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Land-use, land-use history and soil type affect soil greenhouse gas fluxes from agricultural landscapes of the East African highlands

Wanyama, I.[1,2], M.C. Rufino[3], D.E. Pelster[1,4*], G. Wanyama[1], C. Atzberger[5], P. van Asten[6], Louis V. Verchot[7], K. Butterbach-Bahl [1,8]

[1]International Livestock Research Institute (ILRI), P.O Box 30709, Nairobi, Kenya

[2]Center for International Forestry Research (CIFOR), P.O Box 30677, 00100 Nairobi, Kenya

[3]Lancaster Environment Centre, University of Lancaster, Lancaster, LA1 4YQ, United Kingdom

[4]Agriculture and Agri-Food Canada, Science and Technology Branch, 2560 Boul. Hochelaga, Quebec, Canada

[5]Universityof Natural Resources and Applied Life Sciences (BOKU), Peter Jordan–Strasse 82, 1190, Austria

[6]International Institute of Tropical Agriculture (IITA), P.O Box 7878, Kampala, Uganda

[7]International Centre for Tropical Agriculture (CIAT), Cali, Colombia

[8]Instituteof Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Kreuzeckbahnstr. 19, 82467 Garmisch-Partenkirchen, Germany

*corresponding author:

David.Pelster@canada.ca

Abstract

This study aims to explain effects of soil textural class, topography, land-use and land-use history on soil GHG fluxes in the Lake Victoria region. We measured GHG fluxes from intact soil cores collected in Rakai, Uganda, an area characterized by low-input smallholder (<2 ha) farming systems, typical for the East African highlands. The soil cores were air dried and re-wetted to water holding capacities (WHC) of 30, 55 and 80%. Soil CO_2, $CH_4$and N_2O fluxes were measured for 48 hours following re-wetting. Cumulative N_2O fluxes were highest from soils under perennial crops and the lowest from soils under annual crops ($P< 0.001$ for all WHC). At WHC of 55% or 80%, the sandy clay loam soils had lower N_2O fluxes than the clay soils ($P< 0.001$ and $P = 0.041$ respectively). Cumulative soil CO_2fluxes were highest from eucalyptus plantations and lowest from annual crops across multiple WHC ($P = 0.014$ at 30% WHC and $P< 0.001$ at both 55 and 80% WHC). Methane fluxes were below detectable limits, a shortcoming for using soil cores from the top soil. This study reveals that land-use and soil type have strong effects on GHG fluxes from agricultural land in the study area. Field monitoring of fluxes is needed to confirm whether these findings are consistent with what happens *in situ*.

Key words: Soil core incubation, tropical soils, Land-use change, forest, soil texture

1. Introduction

Greenhouse gas (GHG) fluxes from agricultural systems have contributed to increases in the atmospheric concentrations of N_2O, CH_4 and CO_2 and thus, to climate change (Smith et al., 2014). The contribution of GHG fluxes from agricultural activities, including land-use change to total anthropogenic GHG fluxes is estimated at approximately 24% (IPCC, 2014). Non-CO_2 GHG fluxes from agriculture were estimated to have increased annually by 1.1% in the period 2000-2010 (Tubiello et al., 2013), mainly due to the increased use of synthetic fertilizers and increased fluxes from livestock production. Agricultural systems are the greatest source of GHG’s in most developing countries (DeFries & Rosenzweig, 2010), particularly in Sub-Saharan Africa where smallholder farmers dominate agricultural activities (Altieri & Koohafkan, 2008). Initiatives such as the Green Climate Fund aim to support developing countries’ smallholder farmers to improve agricultural productivity under a changing climate while aiming at the same time to mitigate GHG fluxes (Beddington et al., 2012). However, effective targeting for such initiatives requires detailed knowledge of GHG emission hotspots and of promising agricultural practices to reduce GHG fluxes (Olander et al., 2013).

In East Africa, quantification of GHG fluxes from smallholder agriculture is limited and the little information that is available covers few agricultural land-uses and activities (Kim et al., 2016). Quantification of GHG fluxes is constrained by the fact that smallholder systems in East Africa are diverse across climates and soils. Even at the farm scale, soil management practices differ widely, causing pronounced gradients of soil fertility associated with distance to homesteads (Carter & Murwira, 1995; Okumu et al., 2011; Tittonell et al., 2013) due to differential use of agricultural inputs (Giller et al., 2011; Okumu et al., 2011; Tittonell et al., 2010). Additionally, at the landscape scale, spatial variation of soils is common due to geological and edaphic factors as well as processes like erosion and deposition (Scull et al., 2003), challenging the estimation of greenhouse fluxes from tropical agricultural landscapes.

Production and flux rates of N_2O from the soil are governed primarily by the availability of reactive N, soil aeration (Firestone & Davidson, 1989) and gas diffusivity (Balaine et al. 2013), which are related to soil water content and texture (Davidson et al., 2000). Most N_2O from soils is produced by either nitrification or denitrification (Baggs & Philippot, 2010). Most aerobic processes (including nitrification) increase with increasing water content up to approximately 60% water holding capacity (WHC) (Bowden et al., 1998; Linn & Doran, 1984), at which point oxygen availability tends to become limiting for microbes. However, because denitrification requires anaerobic conditions, N_2O fluxes have been found to peak at around 80% WHC (Butterbach-Bahl et al., 2013; Davidson, 1991).

In the tropics, land-use change from natural vegetation (i.e. indigenous forests, woodlands and wetlands) to agriculture land is common. For example, between 1980 and 2000 approximately 83% of new agricultural land in the tropics came from the conversion of intact and/or degraded forests (Gibbs et al., 2010). Land-use change from natural forests to agriculture results in alteration of soil physical and chemical properties (Don et al., 2011; Majaliwa et al., 2010) and affects GHG fluxes (García-Marco et al., 2014; Muñoz et al., 2011; Signor & Cerri, 2013). Additionally, soil temperature, pH and available soil carbon, which vary with slope position, soil texture and land-use (Gregorich et al, 1998), also influence the production of N_2O. For example, the amount of labile C was found to be positively correlated with the N_2/N_2O ratio (Weier et al. 1993), which in turn can also affect the amount of N_2O emitted from soils.

Our objectives were to assess GHG fluxes in controlled incubation experiments of intact soil cores from diverse soil texture classes taken from different land-uses, slope positions, and with various land-use histories at 3 water holding capacities. More specifically, we addressed the following research questions (RQ):

1. To what extent do slope position, soil textural class, and topography affect the soil N_2O, CO_2 and CH_4 flux potential (i.e. the maximum N_2O flux from the soil cores incubated at an optimal WHC) in the study area?
2. Does time since conversion (from natural forests to agricultural land-use) affect the soil N_2O, CO_2 and CH_4 flux potential?

2. Materials and Methods

2.1. Study area

This research was conducted at the Climate Change Agriculture and Food Security (CCAFS) Research Program benchmark site of Rakai, located in Southern Uganda, represented by a 10 km by 10 km area with the center located at latitude -0.667, longitude 31.437. The annual precipitation pattern at Rakai is bimodal with the "short rains" occurring between March and May, and the "long rains" between September and December. Average annual rainfall for the periods 1963 to 1975 and 1999 to 2005 was 1039 mm (Orlove et al., 2010) and the average annual temperature was 21.5°C (Lufafa et al., 2003). This landscape is typical for much of the East Africa highlands, characterized by undulating flat hilltops and numerous elongated hills with valley bottom swamps, including stream wetlands (Langlands, 1964).

Smallholder agriculture dominates the landscapes of the study region, with the farming system classified as "Banana-robusta coffee farming" due to its main cash crops (Taylor et al., 2011). Maize is grown as a secondary cash crop and for domestic consumption. Root crops and several annual or biennial food crops such as beans, sweet potatoes and cassava are also commonly grown (Silvestri et al., 2015). Banana-based farming systems are typical for much of the highlands of Uganda, western Kenya, Tanzania, Rwanda, Burundi and East Democratic Republic of Congo (Van Asten et al., 2004). Besides cropping as an agricultural activity, farmers also keep cattle, goats, and poultry, although typically in small numbers (Silvestri et al., 2015, Kristjanson et al., 2012). Use of external nutrient inputs is low and limited to mulch and manure in 20% and 7% of the banana fields, respectively (Silvestri et al., 2015). Use of external nutrient inputs in other crops is also insignificant (Silvestri et al., 2015).

2.2. Soil types

The soils typically originate from shales and phyllites in the upland areas, although quartz mica and mica schists are common parent materials for the upland soils in the eastern part of the study area. In the lowland areas around lakes, soils are rich in organic matter (FAO, 2009). The majority of soils in the region are Acrisols and Ferralsols with Leptosols on hill tops, while Gleysols are found in valleys and depressions adjacent to wetlands and open water bodies (FAO, 2009). Because the information on soils distribution within the specific study area was rather limited, indigenous knowledge was used for mapping the distribution of farmer-defined soil types in the study area (Gowing et al., 2004; Payton et al., 2003; Macharia, 2005). Three key informants, (i.e. local people who are knowledgeable about soils), characterized the soils at the village scale, which resulted in the identification of five soil types. We then verified the classification by ground-truthing the soil distribution along with local experts. Three of the identified soils were classified as Acrisols but differed in texture of the top layer as follows: clay, sandy clay loam, and silty clay loams with the first two textures the most common in the study area. The fourth type, Leptosols, was widespread on the upper and top slope positions of the landscape, while the fifth soils were the Gleysols in wetlands.

2.3. Mapping of land-use and land cover

To characterize land-use and land cover, World-view 2 images (0.5 cm spatial resolution, 0% cloud cover, taken in July 2013) with 8-band multi-spectral data were selected. In addition to the original spectral bands, the normalized difference vegetation index (NDVI) was calculated as difference between near infra-red (NIR) and visible (VIS) reflectance values over the sum of the two (Rouse Jr et al., 1974). NDVI was used to enhance the differences between vegetated and non-vegetated surfaces as well as for partitioning of different vegetation densities. In addition, wavelet-based texture information was added to the spectral bands and NDVI to aid in identification of some classes that are best distinguished based on texture (Roach & Fung, 1994; Zhu & Yang, 1998). Principal component analysis (PCA) was used to condense the information into three uncorrelated principal components (PC) (Swan et al., 1995). The Mean Shift algorithm Comaniciu &Meer, 2002) then was run on the three PC to produce image-objects; groups of connected pixels that share common properties (i.e. low intra-object variability) while being different from neighboring objects. Since our main focus was on agricultural land-use, particular attention was paid to correctly delineate field boundaries. The RF-classifier algorithm (Breiman, 2001) was used to assign features of a given image-object to one of the 16 user-specified land cover classes. Land cover classes were ground-truthed by resampling 50 points of each of the 16 classes; these were further merged into 7 classes (Table 1). The overall classification accuracy was 80%. Table 1 shows the respective areas of land-uses from the classification.

2.4. Sampling sites selection

We conducted two different laboratory experiments to address each of the research questions, each from a different research site (R1 and R2).

- To study the effects of land-use (LU), soil texture and slope position on GHG flux potentials (R1), we selected sites from three land-uses and two dominant soils that differed in texture (clay and sandy clay loam Acrisols) along two slope positions (lower and mid slope). The LU included (i) perennial crops (coffee-banana intercrop or banana plantation), (ii) annual crops (maize and bean intercrops were dominant, but sorghum and potatoes also occurred), and (iii) eucalyptus plantations. These land-uses formed the major part of the agricultural landscape (Table 1), with our sampling locations distributed across the study area. The lower and mid slope positions were selected because most agricultural activities are focused there. Soils on the upper slope positions are typically shallow and rich in gravel, so they are rarely used for agriculture.
- To study the effects of land-use history on soil GHG flux potentials (R2), soil sampling focused on a small patch of approximately 4.5 ha of remaining natural forest in the study area. This area was selected as a control in order to assess the effect of time since

conversion. We also sampled four fields adjacent to the forest that had been converted to agriculture either 3 or 50 years ago and are currently planted with banana (3 yr + 50 yr) or maize (3 yr and 50 yr). However, the maize field of 50 yr had been left fallow for the previous two years.

2.5. Soil core sampling

Seventeen landscape units (land-use and or combinations of soil and landscape position) were randomly selected, with each type being replicated 3 to 10 times to address R1 and R2. The number of replicates used was related to how common each land use was in the area. We sampled 74 and 22 points for R1 and R2 respectively (Fig.1, Table 2). At each point, the actual farming practice was recorded and farmers were interviewed to obtain information on organic and inorganic fertilizer use, field management and years since conversion from natural vegetation. Fifteen intact soil cores were taken at three points along a transect spanning the site (e.g. a farmers' field or a forest patch). Intact soil core sampling was done using PVC-cylinders (5 cm diameter ID, 5 cm height) with the bottom edge sharpened. After careful removal of the organic layers, these cylinders were pushed into the mineral soil, carefully removed, sealed with Parafilm©, placed in a cooled insulated box and transported within 2 days to the soil and greenhouse gas laboratory of the Mazingira House at the International Livestock Research Institute (ILRI), Nairobi. In addition, a soil sample (5 cm depth) was taken adjacent to each of the three points where the soil cores were taken, and these three additional samples were thoroughly mixed to obtain a composite soil sample for each landscape unit. The composite soil samples were used for determination of pH, texture, total carbon and total nitrogen.

2.6. Soil characterization and treatment

Soil pH was determined in 1:2.5 soil–water slurry using a glass electrode (Jackson, 1958). Soil organic carbon (SOC) and total nitrogen content (TN) were determined on finely grounded air-dried soils by an elemental combustion system (ECS 4010, Costech Instruments, Italy). Because the soils were taken from the top 5 cm and were acidic with a pH < 7 (Table 2), we assumed that there were no carbonates and that the soil organic carbon (SOC) was equal to the total carbon (TC). Out of the 15 soil cores per sampling site, three soil cores were oven dried at 105^{o}C for 24 hours to determine bulk density. The remaining 12 cores were air dried at 30°C for a period of three days. Three of the air-dried soil cores were used to determine the maximum water holding capacity (WHC) (Gardner, 1986). The remaining nine cores were divided into 3 sets and each set was rewetted to a specified level of water holding capacity (30, 55 or 80%) by adding the appropriate amount of distilled, deionized water. These water contents were used for all cores because previous studies in the Lake Victoria region have found that soil moisture often ranges between these values, that there is typically no differences in water-filled pore space (WFPS) between land uses and that peak N_2O emissions tend to occur at soil moisture contents between 55 and 80% WFPS (Pelster et al., 2017; Wanyama et al., 2018).

2.7. Determination of soil greenhouse gas production

To estimate GHG flux rates at different soil moisture contents, the soil cores mentioned above were placed in glass vessels (volume= 847 cm^3) and incubated at 20.5°C in a Lovibond Thermostatic Chamber (Dortmund, Germany). At each sampling time, the lid of the glass vessel was screwed on tightly to ensure the vessel was gas tight. Gas sampling from the headspace of the vessel was done immediately and then after 15, 30 and 45 minutes, via a septum placed in the lid. The gas samples were immediately injected into a gas chromatograph equipped with a ^{63}Ni electron capture detector and a flame ionization detector (GC, SRI 8610C) for analyses of N_2O, CH_4 and CO_2 (using a methanizer) as described by Schindlbacher et al. (2004). The GC system was calibrated several times per day using standard gas mixtures (Linde Gas, Germany). The GC minimum flux detection limits (Parkin et al. 2012) were 0.04 mg CH_4-C m^{-2} h^{-1} for CH_4, 0.07 mg CO_2-C m^{-2} h^{-1} for CO_2 and 0.02 μg N_2O-N m^{-2} h^{-1} for N_2O given a 45 minutes sampling period.

Production/consumption rates of N_2O, CH_4 and CO_2 were calculated from linear changes in headspace gas concentrations over time (0, 15, 30 and 45 minutes) following the gas-tight closure of the vessels. Less than 2% of the headspace was removed for sampling, so no adjustments were made to account for any reductions in headspace pressure with sample withdrawal. GHG flux rates of the three individual cores from each site were first measured under air-dried conditions twice before wetting (none of the GHG fluxes were significantly different from zero). Thereafter, each set of cores was rewetted by addition of distilled/deionized water until a target WHC level (30, 55 and 80%) was reached. We used these water contents because as mentioned earlier, aerobic processes tend to be maximized at around 55% (Howard & Howard, 1993), while denitrification tends to peak at approximately 80% WHC (Bollman & Conrad 1998). This should allow the greatest chance of detecting meaningful differences between the flux potentials of the different land-uses, soil types and slope positions.

GHG production rates were measured at 4, 24 and 48 hours following re-wetting. Soil moisture contents were maintained throughout the experiment by weighing vessels daily and, if needed, adding appropriate amounts of distilled water at least 3 hours prior to taking flux measurements. Cumulative gas fluxes were calculated by integrating the area of all measurement points for the 48-hour period following rewetting.

2.8. Data analysis

Data were analyzed using R 3.0.3 (R Core Team). The fixed effects of land-use, soil type and slope position on potential fluxes were tested using analysis of variance (ANOVA). We used Type III sums of squares because the sample sizes were not the same across the treatment combinations. The analysis was done separately for each WHC. Cumulative GHG fluxes for the 48h period were Log_{10} transformed or Box-Cox transformed where necessary to approximate a normal distribution. The residual plots of the ANOVA model were used to test for homogeneity of variance. Comparisons between means were made using Tukey HSD on the fitted model. Pearson's correlation was used on transformed data to test for relationships between cumulative fluxes and soil properties.

3. Results

3.1. Soil properties

For soils sampled to address research question R1, SOC and TN concentrations were lowest in fields under annual cropping and highest in fields under perennial cropping and eucalyptus plantations (Table 2). There were large differences in SOC and TN concentrations between the different soil textures. The mean (± SE) SOC concentrations were $3.07 \pm 0.31\%$ and $1.99 \pm 0.28\%$ for the clay and sandy clay loam soils respectively, and mean TN concentrations were $0.26 \pm 0.05\%$ and $0.15 \pm 0.02\%$ for the clay and sandy clay loams, respectively. Soil pH ranged from slightly acidic to strongly acidic, with lowest values (between pH 4.3 to 4.8) found in the eucalyptus plantations (Table 2). Unlike land-use and soil texture, slope position had no effect on soil parameters. The C:N ratios ranged from 11.4 to 15.7; the highest was found in soils from eucalyptus plantations.

For R2, the soil textural class was solely silty clay loam with clay contents ranging from 31 to 39% (Table 2). The highest SOC and TN concentrations were found at the natural forest site. Soil pH ranged from 5.6 to 6.4 while C:N ratio varied from 10.9 to 12.1.

3.2. Soil N_2O and CO_2 fluxes from different landscape units (R1)

Cumulative N_2O fluxes from the intact soil cores varied across soil water content, land-uses and soil textural classes. For all sampling sites, N_2O fluxes at 80% WHC were at least one order of magnitude higher than fluxes from soils at 55% and 30% WHC (80% WHC:11.0±1.2, 55% WHC: 0.8±0.2, and 30% WHC: 0.2±0.0 mg N_2O-N m^{-2} 48 h^{-1}). Land-use had an effect on N_2O fluxes at all WHC ($P<0.001$). At 80% WHC N_2O fluxes were highest from soils from perennial crops ($P<0.001$), while fluxes from eucalyptus plantations were similar to those from annual crops (Fig. 2). At 55% WHC, N_2O fluxes from soils under perennial crops were higher than from under annual crops under both soil textural classes ($P<0.001$, Fig. 2). However, soil N_2O fluxes from eucalyptus plantations were similar to fluxes from annual crops for the sandy clay loam soils but not for the clay soils showing an interaction between the soil texture and land-use ($P=0.013$, Fig. 2). The fluxes from clay soils were higher than the fluxes from the sandy clay loam at both 80% ($P=0.041$) and 55% WHC ($P<0.001$; Table 3).

Mean cumulative CO_2 fluxes during the 48 h post re-wetting period across all land-uses ranged from 0.7 to 3.2 g CO_2–Cm^{-2} 48 h^{-1} (Fig. 3). Cumulative soil CO_2 fluxes were similar for soils re-wetted to 80% and 55% ($P=0.91$) WHC and lowest from soils incubated at 30% WHC ($P<0.001$). Cumulative soil CO_2 fluxes from eucalyptus soils were greater than soils from annual and perennial crops at 80% WHC ($P<0.001$), while at 55% WHC eucalyptus plantation and perennial crops fluxes were similar ($P=0.056$, Fig.3). Cumulative CO_2 fluxes from annual crops were lower than those from eucalyptus plantations ($P<0.001$) and perennial crops ($P<0.001$). Slope position and soil texture did not affect CO_2 fluxes from soils at either 55 or 80% WHC (Table 3). However, when the soils were incubated at 30% WHC, the CO_2 fluxes were higher for the sandy clay loam soils than for clay soils (*P* = 0.004, Fig. 3). At all WHC, the effect of land-use was consistent, with higher fluxes from eucalyptus plantations (1361±209 g CO_2–Cm^{-2} 48 h^{-1}) followed by perennial crops (1044±148.4 g CO_2 –Cm^{-2} 48 h^{-1}) and the lowest fluxes from annual crops (708.4±61.4 g CO_2 –Cm^{-2} 48 h^{-1}).

3.3. Effect of conversion age on soil N_2O and CO_2fluxes from agricultural land-uses (R2)

Conversion from natural forest to agricultural land resulted in a reduction (*P*<0.001, Table 4) of cumulative N_2O fluxes regardless of land-use type (annual/ perennial cropping system) at 55% and 80% WHC. At all soil moisture levels, cumulative N_2O fluxes from soil cores taken from the natural forest sites were at least 50% higher than cumulative N_2O fluxes observed for soils from annual or perennial cropping systems (Fig. 4). The highest N_2O fluxes were observed with soil moisture of 80% WHC, exceeding those observed at 55% WHC by at least one order of magnitude (Fig. 4). Time since conversion had an effect on the fluxes at 80% WHC (*P*=0.031, Table 4); with lower N_2O fluxes from recently (3 years or less) converted fields (*P*=0.031) than agricultural sites that had been converted from forest 50 years ago (Table 4).

At all soil moisture levels, soils from natural forest sites showed greater (at least 40% higher) CO_2 fluxes compared to soils from annual or perennial crops (*P*<0.001, Fig. 5). Soil CO_2 fluxes were not affected by land-use (annual *versus* perennial crops) nor by time since conversion. Fluxes were however, affected by WHC, with the highest emissions at 80% WHC and the lowest at 30% WHC (*P*<0.001, Table 4, Fig. 5).

3.4. Soil CH4 fluxes

Methane fluxes from all upland sites, irrespective of land-use, were not significantly different from zero (*P*>0.05). Cumulative CH_4 fluxes were also close to zero and mostly below the detection limit.

3.5. Relationship between cumulative GHG fluxes and soil properties

For all sites and soil moisture levels, TN and SOC were always positively correlated with cumulative CO_2 fluxes. Similarly, soil TN and SOC were positively correlated with cumulative N_2O fluxes for the sites sampled for R1 and R2, with the exception of R1 at 30% WHC. Soil cumulative N_2O fluxes were positively correlated (*P*<0.001) with soil pH for R1 only (Table 5).

Still, for R1 a significant relationship ($P<0.05$) between soil pH and CO_2 fluxes was observed. Soil BD was negatively correlated with both N_2O and CO_2 fluxes at R2 sites.

4. Discussion

Land-use and soil type effects on N_2O and CO_2 fluxes

In the banana-based systems of East Africa, a common perennial system in our study area, farmers retain banana residues and transfer large amounts of organic matter (i.e. manure, the residues from annual crops and organic home refuse) to these plots (Briggs & Twomlow, 2002; Silvestri et al., 2015), which results in a large accumulation of C and N in the soil. Banana plots are subjected to relatively low soil disturbance, which can stimulate further accumulation of C and N in the topsoil (Table 2; Gál et al., 2007). Banana residues, organic home refuse and mulches typically have a low C:N ratio and therefore show high rates of decomposition (Raphael et al., 2012). Therefore, this accumulation of residues with low C:N ratio could result in greater mineralization rates in the soils under the perennial crops, providing additional substrate to both nitrifiers and denitrifiers, which would result in the higher soil N_2O fluxes from perennial crops than annual crops.

Soil N_2O fluxes from perennial crops were higher than fluxes from eucalyptus plantations even though they had similar TN and SOC concentrations. However, the soil pH was lower ($P<0.001$) in the eucalyptus stands (4.3 ± 0.16) compared to the perennial crops (6.4 ± 0.12). Zaman et al. (2012) found that the suitable pH range for nitrification and denitrification is 5 to 8, below which N_2O production is hampered. We found soil pH ranging from 3.9 to 6.7 positively correlated with the N_2O fluxes ($P<0.001$, Table 5). Thus the lower soil pH of eucalyptus plantations (Table 2) likely influenced a lower production of N_2O fluxes.

Lower N_2O fluxes for the sandy clay loam soils than for the clay soils at 55% and 80% WHC were likely associated with lower soil TN and SOC concentrations in the coarser sandy soil (Table 2), as those two soil properties were positively correlated with N_2O fluxes (Table 5). Coarser soils tend to have higher gas diffusivity rates, which decreases the proportion of soil anaerobic microsites (Balaine et al. 2013), leading to less denitrification. We also found an interaction between land-use and soil texture at 55% where N_2O from annual and eucalyptus land-use were the same under sandy clay loams but different under clay soils. Rochette et al. (2008)

reported such an interaction between soil texture and N_2O fluxes. In our case, the additional clay content of the clay soils may have reduced oxygen entry into and diffusivity within the soil (Balaine et al., 2013), while the higher SOC content would have increased the oxygen demand through increased microbial activity. The expected increase in soil microbial activity and reduced gas diffusivity of the clay soils at 55% WHC likely reduced soil oxygen supply leading to the creation of more anaerobic microsites where denitrification could proceed. The lower C content and greater diffusivity of the sandy clay loam soils at 55% WHC likely did not result in sufficient anaerobiosis for denitrification to occur. However, these differences in diffusivity and oxygen demand would be less of a constraint at 80% WHC when both soils would have had sufficient anaerobic conditions.

We expected to measure greater soil N_2O and CO_2 fluxes from the lower landscape positions as previous studies found higher soil N_2O and CO_2 fluxes in lower landscape positions compared to hilltops or mid-slope positions, likely due to higher soil moisture and higher carbon and nutrient depositions (Braun et al., 2013; Negassa et al., 2015, Arias-Navarro et al. 2017). The lack of an effect of slope position on fluxes in our study could be attributed to low soil erosion/ deposition of soil nutrients given the low slope gradient among the slope positions that we studied (mid-slope = 11% and lower slope = 8%), which resulted in no difference in SOC and TN (Table 2).

We also expected the greatest CO_2 fluxes to be measured in the soils of the perennial crops because the mulch, livestock manure and kitchen wastes that farmers put on these soils should be highly labile. Fine roots and leaf litter decomposition rates in eucalyptus plantations tend to be lower than in other vegetation types such as annual and perennial crops (Lemma et al., 2007; Louzada et al., 1997). However, we did not find differences in CO_2 fluxes between eucalyptus plantations and perennial crops at either 30% or 55% WHC; while at 80% WHC the greatest CO_2 fluxes came from the soils of the eucalyptus plantations (Fig. 2). Therefore it is possible that the mulch added to the perennial crops may not be as labile as initially thought. However, the farmers tend to pile the mulch on the soil surface rather than incorporating the mulch into the soils, so much of the labile C in the mulch will be consumed by the microbial community within the mulch itself. As we removed the mulch when collecting the soil cores, the C that was left in our incubations, according to the Microbial Efficiency-Matrix Stabilization framework, would tend to be the more stable microbial products (Cotrufo et al., 2013) that had leached into the underlying soils from the mulch above.

Soil N_2O fluxes can be constrained by the availability of inorganic-N substrate for the microbial processes of nitrification and denitrification as well as the availability of labile organic carbon, which acts as an electron donor during the denitrification process (Swerts et al., 1996). Previous studies have suggested that traditional farming methods i.e. continual cropping with no or low inputs have led to N depletion in most farming systems in Africa (Chianu et al., 2012; Sanchez, 2002; Zhou et al., 2014). The average mineral fertilizer use on arable land for the study area in 2011 was less than 1 kg mineral fertilizer per ha^{-1} yr^{1} (Silvestri et al., 2015), and among the plots we sampled, only one farmer applied fertilizer (Di-ammonium phosphate) during the previous growing season. The low application rates of organic manure are insufficient to compensate for environmental N losses (leaching, gaseous) and N removal through crop harvests (Bekunda et al., 2004). Zhou et al.(2014) found that soil N mining (i.e. N removed or lost from the site without being replaced) averaged approximately 20 kg N ha^{-1} yr^{-1} for the Lake Victoria basin, where our study site at Rakai is located. Similarly, negative soil N balances have been reported for other farming systems in Uganda (Ebanyat et al., 2010; Wortmann and Kaizzi, 1998) and elsewhere in sub-Saharan Africa (Chianu et al., 2012). Since mineralized N has previously been correlated with total soil N (Cornfield, 1952; Winsor & Pollard, 1956), it is likely that, similar to the *in situ* measurements by Pelster et al. (2017), the low N_2O fluxes from the annual crops were at least partially caused by low soil inorganic-N concentrations.

4.1. CH_4 fluxes

Methane fluxes could not be detected as most measurements were below the detection limit in all the upland soils. Methane oxidation and production occur concurrently in upland soils by methanotrophic and methanogenic bacteria, though uptake has been shown to dominate under dry and low soil moisture conditions (Smith et al., 2000). Management practices such as cultivation have been shown to have a long-term negative impact on CH_4 uptake (Jacinthe et al., 2014; Priemé et al., 1997; Ussiri et al., 2009) as a result of the destruction of soil structure causing less favorable micro-environment for methanotrophic bacteria. However, in our study we used only the top 5 cm, while methane uptake and production occurs mainly in deeper soil layers (Hütsch, 1998; Saari et al., 1997; Whalen et al., 1992), which is likely the reason why we measured no methane fluxes.

4.2. Land-use history effects on GHG fluxes

Natural forests had higher N_2O and CO_2 fluxes than perennial and annual crops. Natural forests also had higher SOC and TN compared to crops (Table 2), which were highly correlated with N_2O and CO_2 fluxes (Table5). Reductions in the SOC and TN pools are associated with decreased litterfall (Yang et al., 2007). Management practices such as burning and tillage during land clearing result in loss of SOC and TN stocks (Davidson &Ackerman, 1993; Ma et al., 2004; Post &Mann, 1990), that together with crop nutrient mining lead to negative nutrient balances (Ebanyat et al., 2010; Zhou et al., 2014). The effect of land conversion for N_2O fluxes was largest at 80% WHC ($P<0.001$), with the highest flux reductions for recently converted annual cropping sites (approximately 3 years) compared to sites managed at least 50 years for both annual and perennial cropping. For soil CO_2, there was no difference between long- and short-term conversion histories. We hypothesize that the lower N_2O fluxes from recently converted land was related to field management as sites converted several decades ago are most likely those sites that were most suitable for agriculture and closer to the homestead where they may receive more nutrient inputs such as home wastes (Tittonell et al., 2013). Additionally, for sites to be productive over long periods, farmers manage soil fertility through traditional means like adding animal manure. In contrast, recently converted natural forest might already have been degraded bushland (due to exploitation for firewood), coupled with high nutrient stock turnover due to bush burning and tillage during land clearing.

5. Conclusions

This is one of a first studies analyzing effects of landscape position, land-use, and soil texture on the soil GHG fluxes in East Africa. Spatial variability of GHG fluxes in this system was high with land-use and soil texture as important factors driving this variability. Among the converted land-uses for research question 1, perennial crops exhibited the highest soil N_2O and CO_2 fluxes followed by eucalyptus plantation, while the lowest fluxes were measured in soils from annual crops. However, given that the area occupied by annual crops is twice that of perennial crops, the contribution of annual cropping systems to soil fluxes at the landscape-scale may surpass that of the soils under eucalyptus and equate that of perennial crops. It is important to note however, that these are soil fluxes from incubated soil cores. Hence, these findings need to be considered carefully as they do not include previous gaseous losses (i.e. did the converted land lose most of the C and N in the years before we sampled), nor do incubation studies include information on CO_2 sequestration in plant biomass via photosynthesis. Further *in situ* studies are recommended to address these questions. Converted land-uses showed reduced fluxes compared to natural forest. As a previous study in the region found a correlation between emissions from soil core incubations and annual field emissions (Pelster et al. 2017), we believe that our results also resemble the relative rankings of *in situ* annual fluxes, suggesting that the soils under perennial crops are the most likely to be GHG flux hotspots. However, this needs to be confirmed through measurement of *in situ* GHG fluxes in the region.

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References

Altieri, M. A., and P. Koohafkan (2008), Enduring farms: Climate change, smallholders and traditional farming communities, Third World Network, Environment and Development series No. 6, Penang, Malaysia, 63 pp.

Arias-Navarro, C., Díaz-Pinés, E., Klatt, S., Brandt, P., Rufino, M.C., Butterbach-Bahl, K., and L.V. Verchot (2017), Spatial variability of soil N_2O and CO_2 fluxes in different topographic positions in a tropical montane forest in Kenya,*Journal of Geophysical Research: Biogeosciences* 122(3): 514-527.

Baggs, E., and L. Philippot (2010), Microbial terrestrial pathways to nitrous oxide, in K.A. Smith (Ed), *Nitrous oxide and climate change*, (256 pp. 4-35). London: Earthscan Ltd.

Balaine, N., T. J. Clough, M. H. Beare, S. M. Thomas, E. D. Meenken, and J. G. Ross (2013), Changes in relative gas diffusivity explain soil nitrous oxide flux dynamics, *Soil Science Society of America Journal*, 77(5), 1496-1505.

Beddington, J., M. Asaduzzaman, M. Clark, A. F. Bremauntz, M. Guillou, D. Howlett, M. Jahn, E. Lin, T. Mamo, and C. Negra (2012), What next for agriculture after Durban, *Science*, *335*(6066), 289-290.

Bekunda, M., E. Nkonya, D. Mugendi, and J. Msaky (2004), Soil fertility status, management, and research in East Africa, *East African Journal of Rural Development*, *20*(1), 94-112.

Bollmann, A., and R. Conrad (1998), Influence of O2 availability on NO and N_2O release by nitrification and denitrification in soils, *Global Change Biology, 4*(4), 387-396.

Bowden, R. D., K. M. Newkirk, and G. M. Rullo (1998), Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions, *Soil Biology and Biochemistry*, *30*(12), 1591-1597.

Braun, M., Y. Bai, B. McConkey, R. Farrell, J. Romo, and D. Pennock (2013), Greenhouse gas flux in a temperate grassland as affected by landform and disturbance, *Landscape Ecology*, *28*(4), 709-723.

Breiman, L. (2001), Random forests, *Machine learning*, *45*(1), 5-32.

Briggs, L., and S. Twomlow (2002), Organic material flows within a smallholder highland farming system of South West Uganda, *Agriculture, Ecosystems & Environment*, *89*(3), 191-212.

Butterbach-Bahl, K., E. M. Baggs, M. Dannenmann, R. Kiese, and S. Zechmeister-Boltenstern (2013), Nitrous oxide emissions from soils: how well do we understand the processes and their controls?, *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1621), 20130122.

Carter, S. E., and H. K. Murwira (1995), Spatial variability in soil fertility management and crop response in Mutoko Communal Area, Zimbabwe, *Ambio*, 24, 77-84.

Chianu, J. N., J. N. Chianu, and F. Mairura (2012), Mineral fertilizers in the farming systems of sub-Saharan Africa. A review, *Agronomy for Sustainable Development*, *32*(2), 545-566.

Comaniciu, D., and P. Meer (2002), Mean shift: A robust approach toward feature space analysis, *IEEE Transactions on pattern analysis and machine intelligence*, *24*(5), 603-619.

Cornfield, A. H. (1952), The mineralization of the nitrogen of soils during incubation: Influence of pH, total nitrogen and organic carbon contents, *Journal of the Science of Food and Agriculture*, 3(8), 343-349.

Cotrufo, M. F., M. D. Wallenstein, C. M. Boot, K. Denef, and E. Paul (2013), The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology, 19*, 988-995.

Davidson, E. A., and I. L. Ackerman (1993), Changes in soil carbon inventories following cultivation of previously untilled soils, *Biogeochemistry*, *20*(3), 161-193.

Davidson, E. A., M. Keller, H. E. Erickson, L. V. Verchot, and E. Veldkamp (2000), Testing a conceptual model of soil emissions of nitrous and nitric oxides, *BioScience*, *50*(8), 667-680.

Davidson, E. A., (1991), Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in J. Rogers and W. B. Whitman (Eds), *Microbial production and consumption of greenhouse gases, (*pp 219-235). Washington DC: American Society for Microbiology.

DeFries, R., and C. Rosenzweig (2010), Toward a whole-landscape approach for sustainable land use in the tropics, *Proceedings of the National Academy of Sciences*, *107*(46), 19627-19632.

Don, A., J. Schumacher, and A. Freibauer (2011), Impact of tropical land‐use change on soil organic carbon stocks–a meta‐analysis, *Global Change Biology*, *17*(4), 1658-1670.

Ebanyat, P., N. de Ridder, A. De Jager, R. J. Delve, M. A. Bekunda, and K. E. Giller (2010), Drivers of land use change and household determinants of sustainability in smallholder farming systems of Eastern Uganda, *Population and Environment*, *31*(6), 474-506.

FAO (2009), Harmonized World Soil Database (version 1.1). FAO, Rome, Italy.

Firestone, M. K., and E. A. Davidson (1989), Microbiological basis of NO and N_2O production and consumption in soil, *Exchange of trace gases between terrestrial ecosystems and the atmosphere*, *47*, 7-21.

Gál, A., T. J. Vyn, E. Michéli, E. J. Kladivko, and W. W. McFee (2007), Soil carbon and nitrogen accumulation with long-term no-till versus moldboard plowing overestimated with tilled-zone sampling depths, *Soil and Tillage Research*, *96*(1), 42-51.

García‐Marco, S., S. Ravella, D. Chadwick, A. Vallejo, A. Gregory, and L. Cárdenas (2014), Ranking factors affecting emissions of GHG from incubated agricultural soils, *European journal of soil science*, *65*(4), 573-583.

Gardner, W. H., (1986), Water content, in A. Klute (Ed) *Methods of soil analysis. Part 1. Physical and mineralogical methods*, (pp 493-544). Madison, USA: Soil Science Society of America.

Gibbs, H. K., A. Ruesch, F. Achard, M. Clayton, P. Holmgren, N. Ramankutty, and J. Foley (2010), Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s, *Proceedings of the National Academy of Sciences*, *107*(38), 16732-16737.

Giller, K., P. Tittonell, M. C. Rufino, M. Van Wijk, S. Zingore, P. Mapfumo, S. Adjei-Nsiah, M. Herrero, R. Chikowo, and M. Corbeels (2011), Communicating complexity: Integrated assessment of trade-offs concerning soil fertility management within African farming systems to support innovation and development, *Agricultural Systems*, *104*(2), 191-203.

Gowing, J., R. Payton, and M. Tenywa (2004), Integrating indigenous and scientific knowledge on soils: recent experiences in Uganda and Tanzania and their relevance to participatory land use planning, *Uganda Journal of Agricultural Sciences*, *9*(1), 184-191.

Gregorich, E.G., K. J. Greer, D. W. Anderson, and B. C. Liang (1998), Carbon distribution and losses: erosion and deposition effects, *Soil & Tillage Research*, 47, 291-302.

Howard, D. M., and P. J. A. Howard (1993), Relationships between CO_2 evolution, moisture content and temperatures for a range of soil types, *Soil Biology and Biochemistry*, *25*(11), 1537-1546.

Hütsch, B. (1998), Tillage and land use effects on methane oxidation rates and their vertical profiles in soil, *Biology and Fertility of Soils*, *27*(3), 284-292.

IPCC (2014), Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jacinthe, P.-A., W. A. Dick, R. Lal, R. K. Shrestha, and S. Bilen (2014), Effects of no-till duration on the methane oxidation capacity of Alfisols, *Biology and Fertility of Soils*, *50*(3), 477-486.

Jackson, M.L. (1958), Soil Chemical Analysis. 2nd Edition, Baton Rouge, FL, USA, CRC Press.

Kim, D.-G., A. D. Thomas, D. Pelster, T. S. Rosenstock, and A. Sanz-Cobena (2016), Greenhouse gas emissions fromnatural ecosystems and agricultural lands in sub-Saharan Africa: synthesis of available data and suggestions for further studies, *Biogeosciences*, *13*, 4789-4809.

Kristjanson, P., H. Neufeldt, A. Gassner, J. Mango, F. B. Kyazze, S. Desta, G. Sayula, B. Thiede, W. Forch, P. K. Thornton, and R. Coe (2012), Are food insecure smallholder households making changes in their farming practices? Evidence from East Africa, *Food Security*, 4(3), 381-397.

Langlands, B. (1964), East African landscapes and the study of physical geography, *East African Geographical Review*, *1964*(2), 1-16.

Lemma, B., I. Nilsson, D. B. Kleja, M. Olsson, and H. Knicker (2007), Decomposition and substrate quality of leaf litters and fine roots from three exotic plantations and a native forest in the southwestern highlands of Ethiopia, *Soil Biology and Biochemistry*, *39*(9), 2317-2328, doi:http://dx.doi.org/10.1016/j.soilbio.2007.03.032.

Linn, D., and J. Doran (1984), Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils, *Soil Science Society of America Journal*, *48*(6), 1267-1272.

Louzada, J. N. C., J. Schoereder, and P. De Marco (1997), Litter decomposition in semideciduous forest and Eucalyptus spp. crop in Brazil: a comparison, *Forest Ecology and Management*, *94*(1), 31-36.

Lufafa, A., M. Tenywa, M. Isabirye, M. Majaliwa, and P. Woomer (2003), Prediction of soil erosion in a Lake Victoria basin catchment using a GIS-based Universal Soil Loss model, *Agricultural Systems*, *76*(3), 883-894.

Ma, S., J. Chen, M. North, H. E. Erickson, M. Bresee, and J. Le Moine (2004), Short-term effects of experimental burning and thinning on soil respiration in an old-growth, mixed-conifer forest, *Environmental Management*, *33*(1), S148-S159.

Macharia, P. (2005), Integrating indigenous soil and land classification systems in the identification of soil management constraints in the tropics: a Kenyan case study, *Tropical and Subtropical Agroecosystems*, *5*(2), 67-73.

Majaliwa, J., R. Twongyirwe, R. Nyenje, M. Oluka, B. Ongom, J. Sirike, D. Mfitumukiza, E. Azanga, R. Natumanya, and R. Mwerera (2010), The effect of land cover change on soil properties around Kibale National Park in South Western Uganda, *Applied and Environmental Soil Science*, *2010*.

Muñoz, C., L. Paulino, C. Monreal, and E. Zagal (2011), Greenhouse gas (CO_2 and N_2O) emissions from soils: A review, *Chilean Journal of Agricultural Research*, *70*(3), 485-497.

Negassa, W., R. F. Price, A. Basir, S. S. Snapp, and A. Kravchenko (2015), Cover crop and tillage systems effect on soil CO_2 and N_2O fluxes in contrasting topographic positions, *Soil and Tillage Research*, *154*, 64-74.

Okumu, M., P. Van Asten, E. Kahangi, S. Okech, J. Jefwa, and B. Vanlauwe (2011), Production gradients in smallholder banana (cv. Giant Cavendish) farms in Central Kenya, *Scientia Horticulturae*, *127*(4), 475-481.

Olander, L., E. Wollenberg, F. Tubiello, and M. Herold (2013), Advancing agricultural greenhouse gas quantification*, *Environmental Research Letters*, *8*(1), 011002.

Orlove, B., C. Roncoli, M. Kabugo, and A. Majugu (2010), Indigenous climate knowledge in southern Uganda: the multiple components of a dynamic regional system, *Climatic Change*, *100*(2), 243-265.

Parkin, T. B., R. T. Venterea, and S. K. Hargreaves (2012), Calculating the detection limits of chamber-based soil greenhouse gas flux measurements, *Journal of Environmental Quality*, 41(3), 705-715.

Payton, R., J. Barr, A. Martin, P. Sillitoe, J. Deckers, J. Gowing, N. Hatibu, S. Naseem, M. Tenywa, and M. Zuberi (2003), Contrasting approaches to integrating indigenous knowledge about soils and scientific soil survey in East Africa and Bangladesh, *Geoderma*, *111*(3), 355-386.

Pelster, D., M.C. Rufino, T. Rosenstock, J. Mango, G. Saiz, E. Diaz-Pines, G. Baldi, and K. Butterbach-Bahl. 2017. Smallholder farms in eastern African tropical highlands have low soil greenhouse gas fluxes. *Biogeosciences*, 14, 187-202.

Post, W. M., and L. Mann (1990), Changes in soil organic carbon and nitrogen as a result of cultivation, in A. F. Bouwman (Ed) *Soils and the greenhouse effect*, (pp 401-406). New York, John Wiley & Sons.

Priemé, A., S. Christensen, K. E. Dobbie, and K. A. Smith (1997), Slow increase in rate of methane oxidation in soils with time following land use change from arable agriculture to woodland, *Soil Biology and Biochemistry*, *29*(8), 1269-1273.

Raphael, L., J. Sierra, S. Recous, H. Ozier-Lafontaine, and L. Desfontaines (2012), Soil turnover of crop residues from the banana (Musa AAA cv. Petite-Naine) mother plant and simultaneous uptake by the daughter plant of released nitrogen, *European Journal of Agronomy*, *38*, 117-123.

Roach, D., and K. Fung (1994), Fractal-based textural descriptors for remotely sensed forestry data, *Canadian Journal of Remote Sensing*, *20*(1), 59-70.

Rochette, P., D. A. Angers, M. H. Chantigny, and N. Bertrand (2008), Nitrous oxide emissions respond differently to no-till in a loam and a heavy clay soil, *Soil Science Society of America Journal*, *72*(5), 1363-1369.

Rouse Jr, J. W., R. Haas, J. Schell, and D. Deering (1974), Monitoring vegetation systems in the Great Plains with ERTS.

Saari, A., P. Martikainen, A. Ferm, J. Ruuskanen, W. De Boer, S. Troelstra, and H. Laanbroek (1997), Methane oxidation in soil profiles of Dutch and Finnish coniferous forests with different soil texture and atmospheric nitrogen deposition, *Soil Biology and Biochemistry*, *29*(11), 1625-1632.

Sanchez, P. A. (2002), Soil fertility and hunger in Africa, *Science*, *295*(5562), 2019.

Schindlbacher, A., S. Zechmeister-Boltenstern, and K. Butterbach-Bahl (2004), Effects of soil moisture and temperature on NO, NO_2, and N_2O emissions from European forest soils, *Journal of Geophysical Research: Atmospheres (1984–2012)*, *109*(D17).

Scull, P., J. Franklin, O. Chadwick, and D. McArthur (2003), Predictive soil mapping: a review, *Progress in Physical Geography*, *27*(2), 171-197.

Signor, D., and C. E. P. Cerri (2013), Nitrous oxide emissions in agricultural soils: a review, *Pesquisa Agropecuária Tropical*, *43*(3), 322-338.

Silvestri, S., S. Douxchamps, P. Kristjanson, W. Förch, M. Radeny, I. Mutie, C. F. Quiros, M. Herrero, A. Ndungu, N. Ndiwa, J. Mango, L. Claessens, M. C. Rufino (2015) Households and food security: lessons from food secure households in East Africa, *Agriculture & Food Security*, 4, 23

Smith, K., K. Dobbie, B. Ball, L. Bakken, B. Sitaula, S. Hansen, R. Brumme, W. Borken, S. Christensen, and A. Priemé (2000), Oxidation of atmospheric methane in Northern European soils, comparison with other ecosystems, and uncertainties in the global terrestrial sink, *Global Change Biology*, *6*(7), 791-803.

Smith, P., M. Bustamante, H. Ahammad, H. Clark, H. Dong, E. Elsiddig, H. Haberl, R. Harper, J. House, and M. Jafari (2014), Agriculture, forestry and other land use (AFOLU), *Climate change*, 799-890.

Swan, A. R., M. Sandilands, and P. McCabe (1995).*Introduction to geological data analysis*.Oxford, U.K.: Blackwell Science ltd.

Swerts, M., R. Merckx, and K. Vlassak (1996), Denitrification, N_2-fixation and fermentation during anaerobic incubation of soils amended with glucose and nitrate, *Biology and Fertility of Soils*, *23*(3), 229-235.

Taylor, B., D. Bukenya, P. van Asten, D. Agol, A. Pain, and J. Seeley (2011) The impact of HIV on agricultural livelihoods in southern Uganda and the challenges of attribution, *Tropical Medicine & International Health*, 16(3), 324-333.

Tittonell, P., A. Muriuki, C. Klapwijk, K. Shepherd, R. Coe, and B. Vanlauwe (2013), Soil heterogeneity and soil fertility gradients in smallholder farms of the East African highlands, *Soil Science Society of America Journal*, *77*(2), 525-538.

Tittonell, P., A. Muriuki, K. D. Shepherd, D. Mugendi, K. Kaizzi, J. Okeyo, L. Verchot, R. Coe, and B. Vanlauwe (2010), The diversity of rural livelihoods and their influence on soil fertility in agricultural systems of East Africa–a typology of smallholder farms, *Agricultural Systems*, *103*(2), 83-97.

Tubiello, F. N., M. Salvatore, S. Rossi, A. Ferrara, N. Fitton, and P. Smith (2013), The FAOSTAT database of greenhouse gas emissions from agriculture, *Environmental Research Letters*, *8*(1), 015009.

Ussiri, D. A., R. Lal, and M. K. Jarecki (2009), Nitrous oxide and methane emissions from long-term tillage under a continuous corn cropping system in Ohio, *Soil and Tillage Research*, *104*(2), 247-255.

Van Asten, P., C. Gold, S. Okech, S. Gaidashova, W. Tushemereirwe, and D. De Waele (2004), Soil quality problems in East African banana systems and their relation with other yield loss factors, *InfoMusa*, *13*, 20-25.

Wanyama, I., D. E. Pelster, C. Arias-Navarro, K. Butterbach-Bahl, L. V. Verchot, and M. C. Rufino (2018),Management intensity controls soil N_2O fluxes in an Afromontane ecosystem, Science of the Total Environment, *624*, 769-780.

Weier, K. L., J. W. Doran, J. F. Power, and D. T. Walters (1993), Denitrification and the dinitrogen/nitrous oxide ratio as affected by soil water, available carbon and nitrate, *Soil Science Society of America Journal*, 57(1), 66-72.

Whalen, S. C., W. S. Reeburgh, and V. A. Barber (1992), Oxidation of methane in boreal forest soils: a comparison of seven measures, *Biogeochemistry*, *16*(3), 181-211.

Winsor, G. W., and A. G. Pollard (1956), Carbon‐nitrogen relationships in soil. IV. – Mineralization of carbon and nitrogen, *Journal of the Science of Food and Agriculture*, 7(9), 618-624.

Wortmann, C. S., and C. Kaizzi (1998), Nutrient balances and expected effects of alternative practices in farming systems of Uganda, *Agriculture, Ecosystems &Environment*, *71*(1), 115-129.

Yang, Y.-S., G.-S. Chen, J.-F. Guo, J.-S. Xie, and X.-G. Wang (2007), Soil respiration and carbon balance in a subtropical native forest and two managed plantations, *Plant Ecology*, *193*(1), 71-84.

Zaman, M., M. Nguyen, M. Šimek, S. Nawaz, M. Khan, M. Babar, and S. Zaman (2012), Emissions of nitrous oxide (N_2O) and di-nitrogen (N_2) from the agricultural landscapes, sources, sinks, and factors affecting N_2O and N_2 ratios, *Greenhouse Gases-Emission, Measurement and Management.(Ed. Guoxiang Liu)*, 1-32.

Zhou, M., P. Brandt, D. Pelster, M. C. Rufino, T. Robinson, and K. Butterbach-Bahl (2014), Regional nitrogen budget of the Lake Victoria Basin, East Africa: syntheses, uncertainties and perspectives, *Environmental Research Letters*, *9*(10), 105009.

Zhu, C., and X. Yang (1998), Study of remote sensing image texture analysis and classification using wavelet, *International Journal of Remote Sensing*, *19*(16), 3197-3203.

Table 1. Land-use coverage for the Rakai study area. See also Fig. 1

Land-use	**Area (ha)**	**Total area (%)**
Annual crops	3153	32.0
Perennial crops	1627	16.5
Eucalyptus plantations	331	3.4
Natural forest	7	0.1
Water body	220	2.2
Wetlands	336	3.4
Others	4173	42.4
Total Area	**9847**	**100.0**

Others: buildings and homesteads, non-arable lands, shrubs and roads

Table 2. Topsoil (0 – 5 cm) properties for the intact soil cores collected from different land-use, soil type and slope positions near Rakai, Uganda and used for the different incubation experiments

Soils	Slope position	Land-use	GPS coordinates		N	Time since conversion (yrs)	TC (%)	pH	TN (%)	BD (g cm^{-3})	C:N ratio	Clay (%)
			Lat.	Long.								
Research Site R1												
Sandy clay loam	L	Annual crops	-0.6311	31.4679[a]	7	>20	1.28±0.09d	4.5±0.1	0.09±0.01c	1.29±0.03a	12.9±0.1b	27±5
Sandy clay loam	M	Annual crops			8	>20	1.42±0.13d	5.4±0.2	0.12±0.01cd	1.28±0.04a	11.6±0.5c	26±3
Clay	L	Annual crops			5	>20	2.73±0.19b	5.8±0.2	0.24±0.02b	1.11±0.07cb	11.4±0.4c	43±2
Clay	M	Annual crops			6	>20	2.58±0.41b	5.7±0.2	0.22±0.03b	0.99±0.04c	11.5±0.2c	43±3
Sandy clay loam	L	Eucalyptus plantation			4	>20	2.42±0.99b	3.9±0.0	0.12±0.02c	1.16±0.04b	13.9±1.2b	24±3
Sandy clay loam	M	Eucalyptus plantation			3	>20	2.17±0.44b	4.1±0.4	0.19±0.07b	1.18±0.07b	15.7±2.3a	19±2
Clay	L	Eucalyptus plantation	-0.6433	31.4130[b]	3	>20	3.37±0.84a	4.8±0.7	0.28±0.08a	1.11±0.12b	12.4±0.7bc	36±8
Clay	M	Eucalyptus plantation			3	>20	3.19±0.06a	4.5±0.7	0.25±0.00a	1.15±0.05b	12.7±0.2b	41±7
Sandy clay loam	L	Perennial crops			8	>20	2.28±0.21b	6.1±0.3	0.19±0.02b	1.24±0.03b	11.9±0.4c	23±2
Sandy clay loam	M	Perennial crops			8	>20	2.09±0.24b	6.7±0.2	0.16±0.02bd	1.19±0.04b	13.1±0.6ab	27±3
Clay	L	Perennial crops			10	>20	3.12±0.16a	6.2±0.1	0.27±0.3a	1.13±0.05b	11.6±0.2c	36±3
Clay	M	Perennial crops			9	>20	3.51±0.15a	6.7±0.1	0.29±0.02a	1.08±0.02c	12.0±0.3c	44±1
Research Site R2												
silty clay loam	L	Annual crops	-0.6801	31.4497	4	3	3.02±0.13a	6.1±0.1	0.27±0.02a	1.02±0.05a	11.2±0.3a	35±1
silty clay loam	L	Annual crops	-0.6778	31.4500	4	50	2.36±0.23c	5.6±0.1	0.19±0.01c	1.02±0.05a	12.1±0.5a	35±6
silty clay loam	L	Natural forest	-0.6815	31.4495	6	na	5.81±0.34b	6.3±0.4	0.53±0.03b	0.79±0.03b	10.9±0.2a	31±2
silty clay loam	L	Perennial crops	-0.6794	31.4495	4	3	2.53±0.23ac	6.4±0.2	0.23±0.03a	1.02±0.02a	11.2±0.7a	39±1
silty clay loam	L	Perennial crops	-0.6772	31.4494	4	50	2.56±0.26ac	6.1±0.1	0.23±0.03a	1.06±0.04a	11.5±0.8a	38±2

SOC: Soil organic carbon, TN: Total nitrogen, CN: carbon to nitrogen ratio. Land-Use plant/ crop species; Annual crops (*Zea Mays, Phaseolus spp*.), Perennial crops (*Musa* spp, *Coffea canephora*), Eucalyptus plantation (*Eucalyptus spp.).* Slope positions: L: Lower slope, M: Mid slope, B: Bottom slope. n: number of replicates. na: Not applicable. Note that different lower case letters within each research site indicate differences between treatments ($P < 0.05$)

[a] GPS coordinates for midpoint of clay Acrisols cluster of R1,

[b] GPS coordinates for midpoint of sandy clay loam Acrisols soil type cluster of R1

Table 3: Analysis of Variance comparing the effects of soil texture (sandy clay loam vs clay), slope position (lower and mid slopes) and land-use (eucalyptus plantation, perennial cropping and annual cropping systems) on N_2O and CO_2 cumulative flux rates for a 48 h incubation at three different water holding capacities (WHC) for intact soil cores (n = 74) collected at research site 1 (R1) near Rakai, Uganda

		80% WHC			55% WHC			30% WHC		
N_2O	DF	Mean SS	F value	P value	Mean SS	F value	P value	Mean SS	F value	P value
ST	1	2.21	4.35	***0.041***	4.81	11.834	***<0.001***	0.024	0.17	0.681
SP	1	0.113	0.223	0.638	0.375	0.922	0.341	1.286	8.87	***0.004***
LU	2	9.868	19.46	***<0.001***	11.889	29.233	***<0.001***	1.606	11.077	***<0.001***
ST:SP	1	0.104	0.204	0.653	0.237	0.583	0.448	0.006	0.041	0.839
ST:LU	2	0.115	0.228	0.797	2.289	5.629	***0.006***	0.216	1.492	0.233
SP:LU	2	0.211	0.417	0.661	0.141	0.348	0.707	0.529	3.649	0.031
ST:SP:LUT	2	1.039	2.048	0.138	1.346	3.309	***0.043***	0.313	2.155	0.124
CO_2										
ST	1	0.73	0.913	0.343	0.111	0.179	0.673	0.409	7.159	0.009
SP	1	0.234	0.293	0.59	0.157	0.253	0.617	0.011	0.202	0.654
LU	2	9.41	11.766	***<0.001***	8.315	13.409	***<0.001***	0.260	4.543	0.014
ST:SP	1	0.806	1.007	0.319	0.134	0.216	0.644	0.004	0.082	0.776
ST:LU	2	0.093	0.117	0.89	0.687	0.107	0.337	0.161	2.819	0.067
SP:LU	2	0.755	0.943	0.395	1.666	2.686	0.076	0.040	0.701	0.500
	2	0.433	0.541	0.585	0.931	1.501	0.231	0.094	1.649	0.201

ST= Soil texture, SP=Slope position, LU= Land-use, n= Sample size and DF= Degrees of freedom

Table 4: Analysis of variance table showing contrasts on chronological sequence of land-use conversion from natural forest to agricultural land-use effects on N_2O and CO_2 fluxes from 48h incubated soil cores (n = 22) under different percentage water holding capacities (WHC) at sites used for research question R2 near Rakai, Uganda.

Contrasts		80% WHC			55% WHC			30% WHC		
N_2O	DF	Mean SS	F value	P value	Mean SS	F value	P value	Mean SS	F value	P value
Natural Forest vs Converted Land-use	1	11.23	29.68	***<0.001***	11.554	26.292	<***0.001***	7.48	22.09	***<0.001***
Converted 3 yrs vs 50 yrs	1	2.07	5.480	***0.031***	0.158	0.36	0.556	0.11	0.349	0.562
Annual 3 yrs vs Perennial 3 yrs	1	0.79	2.100	0.165	0.262	0.597	0.45	0.43	1.296	0.271
Annual 50 yrs vs Perennial 50 yrs	1	0.26	0.689	0.418	0.349	0.794	0.385	4.34	12.83	***0.002***
Annual vs Perennial	1	0.98	2.590	0.125	0.608	1.385	0.256	3.77	11.14	***0.004***
CO_2										
Natural Forest vs Converted Land-use	1	0.447	53.764	***<0.001***	9.289	15.638	***0.001***	15.648	47.471	***<0.001***
Converted 3 years vs 50 yrs	1	0.019	2.270	0.15	0.181	0.306	0.588	0.854	2.590	0.126
Annual crops 3 vs Perennial 3 yrs	1	0.003	0.371	0.551	0.010	0.016	0.900	0.141	0.427	0.522
Annual crops 50 vs Perennial 50 yrs	1	0.001	0.123	0.73	0.001	0.002	0.963	4.977	15.100	***0.001***
Annual vs Perennial	1	0.004	0.461	0.506	0.009	0.015	0.990	1.722	5.224	***0.035***

Table 5: Correlation coefficients between soil properties and cumulative N_2O and CO_2emissions at 30, 55 and 80% water holding capacity (WHC)

	Cumulative N_2O			Cumulative CO_2		
Soil Parameter	30% WHC	55% WHC	80% WHC	30% WHC	55% WHC	80% WHC
Sampling site 1 (RQ1)						
pH	**0.54***	**0.56*****	**0.59*****	0.09	0.13	**0.27***
TN	**0.43*****	**0.45*****	**0.53*****	-0.03	**0.38****	**0.41*****
SOC	**0.33****	**0.51*****	**0.56*****	0.01	**0.42*****	**0.36****
BD	-0.17	-0.13	-0.19	0.11	0.02	0.02
C:N	-0.11	-0.08	-0.29	0.15	0.04	**0.26***
Clay	-0.04	0.12	01.2	-0.39***	-0.03	0.1
Sampling site 2 (RQ2)						
pH	0.36	0.08	0.06	0.37	-0.01	0.26
TN	**0.53***	**0.83*****	**0.58****	**0.78*****	**0.73*****	**0.77*****
SOC	**0.56***	**0.77*****	**0.62****	**0.73*****	**0.66*****	**0.76*****
BD	-0.32	**-0.74*****	**-0.5****	**-0.78*****	**-0.74*****	**-0.76*****
CN	-0.21	-0.1	0.16	-0.22	-0.08	-0.11
Clay	-0.07	-0.29	-0.13	-0.25	-0.37	-0.26

*, **, *** significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively.

Figure 1. Map showing the study area in Rakai, Uganda, with its land-use and selected sampling sites. The area used in R2 is highlighted in a black circle; all other points were sampled for R1. Area within blue dotted boundary is predominantly sandy clay loam Acrisols while area within brown solid boundary is predominantly clay Acrisols.

Figure 2. Cumulative N_2O(mg N_2O-N m^{-2}48 h^{-1}) emissions at 30, 55, 80% water holding capacity (WHC) and under different land-uses and soil texture following rewetting of dried soil cores for 48 hours at plots sampled for R1. Same letter(s) indicate lack of significance ($p>0.05$) at respective % WHC. Error bars represent standard error of means. At 30% WHC soil textural class and slope position were not significant so only land-use is presented

Figure 3. Cumulative CO_2 (g CO_2-C m^{-2}48 h^{-1}) emissions at 30, 55, 80% WHC from different land-uses following rewetting of dried soil cores for 48 hours at R2 sites. Same letter(s) indicate lack of significance. Error bars represent standard error of means. At 55 and 80% WHC soil textural class and slope position did not influence emissions so only land-use is presented.

Figure 4. Cumulative soil N_2O (mg N_2O-N m^{-2} 48 h^{-1}) emissions at 30, 55, 80%WHC for rewetted soil cores over a 48 hour period. Soil cores were taken from plots with differences in time of conversion from natural forest (3 or 50 years) and current management (annual crops versus perennial [banana] crops). Same letter(s) above the graphs at respective % WHC indicate lack of significance ($p>0.05$). Error bars represent standard error of means.

Figure 5. Cumulative soil CO_2 (mg CO_2-C m^{-2} 48 h^{-1}) emissions at 30, 55, 80% WHC for rewetted soil cores over a 48 hour period. Soil cores were taken from plots with differences in time of conversion from natural forest (3 or 50 years) and current management (annual crops versus

perennial [banana] crops). Same letter(s) above the graphs at respective % WHC indicate lack of significance ($p>0.05$). Error bars represent standard error of means.

Figure 1.

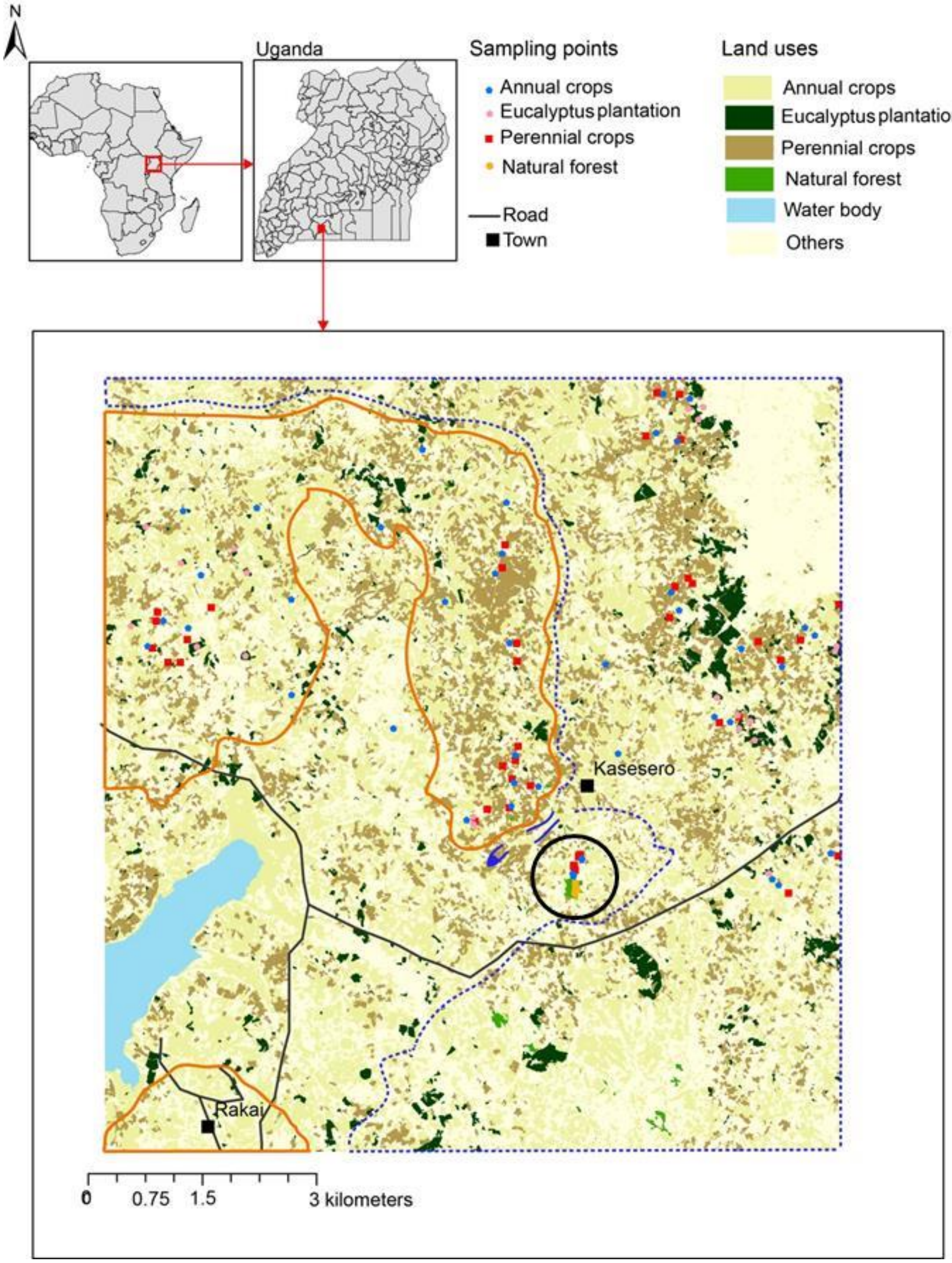

N
Uganda
Sampling points
Annual crops
Eucalyptus plantation
Perennial crops
Natural forest
Road
Town
Land uses
Annual crops
Eucalyptus plantation
Perennial crops
Natural forest
Water body
Others
Kasesero
Rakai
0 0.75 1.5 3 kilometers

Figure 2.

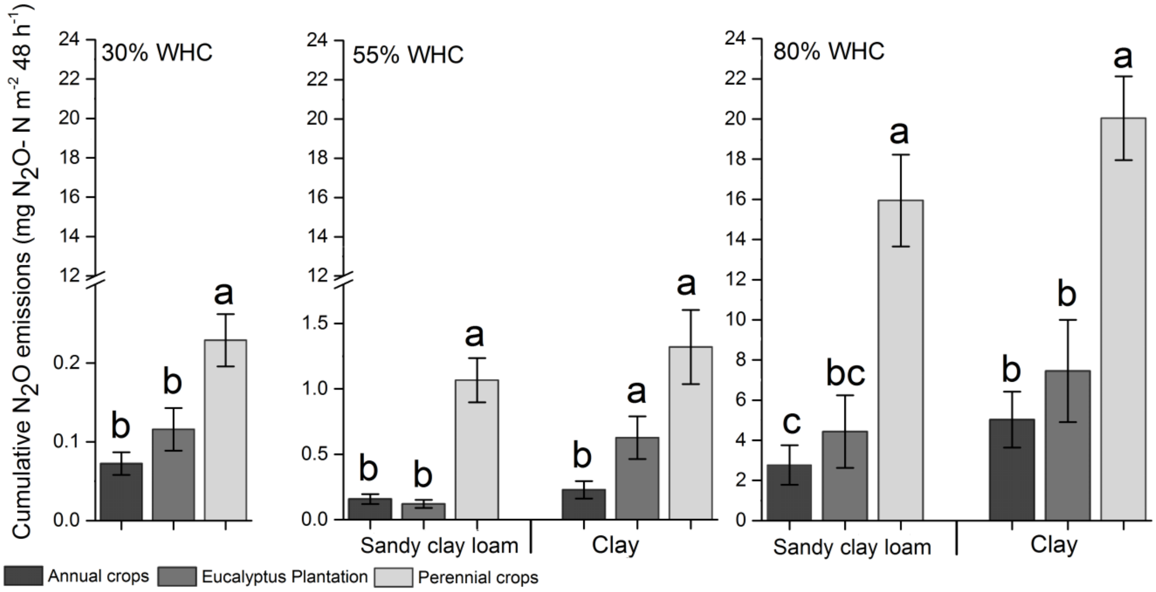

Cumulative N_2O emissions (mg N_2O- N m^{-2} 48 h^{-1})
30% WHC
55% WHC
80% WHC
24
22
20
18
16
14
12
10
8
6
4
2
0
1.5
1.0
0.5
0.0
0.2
0.1
0.0
a
b
bc
c
Sandy clay loam
Clay
Annual crops
Eucalyptus Plantation
Perennial crops

Figure 3.

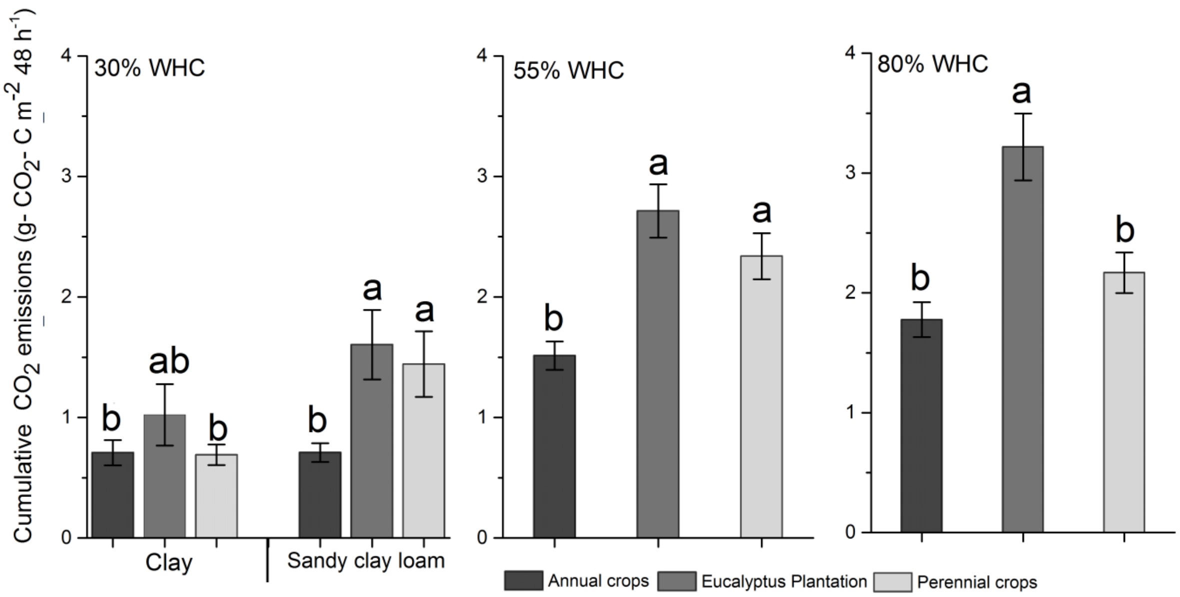

Cumulative CO2 emissions (g- CO2- C m-2 48 h-1)
30% WHC
55% WHC
80% WHC
0
1
2
3
4
b
ab
b
b
a
a
Clay
Sandy clay loam
b
a
a
b
a
b
Annual crops
Eucalyptus Plantation
Perennial crops

Figure 4.

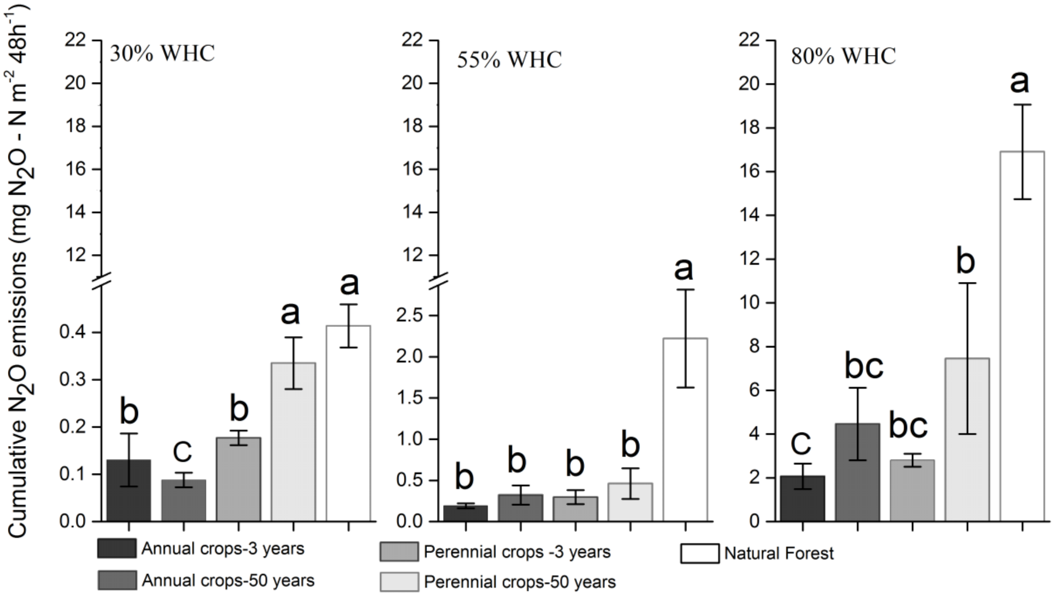
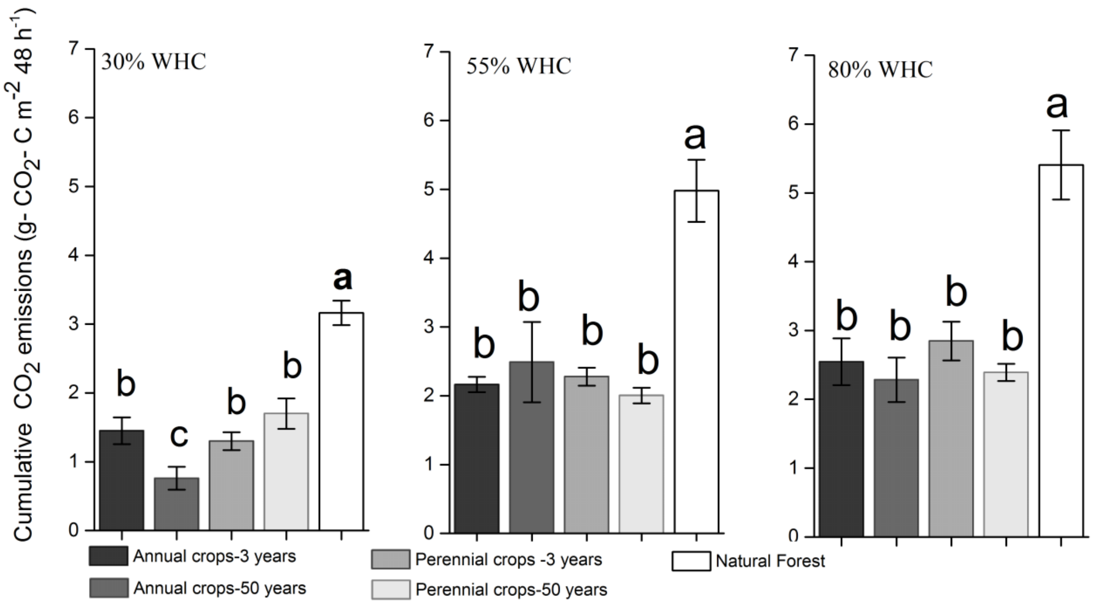

Cumulative N_2O emissions (mg N_2O - N m^{-2} $48h^{-1}$)
30% WHC
55% WHC
80% WHC
22
20
18
16
14
12
0.4
0.3
0.2
0.1
0.0
2.5
2.0
1.5
1.0
0.5
10
8
6
4
2
0
b
c
b
a
a
b
b
b
b
a
c
bc
bc
b
a
Annual crops-3 years
Annual crops-50 years
Perennial crops -3 years
Perennial crops-50 years
Natural Forest

Figure 5.


Cumulative CO2 emissions (g- CO2- C m-2 48 h-1)
30% WHC
55% WHC
80% WHC
0
1
2
3
4
5
6
7
b
c
b
b
a
b
b
b
b
a
b
b
b
b
a
Annual crops-3 years
Annual crops-50 years
Perennial crops -3 years
Perennial crops-50 years
Natural Forest