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WETLAND BIOGEOCHEMISTRY

Effects of Water Table Fluctuation on Greenhouse Gas Emissions from Wetland Soils in the Peruvian Amazon

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Abstract

Amazonian swamp forests remove large amounts of carbon dioxide (CO_2) but produce methane (CH_4). Both are important greenhouse gases (GHG). Drought and cultivation cut the CH_4 emissions but may release CO_2. Varying oxygen content in nitrogen-rich soil produces nitrous oxide (N_2O), which is the third most important GHG. Despite the potentially tremendous changes, GHG emissions from wetland soils under different land uses and environmental conditions have rarely been compared in the Amazon. We measured environmental characteristics, and CO_2, CH_4 and N_2O emissions from the soil surface with manual opaque chambers in three sites near Iquitos, Peru from September 2019 to March 2020: a pristine peat swamp forest, a young forest and a slash-and-burn manioc field. The manioc field showed moderate soil respiration and N_2O emission. The peat swamp forests under slight water table drawdown emitted large amounts of CO_2 and CH_4. A heavy post-drought shower created a hot moment of N_2O in the pristine swamp forest, likely produced by nitrifiers. All in all, even small changes in soil moisture can create hot moments of GHG emissions from Amazonian wetland soils, and should therefore be carefully monitored.

Keywords Carbon dioxide · Greenhouse gas · Laughing gas · Methane · Nitrous oxide · Peat · Peatland · Tropical · Tropics

Resumen

Los bosques pantanosos amazónicos eliminan grandes cantidades de dióxido de carbono (CO_2) pero producen metano (CH_4). Ambos son importantes gases de efecto invernadero (GEI). La sequía y el cultivo reducen las emisiones de CH_4 pero pueden liberar CO_2. La variación del contenido de oxígeno en los suelos ricos en nitrógeno produce óxido nitroso (N_2O), que es el tercer GEI más importante. A pesar de los enormes cambios potenciales, las emisiones de GEI del suelos de los humedales bajo diferentes usos de la tierra y condiciones ambientales rara vez se han comparado en la Amazonía. Medimos las características ambientales y las emisiones de CO_2, CH_4 y N_2O de la superficie del suelo con cámaras opacas manuales en tres sitios cerca de Iquitos, Perú, de septiembre de 2019 a marzo de 2020: un bosque pantanoso de turba prístino, un bosque joven y un campo de yuca de talado y quemado. El campo de yuca mostró una respiración moderada del suelo y emisión de N_2O. Los bosques pantanosos de turba con un ligero descenso del nivel freático emitieron grandes cantidades de CO_2 y CH_4. Una fuerte lluvia posterior a la sequía creó un momento caliente de N_2O en el bosque pantanoso prístino, probablemente producido por nitrificantes. Endefinitiva, incluso pequeños cambios en la humedad del suelo pueden crear momentos calientes de emisiones de GEI de los suelos de los humedales amazónicos y, por lo tanto, deben monitorearse cuidadosamente.

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Introduction

Peatlands are an enormous sink of carbon and nitrogen (Leifeld and Menichetti 2018; Loisel et al. 2021). Natural and human disturbances may release them as greenhouse gases (GHG). The issue is particularly acute in tropical peatlands (IPCC 2019). The Amazon has the largest area of tropical peatlands (Leifeld and Menichetti 2018; Ribeiro et al. 2021). Most of them are isolated from major population centres and roads, and thus inaccessible to logging and agriculture (Lilleskov et al. 2019). C sequestration dominates the GHG balance in natural peat swamps (Frolking and Roulet 2007) whereas disturbances increase GHG emissions (Turetsky et al. 2014; IPCC 2019). In the Amazon, drought is a quickly increasing ecosystem change which is shortening the growth period and imposing tree decline (IPCC 2019). Droughts increase ecosystem respiration (Karhu et al. 2014; Jassey et al. 2021). Specifically, fungi and other microbes that respire much of the CO_2 rapidly acclimatise with the rising temperature which may send the ecosystems down a positive feedback loop (Karhu et al. 2014; Jassey et al. 2021). Thus, drought-induced tree mortality is saturating the Amazon C sink (Hubau et al. 2020). Undisturbed, i.e. permamently waterlogged peat swamp forests accumulate carbon (C) in the peat for tens of thousands of yr (Ruwaimana et al. 2020). However, during dry seasons in a Peruvian peat swamp forest, ecosystem respiration exceeds gross primary production by a steady average of 600 mg C day^{-1} even when the peat remains wet (Griffis et al. 2020). Overall, the impact of water table fluctuations on tropical peatland C balances is unclear and therefore needs research.

Anoxic decomposition of peat under high water table yields methane (CH_4; Teh et al. 2017; Hergoualc'h et al. 2020), a potent greenhouse gas with a global warming potential of 28 CO_2 equivalents (IPCC 2019). The CH_4 produced in a peat layer moves to the topsoil where it can be consumed by methanotrophs or emitted either through the peat or conducted through plants (Soosaar et al. 2022). Therefore, hydroclimate and biogeochemistry of the different peat layers, as well as vegetation type and land use are potential factors of CH_4 emissions in tropical peatlands.

Suboxic processes in nitrogen-rich peat under intermediate (50 to 60%) water content produce nitrous oxide (N_2O; Melillo et al. 2001; Jauhiainen et al. 2012; Rubol et al. 2012; Hu et al. 2015; Pärn et al. 2018; Hergoualc'h et al. 2020). The 5.4 million km^2 Amazon rainforest is the ecosystem with the largest N_2O emissions in the world (Ricaud et al. 2009) producing 1,300 Gg N_2O-N yr^{-1} (Melillo et al. 2001). Brazil is a major contributor to the global increase in N_2O emissions, owing to the increase in nitrogen (N) fertilisation (Thompson et al. 2019). Contribution of swamp forests to the Amazonian N_2O emissions is poorly known (van Lent et al. 2015; Guilhen et al. 2020). A Peruvian palm peat swamp emitted 0.5 to 2.6 kg N_2O-N ha^{-1} yr^{-1} (van Lent et al. 2015) and similar swamp forests in Southeast Asia emitted 2.7 ± 1.7 kg N_2O-N ha^{-1} yr^{-1} (average ± standard deviation; van Lent et al. 2015). However, sources of N_2O (nitrate (NO_3^-) or ammonium (NH_4^+) and their vulnerability to climatic changes, such as water table, oxygen (O_2) and temperature fluctuations, are unclear and need investigation. Denitrification by the sequential reduction of NO_3^- is the most important mechanism behind N_2O production and emission (Butterbach-Bahl et al. 2013; Liengaard et al. 2014; Hu et al. 2015). This has been identified from N_2O profiles and porewater nitrogen forms in wetting experiments on intact soil cores (Butterbach-Bahl et al. 2013; Liengaard et al. 2014; Hu et al. 2015). N_2O is an intermediate product of the denitrification process in either suboxic soil or under varying O_2 availability both in time and between anoxic soil aggregates and air-filled pores (Butterbach-Bahl et al. 2013; Hu et al. 2015). Only after depletion of NO_3^- is N_2O reduced to inert N_2, as Liengaard et al. (2014) observed in denitrification potential incubations of soil from the Brazilian Amazon. However, nitrification, the sequential oxidation of NH_4^+ to NO_3^- is an exceptionally important source of N_2O (10% of N_2O production) in the Amazon (Inatomi et al. 2019). Hergoualc'h et al. (2020) identified nitrifier denitrification as the probable source process for the high N_2O emission in a Peruvian palm peat swamp forest. Thus, evidence on N_2O source mechanisms and on its denitrification potential reduction to inert N_2 (measured in soil incubations) in the tropics is scarce and contradicting. In addition, studies on mineral soil are unreliable for climate change effects on peatlands for their essentially different hydrology and biogeochemistry (Rydin and Jeglum 2013). In peatlands, water table stays above or near the ground surface throughout the dry season, protecting the carbon and nitrogen stocks (Turetsky et al. 2014). Peatland clearing, commonly with fire, renders the peat carbon and nitrogen stocks vulnerable (Turetsky et al. 2014; Lilleskov et al. 2019). Few studies have compared greenhouse gas fluxes across a variety of land uses and water table fluctuations in former and current Amazonian swamps. No study reports O_2 content values in relation to the greenhouse gas fluxes including denitrification potential.

We set an objective to identify environmental drivers of soil respiration, and CH_4 and N_2O production and consumption rates across a common gradients of land use in the Peruvian Amazon peatlands – from pristine peat swamp forest through a secondary forest to arable land – with according differences in soil chemistry and water table. Our specific research questions tested the importance of chemical resources (such as organic C, total N, NH_4^+, NO_3^-) and climatic fluctuations (in temperature, water table, soil moisture and O_2) for soil respiration, and the CH_4 and N_2O fluxes.

Materials and Methods

We measured fluxes of the three GHGs using opaque soil chambers and environmental factors of the GHGs in three current or former swamps with the *Mauritia flexuosa* palm under various disturbance histories (Fig. 1): 1 — 'Swamp', a wet peat swamp forest in the Quistococha lake floodplain (6 m peat, – 0.03 to – 0.125 m water table during the campaigns; see Roucoux et al. 2013 for detailed physical description) located at 3°50'03.9" S, 73°19'08.1" W, 2 — 'Slope', a 12-year old secondary swamp forest grown over a fallow pasture and banana plantation on an alluvial toe slope (0.1 to 0.3 m organic layer; – 0.09 to – 0.70 m water table toposequentially) 3°50'10.7" S, 73°21'45.0" W and 3 — 'Manioc', a slash-and-burn cultivated manioc (*Manihot esculenta*) field (0.03 to 0.15 m peat; – 2 m water table drawn down by the nearby stream channel and further dried by the burn clearing of forest and hand tillage of soil, no fertiliser), 3°51'00.0" S, 73°22'45.8" W. Regionally, rainfall is most pronounced during the 6-month January–June period, with peaks in March–April (Madigosky and Vatnick 2000). Rainfall diminishes sharply during April, with further decline during the next two months. The lowest period of rainfall is July–September (average of 572 cm yr^{-1}). Droughts or periods without rainfall can last for up to 7 consecutive days and dry days can occur for up to 20 days in a single month. In the rainy season (January–June), dry spells are typically much shorter and may last only two days. Although unusual, rainfall can be absent up to 15 days a month (Madigosky and Vatnick 2000).

At the 'Slope' and 'Manioc' sites, we established three toposequent stations at an interval of 15 m with 1.5 m elevation difference between the sequent stations. Water table in the 'Slope' forest varied between – 0.09 and – 0.13 m at the bottom of the transect, between – 0.115 and – 0.15 m at the middle and around – 0.7 m at the upper station. Each station received three chambers three to five meters apart from each other. The 'Swamp' site was located in a flat terrain. Due to a flat uniform terrain, we organised the chambers in the 'Swamp' site in no stations or particular sequence to topographic features. CO_2, CH_4 and N_2O gas concentrations were sampled using the static chamber method with PVC collars of 0.5 m diameter and 0.1 m depth installed in the soil. The inside of collars at the 'Slope' site was covered with sparse < 0.2 m tall *Pteridaceae* ferns while the collars in the 'Swamp' and 'Manioc' sites contained no plants. We used white 65 L PVC truncated conical gas sampling chambers. We did not use extra cover against sunlight but the chamber design is generally regarded as opaque (Hutchinson and Livingston 1993). We calculated individual CO_2, CH_4 and N_2O fluxes using changes in concentration during one hour within the chamber. Gas concentration was

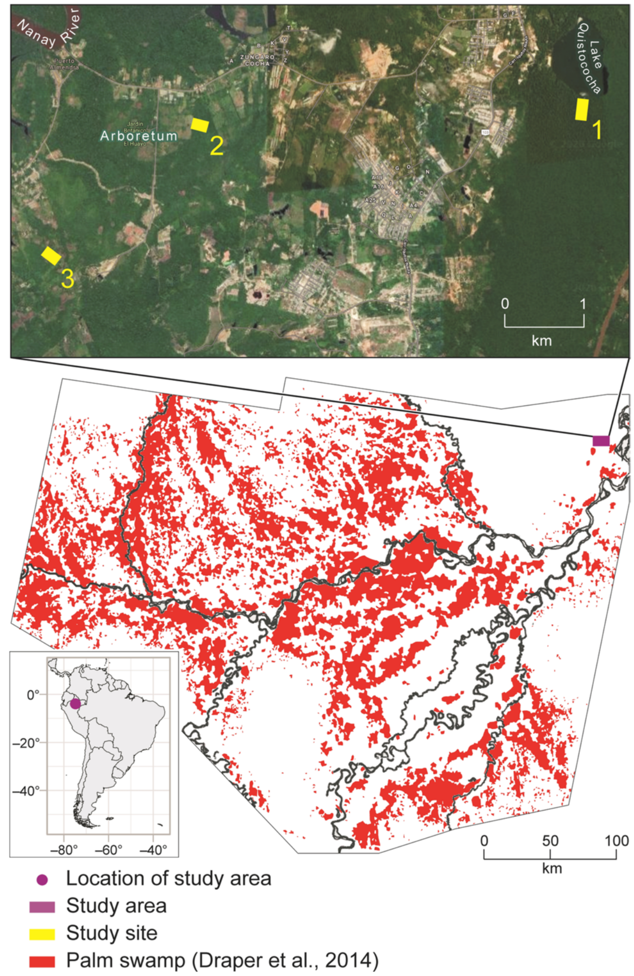

Fig. 1 Location of study sites (1 – 'Swamp', 2 – 'Slope', and 3 – 'Manioc') and distribution of palm swamp forests in the Pastaza-Marañon Basin (data from Draper et al. 2014). Background image for the site location map above – © Google Maps

measured at 20 min intervals (0, 20, 40 and 60 min). The fluxes were measured between 8 and 11 am to represent the average diurnal emissions (according to Figs. 11 and 12 in Griffis et al. 2020). We conducted 9 flux measurements in the 'Swamp' forest (10 collars) from September 2019 to March 2020, four flux measurements in the 'Slope' forest (9 collars) in September 2020 and 9 flux measurements in the 'Manioc' field (9 collars) from September 2019 to March 2020 according to the schedule presented in Table 1. We used five chambers, which we moved between the collars. Before the first sampling in September, young manioc saplings had been planted. By 15 February, they had grown to 3 m height covering the whole field with a sparse canopy (< 30% shading). No manioc plant grew directly out of the stationary gas sampling collars at any time. The manioc was harvested in late February, leaving a bare field for the March sampling. The gas samples were transported to a laboratory at the University of Tartu and analysed by gas chromatography (GC-2014; Shimadzu, Kyōto, Japan) instrumented with an electron capture detector for detection of N_2O and a flame ionisation detector for CH_4, and Loftfield-type autosamplers. An individual gas flux was determined on the basis of linear regression obtained from consecutive concentrations (Hutchinson and Livingston 1993). We closely examined the shape of our gas concentration trends in each individual chambers. Practically all significant deviations from a linear trend were apparently caused by a faulty chamber sealing. We did not observe any signs of ebullition such as jump rises in concentration not followed by a drop in concentration. An only small share of ebullition may be a peculiarity of our long chamber closing time of 1 h. A p level of < 0.05 was accepted for the goodness of fit to linear regression. Out of 216 flux measurements, 14 failed to pass the quality check. Insignificant fluxes ($p > 0.05$) below the accuracy of gas chromatograph (regression change of gas concentration $\delta v < 10$ ppb) were included in the analysis as zeros.

Each station was equipped with a 1 m deep observation well (a 0.05 m perforated PP-HT pipe wrapped in filter textile). Water table height was recorded from the observation wells during the gas sampling. Soil moisture was measured with a GS3 sensor connected to a ProCheck handheld reader (Decagon Devices, Pullman, WA, USA). Soil temperature was measured between 0.1 and 0.4 m depth at an interval of 0.1 m. Soil oxygen (O_2) content was measured with a stand-alone fibre optic oxygen meter (PreSens, Regensburg, Germany) at 0.05 m and 0.005 m depths in September and March.

Table 1 Time schedule of flux measurements in all collars of each study site. X marks a 1-hour flux measurement

Date	Swamp	Slope	Manioc
16.09.2019	X		
17.09.2019	X		
19.09.2019		XX	
20.09.2019		XX	
21.09.2019			XX
22.09.2019			XX
24.09.2019	X		
25.09.2019	X		
04.01.2020			X
11.01.2020	X		
18.01.2020			X
25.01.2020	X		
04.02.2020			X
08.02.2020	X		
15.02.2020			X
22.02.2020	X		
02.03.2020			X
03.03.2020			X
04.03.2020	X		

A 200 g soil sample was collected from each chamber between 0 and 0.1 m depth after the gas flux measurements in September and March. The soil samples were stored and transported at 5 °C to the Estonian University of Life Sciences. At the laboratory, plant-available (KCl extractable) phosphorus (P) was determined on a FIAstar 5000 flow injection analyser (FOSS, Hilleroed, Denmark; Ruzicka and Hansen 1981). Plant available potassium (K) was determined from the same solution by the flame-photometric method, and plant available magnesium (Mg) was determined from a 100 mL ammonium acetate solution with a titanium-yellow reagent on the flow injection analyser (Ruzicka and Hansen 1981). Calcium (Ca) was analysed using the same solution by the flame photometrical method (Ruzicka and Hansen 1981). Soil pH was determined on a 1 N KCl solution. Soil ammonium (NH_4^+) and nitrate (NO_3^-) contents were determined on a 2 M KCl extract of soil by flow-injection analysis (Ruzicka and Hansen 1981). Total N and C contents of oven-dry samples were determined using a dry combustion method on a varioMAX CNS elemental analyser. The soil organic matter (SOM) content of the oven-dry samples was determined by loss on ignition at 360° C.

To measure potential N_2O and molecular nitrogen (N_2) fluxes with the He–O_2 soil incubation technique (Espenberg et al. 2018) at our laboratory in Tartu, Estonia, we collected intact soil cores (0.068 m diameter, 0.06 m height) from the top 0.1 m from each chamber after the last gas flux measurements in September and March. The soil cores were stored and transported at 5 °C. The cylinders with the intact soil cores were placed into special gas tight incubation vessels in a climate-controlled space (own design). Gases were removed by flushing with an artificial gas mixture (21.0% O_2, 358 ppm CO_2, 0.313 ppm N_2O, 1.67 ppm CH_4, 5.97 ppm N_2 and the rest He). The new atmosphere equilibrium was kept by continuously flushing the vessel headspace with the artificial gas mixture at 20 mL per min was established after 12–24 h. The flushing time depended on the soil moisture. The temperature was kept similar to the field temperature during the incubation. Concentrations of N_2O and N_2 were analysed by the GC-2014 (Shimadzu, Japan). Flux rates were calculated from the actual gas concentration of the continuous flow rate from the vessel headspace after subtraction of a blank value from a vessel without a soil core, which is equivalent to concentrations from the artificial He–O_2 gas mixture.

We tested normal distribution of the samples by the Kolmogorov–Smirnov and Shapiro–Wilk's tests using the *stats* package in R. As data for most of the sites were not normally distributed (p > 0.05), we analysed relationships between the GHG fluxes and environmental characteristics by the nonparametric generalised additive models (GAM) usinge the simplest smoothing term (k = 3) in the *mgcv* package in R, and principal component analysis (PCA) using the *stats* package in R. For each cluster of replicate measurements we plotted a normal data ellipse with size defined as a normal probability equal to 0.68. Significance of differences between sites was checked by the unpaired two-sided Wilcoxon rank sum test (the *wilcox.test* function, *stats* package in R).

Results and Discussion

The PCA separated our three sites along gradients of soil respiration, CH_4 and N_2O fluxes (see detailed results in the next sections) and along physicochemical gradients (Fig. 2). Most clearly, the breaks between sites followed a water table gradient as well as soil O_2, temperature and NO_3^- content gradients. The waterlogged swamp peat did not contain a detectable amount of NO_3^-. As no fertiliser was added on our sites (see Methods), the high NO_3^- level in the manioc field was probably produced by nitrification induced by the slash-and-burn and subsequent water-table drawdown. Within the sites, the PCA distinguished the gas-sampling chambers along a soil nutrient gradient (Ca, Mg, pH, P, total N, NH_4^+) independent from the water table changes. The nutrients may have enhanced heterotrophic CO_2 and N_2O production. Within-site differences in water table and macronutrients were still remarkable. In the 'Swamp' forest, water table varied from − 0.12 to − 0.085 m in mid-September, rose to − 0.03 m after a 30 mm shower 6 h before the 24 September session and dropped to − 0.07 m during the next dry day. From January to March, it was steadily − 0.03 m. Soil O_2 content remained < 0.1 mg L^{-1} at both 0.005 and 0.05 m depth throughout the observations.

The dry station (water table − 0.7 m; soil water content 0.26 m^3 m^{-3}; soil temperature around 26 °C at 10 cm depth) of the 12-year old 'Slope' swamp forest respired the

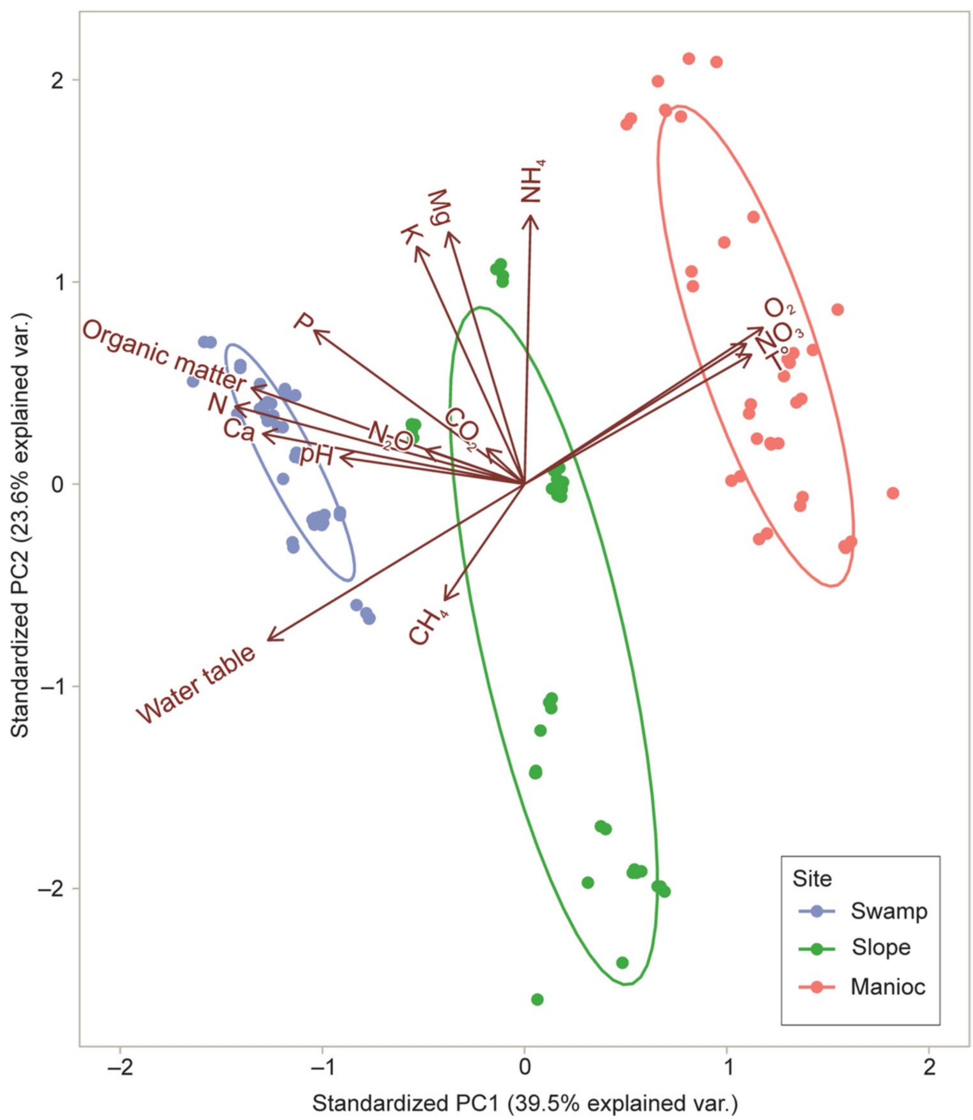

Fig. 2 Principal component analysis (PCA) of GHG fluxes and environmental characteristics in September 2019. Each data point represents one GHG flux replicate measurement. A normal data ellipse is shown around points from each site

largest amount of CO_2 (session averages of 130 to 210 mg C m^{-2} h^{-1}). That station apparently represents the optimal moisture for soil respiration (Byrne et al. 2005; Balogh et al. 2011). The respiration declined with the increase in the water table (session averages of 43 to 91 mg C m^{-2} h^{-1} at the wettest station). The dry 'Manioc' field with higher soil temperature (soil water content 0.15 to 0.24 m^3 m^{-3}; soil temperature 26 to 34 °C at 0.1 m depth during all months) respired 75 to 98 mg C m^{-2} h^{-1} steadily throughout the study period (Fig. 3a). The anoxic 'Swamp' peat (soil dissolved O_2 content < 0.1 mg L^{-1} at both 0.005 and 0.05 m depth) respired 49 to 150 mg C m^{-2} h^{-1} at session average in negative linear relationship with water table (Fig. 4). Two alternative sources of the respiration at high soil water content (> 0.8 m^3 m^{-3}) and no dissolved O_2 in the soil (< 0.1 mg L^{-1} at both 0.005 and 0.05 m depth from 24 September onward). For one, anaerobic CO_2 production from dissolved organic matter diverted from methanogenesis (Heitmann et al. 2007). Second, the aerenchymous palm roots may have provided O_2 in the deeper soil zones (van Lent et al. 2019).

The wet 'Swamp' forest floor emitted session averages of 530 to 9,100 µg CH_4-C m^{-2} h^{-1} (Fig. 3b) owing to the high −0.03 to −0.125 m water table (in agreement with Hergoualc'h et al. 2020). This was less than the 43,000 µg CH_4-C m^{-2} h^{-1} (of mostly ebullition) measured in a nearby peat swamp forest (Teh et al. 2017) and the 14,000 µg CH_4-C m^{-2} h^{-1} from the *Mauritia flexuosa* palm peat swamp forests in Madre de Dios, Peru (Winton et al. 2017), but similarly high to the 1,500 to 3,200 µg C m^{-2} h^{-1} of diffused CH_4 reported from nearby peat swamp forests (Teh et al. 2017; Hergoualc'h et al. 2020). Above the canopy, 600 to 1,300 µg C m^{-2} h^{-1} was measured (with water table between −0.03 and −0.12 m; Griffis et al. 2020). This shows that even during the dry season the palm swamp emits a lot of CH_4 and a large part of it reaches the atmosphere. Our measurements also lay within the range of CH_4 fluxes reported from Brazilian swamp forest soils (*igapo* and *varzea*; Pangala et al. 2017). The dry slash-and-burn 'Manioc' field consumed CH_4 at a session mean rate of 49 to 83 µg C m^{-2} h^{-1} (Fig. 3b).

The swamp forest peat produced session averages of 65 and 58 µg N_2O-N m^{-2} h^{-1} during the 0.085–0.012 m water-table drawdown on 16 and 17 September, respectively. Among the tested factors, water table fluctuation emerged as important. Accordingly, a 30 mm shower on the night before 24 September raised the water table to −0.03 m, caused a 2-fold drop in peat respiration (Fig. 4), and initiated session-average peaks of 360 and 420 µg N_2O-N m^{-2} h^{-1} from the 90–350 mg dry kg^{-1} soil NH_4^+-N on 24 and 25 September. In January to March, a steady average of 11.6 µg N_2O-N m^{-2} h^{-1} (session averages of 2.3 to 27 µg N_2O-N m^{-2} h^{-1}) was produced from the 120 mg dry kg^{-1} soil NH_4^+-N (Fig. 5a) regardless of rainfall immediately before some of the sampling sessions. Across the study period, the fluxes

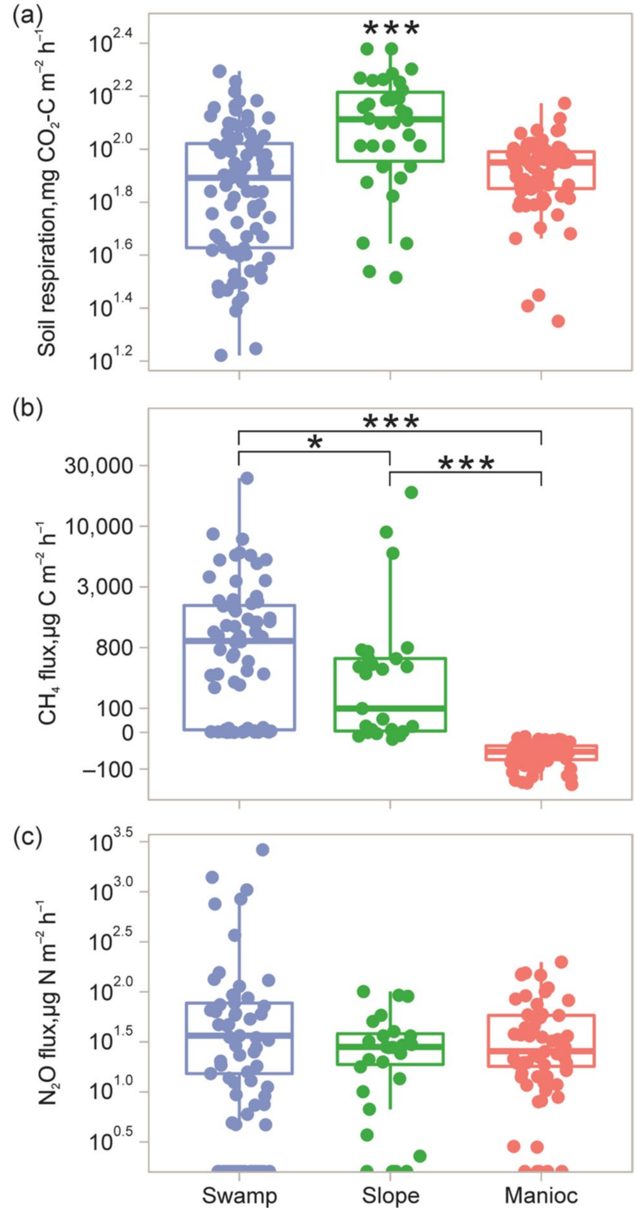

Fig. 3 Individual CO_2 (**a**), CH_4 (**b**) and N_2O (**c**) fluxes in Peru, and their box plots. Significant differences according to Wilcoxon test are shown with asterisks as follows: * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$. Asterisks directly above box without brackets denote significant difference from all other sites in the plot

correlated log-linearly with soil NH_4^+ content (Fig. 5a). Few N_2O flux models consider rainfall events; among them, the DeNitrification–DeComposition model (DNDC; Li et al. 1992) calculates N_2O fluxes driven by decomposition of organic N and denitrification following rainfall events. However, more records of N_2O peaks after rainfall events are needed to feed a model properly. Our measured N_2O emissions contrasted the earlier-reported negligible emissions from a nearby palm peat swamp forest (Teh et al. 2017) and were relatively high compared to the average 31 ± 22 µg

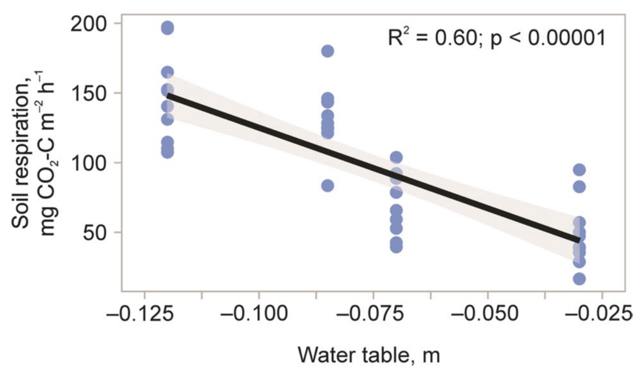

Fig. 4 Soil respiration declined with the rise of water table in the 'Swamp' forest in Peru

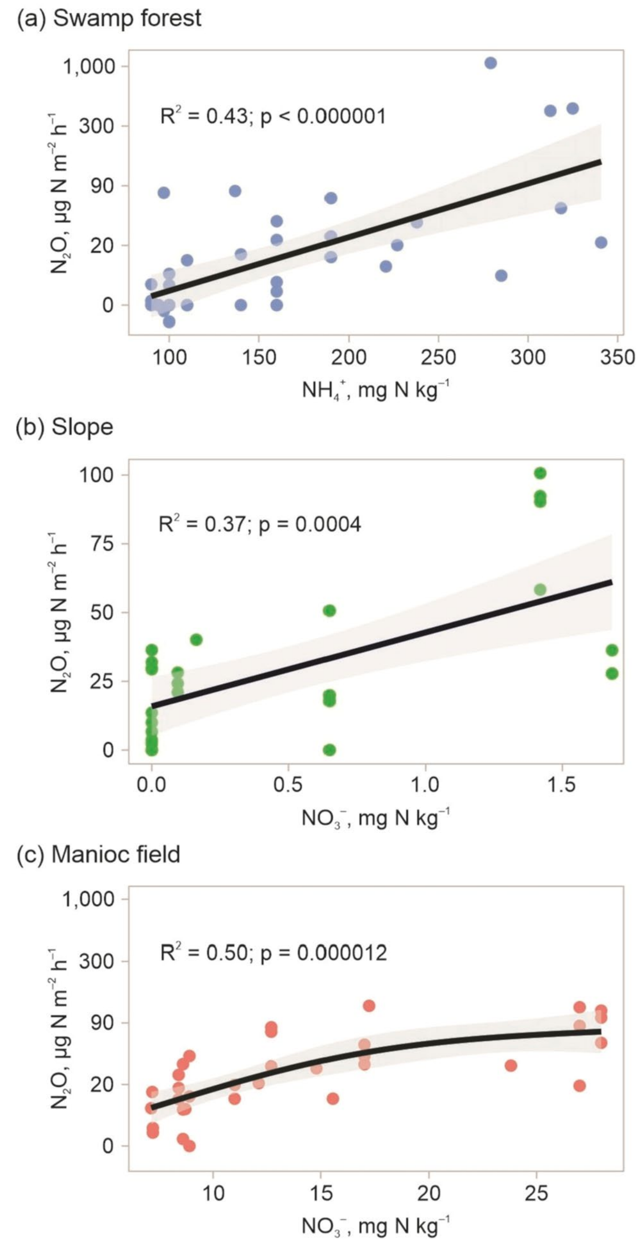

Fig. 5 Relationships between monthly average (**a**, **c**), and individual (**b**) N_2O emissions and soil N forms

N_2O-N m^{-2} h^{-1} (average ± standard deviation across studies) from the 410 ± 120 mg dry kg^{-1} soil NH_4^+-N in Southeast Asian wetland forests (van Lent et al. 2015), despite using an analogous measurement protocol (Hutchinson and Livingston 1993). Our measured fluxes were higher than model-predicted emissions of 21 µg N_2O-N m^{-2} h^{-1} for the Amazon Basin (Guilhen et al. 2020) but agreed with huge N_2O emissions from floodplains soils of the Brazilian Amazon by Figueiredo et al. (2019).

Soil NO_3^- content was below the detection limit in most of the anoxic peat samples, while NH_4^+ varied between 90 and 350 mg N dry kg^{-1}. This contradicts previous knowledge on low-NO_3^- water-saturated peat as a negligible source of N_2O (Rubol et al. 2012; Teh et al. 2017; Pärn et al. 2018). Melillo et al. (2001) reported > 50 µg N_2O-N m^{-2} h^{-1} in an Amazon upland rainforest with low NO_3^- content. Most of anaerobic N_2O production pathways use NO_3^- as the source (Baggs 2011; Butterbach-Bahl et al. 2013; Hu et al. 2015). Among the few exceptions, nitrifier denitrification avoids NO_3^- reducing NO_2^- directly into N_2O (Wrage-Mönnig et al. 2018). Hergoualc'h et al. (2020) identified nitrifier denitrification in the palm swamp. It is a well-documented process in mineralised peats (Wrage-Mönnig et al. 2018; Masta et al. 2020). Alternatively, either the CO_2 produced in the anaerobic respiration of dissolved organic matter (Heitmann et al. 2007) or O_2 from aerenchymous palm roots (van Lent et al. 2019) may have fed incomplete nitrification with the derived NO_3^- immediately used up by plants and denitrifiers in heavy competition on the NO_3^- (Kuzyakov and Xu 2013). The latter in turn may have produced a part of the N_2O in the anaerobic soil zone (in agreement with van Lent et al. 2019). As another possible mechanism, co-denitrification reduces nitrogen dioxide (NO_2^-) or NO into N_2O (Spott et al. 2011; Butterbach-Bahl et al. 2013). As a fourth potential source, we can consider denitrification in cryptogams such as lichens and fungi in other symbioses on the litter (Lenhart et al. 2015). The soil in our dry sites also emitted considerable 43 µg (12 to 55 µg as session average) N_2O-N m^{-2} h^{-1} in positive relationships with soil NO_3^- content (Figs. 3c and 5bc).

Potential N_2 production exceeded the potential N_2O flow by 1 to 2 orders of magnitude (Fig. 6). N_2O production potential in the intact soil cores collected from the 'Swamp' forest after the September hot moment was 64 µg N_2O-N m^{-2} h^{-1}. The soil cores collected in March and from other locations in all other sampling times showed near-zero N_2O production potential. The product potential of N_2 in the palm swamp was 1,100 µg m^{-2} h^{-1} in late September and 5,500 µg m^{-2} h^{-1} in March. This

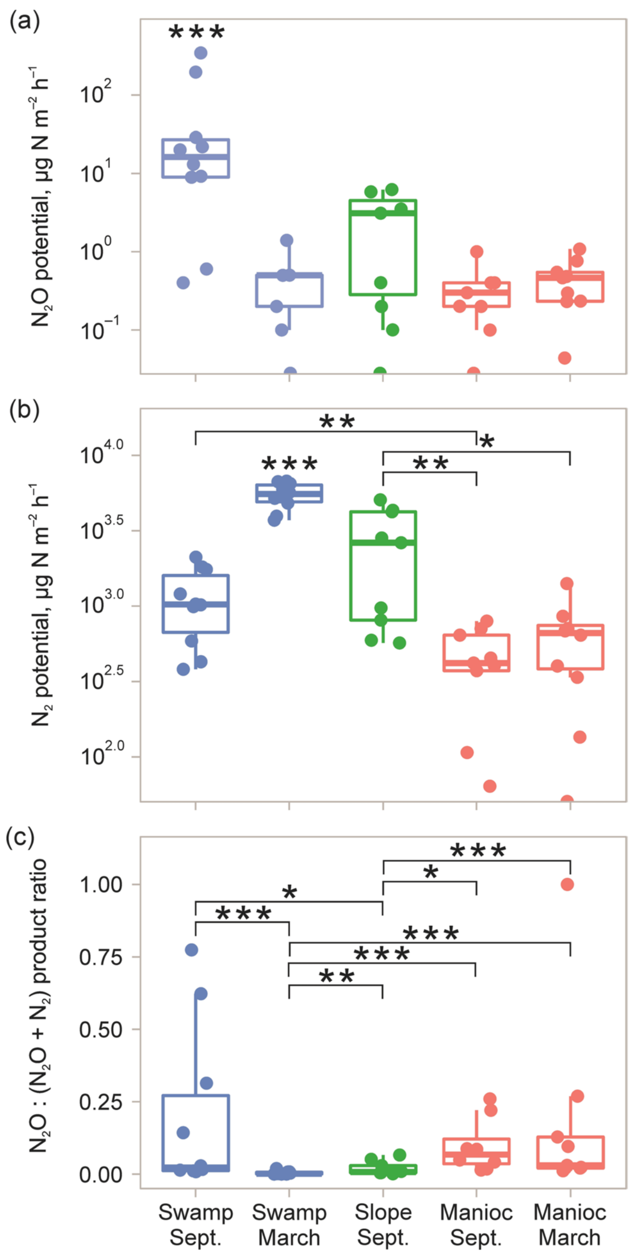

Fig. 6 N_2O and N_2 production potential measured from intact soil cores, and product ratio of field-observed N_2O flux (Figs. 3c and 5) to sum of field-observed N_2O flux and N_2 production potential. Significant differences according to Wilcoxon test are shown with asterisks as follows: * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$. Asterisks directly above box without brackets denote significant difference from all other sites in the plot

shows that denitrification was deficient in September whereas in March practically all N_2O was dentrified to N_2. In the 'Manioc' site, N_2 production potential was low, further explaining the significant N_2O emissions (Fig. 3b) with incomplete denitrification. At the bottom station of Slope, N_2 potential was intermediate between the natural palm swamp and the manioc field, completing the clear N_2 potential gradient according to the previous duration of high water table.

The field N_2O : (N_2O+N_2 potential) product ratio was the highest at the 'Swamp' in September, owing to huge N_2O emission and moderate N_2 potential. These can probably be explained, again, by the water-table drawdown and heavy shower before the sampling. In March the N_2O : (N_2O+N_2) ratio showed near-zero values in the 'Swamp' forest, due to low N_2O emission and very high N_2 potential. Thus, the N_2O likely produced from nitrifier denitrification in March was consumed by denitrification. That likely resulted from the December rainfall after which high water table settled in for months. The 'Slope' also showed a low N_2O : (N_2O+N_2) ratio owing to moderate N_2O emission and high N_2 potential. The N_2O : (N_2O+N_2) ratio in the 'Manioc' site was moderate, due to moderate N_2O emissions and low N_2 potential in the dry soil.

We carefully examined the N_2O and N_2 production potential results for a possible effect of cold storage on the soil for incubations. Studies by Verchot (1999), Arnold et al. (2008) and others have demonstrated adverse impacts on N cycling microbes and thus problematic and could lead to significant treatment effects. Our incubations, however, showed various production potential rates which we assumed were related to their ambient environmental conditions. As a validation point, the N_2O production potentials generally followed the same pattern as the field N_2O measurements, with the 'Swamp' in September emitting hundreds of μg m^{-2} h^{-1} N_2O-N with the rest of the sessions showing small or negligible N_2O fluxes (Figs. 5 and 6b).

Conclusions

The cultivated field in the Peruvian Amazon emitted relatively high amounts of CO_2 and N_2O but the swamp forest under a rising water table topped even that, while retaining their naturally high CH_4 production and part of the CO_2 emission. We observed several indirect signs of temporary oxygen intrusion in the swamp forest soil. The resulting high GHG emissions demand close monitoring of soil moisture and oxygen levels in Amazonian wetand soils. Management of Amazonian swamp forests should be aware of the impact even small changes in soil moisture have on GHG emissions wherefore conservation of swamp forests is still the surest way to minimise the GHG emissions.

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Cordova Horna, Tedi Pacheco Gómez, Jose David Urquiza Muñoz, Rodil Tello Espinoza and Ülo Mander participated in the field sampling. Martin Maddison analysed the denitrification potential samples. Jaan Pärn analysed the data and wrote the paper with significant input from Ülo Mander, Kaido Soosaar, Thomas Schindler, Katerina Machacova and Kristina Sohar. All authors read and approved the manuscript.

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Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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