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1. Introduction

Tropical deforestation for fertilizer-intensive agriculture has increased greatly over the last decades and remains one of the greatest global environmental challenges of the 21st century because it contributes significantly to the emission of greenhouse gases (GHGs; [Ciais et al.,](#)

[2014](#); [Gibbs and Herold, 2007](#); [Pearson et al., 2017](#)). In Uganda, approximately 60% of the forestland (~ 3 million hectares) has been lost to deforestation between 1990 and 2015 ([NEMA, 2017](#)), making this developing nation, one of the countries in tropical Africa that is currently faced with a deforestation crisis ([Josephat, 2018](#)). Deforested areas in Uganda are mostly allocated to large-scale sugarcane

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(*Saccharum officinarum*) cultivation and as a consequence, land area under fertilizer-based sugarcane cultivation has more than tripled in the past 20 years (Mwavu et al., 2018). The expansion of the Ugandan sugarcane sector is largely premised on scaling up of sugarcane production in order to match the per capita increase in sugar demand (currently at 12 kg sugar yr⁻¹; Johnston and Meyer, 2008), improve household incomes (Mwavu et al., 2018), and provide feedstock for the emerging biofuel industry (Isabirye et al., 2013). However, the impact of this land use shift on the temporal and spatial dynamics of the three main biogenic GHGs (carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O)) is still poorly understood.

Tropical deforestation together with the associated biomass burning are reported to not only set free significant amounts of C stored in the aboveground biomass (i.e., ~ 0.6 – 1.2 Gt C.yr⁻¹; Achard et al., 2014) but also lead to long term alterations in the soil-vegetation feedbacks (Runyan et al., 2012). These in turn affect soil properties (particularly bulk density (BD), pH, soil organic carbon (SOC), effective cation exchange capacity (ECEC), base saturation (BS), and C: N ratio) that constrain the microbial production and consumption of the biogenic GHGs in the soil or at the soil-atmospheric interface (Veldkamp et al., 2020). Further, it has been shown that the routine management operations practiced in cropland equally affect soil GHG fluxes (CO₂ (Oertel et al., 2016), CH₄ (Dattamudi et al., 2019), and N₂O fluxes (D'Haene et al., 2008)). For instance, in many croplands, seedbed preparation, weeding, and harvesting operations are usually achieved through a number of tillage operations (Naseri et al., 2020). Tillage, however, exposes the soil surface to higher temperatures resulting in increased organic matter decomposition and increased CO₂ emissions (Six et al., 1998). Moreover, increased traffic of machinery over the fields (during the different tillage and field operations) compacts surface soils resulting in reduced diffusive entry of CH₄ from the atmosphere to the oxidative sites in the soil (Dexter, 2004). Besides tillage, many large-scale sugarcane production systems around the world rely on large doses of nitrogen (N- between 150 and 300 kg N ha⁻¹ yr⁻¹; Kostka et al., 2009) and potassium (K- between 300 and 600 kg K ha⁻¹ yr⁻¹; Thorburn et al., 2010), to maintain high yields both in cane and ratoon fields (Thorburn et al., 2005). However, high N fertilizer doses together with the warm and humid tropical environments where the sugarcane grows (Thorburn et al., 2010) predispose the sugarcane fields to increased N₂O emissions (Dattamudi et al., 2019). It has also been shown that excessive N fertilization inhibits methanotrophic CH₄ uptake due to the increased affinity of the NH₄⁺ ions for the oxidative sites on CH₄-monooxygenases (Veldkamp et al., 2013). Little is known, however, about the effect of N fertilization on CO₂ effluxes from sugarcane fields.

Management of sugarcane residues prior to harvesting of the cane stalks is another practice that has been reported to significantly affect GHG fluxes from sugarcane fields (Tavares et al., 2018). Some sugarcane growers set fields on fire prior to harvesting to speed up harvesting operations (Blair, 2000) while others leave residues standing on the field after harvesting the stalks (also known as the green cane harvesting system—GCHS; Graham and Haynes, 2006) mainly to conserve soil moisture and replenish soil fertility (Robertson and Thorburn, 2007). On the one hand, burning of the residues leads to both increased N and P volatilization (Britts et al., 2016) and higher CO₂ emissions from sugarcane fields (De Figueiredo and La Scala, 2011). On the other hand, GCHS increases C sequestration via increased C inputs to soil (Robertson and Thorburn, 2007) but this gain in SOC stocks is often offset by increased N₂O and CH₄ emissions from the unburnt fields (Dattamudi et al., 2019).

In Uganda, although nearly all sugarcane farmers leave residues standing on the fields and employ tillage operations at seedbed preparation and weeding, fertilizer application practices among these farmers can greatly differ due to financial reasons (Otieno et al., 2019). The majority of the farmers typically apply a one-time standard fertilizer dose of urea ((NH₂)₂CO; 70 kg N ha⁻¹) mixed with muriate of potash (KCl; 23 kg K ha⁻¹) to the sugarcane fields during the growth cycle.

However, there are still farmers that apply either less or more than the recommended standard fertilizer application rate. The different fertilizer application rates in combination with the tillage and residue management practices by farmers are expected to invariably affect soil GHG fluxes. However, there is still no concrete evidence on how replacing tropical forests with sugarcane managed under different fertilization regimes affects soil GHG fluxes, creating major uncertainties in our assessment of the role tropical land use change plays in the soil-atmospheric exchange of C and N. It was for this reason that we quantified soil GHG fluxes (CO₂, CH₄, and N₂O) along with their potential auxiliary controls (water-filled pore space (WFPS), temperature and mineral N) from four reference forest plots and 12 replicate plots of a completely randomized design (CRD) experiment premised in a neighboring 20-year-old sugarcane plantation in northwestern Uganda.

In the following, it was hypothesized that tropical forest conversion for fertilizer-based sugarcane systems would result in:

- (1) Increased CO₂ emissions from the respective sugarcane CRD treatment plots compared to the reference forest plots (low input > standard input > high input > reference forest plots) coming from the continuous loss of forest SOC, until the soils under sugarcane reach a new equilibrium, and the higher autotrophic respiration by the sugarcane fibrous roots.
- (2) Reduced CH₄ uptake in the respective sugarcane CRD treatment plots compared to the reference forest plots (high input < standard input < low input < reference forest plots) resulting from reduced methanotrophic activity under the heavily fertilized and compacted (from machinery traffic) sugarcane fields.
- (3) Increased N₂O emissions from the respective sugarcane CRD treatment plots compared to the reference forest plots (high input > standard input > low input > reference forest plots) attributed to N fertilization and increased mineralization of the retained crop residues.

2. Methods and materials

2.1. Study area

The study was conducted in northwestern Uganda where large-scale deforestation for fertilizer-based sugarcane cultivation has been documented for several decades. The long-term mean annual temperature for the study area is about 25 °C while the annual precipitation is about 1700 mm (Lukwago et al., 2020). Rainfall in the region follows a bimodal distribution pattern divided into two main wet seasons (March to May and August to November), and an extended (December to February) and a short dry season (June to July; Lukwago et al., 2020).

2.2. Experimental design

Two similar test sites with respect to altitude, topography, geology, soils and climate were selected for the study (Table A1). Site 1 (1°44'28.4" N, 31°32'11.0"E) represents the location of the nutrient manipulation experiment (NME) in the forest—Budongo Central Forest Reserve. The forest site characteristics as well as further details about the NME were reported in Manu et al. (2022). The present study builds on an earlier study conducted within the framework of the NME (Tamale et al., 2021) with the aim to disentangle the effect of deforestation for fertilized sugarcane on soil GHG fluxes. In the present study, we compare the soil GHG fluxes measured from the untreated forest plots of the Tamale et al. (2021) study, here after referred to as reference forest plots, to the soil GHG fluxes measured from 12 replicate plots of a completely randomized design (CRD) experiment established in the neighboring sugarcane plantation (1°41'37.9" N, 31°30'6.3" E). The sugarcane CRD experiment plot dimensions (plot size: 40 m x 40 m, inner measurement core: 30 m x 30 m, and guard row: 40 m) were identical to those of the reference forest plots. The CRD experiment

consisted of a one-time standard fertilizer dose (70 kg N (as urea) + 23 kg K (as muriate of potash) ha⁻¹ growth cycle⁻¹), low fertilizer dose (0.5 times standard), and high fertilizer dose (1.5 times standard) as treatments. The fertilizer doses used in the sugarcane CRD experiment represented a gradient of fertilizer application rates used by sugarcane farmers in this region (i.e. low, standard, and high). Each treatment was replicated four times, hence, the sugarcane CRD experiment consisted of 12 plots (n = 12, three treatments x four replications). The treatments were applied to the replicate plots of the CRD on 14 May 2019. Inter-row weeding was done once every 2.5 months in the first eight months using a hand hoe, and none after the eighth month, since the sugarcane canopy had increased significantly to efficiently subdue the weeds. Additionally, the sugarcane fields hosting the CRD experiment were maintained as ratoon crops with residues returned to the fields after every harvest cycle.

2.3. Soil sampling and analysis

Soil physico-chemical characterization (i.e., BD, mineral N, OC, pH, and texture) over 1 m depth was done for both the forest and sugarcane sites prior to the start of soil GHG flux measurements. In the forest, soil samples were obtained from ten random locations within each of the four reference plots for the top 0.10 m depth. However, for depths between 0.10 and 1 m, soil samples were obtained outside the established reference forest plots in order to minimize disturbance to the soil microenvironment within these plots. For 0.10–0.50 m depth, soil samples were obtained from five random points within each of the 16 reconnaissance plots located at ~ 500 m from the current location of reference forest plots while for 0.50–1 m depth, soil samples were taken from 1 m pits dug in the inter plot spaces of the reference plots. At the sugarcane site, soil samples were obtained at three random locations within every established plot of the CRD experiment for three depths (0–0.10 m, 0.10–0.30 m and 0.30–0.50 m), and from four pits (1 m x 1 m x 1.1 m) dug in the inter plot spaces of the established plots for the depths between 0.50 and 1.00 m.

To have an indication, if the SOC stocks after 20 years of sugarcane cultivation had already approached a new C equilibrium, we also took soil samples in 50-year-old ratoon plantations. These plantations were located about 1–2 km from the current location of the 20-year-old sugarcane plantations and both had similar soil types, climate, weed management, residue retention and fertilization practices.

Soil samples obtained from the same depth within a plot or pit were thoroughly mixed and about 500 g of the homogenized soil sample was air dried (~ 25 °C) and submitted to University of Augsburg (Germany) and ETH Zurich (Switzerland) for analysis. Soil samples for C, N, and pH analyses were sieved to 2 mm before being used in the analyses. Soil pH was measured on a 1:2.5 soil water suspension using a pH electrode. Soil BD was determined from the respective oven dry soil sample masses (105 °C for 48 h) together with the Kopecky ring volume (volume = 251 cm³) used in obtaining the soil samples while considering the stone content. Soil C and N concentrations were determined using a C/N analyzer (Vario EL Cube CNS Elementar Analyzer, Germany). The respective soil C and N stocks of every depth interval per plot were calculated based on the soil BD measurements. At both sites (forest and sugarcane), texture was determined using samples obtained from the profile pits for two depths, 0.10 m (for topsoil) and 0.50–0.60 m (for deeper soils) while textural analysis was done using a laser diffractometer (LS 13 320 Laser Diffraction Particle Size Analyzer, Beckman Coulter, United States of America).

2.4. Aboveground and belowground biomass determination

Aboveground biomass (AGB) was estimated for two tree diameter classes (1–10 cm and > 10 cm; [Manu et al., 2022](#)) in the forest while in the sugarcane, only the maximum AGB at harvest was considered. Forest AGB was converted to C based on the widely accepted C fraction

conversion factor for tropical forest biomass (0.50; [Sarmiento et al., 2005](#)) while in the sugarcane, the AGB was converted to C using a C fraction factor of 0.43, determined with the C/N analyzer.

Belowground biomass (BGB) in the sugarcane consisted of only living fine roots (diameter < 2 mm) given the fibrous nature of the sugarcane's root system, and was based on soil monoliths (measuring 0.20 m x 0.20 m x 0.10 m) obtained from one face of every pit (described in [Section 2.3.](#)) following 0.10 m depth increments down to 1 m. The obtained soil materials were thoroughly washed to isolate roots from the soil mass. The root samples were oven dried at 60 °C for 48 h at the National Agricultural Research Laboratories, Kampala, Uganda and weighed to determine the root biomass per depth increment. However, in the forest, BGB consisted of both coarse (diameter > 2 mm) and fine (diameter < 2 mm) roots based on the pits (described in [Section 2.3.](#)). It is worth noting that whereas the pits provided a good estimate of the fine root biomass in the forest, they far underestimated the coarse root biomass because they were dug at a considerable distance away from the bases of big trees in order to minimize ecosystem disturbance. This consequently resulted in exclusion of a significant proportion of coarse roots closest to big tree bases, creating a bias in the pit BGB data. To overcome this bias, we estimated the forest coarse roots from AGB using [Eq. 1](#) proposed by [Cairns et al. \(1997\)](#) before summing it with fine roots determined from pits to obtain the forest BGB. Next, both the forest and sugarcane BGB were converted to C using a C fraction factor of 0.43 determined with a C/N analyzer.

$$BGB_{cf} = e^{(-1.0587 + 0.8836 \ln(AGB_f))} \quad (1)$$

Where BGB_{cf} is the coarse root component of the forest BGB, expressed in kg dry matter ha⁻¹ while AGB_f is the aboveground biomass of the forest, expressed in kg dry matter ha⁻¹.

2.5. Soil greenhouse gas measurements, auxiliary measurements, flux calculation, and soil GHG budget estimation

Soil GHG flux measurements were conducted inside the inner measurement core (measuring 30 m x 30 m) of every plot in the forest (four) and sugarcane (twelve), with every core randomly installed with four chamber bases (made from a 250 mm PN10 PVC pipe, area = 0.044 m², and volume = ~ 12 L) at a depth of about 0.03 m. The installation of chamber bases was done nearly a month before the first gas sampling (May 2019), which together with leaving the chamber bases in place throughout the measurement period, ensured that any potential disturbances to the soil microenvironment under the chamber bases were minimized.

Gas sampling was done on a plot-by-plot basis and completely random to ensure that any effects that the diurnal changes in temperature may have on the measured soil GHG fluxes were minimized. A minute before the gas sampling started, all the chamber bases were fanned to ensure that the concentrations of the GHGs at the soil surface and the atmosphere immediately above the chamber were in equilibrium. Next, all the chamber bases in every plot were simultaneously covered with vented polyvinyl hoods (volume = 6.78 L) fitted with bulkheads (sampling ports). A composite gas sample (60 mL) was obtained at 3, 13, 23, and 33 min by drawing 15 mL of gas sample from the individual chamber head airspaces and pooling them together at every time interval using the protocol of [Arias-Navarro et al. \(2013\)](#). Next, 40 mL of the composite gas sample was flushed through a 12 mL pre-evacuated Labco exetainer (Labco, UK) before transferring the remaining 20 mL into the exetainer and bringing it to an over pressure. Soil GHG fluxes from the reference forest plots were measured monthly throughout the measurement period while for sugarcane, more intensive measurements were done in the first six months following fertilization before switching to monthly measurements for the remaining period of gas sampling. The intensive measurements aimed to capture the expected N₂O emission flush following fertilization in the sugarcane and

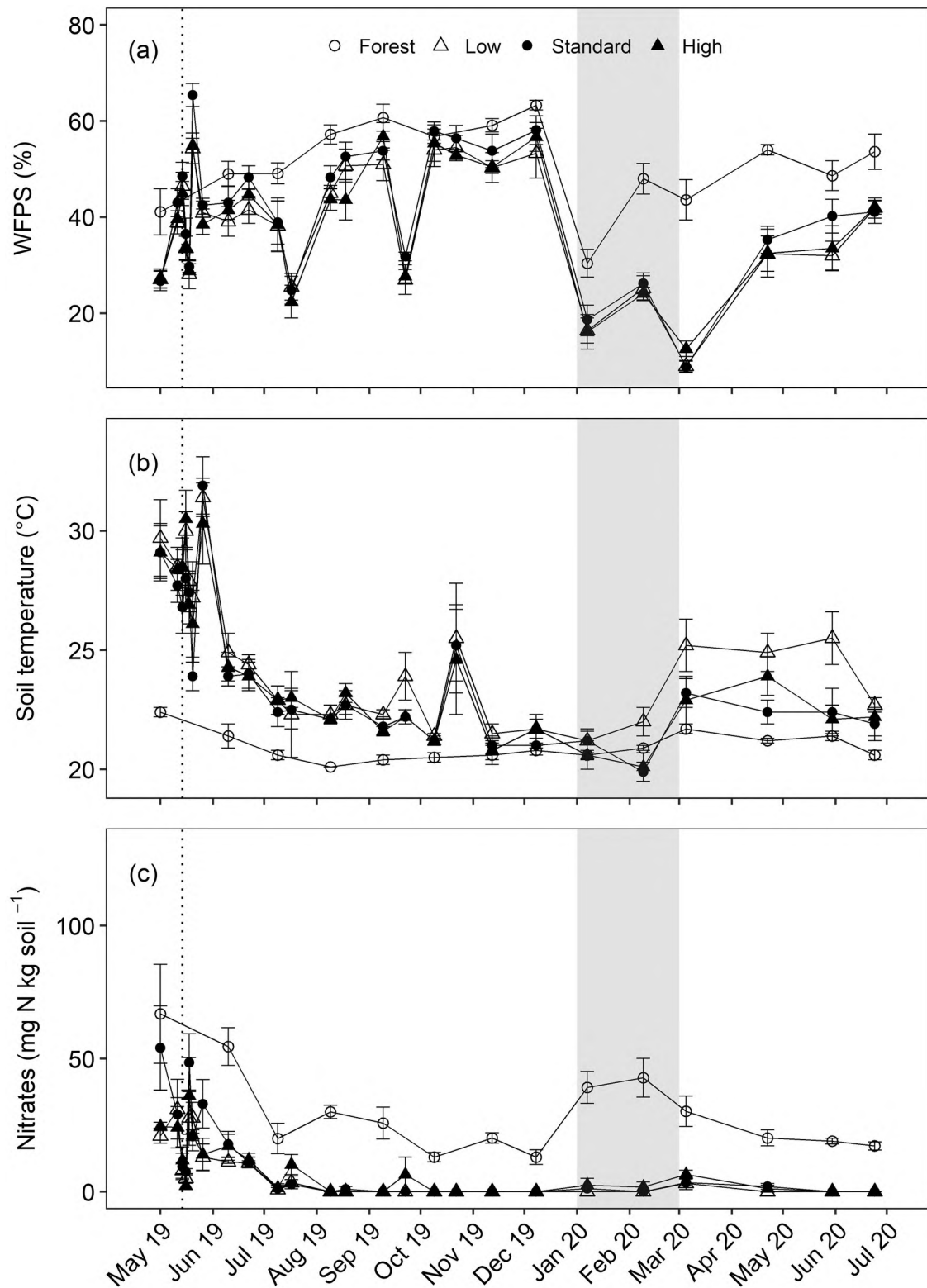


Fig. 1. Mean (\pm standard error, $n = 4$) water-filled pore space (WFPS; a), soil temperature (b) and nitrate (NO_3^-) content (c) measured at 0.05 m (May 2019 to June 2020) from the reference forest plots and the replicate treatment plots in the 20-year-old sugarcane plantation. The mean WFPS, soil temperature, and NO_3^- content result from four plots per treatment for every sampling time. The dashed vertical line indicates the application of urea and muriate of potash fertilizers in the sugarcane plots. The gray shaded rectangle (a-c) indicates the start and end of the dry period (monthly precipitation ≤ 100 mm). Standard equals to $70 \text{ kg N} + 23 \text{ kg K ha}^{-1}$ growth cycle⁻¹, low equals to 0.5 times standard, and high equals to 1.5 times standard.

Table 1

Seasonal mean (\pm SE, $n = 4$) auxiliary controls (water-filled pore space (WFPS), soil temperature, and nitrate (NO_3^-)) and soil greenhouse gas fluxes (CO_2 , CH_4 , and N_2O) measured in the topsoil (at 0.05 m) from the reference forest and the sugarcane under different treatments (low, standard, and high).

Treatment /season		WFPS (%)	Soil temperature ($^{\circ}\text{C}$)	NO_3^- (mg N kg^{-1})	Daily CO_2 fluxes ($\text{mg C m}^{-2} \text{h}^{-1}$)	Daily CH_4 fluxes ($\mu\text{g C m}^{-2} \text{h}^{-1}$)	Daily N_2O fluxes ($\mu\text{g N m}^{-2} \text{h}^{-1}$)
Wet season							
Forest		$53.8 \pm 1.4^{\text{Aa}}$	$21.0 \pm 0.1^{\text{a}}$	$27.5 \pm 2.9^{\text{Aa}}$	$165 \pm 5^{\text{a}}$	$-31.2 \pm 3.3^{\text{Aa}}$	$19.9 \pm 3.7^{\text{a}}$
Sugarcane	Low	39.8 ± 1.3	25.1 ± 0.4	7.1 ± 1.3	228 ± 5	-8.7 ± 2.3	6.2 ± 0.9
	Standard	42.8 ± 1.4	24.1 ± 0.3	10.5 ± 1.9	217 ± 7	-9.8 ± 2.2	7.3 ± 1.2
	High	40.1 ± 1.3	24.5 ± 0.4	8.2 ± 1.3	200 ± 5	-12.5 ± 1.9	5.7 ± 0.9
Mean ^a		$40.9 \pm 0.8^{\text{Ab}}$	$24.6 \pm 0.2^{\text{Ab}}$	$8.6 \pm 0.9^{\text{b}}$	$215 \pm 3^{\text{Ab}}$	$-10.3 \pm 1.2^{\text{Ab}}$	$6.4 \pm 0.6^{\text{b}}$
Dry season							
Forest		$39.2 \pm 3.9^{\text{Ba}}$	$20.8 \pm 0.1^{\text{a}}$	$41.0 \pm 4.4^{\text{Ba}}$	$167 \pm 12^{\text{a}}$	$-60.2 \pm 8.0^{\text{Ba}}$	$20.9 \pm 4.5^{\text{a}}$
Sugarcane	Low	20.8 ± 2.4	21.6 ± 0.3	0.0 ± 0.0	154 ± 7	-27.8 ± 5.6	0.9 ± 1.0
	Standard	22.5 ± 2.2	20.6 ± 0.4	0.6 ± 0.6	146 ± 6	-20.0 ± 10.2	1.7 ± 2.1
	High	20.1 ± 2.3	20.3 ± 0.4	2.1 ± 1.4	150 ± 10	-24.4 ± 2.3	1.8 ± 0.7
Mean ^a		$21.1 \pm 1.3^{\text{Bb}}$	$20.8 \pm 0.2^{\text{Ba}}$	$0.9 \pm 0.7^{\text{b}}$	$150 \pm 4^{\text{Bb}}$	$-24.0 \pm 3.8^{\text{Bb}}$	$1.5 \pm 0.8^{\text{b}}$

^a Mean (\pm SE, $n = 3$) of the treatments (i.e., low, standard and high) of the CRD experiment in the sugarcane. Different lowercase letters indicate significant differences between the sugarcane and forest while different uppercase letters indicate significant differences between seasons within each land use ((Generalized) linear mixed-effects models with Tukey's HSD test at $p \leq 0.05$). Standard equals to $70 \text{ kg N} + 23 \text{ kg K ha}^{-1}$ growth cycle⁻¹, low equals to 0.5 times standard and high equals to 1.5 times standard.

were done as follows; 1- day before fertilization, 3-, 5-, 7-days after fertilization, weekly in the four weeks that followed fertilization, and then bi-weekly from the second to the sixth month after fertilization.

In parallel to gas sampling, auxiliary controls (soil temperature, volumetric water content and soil mineral N) were determined at 0.05 m depth in locations close to the respectively installed chamber bases. Soil temperature was measured using a digital soil thermometer (Greisinger GMH 3230, Germany) while volumetric water content was determined using a calibrated Theta FDR probe (AT Delta-T Devices Limited, United Kingdom). Soil mineral N content (consisting of nitrate (NO_3^-) and ammonium (NH_4^+)) was determined using the RQ10 flex reflectometer (Merck, Germany). It is worth noting that the gas-sampling period (May 2019 to June 2020) was wetter than normal because the precipitation amounts received during this period far exceeded the long-term mean annual precipitation (36%; Table A1).

During the course of the gas sampling campaign, batches of gas-filled exetainers were shipped to ETH Zürich, Switzerland, for analysis at the gas chromatograph (GC; Scion 456-GC Bruker, Germany). The GC has an auto-sampler and is equipped with a thermal conductivity detector (CO_2), flame ionization detector (CH_4), and an electron capture detector (N_2O). Soil CO_2 , CH_4 , and N_2O concentrations in the collected composite gas samples were determined by comparing the peak areas of the samples to the peak areas of a set of standards for the gases of interest. Soil CO_2 , CH_4 , and N_2O fluxes were determined using the "gasfluxvis" scheme described in detail by Hüppi et al. (2018).

Net soil GHG budgets for both the forest and sugarcane plantations were estimated for a 100-year time window by converting the annual soil GHG fluxes to CO_2 equivalents ($\text{CO}_2\text{-eq}$) using factors of 1, 28 and 265 for CO_2 , CH_4 , and N_2O , respectively (IPCC, 2021).

2.6. Statistical analyses

Before conducting any statistical analyses, time series data on soil GHG fluxes and the auxiliary controls were divided into wet and dry seasons in order to understand how seasonality affects both the soil GHG fluxes and auxiliary controls. The wet season data included all sampling points where monthly precipitation was greater than 100 mm and the reverse was true for the dry season. It is worth noting that although both soil NH_4^+ and NO_3^- concentrations were monitored throughout the GHG sampling period, only the NO_3^- dataset is presented in the paper because the NH_4^+ concentration at both sites were mostly low and sometimes below the reflectometer detection limit. All data were inspected for normality and homoscedasticity prior to running any of the parametric tests (particularly one-way analysis of variance (ANOVA) and linear mixed effects models (LMEMs)) using quantile-quantile plots and

Shapiro test, and Levene test, respectively. In case diagnostic plots or (and) tests revealed skewness of the data or heteroscedasticity, a Tukey transformation was applied to the data, followed by running the normality and homoscedasticity tests again. However, if after transformation, normality and homoscedasticity were not restored, an equivalent nonparametric statistical test was selected. These included the generalized linear mixed effects models (GLMMs), spearman-rank correlation coefficient test, and the Kruskal-Wallis test. The GLMMs and LMEMs included the respective soil GHG fluxes (CO_2 , CH_4 , and N_2O) and auxiliary controls (WFPS, temperature, and mineral N) as response variables, land use type (forest and sugarcane under different fertilization regimes) as the fixed effects, plot numbers and sampling days as random effects. In some cases, the LMEMs were extended to cater for heteroscedasticity and correlation between measurements taken at closely spaced intervals. Extension of the LMEMs was only done if it improved the relative goodness of fit of the model reflected by a lower Akaike information criteria value. Annual soil CO_2 , CH_4 , and N_2O fluxes were approximated through application of a trapezoidal interpolation on the time intervals between measured soil GHG flux rates, assuming a constant daily flux rate.

The differences in soil physico-chemical characteristics between the sugarcane and forest were checked with either one-way ANOVA or Kruskal-Wallis test. The respective ANOVA models included different soil properties as response variables and land use types as predictor variables. The spearman-rank correlation coefficient test was used to determine the relationship between the measured soil GHG fluxes and auxiliary controls. Throughout the paper, statistical analyses were done in R 3.6.3 (R Development Core Team, 2019) using *car* (ANOVA), *nlme* (LMEMs), *MASS* (GLMMs), and inbuilt packages (for spearman-rank correlation coefficient test and Kruskal-Wallis test), with statistical significance for all the tests set at $p \leq 0.05$.

3. Results

3.1. Auxiliary controls and soil GHG fluxes

Topsoil (measured at 0.05 m depth) WFPS, temperature, and NO_3^- did not significantly differ between the treatments of the sugarcane CRD experiment despite application of varying quantities of N and K fertilizers (i.e., low, standard, and high) as treatments for the CRD experiment (Fig. 1; Table 1). Soil WFPS ranged between 6% and 72% in the sugarcane and between 24% and 69% in the forest. WFPS exhibited seasonal variability, with larger WFPS measured in the wet season compared to the dry season both in the forest (14%; Table 1; $p < 0.001$) and in the sugarcane (20%; Table 1; $p < 0.001$). Significantly higher

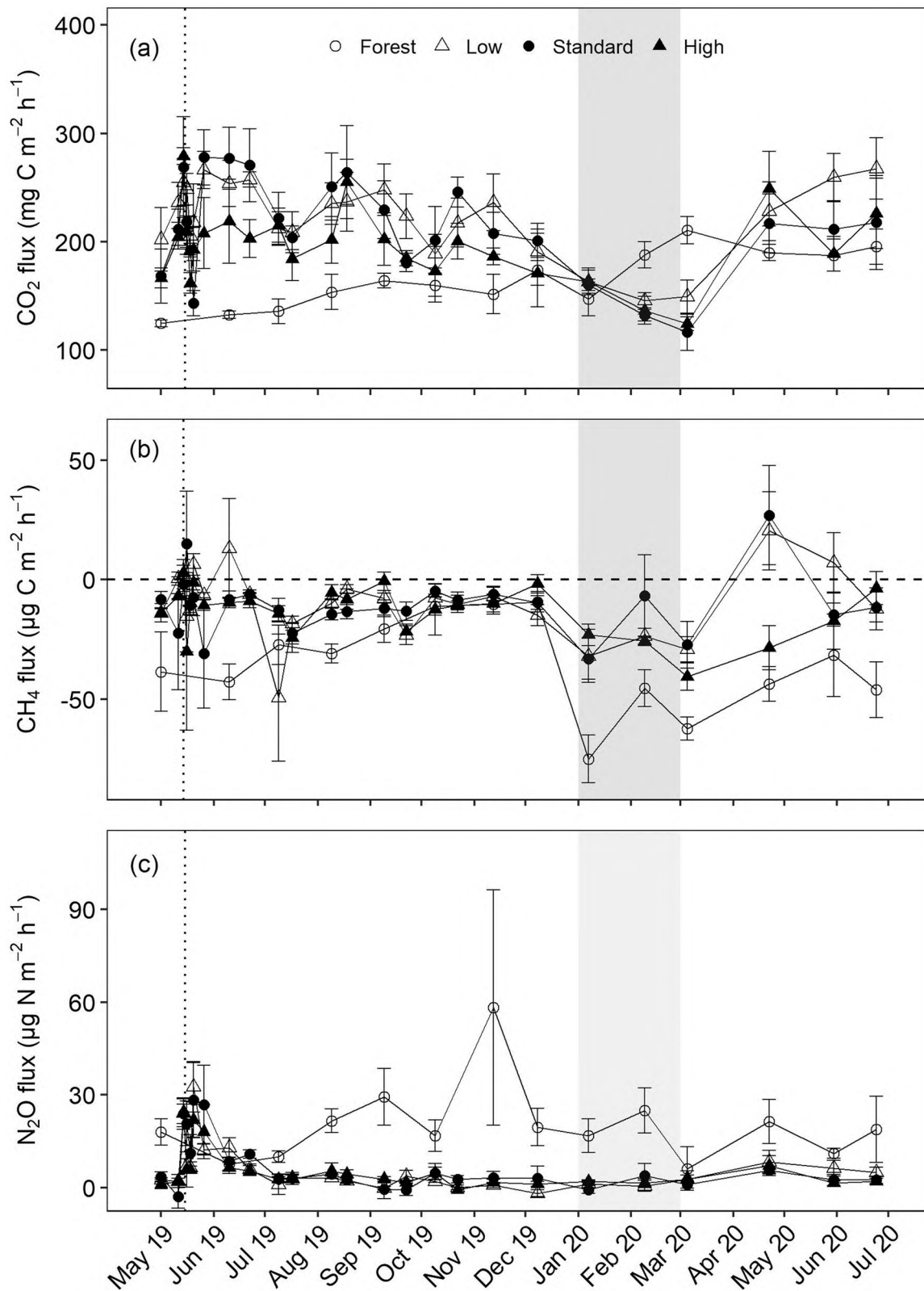


Fig. 2. Mean (\pm standard error, $n = 4$) soil CO_2 (a), CH_4 (b) and N_2O fluxes (c) measured between May 2019 and June 2020 from the forest and the sugarcane plots. The mean soil GHG fluxes result from measurements of four plots per treatment for every sampling time point. The dashed vertical line indicates the application of urea and muriate of potash fertilizers in the sugarcane. The gray shaded rectangle (a-c) indicates the start and end of the dry period (monthly precipitation ≤ 100 mm). Standard equals to $70 \text{ kg N} + 23 \text{ kg K ha}^{-1}$ growth cycle $^{-1}$, low equals to 0.5 times standard and high equals to 1.5 times standard.

Table 2

Spearman-rank correlation coefficients (*r*) between soil CO₂ fluxes (mg C m⁻² h⁻¹), soil CH₄ fluxes (μg C m⁻² h⁻¹), soil N₂O fluxes (μg N m⁻² h⁻¹), and auxiliary controls (WFPS (%), soil temperature (°C), nitrate (NO₃⁻; mg N kg soil⁻¹)) measured at 0.05 m depth from the reference forest and sugarcane. The spearman-rank correlation coefficients were calculated using means of the four reference plots under forest and 12 replicate treatment plots under sugarcane based on daily, weekly, biweekly, and monthly measurements under sugarcane, and only monthly measurements under forest.

Land use	Variable	WFPS	Soil temperature	NO ₃ ⁻
Forest	CO ₂ flux	0.11	0.08	-0.37
	CH ₄ flux	0.78**	-0.40	-0.51
	N ₂ O flux	0.59*	-0.47	-0.08
Sugarcane	CO ₂ flux	0.38	0.31	-0.08
	CH ₄ flux	0.68**	0.10	-0.14
	N ₂ O flux	0.10	0.49*	0.40*

Significance codes: *** *p* ≤ 0.01; and ** *p* ≤ 0.05.

WFPS was measured in the forest compared to the sugarcane both in the wet (13%; Table 1; *p* < 0.001) and in the dry season (18%; Table 1; *p* < 0.001). In contrast, there was a minimal to negligible variation in soil temperature (0.2 °C) in the forest across the wet and dry season (Fig. 1b; Table 1) compared to the sugarcane where the wet season soil temperature was 3.8 °C higher than the dry season (Fig. 1b; Table 1; *p* < 0.001). Forest NO₃⁻ concentrations in soil solution measured in the dry season were nearly twofold higher than in the wet season (Table 1; *p* < 0.001). However, under sugarcane, no significant differences in soil NO₃⁻ concentrations were detected between the wet and dry season in spite of measuring higher soil NO₃⁻ concentrations in the wet season compared to the dry season (Table 1). Overall, the forest had significantly larger soil NO₃⁻ concentrations than the sugarcane both in the wet and dry seasons (Table 1; *p* < 0.001).

Similarly, soil GHG fluxes did not significantly differ among the treatments of the CRD experiment in the sugarcane (both in the wet and dry seasons), despite application of varying fertilization rates as treatments for the CRD experiment (Table 1). During the measurement period (May 2019 to June 2020), daily soil CO₂ effluxes varied across space and time ranging between 67 and 386 mg C m⁻² h⁻¹ under sugarcane and between 78 and 240 mg C m⁻² h⁻¹ under forest. Interestingly, forest soil CO₂ effluxes were unaffected by seasonality (Table 1). However, under sugarcane, significantly higher CO₂ effluxes were measured in the wet season compared to the dry season (Table 1; *p* < 0.001). During the wet season, sugarcane soil CO₂ respiration was 1.3 times larger than the forest soil CO₂ respiration (Table 1; *p* < 0.001), while the reverse was found for the dry season (Table 1; *p* = 0.018). The highest soil CO₂ effluxes were measured in June 2019 for sugarcane and in March 2020 for the forest (Fig. 2a), with both periods representing a transition from either wet to dry season (sugarcane) or dry to wet season (forest), and were characterized by moderate WFPS (about 40%; Fig. 1a). Both forest and sugarcane soil CO₂ effluxes positively correlated to WFPS and soil temperature, although, these correlations were weak (Table 2; *p* ≤ 0.05; *r* < 0.5). In contrast, soil CO₂ effluxes from both the forest and sugarcane were negatively correlated to NO₃⁻, and both relationships were similarly weak (Table 2; *p* ≤ 0.05; *r* < 0.5).

Soil CH₄ fluxes exhibited both a high spatial and temporal

variability. Spatially, soil CH₄ uptake varied between an uptake of -94.5 μg C m⁻² h⁻¹ and emission of 15.4 μg C m⁻² h⁻¹ under forest, and an uptake of -128.7 μg C m⁻² h⁻¹ and a release of 80.4 μg C m⁻² h⁻¹ under sugarcane throughout the measurement period. Temporally, soil CH₄ uptake measured in the dry season was two times higher than the soil CH₄ uptake measured in the wet season, both under forest (Fig. 2b; Table 1; *p* = 0.003) and under sugarcane (Fig. 2b, Table 1; *p* < 0.001). Although 5% and 17% of the measured CH₄ fluxes from the forest and sugarcane, respectively, were emissions, the soils at the two sites remained net sinks of CH₄ both in the dry and wet seasons (Table 1). Forest soils were stronger net sinks of CH₄ than the sugarcane soils across the dry and wet seasons (Fig. 2b, Table 1; *p* < 0.001). At both sites, soil CH₄ uptake not only strongly and positively correlated to WFPS (Table 2; *p* ≤ 0.01; *r* > 0.5) but also weakly and negatively correlated to NO₃⁻ (Table 2; *p* ≤ 0.05; *r* < 0.5). There were, however, counteracting and weak responses of soil CH₄ uptake to temperature at the two sites (Table 2; *p* ≤ 0.05; *r* < 0.5), namely negative and positive correlations to temperature in the forest and sugarcane, respectively (Table 2).

Soil N₂O fluxes were equally highly variable in space and time ranging between an uptake of -1.5 μg N m⁻² h⁻¹ and a release of 172 μg N m⁻² h⁻¹ under forest and between an uptake of -12.2 μg N m⁻² h⁻¹ and a release of 61.5 μg N m⁻² h⁻¹ under sugarcane. Although fertilization in the sugarcane resulted in slightly elevated soil N₂O fluxes in the week that followed fertilization (reaching magnitudes of 61.5 μg N m⁻² h⁻¹), soil N₂O fluxes were mostly low for the greater part of the sampling period (Fig. A1, Fig. 2c). Hence, the soils under sugarcane cultivation were a weaker source of N₂O compared to the forest soils (Table 1, Table 3), which were significant emitters of N₂O both in the wet and dry season (Fig. 2c, Table 1, Table 3; *p* < 0.001). Soil N₂O fluxes from the forest did not show a clear seasonal pattern (Fig. 2c, Table 1), so were the soil N₂O fluxes from sugarcane (Fig. 2c, Table 1). Soil N₂O fluxes were positively correlated to WFPS at the two sites, however, this relationship was only strong for the forest (Table 2; *p* ≤ 0.05; *r* > 0.5). Soil N₂O fluxes were negatively and positively correlated to temperature under forest and sugarcane, respectively (Table 2; *p* ≤ 0.05; *r* < 0.5). Similarly, Soil N₂O fluxes were negatively and positively correlated to the NO₃⁻ under forest and sugarcane, respectively (Table 2; *p* ≤ 0.05; *r* < 0.5).

3.2. Carbon stocks in biomass and soil

The forest stored more C in its AGB compartments compared to the fertilized sugarcane (Fig. 3a). Fertilization under sugarcane resulted in increased AGB along the fertilizer intensification gradient (low < standard < high), but significant differences were only detected between high and low fertilization regimes (Fig. 3a). The BGB was also much higher in the case of the forest than the sugarcane (Fig. 3b). However, focussing on fine roots, the sugarcane produced significantly higher stocks for all evaluated soil depths (Fig. 3c). Interestingly, the mean SOC stocks (0–1 m) for all sugarcane plots were significantly higher compared to the mean of all forest plots (26%; Fig. 3d). The largest difference in SOC stocks between sugarcane and forest plots was found for the 0.10 – 0.30 m depth, with a nearly twofold increase in the SOC stocks under sugarcane compared to under forest for this depth

Table 3

Annual soil GHG fluxes based on measurements conducted between May 2019 and June 2020 from the reference forest and sugarcane plantations.

Land use	Annual soil GHG fluxes			Annual soil GWP (Mg CO ₂ -eq ha ⁻¹ yr ⁻¹)			Net soil GWP (Mg CO ₂ -eq ha ⁻¹ yr ⁻¹)
	CO ₂ flux (Mg C ha ⁻¹ yr ⁻¹)	CH ₄ flux (kg C ha ⁻¹ yr ⁻¹)	N ₂ O flux (kg N ha ⁻¹ yr ⁻¹)	CO ₂	CH ₄	N ₂ O	
Forest	14.5 ± 0.1 ^a	-3.1 ± 0.0 ^a	1.8 ± 0.0 ^a	14.5 ± 0.1	-0.09 ± 0.0	0.5 ± 0.0	14.9 ± 0.1
Sugarcane	17.6 ± 0.0 ^b	-1.1 ± 0.0 ^b	0.3 ± 0.0 ^b	17.6 ± 0.0	-0.03 ± 0.0	0.1 ± 0.0	17.7 ± 0.0

Notes: The presented values are means with standard errors (SE). Means followed by different lower-case letters indicate significant differences in the annual soil GHG fluxes between the forest and sugarcane (ANOVA with Tukey's HSD test or Kruskal-Wallis with a multiple-comparison extension test at *p* ≤ 0.05). The annual soil GHG fluxes were based on four reference plots under forest (± SE; *n* = 4) and 12 replicate plots under sugarcane (± SE; *n* = 12). GWP means net global warming potential.

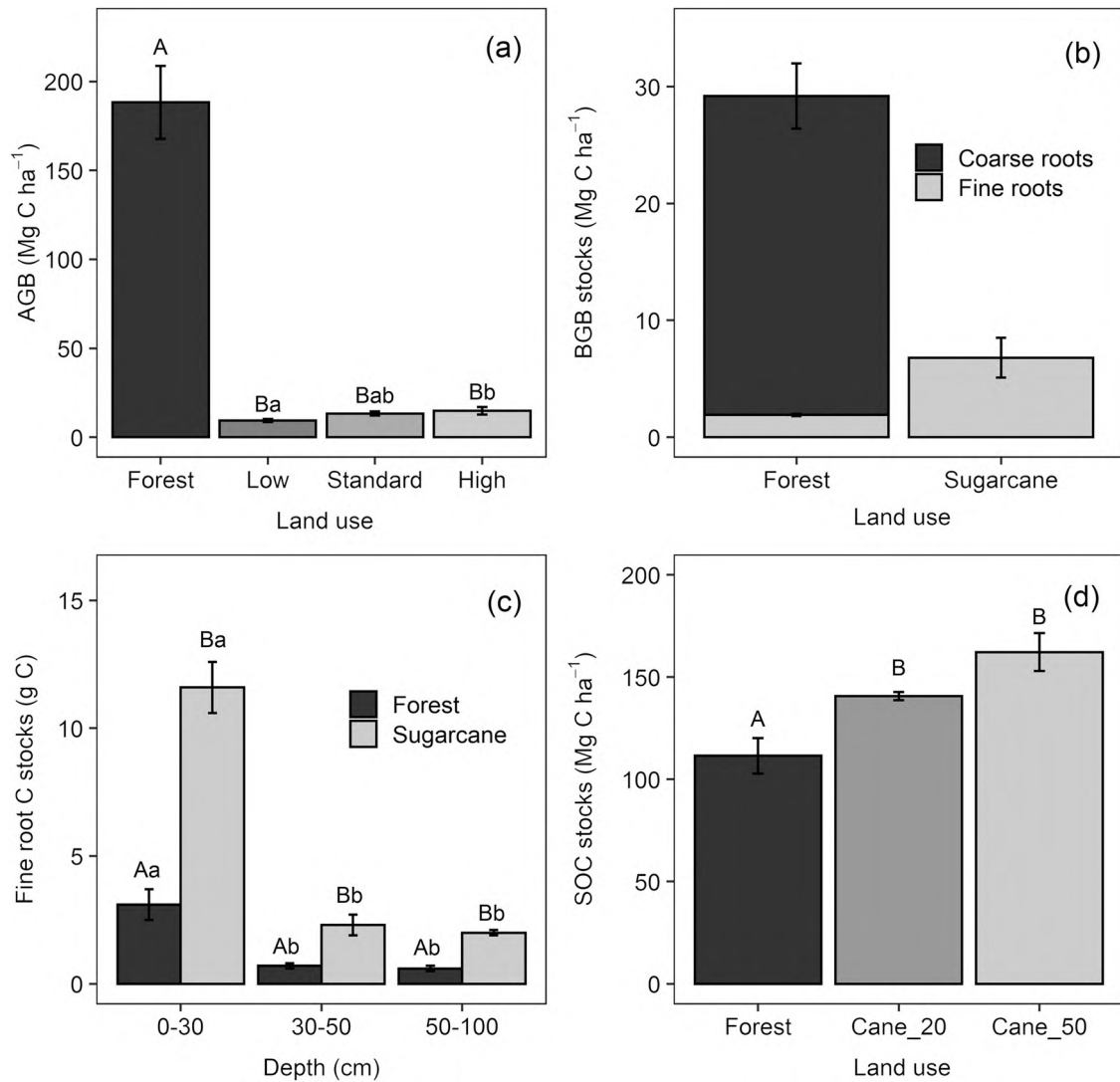


Fig. 3. Mean (\pm standard error, $n = 4$) aboveground biomass (AGB; a), belowground biomass (BGB; b), fine root (c) and soil organic carbon stocks to 1 m depth (SOC; d). Different uppercase letters indicate significant differences between the forest and sugarcane sites while different lowercase letters indicate significant differences either between the sugarcane treatments (Fig. 3a) or different soil depths (Fig. 3c). Low, standard, and high (Fig. 3a) refer to the fertilization treatments of the sugarcane plots. Standard equals to 70 kg N + 23 kg K ha⁻¹ growth cycle⁻¹, low equals to 0.5 times standard, and high equals to 1.5 times standard. Cane_20 and Cane_50 in Fig. 3d stand for 20- and 50-year-old sugarcane fields, respectively.

(Table A2). Even higher SOC stocks were found for older plantations (45%; Fig. 3d).

4. Discussion

4.1. Soil GHG flux dynamics in the reference forest and sugarcane plantations

In this study, soil GHG flux measurements from both the forest and neighboring sugarcane plantations indicate that tropical forest conversion to fertilized sugarcane increases soil CO₂ effluxes (Table 1; Table 3), decreases soil CH₄ uptake (Table 1; Table 3), and significantly affects soil N₂O emissions shortly after fertilization (Fig. A1). The increase in soil CO₂ effluxes under sugarcane relative to the forests is consistent with our first hypothesis, agrees with studies that reported significantly larger soil CO₂ effluxes from cropland compared to the reference forest (Aini et al., 2020; Aryal et al., 2018; Kim and Kirschbaum, 2015), but contrasts those that reported a decrease in soil respiration following tropical land-use change (Verchot et al., 2020; Wanyama et al., 2019). We measured significantly larger soil CO₂ effluxes from the sugarcane

than the forest because of the higher soil C input (via the decay and decomposition of the dense fine root biomass) under sugarcane compared to the forest (Fig. 3). SOC stocks and soil respiration are known to follow first order kinetics (Menichetti et al., 2019; Riggers et al., 2021), hence higher C input to soil would likely result in higher soil respiration rates (Scala et al., 2009). Additionally, ploughing operations in the sugarcane plantations will have exposed the larger SOC stocks to microbial decomposition, especially in the wet season when the soil conditions were warm and moist leading to increased soil CO₂ effluxes (Table 1). Reinsch et al. (2018) found significantly higher soil respiration rates from ploughed grassland plots compared to the control swards, and they attributed this to increased decomposition of the native soil organic matter in the ploughed fields, and the fact that ploughing was done at a time when large amounts of plant residues were standing on the fields. Similarly, we observed that not only did sugarcane farmers in northwestern Uganda retain substantial amounts of residues on their fields (14.6 Mg C ha⁻¹ yr⁻¹; Fig. 4), but also carried out all tillage operations related to weeding at the time when a significant proportion of residues from the previous crop was still present on the fields, leading to higher soil CO₂ effluxes. Furthermore, we postulate that fertilization

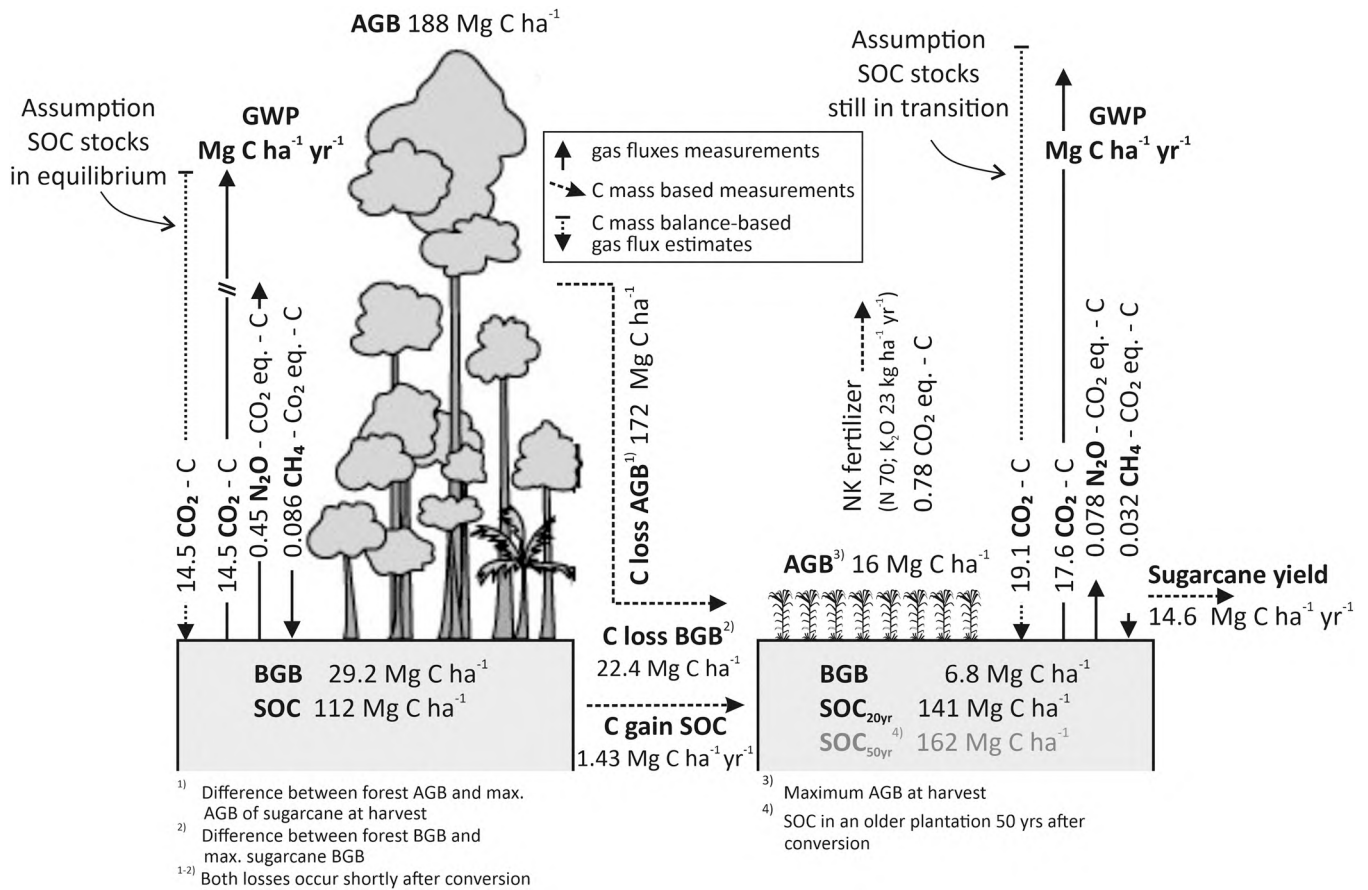


Fig. 4. Schematic illustration of the implication of forest replacement with fertilizer-based sugarcane production on the net ecosystem C fluxes. AGB is aboveground biomass, BGB is belowground biomass, SOC_{20 yr} and SOC_{50 yr} are the soil organic carbon stocks in the sugarcane fields after 20 and 50 years of establishment (deforestation), respectively. The fertilizer application rates, maximum AGB and yield for the sugarcane system represent a typical standard sugarcane system (i.e., Standard equals to 70 kg N + 23 kg K ha⁻¹ growth cycle⁻¹) in northwestern Uganda.

under sugarcane will have enhanced root activity resulting in increased autotrophic respiration by the sugarcane roots (Paradiso et al., 2019; Sun et al., 2017) and increased production of root exudates, which concomitantly stimulated microbial consumption of organic acids in the rhizosphere (Fujii et al., 2021). Surprisingly, in this study, the response of soil CO₂ effluxes to seasonal changes in soil moisture or temperature seemed ecosystem dependent. For instance, under sugarcane, soil CO₂ effluxes measured during the wet season were significantly higher than the dry season (Table 1), mainly because of the higher soil temperatures and moisture for the wet season compared to the dry season (Table 1). However, under forest, soil CO₂ effluxes were unaffected by seasonality-mediated changes in auxiliary controls (Table 1), and we attribute this to the negligible fluctuation in soil temperature throughout the measurement period (Tamale et al., 2021). Furthermore, despite WFPS varying significantly between the dry and wet season, it also remained within the optimal range for soil microbial activity (35–45%; Fig. 1a; Hall et al., 2013; van Straaten et al., 2019), hence did not affect soil CO₂ effluxes as previously reported by Davidson et al. (2000), Itoh et al. (2012), and van Straaten et al. (2011).

The conversion of the tropical forests to sugarcane fields, not only reduced the CH₄ uptake strength of the sugarcane soils (Table 1; Table 3), but also turned them into a CH₄ source under wet conditions (Fig. 2b). These findings confirm the second hypothesis and agree with studies where forest conversion to cropland resulted in lower soil CH₄ uptake (Petitjean et al., 2019; Verchot et al., 2020). Usually, the decline in soil CH₄ uptake in croplands is typically associated with heavy N fertilization (Chen et al., 2021; Oertel et al., 2016) and increased compaction of topsoil due to heavy machinery (Drewer et al., 2021;

Tullberg et al., 2018; Veldkamp et al., 2020). However, we found the contrary. Firstly, N fertilization in the sugarcane did not affect soil CH₄ uptake, probably because the sugarcane soil NH₄⁺ concentrations were too low to interfere with the functioning of methanotrophs. These findings, however, contrast studies that reported either a stimulation (Liu and Greaver, 2009; Shang et al., 2011) or inhibition effect of N fertilization on soil CH₄ uptake (Aronson and Helliher, 2010; Dalal et al., 2008; Ding et al., 2004). Secondly, frequent ploughing in the sugarcane fields did not significantly increase the soil BD there compared to the undisturbed forest. Instead, we measured significantly higher soil BD in the top 30 cm of the reference forest plots (Table A2) than the sugarcane plots. Even then, both the higher BD (Table A2) and the greater WFPS of the forest soils surprisingly did not translate to significantly higher CH₄ production (Table 1; Table 3). We suspect that this was because (1) of the slightly coarser texture of the forest topsoils compared to the sugarcane (Table A2) and (2) that the conversion to sugarcane may have altered the abundance of methanotrophs in the sugarcane soils lowering their CH₄ oxidation potential. With respect to the latter, Täumer et al. (2021) found a higher abundance of *Alphaproteobacteria* microbial communities in the temperate forest than the neighboring grasslands, and as a consequence, forest soils sequestered more CH₄ than the grasslands. We measured higher soil CH₄ uptake in the dry season than in the wet season at both sites (Fig. 2b, Table 1), highlighting the dependence of soil CH₄ uptake on WFPS in well-aerated upland tropical soils (Oertel et al., 2016; Tamale et al., 2021; Wanyama et al., 2019).

Contrary to the third hypothesis, fertilization in the sugarcane only resulted in the expected soil N₂O flush shortly after fertilization (Fig. A1) but did not result in significant differences in soil N₂O fluxes among the

treatments of the sugarcane CRD experiment. Equally unexpected were the significantly lower soil N_2O fluxes from the fertilized sugarcane plots compared to the reference forest (Table 1; Table 3). While the soil N_2O flush shortly after fertilization in our study (Fig. A1) was consistent with the findings of Allen et al. (2010) and Wang et al. (2016) conducted in the Australian sugarcane fields, we measured much lower annual soil N_2O fluxes compared to Allen et al. (2010) and Wang et al. (2016). We postulate that this was due to the much higher N fertilization rates used in these studies ($80\text{--}200\text{ kg N ha}^{-1}$) compared to our study ($35\text{--}105\text{ kg N ha}^{-1}$). Besides the disparity in fertilization rates among these studies, we also attribute the unexpectedly low soil N_2O fluxes from our fertilized sugarcane fields to the likely leaching of the added N fertilizer (given the sandy texture of the soils; Table A2) or its immediate uptake by the vigorously growing sugarcane crop potentially reducing N_2O emissions. The latter was indeed corroborated by the measured increase in the aboveground biomass along the fertilizer intensification gradient (low < standard < high; Fig. 3a), potentially explaining why both the sugarcane soil NO_3^- contents and N_2O fluxes remained significantly lower than the forest (Fig. 1c, Fig. 2c, Table 1). Furthermore, we suspect that surface application of urea fertilizers without subsequent incorporation into the soil likely exposed the added N fertilizers to ammonia volatilization thereby removing excess N for de (nitrification) processes. Separate studies by Li et al. (2015) and Schwenke et al. (2014) reported a 30% loss of the added N fertilizers to ammonia volatilization, and attributed this to the surface placement of these N fertilizers. Although the hole-in-the-pipe conceptual model suggests that soil N_2O fluxes are limited by both soil water content and N availability (Davidson and Verchot, 2000), soil N_2O fluxes from both the forest and sugarcane fields did not respond to seasonal variation in WFPS and soil NO_3^- contents (Table 1). We think that this was due to counteracting responses in both soil WFPS and nitrate contents during the wet and dry seasons in the forest. It is evident that soil WFPS increased during the wet season and declined during the dry season while soil NO_3^- content declined during the wet season and increased during dry season (Fig. 1a, Table 1). However, under sugarcane, background soil NO_3^- contents were consistently too low throughout the measurement period (Fig. 1c) to significantly affect N_2O fluxes (Fig. 2c). Notably, however, the measured soil N_2O fluxes under sugarcane positively correlated to both WFPS and soil nitrate content (Table 2) as similarly reported by Butterbach-Bahl et al. (2013) and Davidson and Verchot (2000).

4.2. Implications of forest-sugarcane conversion for global change

Deforestation for sugarcane cultivation results in a large immediate release of C stored in forest AGB as much of the standing biomass is cut down or burnt (172 Mg C ha^{-1} ; Fig. 4). This is subsequently followed by the gradual decomposition of forest BGB in the years after forest clearing (22.4 Mg C ha^{-1} ; Fig. 4). Once converted to sugarcane, soil CH_4 uptake rapidly declines relative to the forest (Table 3). At the same time, C is sequestered by the growing sugarcane, but this sequestration is short lived as it is again released to the atmosphere ($14.6\text{ Mg C ha}^{-1}\text{ yr}^{-1}$; Fig. 4) when the sugarcane is harvested (at about 18 months) and processed. Equally remarkable though unexpected, are the significantly larger SOC stocks in both the 20- and 50-year-old sugarcane plantations compared to the forest (Fig. 3d). We had expected that SOC stocks would decline after deforestation because there will be reduced litter input to soils (Guo and Gifford, 2002). Further, the warmer soil temperatures and tillage activities (to 30 cm) in sugarcane will certainly have increased the vulnerability of both the old and new SOC stocks to microbial decomposition (Six et al., 1998). Instead, we measured a 26–44% increase in SOC stocks in the sugarcane plantations in comparison to the forest (Fig. 3d). On the one hand, we suspect that the net SOC accumulation in sugarcane reflects: (1) slower leaf litter decomposition rates

because sugarcane leaves have a higher C:N ratio than the forest litter, and (2) increased root productivity will result in increased allocation of C to the root network (Anderson-Teixeira et al., 2013). On the other hand, the 15% difference in SOC stocks (21.5 Mg C ha^{-1} ; Fig. 3d) between the 20- and 50-year-old sugarcane plantations likely suggests that the SOC stocks under sugarcane were not yet in equilibrium. These results imply that the SOC stocks in sugarcane may take several decades after deforestation before they reach a new SOC equilibrium, which contrasts some studies that reported 10–20 years for the equilibration of SOC stocks under converted land uses (de Blécourt et al., 2013; van Straaten et al., 2015). However, due to the lack of other constraining data to identify the source and age of C in soil along the conversion gradient, we cannot finally verify this interpretation. It is equally possible that our results of increasing SOC stocks are in fact not related to C increases after conversion to sugarcane, but rather a selective preservation of forest SOC on low fertility agricultural fields (Cadisch et al., 1996).

5. Conclusions

Tropical deforestation is assumed to represent a significant anthropogenic source of soil-borne GHG emissions. However, soil GHG flux estimates for the deforestation hotspots in tropical Africa are still limited. It was for this reason that we measured soil GHG fluxes along with their potential auxiliary controls from four reference forest plots and 12 replicate plots of a CRD experiment in the 20-year-old sugarcane plantation in northwestern Uganda. Despite the use of different fertilizer application rates (low, standard, and high) as treatments for the sugarcane CRD experiment, no significant differences were detected in both the auxiliary controls and soil GHG fluxes among the CRD treatments. This was largely because, the applied fertilizers were immediately taken up by the vigorously growing sugarcane crop, which is also consistent with the measured increase in the sugarcane aboveground biomass along the fertilizer intensification gradient (low < standard < high). Soil CO_2 effluxes were larger in the sugarcane fields compared to the native forest because of the likely exposure of the sugarcane's surprisingly larger SOC stocks to microbial decomposition and the increased autotrophic respiration from its high fine root biomass. The forest soils were a stronger net sink of CH_4 than the sugarcane soils despite them (forest soils) having both higher bulk densities and larger water filled pore space (WFPS). Although there was a marginal increase in both the soil NO_3^- content and N_2O emissions in the two weeks that followed fertilization in the sugarcane, this never matched the already stronger net release of N_2O from the forest soils given their inherently larger N cycling rates. Only seasonal variability in WFPS, among the auxiliary controls, affected CH_4 uptake at both sites and soil CO_2 effluxes in the sugarcane. Noteworthy, soil N_2O fluxes from both sites were unaltered by seasonality. Overall, the study highlights that even in the case of increased SOC sequestration under the sugarcane fields (as indicated in this study) and the lower N_2O emissions compared to the forest sites, the forest-sugarcane conversion leads to a substantial C loss to the atmosphere. This is because such a land use shift results in an immediate loss of a significant amount of C stored both in the above and belowground biomass of the forest, followed by increased emission of CO_2 (soil respiration, fertilizer use and harvest) and reduced uptake of CH_4 under sugarcane on the long term.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Appendix [Fig. A1](#) and [Tables A1](#) and [A2](#).

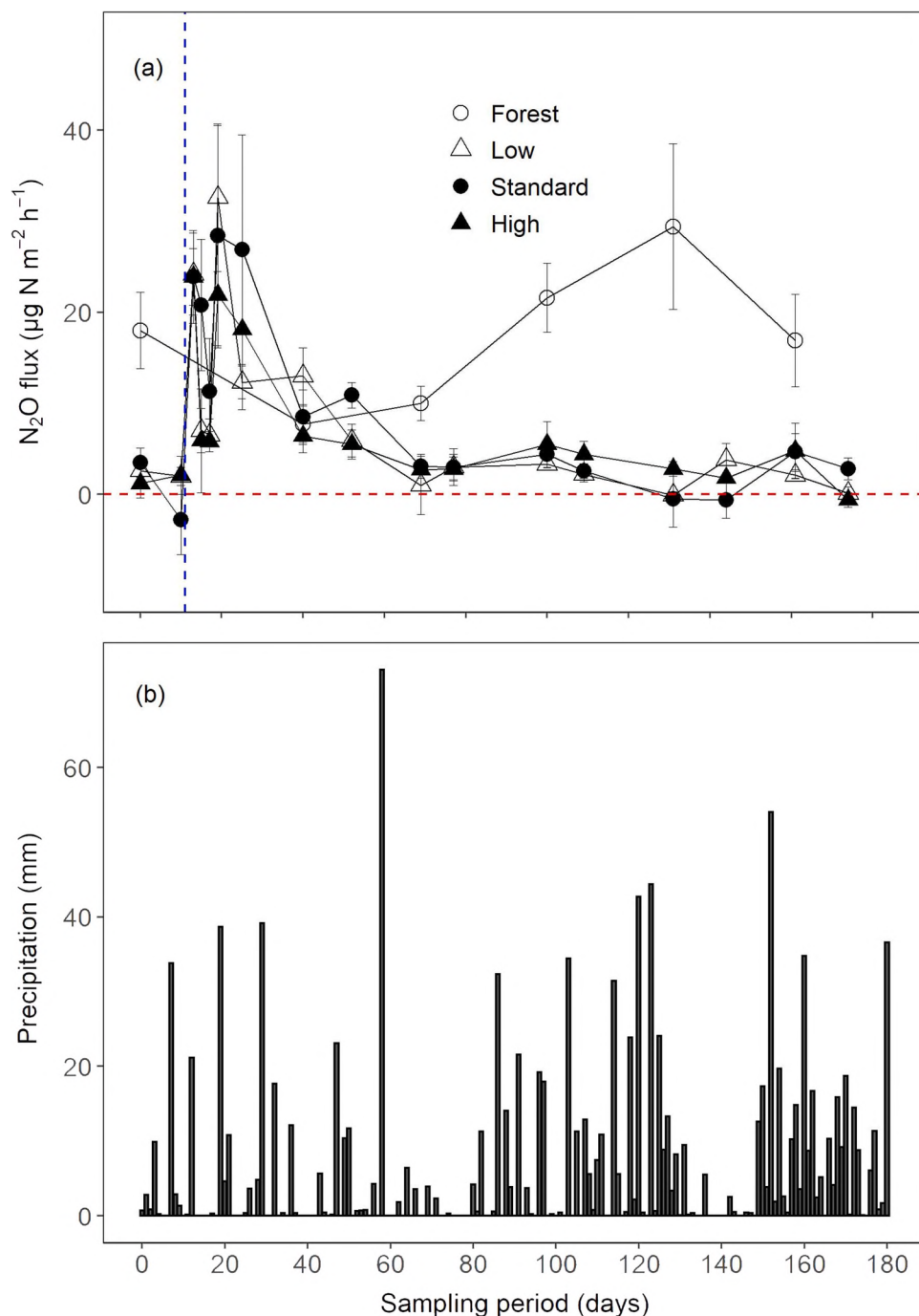


Fig. A1. Mean soil N_2O fluxes (a) measured between May and October 2019 from the reference forest plots and replicate treatment plots of the complete randomized design (CRD) experiment established in the 20-year-old sugarcane plantation, and the bars (b) represent the daily precipitation measured between May and October 2019 from both the forest reference plots and sugarcane plots. The mean soil GHG fluxes in window “a” result from four plots per treatment for every sampling time point. The dashed vertical blue line indicates the timing of the application of the single combined dose of urea and muriate of potash fertilizers in the sugarcane. The dashed horizontal line indicates the background level of the soil N_2O fluxes from both the reference forest and sugarcane plots. Standard equals to $70 \text{ kg N} + 23 \text{ kg K ha}^{-1} \text{ growth cycle}^{-1}$, low equals to 0.5 times standard and high equals to 1.5 times standard.

Table A1
Site-specific topographic, geological, soil and climatic characteristics.

Site	Elevation (m.a.s.l.)	Slope ^a (%)	Geology ^d	Soil type ^b	Precipitation ^c (mm)	Air temperature ^c (°C)
Forest	1058	< 5	Precambrian basement complex comprising of granite and gneisses	Haplic Ferralsols to Xanthic Lixisols	2321	23.1 ± 0.0
Sugarcane	1064	< 5	Precambrian basement complex comprising of granite and gneisses	Pisoplinthic Rhodic Ferralsols	2291	22.7 ± 0.1

^a Slope extracted from a 30 m digital elevation model obtained from the Department of Geology, Ministry of Lands and Survey, Entebbe, Uganda.

^b Soil classification according IUSS Working Group WRB (2014).

^c Climatic data for the gas-sampling period (May 2019 to June 2020) obtained from climatic weather stations installed about 2 km and 0.2 km from the forest and sugarcane sites, respectively.

^d Lehto et al. (2014).

Table A2
Soil physico-chemical characteristics (mean ± SE) of the reference forest and sugarcane study sites in northwestern Uganda.

Depth (cm)	Bulk density (g cm ⁻³)	TOC (Mg ha ⁻¹)	TON (Mg ha ⁻¹)	pH (H ₂ O)	C:N	Soil texture		
						Sand (%)	Silt (%)	Clay (%)
Forest (n = 4)								
0–10	1.3 ± 0.1 ^a	40.2 ± 3.9 ^a	4.1 ± 0.3 ^a	7.2 ± 0.2 ^a	9.7 ± 0.1 ^a	59 ± 0	29 ± 0	12 ± 0
10–30	1.6 ± 0.0 ^a	30.9 ± 4.9 ^a	1.9 ± 0.2 ^a	6.8 ± 0.2 ^a	8.0 ± 0.4 ^a	–	–	–
30–50	1.2 ± 0.0	14.0 ± 2.3 ^a	1.0 ± 0.1 ^a	6.0 ± 0.3	7.7 ± 0.2 ^a	–	–	–
50–100	1.3 ± 0.0 ^a	26.4 ± 2.2 ^a	0.6 ± 0.1 ^a	5.9 ± 0.4	8.4 ± 0.3 ^a	46 ± 2	25 ± 1	29 ± 0
Sugarcane (n = 12)								
0–10	1.1 ± 0.0 ^b	29.0 ± 0.7 ^b	1.9 ± 0.0 ^b	5.5 ± 0.1 ^b	14.8 ± 0.2 ^b	45 ± 0	34 ± 0	21 ± 0
10–30	1.2 ± 0.0 ^b	49.0 ± 1.0 ^b	3.4 ± 1.1 ^b	5.5 ± 0.0 ^b	14.4 ± 0.2 ^b	–	–	–
30–50	1.2 ± 0.0	26.7 ± 1.2 ^b	2.3 ± 0.1 ^b	5.5 ± 0.0	11.7 ± 0.2 ^b	–	–	–
50–100	1.1 ± 0.1 ^b	36.1 ± 2.0 ^b	3.5 ± 0.1 ^b	5.4 ± 0.1	10.4 ± 0.0 ^b	45 ± 1	19 ± 0	36 ± 1

Notes: Different lowercase letters indicate significant differences between the two land uses (ANOVA with Tukey's HSD test or Kruskal-Wallis with a multiple-comparison extension test at $p \leq 0.05$). TOC means total organic carbon and TON means total organic nitrogen

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