (Rosenstock et al. 2016) and 10 to 15 Mg CO_2–C ha^{-1} $year^{-1}$ for grazing lands in eastern Amazonia, Brazil (Davidson et al. 2000). The higher soil CO_2 fluxes from the grazing lands in our study were also much higher than fluxes from all other land use types. These higher CO_2 fluxes are not directly comparable to these other studies, so that microbial respiration plus aboveground and belowground plant and soil respiration were likely measured. At all other sites (tea and eucalyptus plantations and the natural forest) soils were bare without ground cover, so that only microbial plus root respiration were measured. A study by Zhu et al. (2015) in grasslands in China reported that soil CO_2 fluxes from ecosystem respiration, i.e. including plant respiration, were approximately double the fluxes from soil respiration alone. In addition, *Pennisetum clandestinum*, the dominant grass species in the grazing plots in our sites, is a C4 grass that produces relatively greater amounts of root exudates that result in higher rates of root respiration compared to tea and eucalyptus which use C3 photosynthetic pathways (Roberts and Keys 1978; Leuning et al. 1991; Chen et al. 2016). Furthermore, the soil carbon concentrations (7.1%) in the 0–0.2 m soil layer of the grazing lands in our study were 2–3 times higher than in the grazing lands in the study by Pelster et al. (2017) (2.3%) and that by Rosenstock et al. (2016) (2.2–3.7%) with similar bulk densities, which could partly explain the higher soil CO_2 fluxes in our study.

Strong responses of soil CO_2 to soil temperature have been reported in studies where variations in soil temperature are wide, for instance in a study by Fan et al. (2015) at a forest site exposed to a subtropical monsoon climate in Eastern China, with soil temperatures varying over the year in a range of 0 to 35 °C. However, variations in soil temperature in our study region were smaller than the variation in temperate zones (ranging between 14 and 18 °C for the forest, tea plantations, eucalyptus plantations and croplands, and ranging between 17 and 22 °C for the grazing lands). The Q_{10} value of soil respiration was found to be approximately 2.4 (Raich and Schlesinger 1992), meaning that a 10 °C increase in temperature can cause a 2.4-fold increase in soil respiration. The threefold increase in CO_2 flux in the grazing plots from a 2 to 2.5 °C increase in soil temperature suggests a Q_{10} value of approximately 12, which is inconsistent with previous studies, suggesting that the variation in fluxes was most likely due to other factors.

Soil respiratory CO_2 fluxes were explained by soil pH, C:N ratio, bulk density as well as the interaction between soil pH and C:N ratio. Soil pH moderates microbial activities through which CO_2 is produced (Treseder 2008). Cuhel et al. (2010) found that the highest soil CO_2 emissions occurred around neutral soil pH. Our data showed spatial variation in soil pH and this can be attributed to management activities such as application of inorganic fertilizers in the tea plots. In combination with soil C:N ratio, soil pH explained the greatest portion of variation in CO_2 fluxes. Soil C:N ratios indicate the ease with which SOC is decomposed by soil microbes, thus lower C:N ratios lead to higher soil CO_2 fluxes (Sylvia et al. 2005). Bulk density influenced negatively CO_2 fluxes, likely because the higher BD is associated with less pore space, reducing gas diffusivity through the soil (Fujikawa and Miyazaki 2005), resulting in less gaseous exchange between soil and atmosphere.

Tropical forest soils within our study area acted predominantly as sinks for atmospheric CH_4, similarly to previous studies summarized by Veldkamp et al. (2013), Dalal and Allen (2008) and Dutaur and Verchot (2007). Annual CH_4 fluxes at the natural forest plots of the smallholder site (− 3.2 kg CH_4–C ha^{-1}year^{-1}) were comparable to annual CH_4 fluxes observed for tropical montane forests soils in Ecuador (-3.1 kg CH_4–C ha^{-1}year^{-1}; Wolf et al. 2012) and Tanzania (range − 2.7 to − 3.9 kg CH_4–C ha^{-1} year^{-1}; Gütlein et al. 2017), but higher than those found for a montane forest in Indonesia (− 1.5 kg CH_4–C ha^{-1} year^{-1}; Purbopuspito et al. 2006). The lower soil uptake CH_4 rates (− 1.5 kg CH_4–C ha^{-1} year^{-1}) in the study by Purbopuspito et al. (2006) were due to a very thick organic layer at the soil surface, which not only hampered gas diffusion but might have also stimulated CH_4 production. The annual CH_4 uptake rates of the natural forest soils at the tea estate site were greater (− 5.9 kg CH_4–C ha^{-1} year^{-1}) than those measured in the studies from montane tropical environments mentioned above, but similar to the annual flux rate reported for the Kakamega rainforest in Kenya (− 4.8 kg CH_4–C ha^{-1} year^{-1}; Werner et al. 2007), which is at a lower elevation (1530 m asl.), but with similar soil texture as our sites.

Our study showed reductions in CH_4 uptake by soils converted to other land use types compared to native forest soils. Converted land use types in our study were characterized by livestock trampling in grazing lands, tillage during land preparation and trampling by humans and vehicular traffic in tea and eucalyptus plantations. All of these activities were observed to change the soil hydrologic properties (Owuor et al. 2018), which can alter CH_4 production and consumption. The increased soil bulk density and higher water content measured in the tea and eucalyptus plantations and grazing lands reduced oxygen and CH_4 diffusion and increased occurrence of anaerobic conditions in the soil so that the observed net CH_4 uptake at the soil surface decreases as CH_4 production is stimulated while CH_4 oxidation decreases (Jacinthe et al. 2014). The cumulative CH_4 uptake in our study was negatively correlated with both WFPS and soil bulk density, also indicating that reduced oxygen diffusion and increased incidence of anaerobiosis result in a promotion of CH_4 production at the cost of uptake. The contribution of soil water content (WFPS) and bulk density explained over 49% of the total variation in soil CH_4 fluxes (Table 6). This is consistent with Smith et al. (2000), who observed a steady decrease in CH_4 uptake with increasing soil bulk density and soil water content.

Soil CH_4 uptake rates were negatively correlated with NH_4^+–N intensity, i.e. CH_4 uptake decreased with increasing NH_4^+–N availability. The inhibition of methanotrophic activity by increased availability of NH_4^+ has been explained not only by the competition of CH_4 and NH_4^+ for the methane mono-oxygenase enzyme, which catalyzes the conversion of CH_4 to CO_2 and can also oxidize NH_4^+ to nitrite (Bédard and Knowles 1989), but also by toxic effects of intermediates and endproducts of NH_4^+oxidation (i.e. hydroxylamin and nitrite) on methanotropic avtivity (Bodelier and Laanbroek 2004). Heavy grazing of cattle also leads to increased bulk densities, reduced gas diffusion and increased abundance and activity of methanogenic archaea (Radl et al. 2007; Kim et al. 2014). Both effects have been shown to lead to increased CH_4 production in the soil (Ho et al. 2015), which might also explain reduced rates of CH_4 uptake in the grazing plots in this study. Some studies observed increased CH_4 uptake with increasing temperature (Schaufler et al. 2010) in upland soils, as such we expected high methane uptake in grazing lands but this was not the case in our study. This is likely due to fact that methane uptake is in most cases primarily governed by gas diffusion (Dutaur and Verchot 2007) and the effect of temperature was likely masked by in gas diffusion limitations.

Strong seasonal patterns for both soil CO_2 and CH_4 fluxes were observed (Table 4), which reflect the influence of soil moisture on the fluxes. The wet season at our study sites was characterised as period when soil moisture contents were between 41 and 85% WFPS. A soil core study by Arias-Navarro et al. (2017b) at the same site reported soil CO_2 fluxes increased with increasing WFPS up to a moisture level of 90%. Also in other studies soil CO_2 fluxes increased with increasing soil water content up to a maximum flux at field capacity (Schaufler et al. 2010). Methane uptake was highest during the dry period, this is expected as lower soil moisture content during the dry period facilitates gas diffusion and an aerobic environment under which methane uptake is high (Dutaur and Verchot 2007).

The soil fluxes measured in the forest may not have captured the high spatial variability driven by differences in elevation (Jones et al. 2016). For example, in a previous study in the Mau forest, it was shown that soil CO_2 fluxes were dependent on slope position and varied significantly at scales of 10–100 m (Arias-Navarro et al. 2017a). In our study neither elevation nor slope effects on soil CO_2 fluxes were studied. Additionally, we only measured fluxes for one soil type in one agro-ecological zone, while in the mountainous Mau forest region various soil types can be found and rainfall varies on short distance due to elevation and exposition effects (Kinyanjui et al. 2014). Our study is however, the first empirical assessment of atmospheric C exchange on the soil/vegetation to atmosphere interface before and after forest conversion to the dominant land use types of this montane ecosystem.

Conclusion

Our study is the first of its kind reporting on in situ CO_2 and CH_4 fluxes from forest and converted land use types in the Mau forest of Kenya. Soil respiratory CO_2 fluxes were influenced by land use with the converted land use types, with the exception of the grazing lands, generally exhibiting lower soil CO_2 fluxes compared to natural forests. Methane uptake by soils was significantly reduced in managed land compared to soils of natural forests. This indicates that conversion of forest reduces the potential of soil to consume atmospheric CH_4 in tropical montane regions. Reduction in CH_4 consumption was mainly related to reduction in gas diffusion as reflected by soil water content and bulk density. The importance of changes in soil bulk density and soil moisture regime indicate that gas diffusion was the main driver of spatial CH_4 fluxes. For both gasses, we observed differences in fluxes between forests and the converted land use types indicating that land use significantly affect fluxes for the two GHG. These spatial changes can be linked to management practices such as tillage, grazing intensity and N fertilization in the converted land uses. While our study provides the first estimates on the effect of land use on soil CO_2 and CH_4 fluxes in the Mau forest (the largest contiguous tropical montane forest in east Africa), additional measurements comparing fluxes from different land use types on other soil types in different climate zones of these montane forests are needed to provide a thorough understanding of how land use change has affected soil CO_2 and CH_4 fluxes in forest ecosystems of this region.

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Appendix

See Table 7.

Table 7 Table showing characteristics of the plots studied in Mau forest area. *Source* Wanyama et al. (2018)

Site/Land use	Code	Rep	Latitude	Longitude	Elevation (m)	Year established	Management	Inputs	Management intensity
Smallholder agriculture									
Forest	SHF1	1	− 0.2978	35.4397	2305	Native vegetation	Charcoal burning	N	1
Forest	SHF2	2	− 0.2995	35.4354	2267	Native vegetation	Wood collection	N	1
Forest	SHF3	3	− 0.3032	35.4235	2234	Native vegetation	Open (low tree density)	N	1
Grazing land	SHG1	1	− 0.2942	35.4365	2319	1997, annual crops before	Grazing cattle,excreta deposited	Y	3
Grazing land	SHG2	2	− 0.2959	35.4339		1970, forest before	Grazing cattle,excreta deposited	Y	3
Grazing land	SHG3	3	− 0.2985	35.4203	2283	2005, annual crops before	Low density cattle, little excreta	N	2
Tea	SHT1	1	− 0.2936	35.4371	2320	1999, shrubland before	Fertilizer at 125 kg N ha^{-1} $year^{-1}$	Y	3
Tea	SHT2	2	− 0.2964	35.4327	2291	1985, forest before	Fertiliser at 40 kg N ha^{-1} $year^{-1}$	Y	3
Tea	SHT3	3	− 0.2987	35.4196	2294	2012, shrubland before	No fertilizer applied	N	2
Tea estates									
Forest	TEF1	1	− 0.3165	35.3985	2169	Native vegetation	Little disturbance	N	1
Forest	TEF2	2	− 0.3194	35.3964	2173	Native vegetation	Little disturbance	N	1
Forest	TEF3	3	− 0.3225	35.3947	2170	Native vegetation	Little disturbance	N	1
Eucalyptus plantation	TEP1	1	− 0.3143	35.3973	2198	2000, eucalyptus before	Timber harvested	N	2
Eucalyptus plantation	TEP2	2	− 0.3172	35.3956	2163	2000, eucalyptus before	Timber harvested	N	2
Eucalyptus plantation	TEP3	3	− 0.3199	35.3922	2146	2000, eucalyptus before	Timber harvested	N	2
Tea	TET1	1	− 0.3133	35.3968	2208	1973, forest before	Fertiliser at 150 kg N ha^{-1} $year^{-1}$	Y	3
Tea	TET2	2	− 0.3159	35.3943	2176	1973, forest before	Fertiliser at 250 kg N ha^{-1} $year^{-1}$	Y	3
Tea	TET3	3	− 0.3187	35.3911	2168	1973, forest before	Fertiliser at 150 kg N ha^{-1} $year^{-1}$	Y	3

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