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Aquatic and Soil CO_2 Emissions from forested wetlands of Congo's Cuvette Centrale

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Abstract. Within tropical forest ecosystems, wetlands such as swamp forests are an important interface between the terrestrial and aquatic landscape. Despite this assumed importance, there is a paucity of carbon flux data from wetlands in tropical Africa. Therefore, the magnitude and source of CO_2 fluxes, carbon isotopic ratios, and environmental conditions were measured for three years between 2019 to 2022 in a seasonally flooded forest and a perennially flooded forest in the *Cuvette Centrale* of the Congo Basin. The mean surface fluxes for the seasonally flooded site and the perennially flooded site were 2.36 ± 0.51 µmol m^{-2} s^{-1} and 4.38 ± 0.64 µmol m^{-2} s^{-1} respectively. The time series data revealed no discernible seasonal pattern in CO_2 fluxes. As for the environmental drivers, the fluxes at the seasonally flooded site exhibited a positive correlation with soil temperature and soil moisture. Additionally, the water table depth appeared to be a significant factor, demonstrating a quadratic relationship with the soil fluxes at the seasonally flooded site. $\delta^{13}C$ values showed a progressive increase across the carbon pools, from above-ground biomass, then leaf litter, to soil organic carbon (SOC). However, there was no significant difference in $\delta^{13}C$ enrichment between SOC and soil respired CO_2.

An *in-situ* derived gas transfer velocity (k_{600} = 2.95 cm h^{-1}) was used to calculate the aquatic CO_2 fluxes at the perennially flooded site. Despite the low k_{600}, relatively high CO_2 surface fluxes were found due to very high dissolved pCO_2 values measured in the flooding waters. Overall, these results offer a quantification of the CO_2 fluxes from forested wetlands and provide an insight of the temporal variability of these fluxes as well as their sensitivity to environmental drivers.

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1 Introduction

Along with the oceans and Northern Hemisphere forests, tropical forests represent one of the three main components of the global carbon sink (Mitchard 2018). However, due to relatively high gross primary productivity, temperature and soil moisture, tropical forest soils also constitute a large terrestrial source of carbon dioxide (CO_2). Indeed, tropical regions are estimated to contribute up to 64% to the global soil respiration, rendering it as the largest flux of CO_2 from terrestrial ecosystems to the atmosphere (Hashimoto et al. 2015; Huang et al. 2020).

In the tropical Congo Basin, the *Cuvette Centrale* covers approximately 167,600 km^2 and hosts lowland and swamp forests, including the largest peatland complex across the tropics (Crezee et al. 2022). With catchment drainage from north and south of the equator as well as sustained rainfall at the center of the basin (Runge 2007; Breitengroß 1972), the *Cuvette Centrale* shows near permanent inundation. This is especially important since inland waters are increasingly recognized as significant sources of greenhouse gases (GHG) within the terrestrial landscape (Bastviken et al. 2011; Raymond et al. 2013; Drake, Raymond, and Spencer 2018; Borges et al. 2015; Rosentreter et al. 2021). Recent data additionally suggests that the Congo Basin's inland waters might emit more carbon (C) per area than their counterparts in the Amazon Basin (Alsdorf et al. 2016). Profound hydrological (Alsdorf et al. 2016), structural (Lewis et al. 2013), ecological (Slik et al. 2015; Parmentier et al. 2007), aquatic biogeochemical (Borges, Abril, et al. 2015), and terrestrial biogeochemical (Hubau et al. 2020) differences indicate that GHG flux estimates cannot simply be transferred from the Neotropics to the Afro-tropics. However, while recent research on GHG emission from the Congo Basin has focused on either riverine (Bouillon et al. 2012; Mann, Tfaily, et al. 2014; Upstill-Goddard et al. 2017; Borges et al. 2019) or terrestrial fluxes (Baumgartner et al. 2020; Gallarotti et al. 2021; Barthel et al. 2022; Daelman et al. 2024), direct measurements from forested wetlands are still lacking. Despite its immense global importance, probably only one study thus far has been looking into GHG emissions, specifically methane (CH_4), from Congo's wetlands (Tathy et al. 1992).

Forested wetlands/swamp forests are located at the transition zone between the terrestrial and the aquatic realm. The duration and seasonality of the flooding in the forests will constrain the contribution from/to the river system. While flooded, the swamp forests are connected to the river system and receive and/or discharge materials from/to the river network (Aufdenkampe et al. 2011). Variations of riverine greenhouse gas concentrations have been shown to be driven by fluvial-wetland connectivity for the *Cuvette Centrale* based on data from 10 expeditions across the Congo River network (Borges et al. 2019). Furthermore, streams and rivers draining Congo's flooded forests were found to have the highest dissolved concentrations of CO_2 among different land cover types in the Basin, indicating the substantial contribution of forested wetlands on the overall inland water GHG budget (Mann, Spencer, et al. 2014).

Here, we report three years of carbon dioxide (CO_2) fluxes measured from two sites situated within the *Cuvette Centrale*: a seasonally flooded forest site and a perennially flooded forest site. During the observation period, surface CO_2 fluxes whether soil or aquatic, were measured fortnightly to capture the seasonal and inter-annual variation of the fluxes. Additionally, at the seasonally flooded site, environmental parameters (temperature, soil moisture and water table level) were monitored and their effects on the soil fluxes quantified. At the perennially flooded site, the carbon to nitrogen ratio (C:N), dissolved organic carbon (DOC) and pH were also measured to investigate their potential effect on CO_2 fluxes. Hence, these results provide insights into the temporal dynamics of CO_2 fluxes in forested wetlands across two different flooding regimes.

2 Materials and Methods

2.1 Study sites

The sites were located near the town of Mbandaka (Democratic Republic of the Congo, Équateur province), which is located at the Ruki-Congo confluence within the *Cuvette Centrale* (Figure 2). The mean annual precipitation and mean annual temperature of the sampling area are 1588 mm and 25 ºC, respectively (see the measurements detailed below). Here, surface CO_2 fluxes were measured at two different sites across two different hydrological regimes, one in a seasonally flooded forest (N 0.06335, E 18.31054, 300 m a.s.l.) – referred to as SFF site –and in a perennially flooded forest (S 0.03135, E 18.3102, 305 m a.s.l.) – referred to as PFF site (Figure 1).

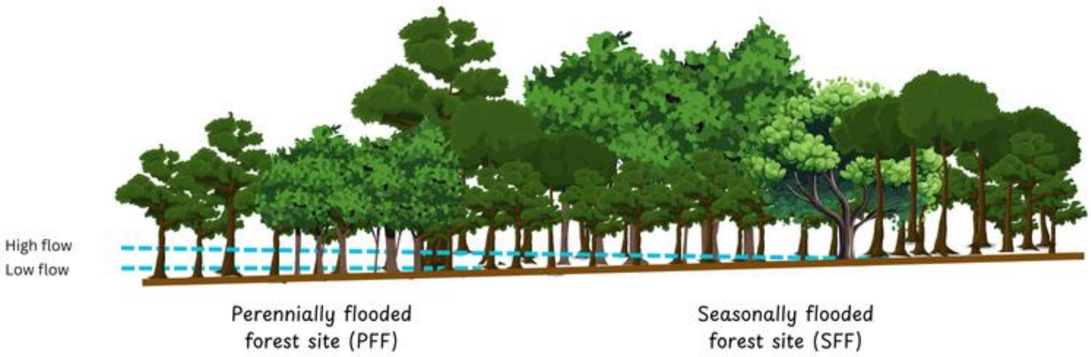

Figure 1. Diagram showing the location of the two experimental sites (PFF and SFF) relative to the hydrological gradient.

The seasonally flooded forest site (SFF) investigated was located within a botanical garden 7 km from the center of Mbandaka (*Jardin Botanique d'Eala,* operated by the *Institute Congolais pour la Conservation de la Nature* (ICCN)). The botanical garden comprises 371 ha of land consisting of 35% dense swamp forest, 14% forest on firm ground, 32% open forest, and the remaining area consisting of secondary forest, grassland, and deforested land, of which 189 ha are protected forest area. There are 3500 different trees and herbaceous plant species, with the main tree species being *Hevea brasiliensis*, *Ouratea arnoldiana*, *Pentaclethra eetveldeana*, *Strombosia tetandra*, and *Daniella pynaertii*. The soil at the site, covered by a thick litter layer, was characterized as Eutric Gleysols (texture 42/50/8 sand/silt/clay in %, bulk density 1.27 g cm^{-3}). The litter layer harbors a dense mesh of fine roots, whereas almost no roots were found to penetrate the upper mineral soil layer (0-30 cm). The SFF site is seasonally flooded from about December to January (~ 2 months) due to its vicinity to the Ruki river.

At the SFF site, combined soil moisture and temperature sensors (ECH_2O 5TM, Meter Group, Inc. USA) connected to loggers (Em50, Meter Group, Inc., USA) were installed at 30 cm depth, and data was recorded every 6 h. Unfortunately, one logger was stolen and the other logger stopped working during deployment; thus, data is only available from November 2019 to July 2020 (Figure 2). In addition, TMS-4 dataloggers (TOMST, Czechia) were installed in December 2020 to record volumetric soil water content and soil temperature in 15-minute intervals. Raw data (soil moisture count) retrieved from TMS-4 dataloggers was converted into soil VWC with calibrations curves, following Wild et al. (2019), using site-specific soil properties (soil texture: 42/50/8 sand/silt/clay in %, bulk density 1.27 g cm^{-3}) and measured soil temperatures. The values from the ECH_2O 5TM sensors showed a systematic offset compared to those obtained from the TMS-4 dataloggers. This was attributed to instrument artefact and corrected by using the difference between maximum values. Furthermore, precipitation, air temperature, relative humidity, solar radiation, and wind speed data were retrieved for the observation period from the Trans-African Hydro-Meteorological Monitoring Observatory (TAHMO) station located in close vicinity to the forest site (ATMOS 41, Meter Group, Inc., USA).

The perennially flooded forest (PFF) site is located about 8 km upstream of the Congo-Ruki confluence, following a small side tributary named Lolifa. The headwater stream area is completely flooded for most of the year, making the stream bed channel indistinguishable. This creates a continuous wetland area where the PFF site is located. While the water is mostly stagnant at the site, a small drainage flow appears during the dry season (late June to early September). The site was accessed with a motorized dugout canoe, and sampling was done fortnightly from the side of the canoe. The main tree species at the PFF site were *Uapaca sp, Irvigia smitii, and Daniella pynaertii De Wild*. Additional to the surface CO_2 fluxes, water samples were collected on the same day to measure pH, dissolved organic carbon (DOC) and total dissolved nitrogen (TDN). The presented C:N ratio was thus calculated using TDN rather than dissolved organic nitrogen (DON). Previous analyses showed that TDN consistently comprised an average of 90% of DON and thus reflected well the relative changes of concentrations. The specific methods used for sample processing and analysis as well as the calculations are described in Drake et al., (2023).

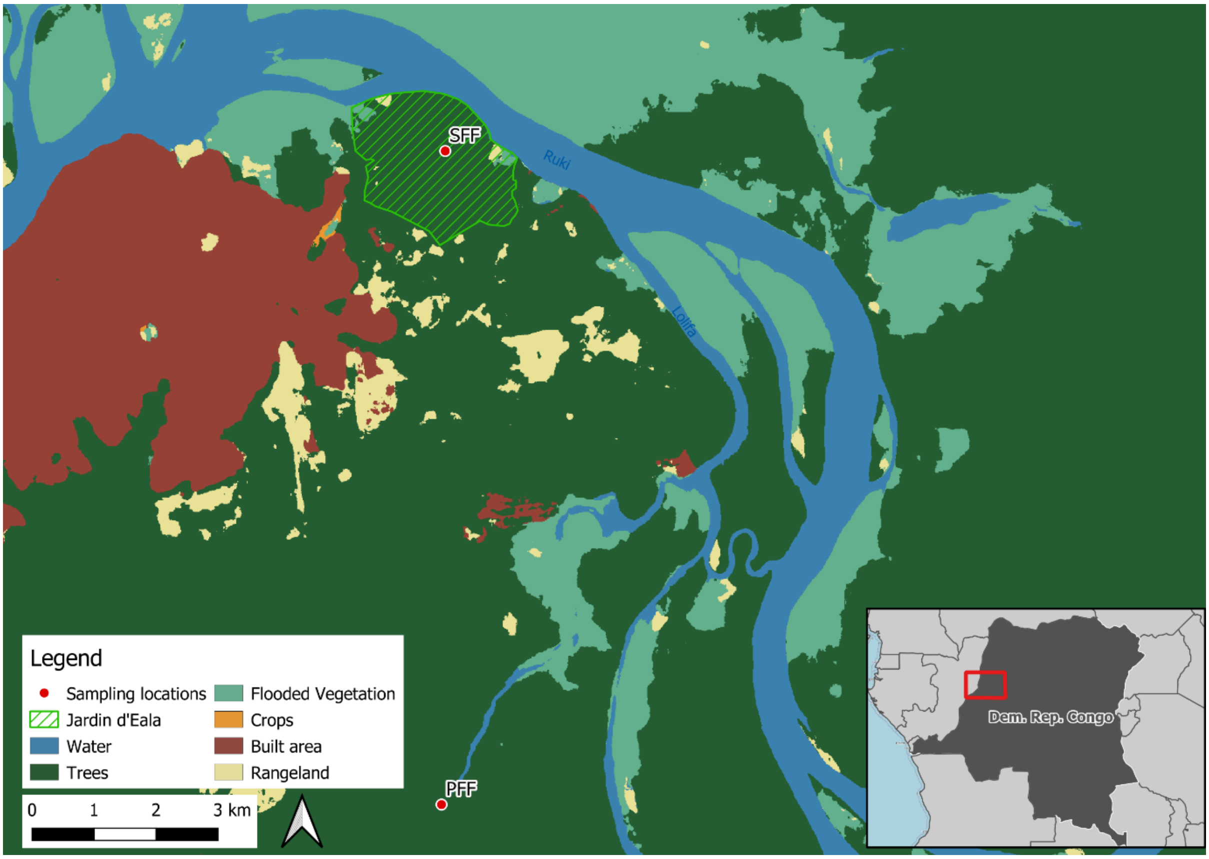

Figure 2. Map presenting the two sampling sites in the vicinity of Mbandaka (Democratic Republic of the Congo). The boundaries of the Jardin botanique d'Eala are highlighted. Maps data: © 2020-2023 Impact Observatory, Inc. and GADM.

2.2 CO_2 fluxes

2.2.1 CO_2 surface fluxes at the SFF site

A total of six polyvinylchloride soil flux chambers (h = 0.3m, ø = 0.3m) were installed in November 2019 at the SFF site. Chambers affected by seasonal flooding were measured for as long they were not completely submerged at which point floating chambers (V = 17L) were used instead. Sampling with the soil chambers was conducted fortnightly for three consecutive years (2019/11 – 2022/12), totalling 403 flux measurements. Sampling was interrupted once for about six months due to logistical constraints (first half of 2022).

Each chamber lid was equipped with a thermocouple to measure headspace temperature, a vent tube to avoid pressure changes, and a sampling port. The sampling port had a 3-way Luer valve attached, connecting the syringe, needle, and chamber. Before withdrawing each gas sample from the headspace, chamber air was mixed by moving the syringe plunger several times; for soil GHG flux determination, gas samples were taken at timesteps of 20 min throughout 1 h (t1 = 0 min, t2 = 20 min, t3 = 40

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min, t4 = 60 min). At each timestep, 20 mL of gas sample were stored in 12 mL pre-evacuated vials (Labco, UK) using a gas-tight disposable plastic syringe (20 mL). The resulting vial overpressure prevents air ingress due to temperature and pressure changes potentially occurring during transport and is required for sample withdrawal by the GC autosampler. Soil CO_2 fluxes were calculated via linear concentration increase over time using the ideal gas law PV = nRT:

$$n = \frac{PV}{RT} \text{ (1) and } \quad F = \frac{\Delta n}{\Delta t} S^{-1} \quad (2)$$

with n moles of gas [mol], P partial pressure of trace gas [atm µmol mol^{-1}], R gas constant 0.08206 [L atm K^{-1} mol^{-1}], T headspace temperature [K], F flux of gas [µmol m^{-2} s^{-1}], $\frac{\Delta n}{\Delta t}$ rate of change in concentration [mol s^{-1}], V chamber volume [L], and S surface area enclosed by chamber [m^2]. The coefficient of determination (r^2) for the linear regression of CO_2 yielded a $r^2 > 0.95$ for 95% of the data (Supp. Fig. 1). All data with $r^2 > 0.1$ was kept for the statistical analyses.

2.2.2 Aquatic surface fluxes at the PFF site

The aquatic surface flux to the atmosphere (F_{CO2}, µmol m^{-2} s^{-1}) from the PFF site was estimated according to a simple gas transfer model (Mann et al. 2014):

$$F_{CO_2} = k_x \cdot K_H \cdot (pCO_{2w} - pCO_{2a}) \quad (3)$$

where k_x is the freshwater gas transfer velocity of CO_2 [m s^{-1}], K_H is the Henry's constant for CO_2 [mol m^{-3} atm^{-1}], $pCO_{2w,a}$ the partial pressure of CO_2 in water and atmosphere, respectively [µatm].
Since the magnitude of the gas transfer velocity is governed by numerous factors (e.g., wind speed, water current velocity, slope), an *in-situ* gas transfer velocity k was calculated as 3.5 cm h^{-1} using the aquatic fluxes from the SFF site sampled between 2022-07 to 2022-12 with the above-mentioned floating chamber (V = 17 L) and the corresponding dissolved CO_2 concentrations of the inundation water at the same site. The value of 3.5 cm h^{-1} was then applied to the perennially flooded forest dataset where no floating chamber measurements existed. Hence, fluxes from the PFF site were derived using the measured gas transfer velocity from the SFF site (3.5 cm h^{-1}).
In order to compare the *in-situ* derived velocity k_x with the temperature normalized transfer velocity (k_{600}) for tropical wetlands of 2.4 cm h^{-1} (Aufdenkampe et al. 2011), we used the equation from Pelletier et al. (2014) to convert k_x to k_{600}.

$$k_x = k_{600} \left(\frac{S_c}{600}\right)^{-b} \quad (4)$$

Where S_c is the gas specific Schmid number and b derived from literature (0.66 for wind speed ≤ 3 m/s; Pelletier et al. 2014). The gas specific Schmid number is a function of water temperature (T in °C) as defined by Wanninkhof (2014) :

$$S_{cCO_2} = 1923.6 - 125.06T + 4.3773T^2 - 0.085681T^3 + 0.00070284T^4 \quad (5)$$

For pCO_{2a}, the tropospheric mean value from the year 2020 (400 µatm) was used while pCO_{2w} was determined using the headspace equilibration technique. That is, 6 mL of bubble-free water sample were injected with a syringe into a 12 mL N_2-pre-flushed vial (Exetainer®, Labco, UK) pre-poisoned with 50µL of 50% $ZnCl_2$ to stop the microbial activity. After sufficient equilibration time, the remaining headspace was analysed for CO_2 concentrations using a gas chromatograph (see Section below), and total dissolved concentrations were calculated based on Henry's law (see a detailed method in Supplementary). For each date, pCO_{2w} samples were taken in triplicate with an average coefficient of variation (CV) of 8%.

2.3 Gas Chromatography

Gas samples were analysed at ETH Zurich using a gas chromatograph (Bruker, 456-GC, Scion Instruments, Livingston, UK) separating CO_2 from residual air. After separation, the concentration of CO_2 was measured on a thermal conductivity detector. GC calibration was done with a suite of three standards (Carbagas AG, Switzerland; PanGas AG, Switzerland) across a concentration range from 249 to 3040 ppm CO_2. Each standard was analysed ten times at start, middle, and end of each set of 140-180 samples. Moreover, because of occasional high CO_2 sample concentrations, an entire system flush was done between each sample measurement to avoid any carry-over effects. The same GC setup was used for both flux samples and dissolved CO_2 samples.

2.4 $\delta^{13}C$ of soil- derived CO_2 fluxes and dissolved CO_2

The carbon isotopic composition of the CO_2 samples was analysed for one SFF CO_2 flux sample set of each month. That is, after CO_2 concentration measurement with the GC, the same samples were analysed for $\delta^{13}C$ of CO_2 with a modified Gasbench II periphery (Finnigan MAT, Bremen, D) coupled to an isotope ratio mass spectrometer (IRMS; Delta^{plus}XP; Finnigan MAT) as described in Baumgartner et al. (2020). Post-run off-line calculation and drift correction for assigning the final $\delta^{13}C$ values on the V-PDB scale was done following the "IT principle" (R. A. Werner and Brand 2001). The $\delta^{13}C$-values of the laboratory air standards were determined at the Max-Planck-Institute for Biogeochemistry (Jena, Germany), according to Werner, Rothe, and Brand (2001). The final soil CO_2-$\delta^{13}C$ values were calculated using the Keeling plot approach (Keeling 1958) (Supp. Fig. 2).

$\delta^{13}C$ of dissolved riverine CO_2 was determined using the headspace equilibration technique as described in section 2.2.2. Instead of concentration, $\delta^{13}C$ of the headspace was analysed via IRMS as described above. Samples were taken each month from the Ruki river between 10-2022 to 06-2023 with 2-3 replicates per sampling (Supp. Fig. 4).

2.5 δ^{13}C of leaves, litter, and soils

Fresh leaf samples were taken from a range of the most representative tree species at two different timepoints (2019-11; 2023-11). In addition, litter samples were collected at the same time and both were used to analyze the carbon isotopic composition (δ^{13}C). Before analysis samples were dried, homogenized, and ground. Soil samples were taken in 2019-11, 2020-02 and 2023-11 at 0-30 cm depth and air dried, sieved, and milled. All samples were analyzed using an elemental analyzer (Flash EA 1112 Series, Thermo Italy, former CE Instruments, Rhodano, Italy), interfaced with an IRMS (Finnigan MAT Delta^{plus}XP, Bremen, Germany) via a 6-port valve (Brooks et al. 2003) and a ConFlo III (Werner et al. 1999). Soil samples are subsequently referred to as soil organic carbon (SOC) samples. Calibration of laboratory standards (acetanilide, caffeine, tyrosine) was done by comparison to the corresponding international reference materials provided by the IAEA (Vienna, Austria).

2.6 Water table level

Direct measurements of the water table level were not available for the whole observation period. Previous work showed a linear relationship between the water level of the Congo River and the Ruki river (unpublished, Supp. Fig. 3). Additionally, the rainfall and/or the hydrological dynamics of the river influence the water levels in the wetlands. In the *Cuvette Centrale*, Georgiou et al. (2023) showed that the water levels of riverine locations in the DRC correlate more with the hydrological dynamics of the river system than with the rainfall input. Hence, available daily measurements of the water level of the Congo River in Mbandaka were used as a proxy of the water table level (Supp. Fig. 6). This data was extracted from an almost continuous record of water gauge readings, collected by the Congolese public institution, *Régie des Voies Fluviales*, since 1913.

2.7 Statistics

Daily environmental conditions were used to explain variability in the measured soil CO_2 fluxes ($n = 403$) at the SFF site. For this, a linear mixed effects model was fitted using soil temperature, volumetric soil water content, and river level as fixed effects. River level showed a non-linear relationship with surface fluxes. Hence, a quadratic term was tested to account for the non-linear effect. The predictor variables were standardized before fitting the models. All models controlled for repeated measurements in the same chambers, by adding chamber ID as a random intercept. Models were fitted by the restricted maximum likelihood method using *lme4* (Bates et al. 2015). Full and reduced models were compared using likelihood ratio test and adjusted R^2 values using *MuMin* package (Barton 2020). Furthermore, a backward stepwise regression analysis was conducted on the full model, incorporating all effects and interaction terms, to identify the most parsimonious model with highest explanatory power (Kuznetsova et al., 2017). The resulting model included an additional interaction term between soil moisture and river level. However, this term was subsequently removed due to multicollinearity and its lack of practical significance. Marginal and conditional R^2 values for mixed effects were calculated using Nakagawa, Johnson, and Schielzeth (2017) and p-values were estimated using Satterthwaite's approximation using *lmerTest* package (Kuznetsova et al., 2017).

Additionally, confidence intervals for the effect estimates were computed to confirm the interpretation of the estimated parameters. The assumptions of the model were validated by verifying the linearity, normality and homoscedasticity of the residuals. Multicollinearity between the predictor variables was also estimated (Variance Inflation Factor (VIF) inferior to 3). Statistical and graphical data analysis was done in R v.4.3.2 (R Core Team 2023) via RStudio v.2023.12.0 (RStudio Team 2023), using the packages *tidyverse* v.2.0.0, *tydr* v1.3.0 , *dplyr* v.1.1.4 (Wickham et al. 2023), *ggplot2* v. 3.4.4 (Wickham 2009), sjPlot (Lüdecke 2013) and *lubridate* v.1.9.3 (Grolemund and Wickham 2011). QGIS version 3.16 was used to compile the map of the sampling locations.

3 Results

3.1 Precipitation, soil moisture, and temperature

Annual precipitation was the highest in 2020 with 1855 mm and lowest in 2022 with 1417 mm. The highest weekly precipitation occurred in July and September of each year with 120 – 182 mm (Figure 2A). Overall, the weekly precipitation ranged from 0 – 182 mm, with a monthly average of 31mm (Figure 2A).

Volumetric soil water content averaged 0.60 ± 0.09 m^3 m^{-3}, ranging between 0.35 to 0.76 m^3 m^{-3} for the observation period (Figure 2A). In general, the soil moisture showed strong seasonality, with an increase in November and peak values observed in January. Thereafter, the soil moisture decreased before stabilizing until the following wet season. This pattern was less pronounced over the 2021-2022 season (Figure 2A).

Soil and air temperatures were stable throughout the observation period (Figure 2B).
Recorded mean air temperature at the weather station was 25.0 °C (± 0.7 °C), and mean soil temperature at the SFF site was 24.7 °C (± 0.3°C) for the observation period.

3.2 Soil and aquatic CO_2 fluxes

Over the observation period, CO_2 fluxes from the PFF site were higher than from the SFF site (Figure 2C). The highest fluxes were recorded in June and August of 2020 with 5.71 and 5.76 µmol m^{-2} s^{-1}, whereas the lowest values were observed in September and October 2020 with 3.35 and 3.42 µmol m^{-2} s^{-1}. Mean weekly surface fluxes (F_{CO2}) from the PFF site ranged from 3.35 to 5.76 µmol m^{-2} s^{-1} with an average flux of 4.38 ± 0.64 µmol m^{-2} s^{-1} using the *in-situ* derived gas transfer velocity of 3.5 cm h^{-1} (Figure 2C). Mean weekly surface fluxes (F_{CO2}) from the SFF site ranged from 0.87 to 3.64 µmol m^{-2} s^{-1} with an average of 2.36 ± 0.51 µmol m^{-2} s^{-1}. Here, the lowest flux was observed in July 2022 with 0.87 µmol m^{-2} s^{-1} while peaking in May 2020 with 3.64 µmol m^{-2} s^{-1} (Figure 2C).

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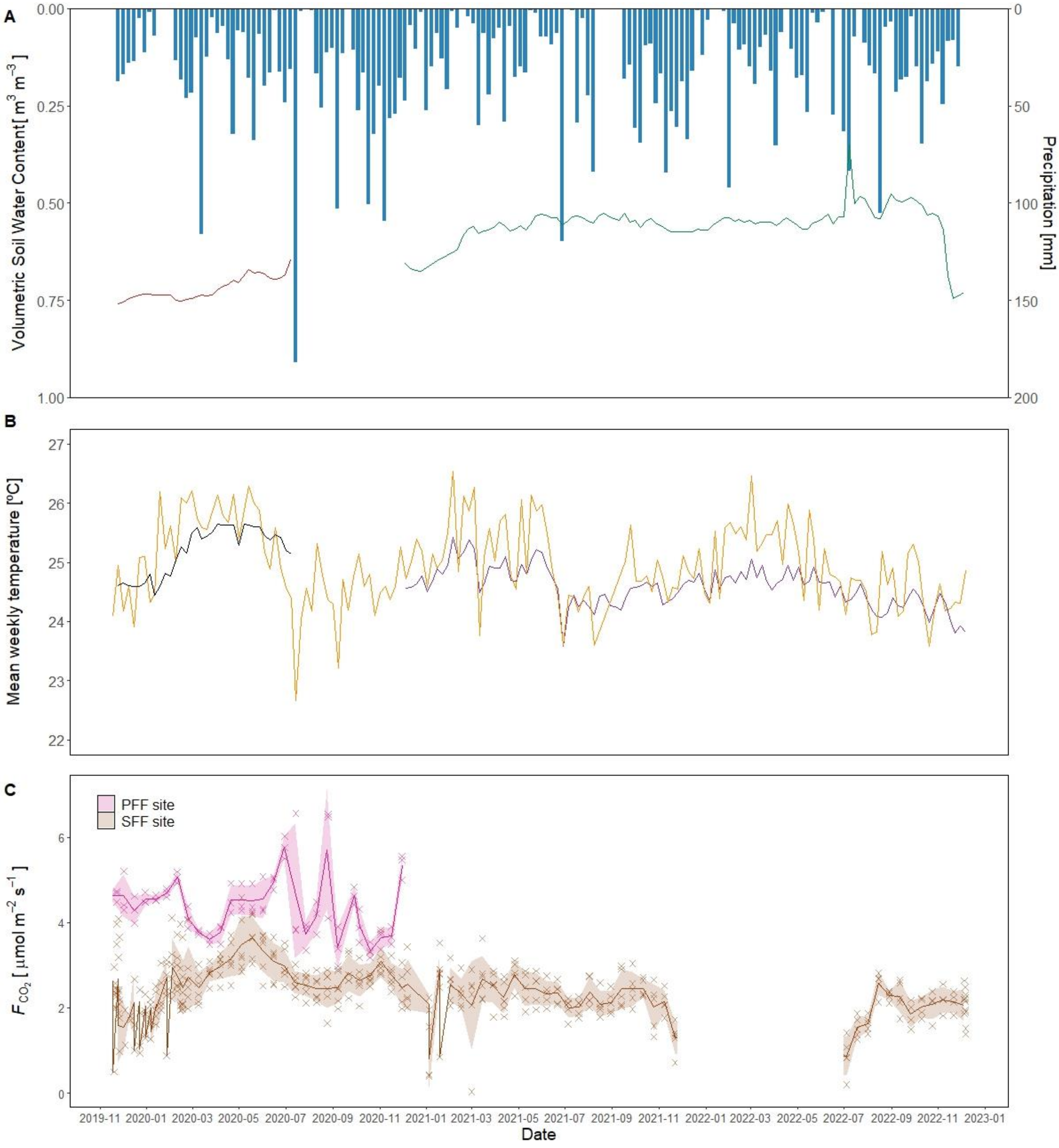


Figure 3. Weekly precipitation, volumetric soil water content, temperature, and CO_2 fluxes. (A) The sum of the weekly precipitation [mm] obtained from the Trans-African Hydro-Meteorological Monitoring Observatory and mean volumetric soil water content [m^3 m^{-3}] measured with soil moisture sensors (ECH_2O 5TM = brown, TMS-4 dataloggers = dark green). (B) Mean weekly air temperature [°C] (gold) was obtained from the Trans-African Hydro-Meteorological Monitoring Observatory. The mean weekly soil temperature [°C] was measured with soil temperature sensors (ECH_2O 5TM = black, TMS-4 dataloggers = purple). (C) Calculated mean weekly surface CO_2 fluxes (F) [µmol m^{-2} s^{-1}] from the SSF site (brown) and PFF site with a calculated K of 3.5 cm h^{-1}(pink). All measurements (cross) and the standard error of the mean are displayed.

3.2.1. Controls on surface CO_2 fluxes at the SSF site

The linear mixed effects model (n = 324) explained 43.0 % of the total variability, of which 35.4 % is allocated to the fixed effects (river level and soil temperature; Table 1). The soil temperature and soil moisture are positively correlated with surface CO_2 fluxes. The river level, used as a proxy for the water table level, exhibited a quadratic relationship with the CO_2 fluxes measured at the SFF site (Table 1; Figure 4C). The nonlinear component exhibited a negative sign, describing an inverse U-shaped curve (Figure 4C). Initially, the relationship had a positive slope at lower river levels, reaching a maximum point before transitioning to a negative slope. As the river level is used as a proxy of the water table depth, a short-term campaign was done during the wet season 2023-2024 to confirm the influence of the water table depth with direct measurements (Unpublished; Supp. Fig. 7). Finally, the significant positive interaction term between temperature and river level suggests a synergistic effect where the combined influence of these two variables on surface fluxes is greater than the addition of their respective individual effects (Figure 4).

Table 1. Fixed effect estimates for soil CO_2 fluxes, including a) river level and soil temperature; b) water table level (cm). For each effect, standard error and p-values (Sattherhwaite's method) are estimated as well as the marginal (m) and conditional (c) R^2_{adfj} (Nakagawa, Johnson, and Schielzeth 2017)

Response	Effect	Estimate	SE	P-value	$R^2_{adj, m}$ / $R^2_{adj, c}$
Soil CO_2 flux	Intercept	2.61	0.09	< 0.001	0.354/0.430
	River level [1st degree]	-0.01	0.04	**0.833**	
	River level [2nd degree]	-0.19	0.04	< 0.001	
	Soil temperature	0.18	0.04	< 0.001	
	Soil moisture	0.28	0.05	< 0.001	
	River level: Soil Temperature[1]	0.18	0.04	< 0.001	

[1] Interaction term between soil temperature and river level

Individual relationships between surface fluxes and the different variables (soil temperature, river level, and soil moisture) as well as the effect of the interaction between the soil temperature and rivel level are visualized in Figure 4. Individual relationships between soil CO2 fluxes and the environmental parameters (soil temperature (A), volumetric soil water content (VWC) (B) and river level (C)). Measures taken while the soil chamber was partially flooded are represented in green. Regression lines are displayed in brown. The interaction between soil temperature and river level is illustrated (D). Values were predicted based on the LMER model (Table 1). Figure 4.

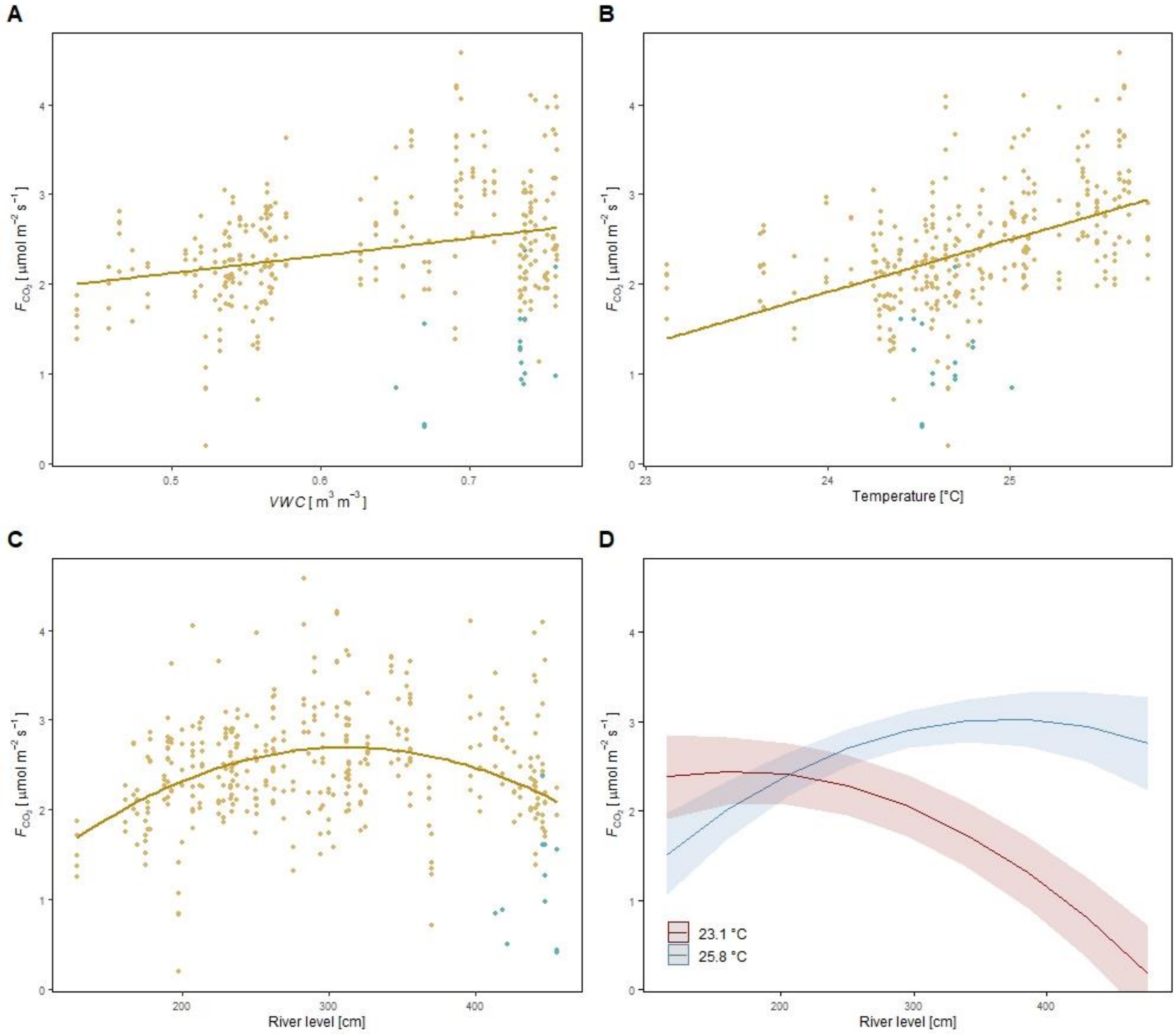
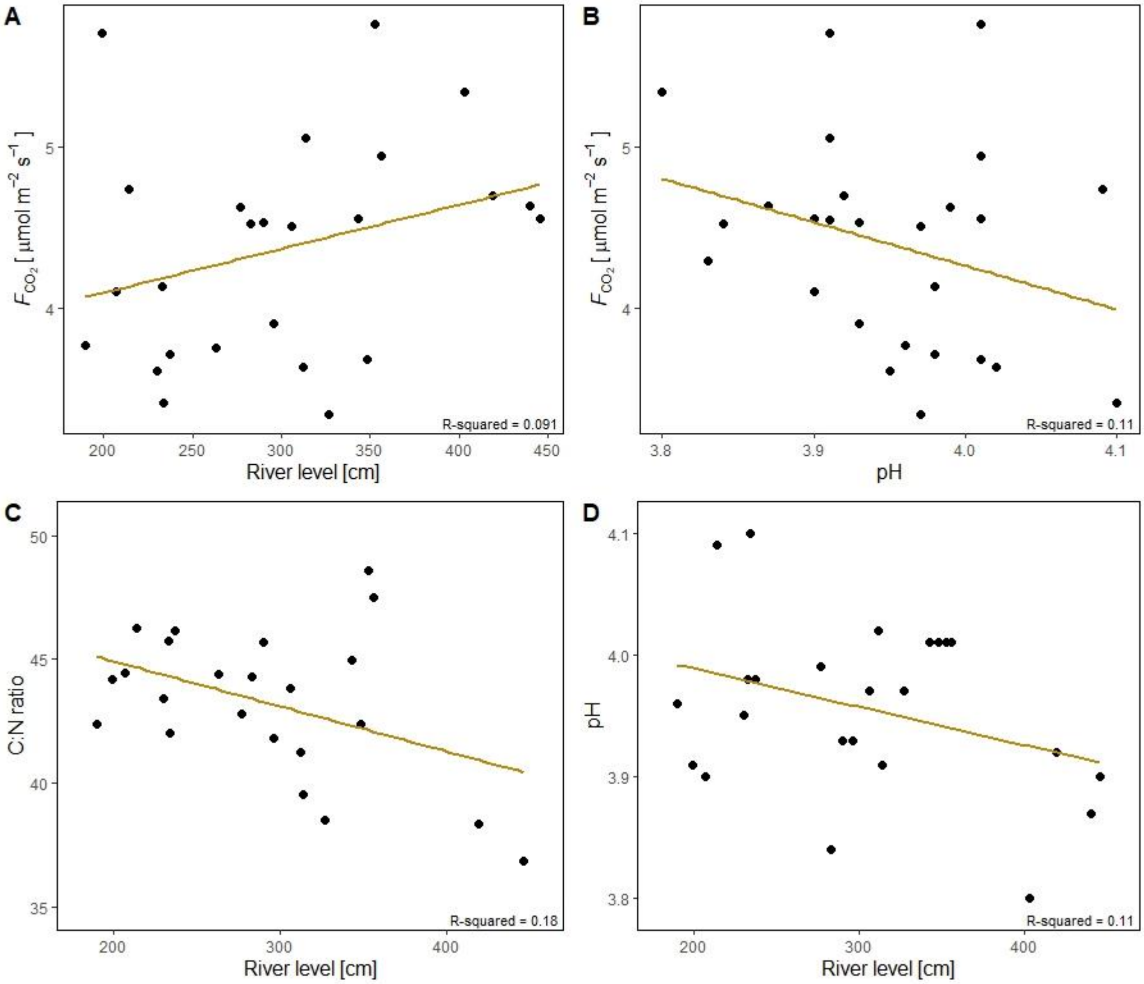


Figure 4. Individual relationships between soil CO2 fluxes and the environmental parameters (soil temperature (A), volumetric soil water content (VWC) (B) and river level (C)). Measures taken while the soil chamber was partially flooded are represented in green. Regression lines are displayed in brown. The interaction between soil temperature and river level is illustrated (D). Values were predicted based on the LMER model (Table 1).

3.2.2. Controls on surface CO_2 fluxes at the PFF site

At the PFF site, surface CO_2 fluxes exhibited a slight increase with the river level, while pH demonstrated opposing trends (Figure 5 A-B). Following this pattern, the aquatic CO_2 fluxes decreased with pH increase. It is important to note, however, that these observations reflect visual trends rather than statistically significant findings. No relationship between the carbon to nitrogen ratio (C:N), dissolved organic carbon or biodegradable dissolved organic carbon and CO_2 fluxes was observed.



305 **Figure 5. Aquatic CO_2 fluxes correlated with the river level at the gauging station (A), and pH (B); C:N ratio (C) and pH (D) correlated with the river level. Linear regression lines are displayed in brown. R-squared values are displayed at the bottom of the respective graphs.**

3.3 δ^{13}C of leaves, litter, soils, soil CO_2 flux, and riverine dissolved CO_2

The measured δ^{13}C values increased from leaves over litter and SOC to soil CO_2 fluxes and became more positive along this cascade of organic matter transformation (Figure 3). δ^{13}C of leaves ranged from -37.1 to -28.9‰ with a mean of -33.8 ± 2.1‰. 310 The δ^{13}C signature of litter was between -32.6 and -28.7‰ and, on average -30.5 ± 1.0‰. SOC had δ^{13}C of -30.1 to -22.3‰, while the mean was -27.4 ± 1.9‰. The δ^{13}C of soil-derived CO_2 (F_{CO2}) was in the range of SOC values for the SFF site (Figure 6) and very stable throughout the measurement period (Supp. Fig. 4). Here, measured δ^{13}C values were -30.2 to -26.5‰ with a mean of -28.5 ± 0.8‰. Contrary, the carbon isotopic composition of CO_2 fluxes from the SFF site during flooding was strongly ^{13}C enriched with -24.8 to -13.3‰ and an average of -20.4 ± 3.4‰ The $\delta^{13}C$ of the inundated soil CO_2 fluxes was higher throughout the whole measurement period (Supp. Fig. 4). The $\delta^{13}C$ value of dissolved CO_2 from the adjacent Ruki river was highly stable throughout the measurement period from 2022-10 to 2023-06 ranging from -24.9 to -23.3‰ with a mean of -24.3 ± 0.5‰ (Supp. Fig. 4).

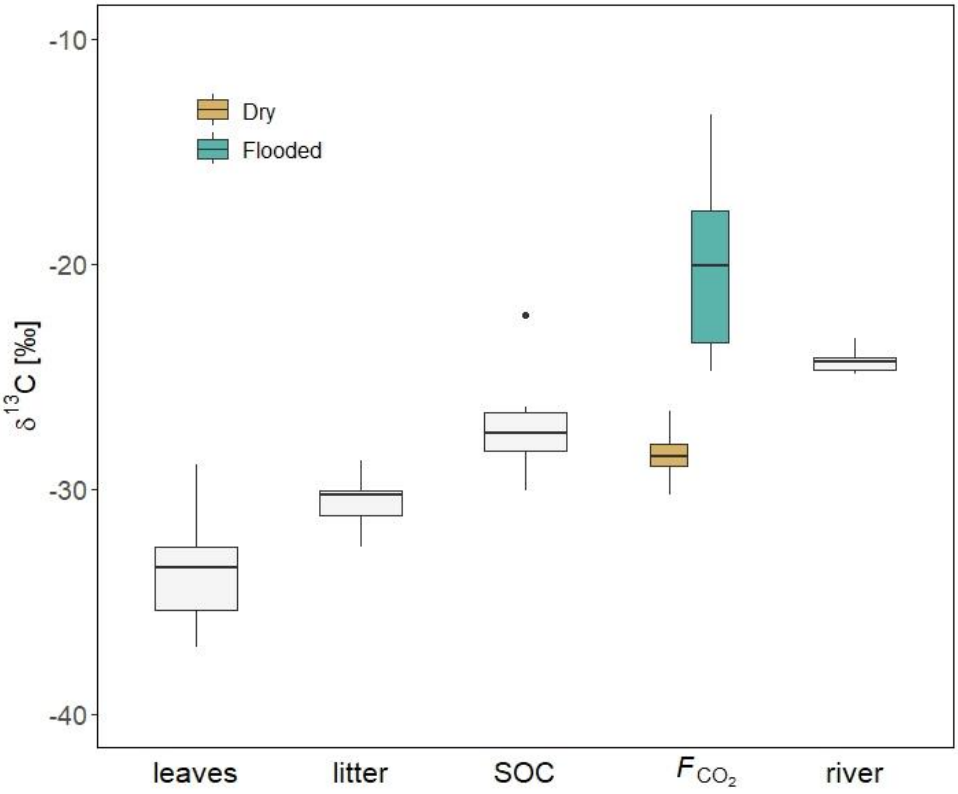


Figure 6. $\delta^{13}C$ values of leaves, litter, soil organic carbon (SOC), soil CO_2 flux (F) at the SFF site as well as riverine dissolved CO_2 (Ruki river). Surface CO_2 flux (F) is further separated into dry and inundated based on chamber type (floating, static).

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4 Discussion

4.1 CO_2 fluxes

The surface CO_2 flux dataset from the SFF site, measured for three consecutive years, showed intra-seasonal and interannual variability. However, no clear seasonal patterns were observed. The reported mean flux of 2.36 ± 0.51 µmol m^{-2} s^{-1} from the SFF site was lower compared to previous studies in the Congo Basin. These studies found mean values of respectively 3.13 ± 1.22 µmol m^{-2} s^{-1} , 3.45 ± 1.14 µmol m^{-2} s^{-1} in montane and lowland forests (Baumgartner et al. 2020) and 4.07 ± 0.90 µmol m^{-2} s^{-1} in a lowland secondary forest of Cameroon bordering the Congo Basin (Verchot et al. 2020). Compared to similar tropical forest studies, our values are at the low end of the range reported across the pantropical forest realm (Table 2).

The perennially flooded forest site (PFF), located at the interface between terrestrial (forest) and aquatic (stream) ecosystems showed relatively high emissions (4.38 ± 0.64 µmol m^{-2} s^{-1}) when compared to other tropical flooded forests, tropical forests, or to those streams draining catchments dominated by seasonally or continually inundated swamp forests (Table 2). As a constant gas transfer velocity was used in the present study, short-term changes in aquatic CO_2 fluxes reflect the variations in carbon dioxide concentrations (pCO_2) in the water. Moreover, the generally low gas transfer velocity (3.5 cm h^{-1}) reflects further the very high pCO_2 concentrations (10197 – 17260 ppm) measured at the PFF site. These values are significantly higher than the range (3069 – 9088 ppm) found on the adjacent Ruki river (Drake et al. 2023). However, the adjacent Ruki water has a long transit time compared to a swamp and a stronger current which in turn results in higher CO_2 outgassing. Generally, the pCO_2 concentration itself is driven by factors such as terrestrial inputs, gas exchange with the atmosphere, water temperature (gas solubility), water chemistry (pH, alkalinity), and in-stream metabolism.

Finally, the *in-situ* derived gas transfer velocity (k_x) expressed as normalized k_{600} (2.95 cm h^{-1}) was slightly higher than the global normalized estimate (k_{600}) for tropical wetlands (2.4 cm h^{-1}; Aufdenkampe et al. 2011). The gas transfer velocity itself changes by factors influencing the near-surface water turbulence (wind speed, water current velocity). A non-significant positive relationship between water level and pCO_2 was found (Figure 5). Generally, assuming a constant gas transfer velocity (k_x), as applied in this study, has its limitations since it likely varies throughout the year with increased values during the dry season when the water is flowing in the stream bed channel.

Table 2. Reported mean values of surface CO2 fluxes across various tropical forested environments

Country/Basin	**Environment**	**Temporal coverage**	**F_{CO_2} (µmol m^{-2} s^{-1})**	**Source**
DRC / Congo Basin	**Seasonally flooded forest** **Perennially flooded forest**	**3 years** **1 year**	**2.36 ± 0.51** **4.38 ± 0.64**	**This study**
DRC / Congo Basin	Montane and lowland (*terra firme*[1]) forests	3 years, at varying temporal resolution	3.13 to 3.45	Baumgartner et al. (2020)
ROC / Congo Basin	Streams (< 100 m wide) draining swamp forests	3 punctual campaigns over the hydrological year	3.61 ± 1.46	Mann, Spencer, et al. (2014)
Cameroon	Lowland (*terra firme*[1]) forest	17 months	4.07 ± 0.90	Verchot et al. (2020)
Kenya	Montane (*terra firme*[1]) forest	2-3 months, dry season and transition period	1.04 to 1.66	Arias-Navarro et al. (2017); Werner, Kiese, and Butterbach-Bahl (2007)
Panama	Lowland poorly drained forest	3 years	4.26 ± 0.16	Rubio and Detto (2017)
Brazil / Amazonian Basin	Seasonally flooded forest	From 1 to 2 years, at varying temporal resolution	2.2[2] to 5.28	Amaral et al. (2020); Borges Pinto et al. (2018); Zanchi et al.(2011)
Brazil / Rio Negro Basin	Perennially flooded forest	Punctual campaigns (low and high-water periods)	0.52 ± 0.21	Scofield et al. (2016)
Brazil / Amazonian Basin	Streams (< 100m wide) draining Amazonian wetlands	Punctual field campaigns integrating low and high flow periods	5.45 ± 3.39 to 5.49 ± 3.16	Alin et al. (2011); Rasera et al. (2008)
Amazonian Basin	Lowland (*terra firme*[1]) forest	Variable	2.30 to 5.30	(Davidson, Ishida, and Nepstad (2004); Doff sotta et al. (2004); Sousa Neto et al. (2011); Sotta et al. (2007); Garcia-Montiel et al. (2004); Borges Pinto et al. (2018); Janssens, Têtè Barigah, and Ceulemans (1998); Buchmann et al. (1997); Bréchet et al. (2021); Epron et al. (2013); Courtois et al. (2018);
Thailand	Lowland (*terra firme*[1]) forest	Punctual measurements over 2.5 years	6.57 ± 3.42[3]	Adachi et al. (2009)

Malaysia	Lowland (*terra firme*[1]) forest	Punctual measurements over 2 and 4 years	5.32 ± 2.85 to 5.7 ± 1.9	Katayama et al. (2009); Ohashi et al. (2007)
Australia	Seasonally flooded forest	13 months	1.4 ± 1.0 / 2.4 ± 1.4 (dry season / wet season)	Goodrick et al. (2016)

[1] Terra firme forests refer here to non-flooding forests.
[2] Measurements done only during the inundated period
[3] Mean soil respiration for the wet season

4.2 Temperature, soil moisture and water table depth controls

While the observed CO_2 fluxes at the SFF site showed no clear seasonal pattern, soil temperature, soil moisture and the river level as proxy of the water table emerged as significant controls. While the positive effect of temperature and soil moisture on soil CO_2 fluxes is well known and used to model soil CO_2 fluxes (Nissan et al. 2023) the effect of water table is less well understood. The observed quadratic relationship with water table depth suggests an optimal water level beyond which further increases lead to reduced CO_2 fluxes. This optimal point likely corresponds to the shift to water saturated conditions in the organic-rich surface soil transitioning from oxic to anoxic conditions. A negative effect of water table beyond a critical threshold aligns well with the results of Goodrick et al., (2016). That study found maximal soil CO_2 fluxes associated with a table depth between 1.5 and 2 m below ground and minimal fluxes when the water table was within 0.15 m of the surface for a tropical riparian swamp forests in Australia (Goodrick et al. 2016). Similarly, Rubio and Detto (2017) found a quadratic relationship between CO_2 fluxes and soil water content in the Amazonian basin. CO_2 fluxes can be reduced in both high and low soil water content, and fluctuations in water table depth introduce additional factors beyond its influence on soil saturation. Both heterotrophic and autotrophic soil respiration are reduced under dry conditions due to limited microbial activity and reduced photosynthetic activity through stomatal closure (Baumgartner et al. 2020). Conversely, increased soil moisture generally enhances respiration. However, high moisture conditions (due to strong rain events or high water tables) can also hinder substrate decomposition by physically impeding the diffusion of atmospheric oxygen and respired CO_2 through the soil pores, thereby limiting both the production and diffusion of CO_2 (Courtois et al. 2018; Nissan et al. 2023). Furthermore, fluctuations in the water table depth can influence soil respiration through physical processes like flushing out soil CO_2 during rising phases, enhanced lateral movement of dissolved CO_2, as well as air ingress and redistribution of organic material during receding phases (Goodrick et al. 2016; Dalmagro et al. 2018). Finally, the positive interaction between soil temperature and water table level suggests that higher temperatures will reinforce the effect of the water level and shift the maximum soil flux towards higher levels of the water table, delaying its inhibitive effect (Figure 4).

Nevertheless, it is important to note that both the water table level and soil moisture measurements exhibit seasonal patterns but do not capture well the short-term changes of the soil CO_2 fluxes. Furthermore, the CO_2 fluxes exhibit unclear seasonal

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pattern (Supp. Fig. 6). This suggests that other factors, such as aboveground inputs, deposition, and rain-induced events, may significantly influence soil CO_2 fluxes, both in the short term and over longer timescales. Overall, while soil water content and temperature are often considered primary drivers of soil CO_2 fluxes (Courtois et al. 2018; Oertel et al. 2016; Nissan et al. 2023), our findings also indicate that incorporating water table depth can help to unravel the variability of the fluxes for lowland forests with shallow water tables.

At the PFF site, on the other hand, we did not find any statistically significant relationships between potential drivers (DOC, BDOC, water table, pH, C:N) and pCO_{2w}. This suggests that the chemical composition of the water is relatively homogenous throughout the year and that allochthonous rather than autochthonous processes determine pCO_{2w} concentrations.

4.3 Isotopic indicators

The general carbon isotopic composition of plant tissue is determined by the degree of ^{13}C discrimination at the leaf level (Brüggemann et al., 2011). Due to the high photosynthetic activity of tropical plants, ^{13}C discrimination is also high, resulting in very negative $\delta^{13}C$ values at the leaf level as observed in this study -37.06 to -28.89‰). As the C moves across the various ecosystems C pools, the substrate becomes gradually enriched in ^{13}C due to kinetic isotope fractionation. In the case of the studied SFF site, a total ^{13}C enrichment of 5.27‰ was observed when moving down the cascade from leaves, litter, SOC to respired CO_2 under dry conditions (Figure 6). Particularly interesting here is the absence of ^{13}C fractionation between SOC and soil respired CO_2, which might initially be interpreted as a result of closed system dynamics where the substrate is limited, and organic decomposition tends to be complete. However, soil respired CO_2 is a two-component flux, comprised of heterotrophic and autotropic respiration. In order words, SOC is not the sole factor governing soil respired CO_2. Indeed, autotropic respiration is to a large degree fueled by recently photosynthesized ^{13}C depleted C (Högberg et al, 2001, Barthel et al., 2011) which in turn can decrease the overall soil respired $\delta^{13}C$ value relative to SOC (depending on the relative contribution of autotrophic vs heterotrophic soil respiration). Transport rates from above to belowground can reach up to 0.5 m h^{-1} (Kuzyakov and Gavrichkova 2010). Thus, whether the similar $\delta^{13}C$ values between SOC and respired CO_2 are driven by substrate limitation or a strong influence of autotrophic respiration requires further investigation.

The highest ^{13}C enrichment observed was from CO_2 emitted during flooding at the SFF site (-20.4‰). These $\delta^{13}C$ values were even higher than the $\delta^{13}C$ values measured in the adjacent Ruki river (-24.30 ‰). The reason for such highly ^{13}C enriched CO_2 outgassing during inundation remains unclear but given that the water in the inundated forest likely experiences relatively long residence times compared to the river, the outgassed CO_2 might become this heavily ^{13}C-enriched due to extensive outgassing. Moreover, the standing water allows the growth of methanogenic archea which use simple carbon compounds such as acetate as electron donors (Conrad et al., 2021). The CO_2 molecules obtained from acetate cleavage is another fractionation process which potentially influences the overall isotopic composition of outgassed CO_2. Lastly, as the inundation of the SFF site is mainly driven by backflow from the river system, the dissolved CO_2 in the inundated water could be a mix of riverine and locally soil-respired CO_2 that undergoes further *in-situ* ^{13}C enrichment.

5 Conclusion

This study presents a multi-year dataset of CO_2 fluxes from two forested wetland sites along a flooding gradient : a seasonally flooded forest (SFF) and a perennially flooded forest (PFF). While exhibiting short-term and interannual fluctuations, CO_2 fluxes showed limited seasonal patterns. At the SFF site, surface emissions increased with rising soil moisture and temperature, while the water table level demonstrated a significant quadratic relationship. Despite the significant sensitivity to environmental conditions over the observation period, the short-term variability observed at both sites, as well as the interannual variability at the SFF site, were incompletely explained, suggesting the influence of additional factors in regulating emissions.

Our results emphasize that groundwater level, alongside soil temperature and soil moisture, significantly affects surface CO_2 fluxes in lowland areas with shallow, fluctuating water tables. Future research should include direct measurements of the water table over the entire hydrological year to elucidate the temporal dynamics of this relationship. Overall, the reported measurements contribute to filling the data gap for soil respiration rates of tropical forests in the Congo Basin and provide baseline fluxes for parametrizing earth system models.

Data Availability

All data used in this study will be made available through the soil respiration database (SRDB; Jian, J. et al. 2021).

Author contributions

Mbarthel, MBauters, TWD, KVO, and JS were responsible for study design and conceived the study. Fieldwork was conducted by Mbarthel, Mbauters, TWD, SB, NBM, JC, ADC, and CE. Lab work was conducted by Mbarthel, RAW, SB and JC. Data analyzes and interpretation was performed by ACHJ, ADC, Mbauters and Mbarthel. ADC and ACHJ wrote the manuscript with contributions from all co-authors.

Competing Interests

At least one of the (co-)authors is a member of the editorial board of Biogeosciences.

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