Seasonality, drivers, and isotopic composition of soil CO_2 fluxes from tropical forests of the Congo Basin

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Abstract.

Soil respiration is an important carbon flux and key process determining the net ecosystem production of terrestrial ecosystems. To address the lack of quantification and understanding of seasonality in soil respiration of tropical forests in the Congo Basin, soil CO_2 fluxes and potential controlling factors were measured annually in two dominant forest types (lowland and montane) of the Congo Basin over two years at varying temporal resolution. Soil CO_2 fluxes from the Congo Basin resulted in 3.45 ± 1.14 and 3.13 ± 1.22 $\mu\text{mol}\,CO_2\,m^{-2}\,s^{-1}$ for lowland and montane forests, respectively. Soil CO_2 fluxes in montane forest soils showed a clear seasonality with decreasing flux rates during the dry season. Montane forest soil CO_2 fluxes were positively correlated with soil moisture while CO_2 fluxes in the lowland forest were not. Smaller differences of $\delta^{13}C$ values of leaf litter, soil organic carbon (SOC) and soil CO_2 indicated that SOC in lowland forests is more decomposed than in montane forests, suggesting that respiration is controlled by C availability rather than environmental factors. In general, C in montane forests was more enriched in ^{13}C throughout the whole cascade of carbon intake via photosynthesis, litterfall, SOC, and soil CO_2 compared to lowland forests, pointing to a more open system. Even though soil CO_2 fluxes are similarly high in lowland and montane forests of the Congo Basin, the drivers of them seem to be different, i.e. soil moisture for montane forest and C availability for lowland forest.

1 Introduction

Soil basal respiration, the sum of carbon dioxide (CO_2) produced both autotrophically by roots and heterotrophically by bacterial and fungal respiration, represents the biggest natural transfer of carbon (C) from the terrestrial biosphere to the atmosphere (Raich and Schlesinger, 1992). Globally, soil respiration is the second-largest terrestrial C flux after photosynthesis, emitting 120 Pg of C per year as CO_2 (Friedlingstein et al., 2019). As such, the flux of CO_2 from soils represents a significant component of net ecosystem production (NEP). Research into the abiotic and biotic controls of this flux are thus critical for understanding the overall C balance of ecosystems.

There are a number of different parameters that can influence soil CO_2 efflux, with soil temperature and soil moisture being the most important drivers (Rustad et al., 2000; Ruehr et al., 2010). Soil temperature affects biological activity whereas soil moisture affects the diffusion of C substrate, atmospheric oxygen and respired CO_2 through soil pores (Janssens et al., 1998; Doff Sotta et al., 2004; Sousa Neto et al., 2011; Courtois et al., 2018). Furthermore, soil pH (Courtois et al., 2018), through its effects on microbial communities, and root density can also affect soil CO_2 production (Janssens et al., 1998). Another particularly important driver is photosynthetic activity, as it describes the rate of carbohydrate supply from leaves to roots, where both root and rhizo-microbial respiration occur (Ekblad, 2001). While the magnitude of soil CO_2 fluxes can vary significantly between and within different ecosystems, soil CO_2 fluxes from tropical forests are generally higher than from any other vegetation type, due to high soil temperature, high soil moisture (Raich et al., 2002), and weak C stabilization (Doetterl et al., 2018). Although tropical forests experience high soil CO_2 fluxes and high production, as as a whole, the tropical terrestrial biosphere acts as a net C sink by production outbalancing the high soil respiration (Melillo et al., 1993; Pan et al., 2011; Palmer et al., 2019).

Despite the importance of tropical forests for the global C cycle, there is a lack of research into CO_2 fluxes from soils in these ecosystems. The Congo Basin in central Africa, hosts the second largest tropical forest on Earth, but has been particularly neglected in biogeochemical research and only one study from 1962 reporting soil CO_2 fluxes from these forests (Maldague and Hilger, 1962) are available. Hence, while many studies model soil and ecosystem respiration in the Congo, there are almost no empirical data on soil CO_2 fluxes to validate the models. Eddy-covariance towers are the most common methods to measure CO_2 fluxes over different ecosystems and larger areas. However, continuous measurements of soil CO_2 fluxes close to the surface are needed to assess temporal trends of processes controlling soil CO_2 production (Ogle, 2018). This is particular important in light of recent data that show that the ratio of soil respiration to primary production has increased over time (Bond-Lamperty et al., 2018). In particular, heterotrophic respiration has increased as soil microbes became more active in response to increasing temperatures (Bond-Lamperty et al., 2018). If this process proceeds such that ecosystem respiration exceeds primary production, terrestrial ecosystems could be transformed from sinks to sources of C. Thus, understanding baseline rates of soil respiration and the role of environmental drivers is crucial to assess future responses to climate change. This is especially important in the Congo Basin, as a recent study showed that the length of dry seasons have increased by 6.4-10.4 days per decade since 1988 (Jiang et al., 2019). These changes in precipitation and temperature could trigger an ecosystem response, including shifts in soil respiration. Furthermore, short-term events, such as extreme rain or prolonged dry periods, are predicted to occur more frequently with climate change and will most likely impact soil respiration rates (Hopkins and Del Prado, 2007; Borken and Matzner, 2009).

It is well known that soil respiration and canopy processes are linked in forests (Ekblad, 2001). Carbohydrates produced by photosynthesis are subsequently transported to the roots and rhizosphere, where they are respired by root or microbial respiration (Ruehr et al., 2009). Thus, the isotopic signature of soil-derived CO_2 is mostly governed by isotope fractionation processes that occur at the leaf scale, since a significant portion of soil respired CO_2 is supplied by recent photoassimilates (Högberg et al., 2001; Brüggemann et al., 2011; Barthel et al., 2011). Generally, all environmental parameters affecting photosynthesis and thus CO_2 discrimination are likely to influence the δ^{13}C signal of soil respiration (e.g. precipitation, vapor pressure deficit) (Bowling et al., 2002). Furthermore, the differences of the stable isotope signatures between different C compartments (litter, soil C, soil CO_2, stream dissolved CO_2) can give information about the opennesss' of a system. To an 'open system' we refer if the system experiences a continuous supply of substrate, while products are lost from the system, whereas a 'closed system' lacks new inputs of substrate. The fractionation between compartements is higher in a more open system (Fry, 2006).

In light of these issues, the objectives of this study were to provide 1) the first empirical quantification of annual soil CO_2 fluxes from forests of the Congo Basin, 2) gauge variability between two dominant forest types within the basin, and 3) assess whether and to what extent soil temperature and moisture influence CO_2 fluxes. We hypothesized higher soil CO_2 fluxes in the lowland forest due to higher temperature and soil moisture regimes compared to the montane forest. Soil CO_2 fluxes were measured weekly to assess the role of seasonality and environmental drivers of soil CO_2 fluxes. Additionally, stable C isotopic signatures (δ^{13}C) of leaf-litter, soil organic carbon (SOC), soil-respired CO_2 and dissolved stream water CO_2 were measured to give us more information about sources and fate of soil respired CO_2.

2 Methods

2.1 Study sites

Old-growth forest sites in the Democratic Republic of Congo (DRC), contrasting in altitude, were selected to conduct long-term static manual chamber CO_2 flux measurements. The first site (KB) is situated in the Kahuzi-Biéga National Park (S 02.215°, E 28.759°) northwest of the city of Bukavu in the South-Kivu province and represents a montane tropical mixed forest at an altitude of 2120 m a.s.l with an mean annual temperature of 15 °C and an mean annual rainfall of 1500 mm (Bauters et al., 2019). Species composition of this forest is well described in Imani et al. (2016) and main species are *Maesa lanceolata, Lindackeria kivuensis* and *Allophyllus kiwuensis*. Rainfall peaks in both April and October, with a dry season from June to September in between (Alsdorf et al., 2016). The soils in KB are broadly classified as Umbric Ferralsols (Jones et al., 2013) with a sandy loam (upper 15 cm) to silt loam (15-30 cm) texture. The second site (YO) is situated in the Yoko Forest Reserve, south of the city of Kisangani in the Tshopo province (N 0.294°, E 25.302°) with a mean annual temperature of 24.2 °C and a mean annual rainfall of 1800 mm (Bauters et al., 2019). The YO site consists of two dominant forest types, a lowland tropical mixed forest and a mono-dominant forest, where more than 60 % of the basal area consists of the species *Gilbertiodendron dewevrei*. The mixed forest plot is a classic African lowland rainforest with about 70 species per hectare and a canopy height up to 40 m and a basal area of 34 m^2 ha^{-1} (Doetterl et al., 2015; Kearsley et al., 2017). Like KB, there are two wet seasons, a short one from March to May and a longer one from August to November. The soils in YO are deeply weathered and nutrient poor Xanthic Ferralsols (Jones et al., 2013) with a loamy sand texture (0-30 cm). Because lowland forests are the main forest type within the Congo Basin, two additional lowland forest sites (Djolu and Yangambi) were selected to conduct short term campaigns, assessing spatial robustness of the results (Figure 1). Yangambi is a UNESCO biosphere reserve and lies at the river bank of the Congo river about 100 km west of the city of Kisangani (Figure 1). Djolu is a territory just north of the equator

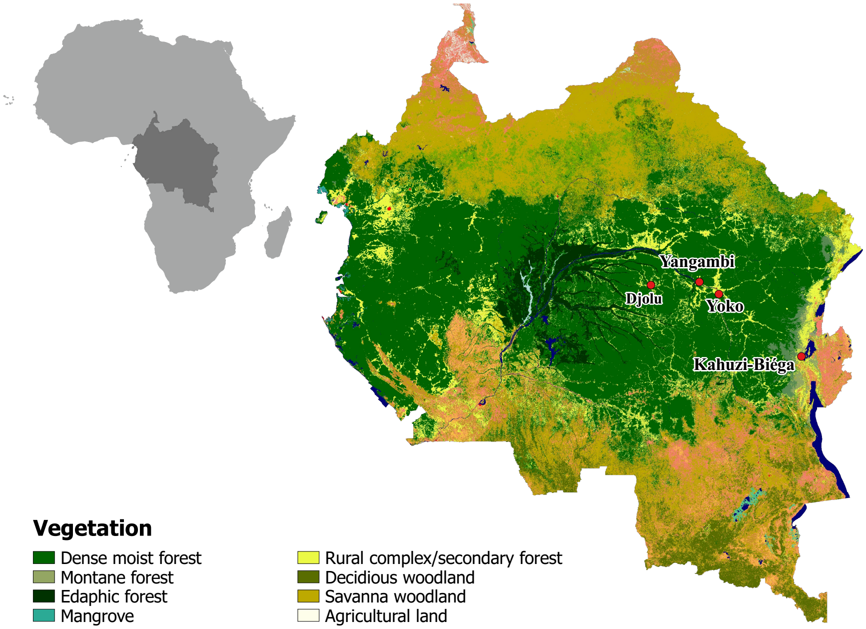

Figure 1. Map of part of the Congo Basin with the different vegetation types. Red dots indicate sampling locations. Lowland: Djolu, Yangambi, and Yoko. Montane: Kahuzi-Biéga. Map modified based on Verhegghen et al. (2012).

roughly 300 km west of the city of Kisangani, in the north-east of Tshuapa province where measurements were conducted in protected forest areas (Figure 1). In KB, one plot (40 by 40 m) in a mixed forest was installed. In Yoko and Yangambi, two plots for each site were installed, one in a mixed forest and one in a mono-dominant forest. In Djolu measurements were conducted in one plot in an old-growth mixed forest sites.

2.2 Soil CO_2 flux measurements

Flux chamber measurements were carried out at different time intervals during 2016-2019. Weekly to fortnightly sampling in YO was conducted from November 2016 to March 2019 and in KB from April 2017 to March 2019. In addition, several 2-week sampling campaigns with daily and sub-daily sampling were conducted to rule out diurnal soil respiration cycles (Figure A3). These short-term sampling campaigns were conducted in KB (September 2016, April 2017), YO (October 2016, Mai 2017), Yangambi (September 2016) and in Djolu (May 2016). Sampling was done using the static manual chamber method, as described in Hutchinson and Mosier (1981). In the montane sampling plot, seven chambers were installed for the short-term campaigns. Due to material and logistical constrains, we started the first year of long-term measurements with three chambers and increased the number of chambers to five in the second year of long-term sampling in the montane forest. In YO, short-term campaigns were conducted with four chambers in the mixed forest plot and three chambers in the mono-dominant plot. We then started the long-term campaign in YO with four chambers in the mixed forest and two chambers in the mono-dominant forest and after one year, we proceeded with five chambers in the mixed forest while we stopped the sampling in the mono-dominant plot. Fluxes in Djolu were measured with four chambers. In every plot the chambers were randomly placed between trees and we avoided hills and depressions. PVC chambers with a diameter of 0.3 m, a height of 0.3 m, an airtight lid, and a vent tube to avoid pressure disturbances were installed. A thermocouple (Type T, Omega Engineering Deckenpfronn, Germany) was inserted through a gas tight cable gland to measure temperature in the chambers at each sampling time point. Following established methods, the chambers were inserted into the forest floor at least 12 hours prior to taking the first sample to avoid altered results due to soil disturbance. The chambers remained in place throughout the measurement campaign. For each flux measurement, the lids of the chambers were closed for one hour and 20 mL headspace gas samples were withdrawn every 20 minutes (t0, t20, t40, and t60) with a 20 mL syringe. Gas samples were stored in pre-evacuated 12 mL vials with airtight septa (Exetainer; Labco Ltd, High Wycombe, UK). To avoid gas leakage issues as described by Knohl et al. (2004), the septa were additionally sealed with a thin layer of silicon. To ensure that the headspace was well-mixed and that there was no static concentration gradient inside the chamber, the syringe was flushed with air from the chamber headspace and reinjected into the chamber prior to sample withdrawal. The chambers were only closed for the duration of the measurements. Soil moisture probes (ECH$_2$O-5, Meter Environment, Pullman, U.S.) and air temperature data loggers (iButton, Maxim Integrated, San Jose, U.S.) were installed at each chamber cluster. Soil temperature was measured during each sampling event at 20 cm depth using a thermocouple (Type T, Omega Engineering, Deckenpfronn, Germany). To standardize soil moisture data between sites and soil types, the water filled pore space (WFPS) was calculated for each volumetric water content measurement using bulk soil density data provided from Bauters et al. (2019) and particle density of soil minerals of 2.65 g cm^{-2}.

Gas samples were analyzed for concentrations of CO$_2$ at ETH Zurich (Zurich, Switzerland) using gas chromatography (Bruker, 456-GC, Scion Instruments, Livingstone, U.K.). Soil gas fluxes were calculated using the linear increase of the gas concentration in the head space of the chambers over time, corrected for pressure and temperature according to the ideal gas law, divided by chamber area (Hutchinson and Mosier, 1981). Using the micrometeorological convention, a flux from the soil to the atmosphere is denoted as positive flux.

2.3 δ^{13}C-CO$_2$ of streams and soil respiration

After concentration measurements, the remaining gas was analyzed for δ^{13}C of CO$_2$ for one week of each month and site to derive a representative δ^{13}C signature of the monthly soil-derived CO$_2$ via the Keeling plot approach (Keeling, 1958). All Keeling plots yielded an $r^2 > 0.99$ (Fig A1). Post-run off-line calculation and drift correction for assigning the final δ^{13}C values on the V-PDB scale were done following the "IT principle" as described by Werner and Brand (2001). The δ^{13}C-values of the laboratory air standards were determined at Max-Planck-Institute for Biogeochemistry (Jena, Germany) according to Werner et al. (2001). Briefly, linking measured δ^{13}C values of CO$_2$ gas isolated from standard air samples relative to the carbonate V-PDB scale was done via the Jena Reference Air Standard (JRAS), perfectly suited to serve as a primary scale anchor for CO$_2$-in-air measurements. The measurement of the aliquots of the laboratory standards is routineously better than 0.15‰. In addition to soil CO$_2$, dissolved CO$_2$ samples of six pristine headwater streams near the chamber sites were taken in April (wet season) and September 2018 (dry season) using the headspace equilibration technique. At each stream site, 20 mL of unfiltered water sampled from the thalweg was injected into 110 mL, N_2-flushed (Alphagaz 2, Carbagas, Gümlingen, Switzerland) serum crimp vials containing 50 μL of 50 % ZnCl. From the headspace of the crimp vials, three analytical replicates were subsampled into evacuated 12mL exetainers (Labco Limited, High Wycombe, UK) following Bastviken et al. (2008). To avoid underpressure problems when withdrawing samples from the 110 mL vials, a luer-stopcock between syringe and needle was used. After withdrawl of 25 mL of sample-headspace, the luer-stopcock valve was closed and the syringe was removed from the headspace. After, the plunger was pushed to 20 mL before opening the valve and injecting the subsample to the new vial. The precision of the three analytical replicates was excellent, with a maximum standard deviation of 0.25 ‰. According to Szaran (1998) only 1.03 ‰fractionation occurs between dissolved and gas phase, thus δ^{13}C of headspace CO_2 can be used as a representative measure for dissolved δ^{13}C of CO_2. All CO_2 samples were analyzed for δ^{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; modification as described by Zeeman et al. (2008)) (see Supplemental Information).

2.4 δ^{13}C of litter and soil

Litterfall collected fortnightly between 2015 and 2016 from traps installed at the same sites was used to determine δ^{13}C of leaves. Eight litterfall traps were installed per plot and arranged in two rows of four with a distance of eight meters between traps. At each site, the leaves were combined into monthly samples which were subsequently dried, homogenized, and ground (Bauters et al., 2019). Soil samples were taken at the montane and the lowland forest plots at 0-30 cm depth and three random positions and subsequently air dried, sieved and milled. Litter and soil samples were analyzed using elemental analyzer (Automated Nitrogen Carbon Analyser; ANCA-SL, SerCon, UK), interfaced with an Isotope Ratios Mass Spectrometer (IRMS; 20-20, SerCon, UK).

2.5 Statistical Analyses

In total 1108 single flux measurements have been conducted (398 in the montane forest and 710 in the lowland forests, respectively). As the campaigns from the different sites were spread over several years, all data were compiled and averaged into weekly bins prior to plotting time series of the data assuming little year-to-year variability. In that way, yearly site averages were not weighed by periods of intensive sampling as each single week had an assigned median value regardless of measurement frequency. This compiling was only conducted for easier representation of the data. For statistical analysis of the effects of soil temperature and WFPS on the soil CO_2 flux, we used the individual fluxes with the actual soil temperature and WFPS conditions during each flux measurement. Effects of soil temperature and WFPS on the soil CO_2 flux from each forest type were quantified using linear mixed effects models, including all fluxes that were measured, and controlling for the soil chamber via a random intercept. Because a full model was not converging for soil CO_2 flux, including all interaction terms between the predictors, interaction between WFPS and soil temperature were omitted. Likewise, two models, one for the wet season and one for the dry season, were fitted to explain effects of ecosystem compartment (litter, soil CO_2 flux and stream CO_2) on δ^{13}C values in the lowland and montane forests, including sample spot (litterfall trap, soil flux chamber and sampled stream) as a random effect. Models were fitted using maximum likelihood methods via the lmerTest package (Kuznetsova et al., 2017).

P-values of the fixed effects - elevation, transect and their interaction - were determined based on the denominator degrees of freedom calculated with the Satterthwaite approximation. Marginal (m) and conditional (c) R^2_{adj} are proxies for the variation explained by the fixed effects, and both the random and fixed effects, respectively, were calculated following Nakagawa and Schielzeth (2013), via the MuMIn package (Barton, 2019). For all statistical analyses, the R-software was used (R Development Core Team, 2019). All model fits were validated by checking normality and homoscedasticity of the residuals. QGIS version 2.18 was used to compile the map of the Congo Basin.

3 Results

3.1 Temperatures and Soil Moisture

Weekly mean soil and air temperature were both stable throughout the year in both forest types (Figure 2a). Mean soil temperatures were 24.0 in the lowland forest sites and 15.3 °C in the montane forest. Air temperatures were slightly lower in both lowland and montane sites, averaging 23.5 and 14.7 °C, respectively. The WFPS at 30 cm depth in the lowland forest was quite constant. However, a decrease in WFPS was observed during dry season in the montane forest (Figure 2b). Mean annual WFPS in the montane forest was higher (51.4 %) than in the lowland (29.6 %).

3.2 Soil CO_2 fluxes

Mean annual soil CO_2 fluxes were (mean $^{maximum}_{minimum}$ ± SD) 3.45 $^{9.20}_{1.22}$ ± 1.14 μmol m^{-2} s^{-1} for the lowland forests and 3.13 $^{10.57}_{0.33}$ ± 1.22 μmol m^{-2} s^{-1} for the montane forest. Soil CO_2 fluxes in the montane forests were lowest during the dry season from June to September (2.42 $^{5.40}_{0.97}$ ± 0.87 μmol m^{-2} s^{-1}) and highest during the wet season from October to May (3.71 $^{10.57}_{0.33}$ ± 1.16 μmol m^{-2} s^{-1}) (Figure 2c). Lowland fluxes were more stable throughout the year, with only a small increase at the end of the wet season in June (3.50 $^{9.20}_{1.22}$ ± 1.15 μmol m^{-2} s^{-1}) (Figure 2c). The results from the intense sampling campaigns showed that there is not a big variability in soil CO_2 fluxes between chambers within a site (lowland: CV = 24%, montane: CV = 18%) and also between the different lowland forest sites (Figure A3 b, CV = 28%) and that fluxes are stable within a site and throughout a day (Figure A3 d). The linear mixed-effect model for soil CO_2 flux in the lowland explained 48 % of the overall variability, whereas the model for the montane soil CO_2 fluxes explained 69 %, all allocated to fixed effects (forest type, soil temperature and WFPS) (Table 1).The linear mixed effect model showed a negative effect of soil temperature on soil CO_2 flux in the lowlands (P-value = 0.03) but a positive effect in the montane forest (P-value <0.001). In the montane and lowland forest, a positive effect of WFPS on soil CO_2 flux (P-value <0.05) was observed (Table 1).

3.3 δ^{13}C values of leaf, litter, soil respired CO_2, and dissolved CO_2 in headwater streams

For each category (litter, soil, soil CO_2, stream CO_2), the δ^{13}C values in the lowland sites were always more negative than in the montane forest (Figure 3). The most negative values were found in leaf litter (-29.91 ± 0.94 for the lowland forest and -28.56 ± 0.85‰ for the montane forest). The highest values were found in stream dissolved CO_2, with -22.74 ± 2.34

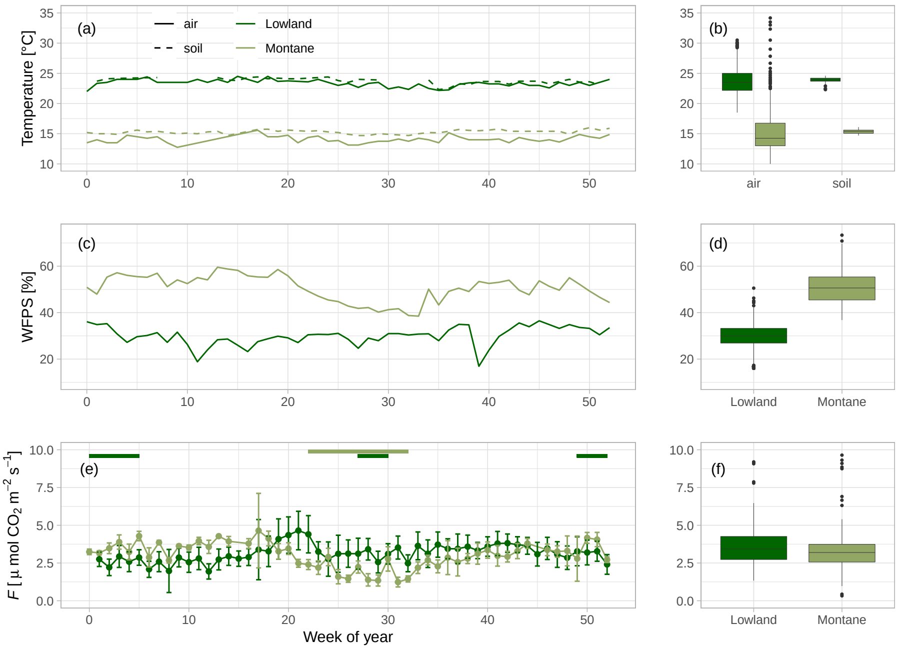

Figure 2. (a) Mean weekly air (solid line) and soil temperature at 20 cm depth (dashed line) in the lowland (dark green) and montane (light green) forest sites. (b) Yearly median air- and soil temperature. (c) Mean weekly water-filled pore space (WFPS) [%] in the lowland and montane forest soils at 30 cm depth. (d) Median WFPS in the lowland and montane forest. (e) Weekly median soil CO_2 fluxes (F) with error bars indicating the standard deviation. Green horizontal bars on top of panel C indicate the dry seasons in the lowland and in the montane forests, respectively. (f) Median soil CO_2 fluxes i the lowland and montane forests.

Table 1. Fixed effects estimates for CO_2 fluxes in the lowland and montane forests, including water-filled pore space (WFPS in %), soil temperature (in °C) as predictors for the soil CO_2 efflux (in μmol m^{-2} s^{-1}). For each effect, estimated standard error and estimated P-values is given, along with the estimated marginal (m) and conditional (c) R^2_{adj} (Nakagawa and Schielzeth, 2013)

Response	Effect	Estimate	SE	P-value	$R^2_{adj,m}$	$R^2_{adj,c}$
CO_2 flux - Lowland	Intercept	9.202	3.14	<0.01	0.07	0.48
	WFPS	0.024	0.01	0.05		
	Soil temperature	-0.279	0.13	0.03		
CO_2 flux - Montane	Intercept	-10.888	1.87	<0.001	0.69	0.69
	WFPS	0.106	0.01	<0.001		
	Soil temperature	0.561	0.13	<0.001		

in lowland streams and -16.68 ± 0.95‰ in montane streams. In both forest types, the δ^{13}C values increased from litter via SOC and soil respired CO_2 to dissolved CO_2 in streams. Only soil $\delta^{13}C\text{-}CO_2$ in the montane forest showed a small decrease

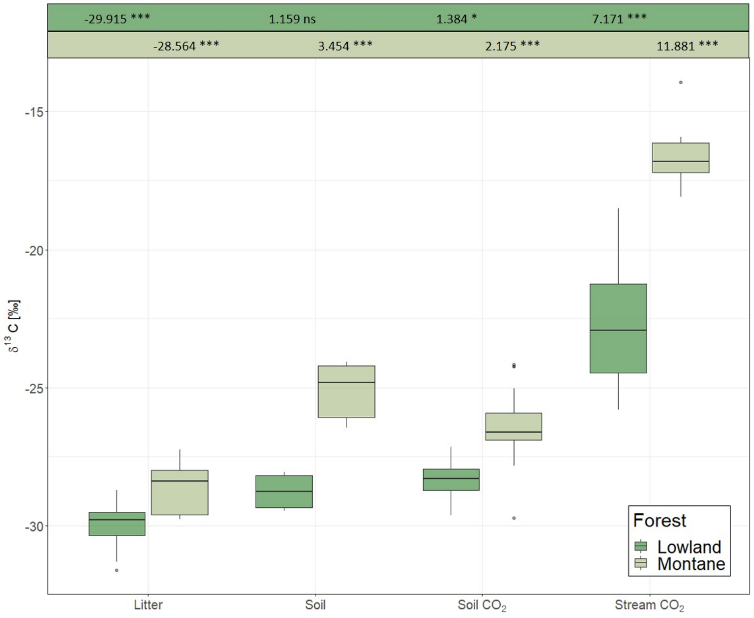

Figure 3. δ^{13}C values of litter, soil organic carbon, soil respired CO_2 and dissolved CO_2 in headwater streams adjacent to the monitoring sites in the lowland and montane forests. Numbers on top indicating the effect sizes of the two separate (lowland and montane) linear mixed effects models. Left numbers are intercept, all subsequent numbers - soil, soil CO_2 and stream CO_2 - are effect estimates relative to the litter.

relative to soil C (Figure 3). Monthly leaf litter δ^{13}C did not show temporal variability (Figure A2d). The mean δ^{13}C value of soil respired CO_2 was -28.35 ± 0.58 in the lowland forest and -26.39 ± 1.03‰ in montane forests. The linear mixed model showed a statistical difference in the δ^{13}C values of soil CO_2 in the montane forest between the wet and dry season, however, no difference was found in the lowland forest. Both, lowland and montane forests, showed significant differences in ^{13}C values of dissolved CO_2 between wet and dry season in streams, where the δ^{13}C-CO_2 signature is more depleted in the wet season compared to the dry season (Figure A4).

4 Discussion

4.1 Soil CO_2 Fluxes

Long term studies of soil CO_2 fluxes in tropical forests are scarce, especially in the Congo Basin. Here we present high temporal resolution data with 1108 individual soil CO_2 flux measurements over a period of more than 2 years. The mean annual values from forests of the Congo Basin reported in this study, which are 3.13 ± 1.22 μmol m^{-2} s^{-1} for the montane forest and 3.45 ± 1.14 μmol m^{-2} s^{-1} for lowland forests, are within the range of reported values from other tropical forests. It is, reported mean soil CO_2 fluxes from South and Central American tropical forests were for French Guiana (2.30 to 5.30 μmol m^{-2} s^{-1}, (Buchmann et al., 1997; Janssens et al., 1998; Bréchet et al., 2011; Epron et al., 2013; Courtois et al., 2018)), Brazil (2.64 to

4.30 μmol m^{-2} s^{-1}, (Davidson et al., 2004; Doff Sotta et al., 2004; Sousa Neto et al., 2011; Sotta et al., 2007; Garcia-Montiel et al., 2004)), and Panama (5.20 μmol m^{-2} s^{-1}, (Pendall et al., 2010)). To our knowledge, the only reported soil CO_2 fluxes from a tropical forest in Africa in recent years are from Kenya (Arias-Navarro et al., 2017; Werner et al., 2007) and they were rather low compared to our flux rates (i.e., between 1.04 and 1.66 μmol m^{-2} s^{-1}). Higher fluxes were reported in tropical forests in Hawaii (6.96 μmol m^{-2} s^{-1}, (Townsend et al., 1995)) and Thailand (9.76 μmol m^{-2} s^{-2}, (Hashimoto et al., 2004)). The data presented here are the first from tropical forests within the Congo Basin since Maldague and Hilger (1962) reported soil CO_2 fluxes from lowland forests in the DR Congo of 3 to 4 μmol m^{-2} s^{-1}. These values from the year 1962 lie exactly within the range of the values measured in this study, although it is important to note that the 1962 fluxes were derived from only four observations.

4.2 Seasonality of CO_2 Fluxes

Fluxes in the montane forest showed marked seasonality, with a 34 % decrease during the dry season, whereas fluxes in the lowland forests did not show any seasonality (Figure 2c). Courtois et al. (2018) have shown a similar trend of decreased fluxes during the dry season (15.7 % decrease) in tropical forests in French Guiana, however, the decrease they found was not as pronounced as in the montane forests we sampled. One possible reason for the seasonal difference between montane and lowland forests is that the lowland dry season is not as distinct as in the montane regions. Rainfall events during the "dry season" in the lowlands are not uncommon (Figure A2). A model study by Raich et al. (2002) concluded that in seasonally dry biomes, soil CO_2 emissions positively correlate with precipitation. Precipitation was also identified as the main driver of maximum C assimilation rates in 11 Sub-Saharan ecosystems, which in turn was an ultimate driver of soil CO_2 fluxes (Merbold et al., 2009). Thus, given the results of the present study and the projected increase in dry season length in the Congo Basin, as recently reported by Jiang et al. (2019), one would expect a future decrease of C fluxes in the montane forests while little to no effect might be expected in the lowland forests. However, a change in rainfall patterns can also lead to more extreme drying-rewetting events and this might affect soil CO_2 fluxes, as potential CO_2 pulses after rewetting compensate for the possible reduced soil respiration (Waring and Powers, 2016).

4.3 Temperature and Soil Moisture Controls

Despite the markedly different temperature regimes between the lowland and montane forests, yearly averaged soil CO_2 fluxes were almost identical (Figure 2 f). Such inter-site temperature independence of soil CO_2 flux is unique compared to other tropical (e.g. Brazil (Doff Sotta et al., 2004; Sousa Neto et al., 2011) or temperate forests (e.g. Switzerland (Ruehr et al., 2010)), where strong correlations between soil CO_2 fluxes and soil temperature were found. However, in addition to temperature, soil geochemistry can play a crucial role in controlling soil CO_2 fluxes, particularly via soil C stabilization processes and their rates (Doetterl et al., 2018). Short-term changes in C fluxes are mostly related to respiration of non-protected soil C (plant residues, root exudates, rhizodeposition) while the majority of stored C in soils is stabilized within the mineral matrix (Doetterl et al., 2018). Thus, a potential increase in CO_2 efflux due to change in soil temperatures in the lowland might be counteracted by higher C protection due to soil geochemistry. Within sites, a statistically significant correlation between soil temperature and

CO_2 flux was found, however, montane and lowland forest displayed opposite relationships with soil temperature (Table 1). The negative relationship with soil temperature in the lowland forest indicates that soil temperatures are already too high for an optimal microbial activity. Nevertheless, it is important to note that the soil temperatures within different forest types of the Congo Basin are relatively stable throughout the year (Figure 2 a), with standard deviations of 0.34°C and 0.42°C for montane and lowland soil temperature, respectively. Thus, given the lack of variability in soil temperatures, the accuracy of detected relationships could be questioned and extrapolations of the here found CO_2 flux responses beyond the soil temperature ranges observed in this study should be handled with care. For better understanding of temperature dependencies of soil respiration in these forest soils, warming experiments (incubation or field) are needed.

Despite the higher total annual rainfall in the lowlands (Figure A2), the montane forest soils exhibited higher WFPS (Figure 2 b). The lower relative WFPS in the lowlands was likely due to the sandier soil texture leading to faster drainage. Moreover, the montane forest site showed a clear positive relationship between soil CO_2 and WFPS, whereas in the lowland site the effect size of WFPS on soil CO_2 flux was a lot smaller (Table 1). Soil moisture can influence soil respiration physically and biologically. Physically, soil moisture can limit the transport of C substrate to soil microorganisms (at low soil moisture conditions) and the diffusion of gases through soils, including both oxygen required for aerobic respiration and respiratory CO_2 (in high soil moisture conditions) (Manzoni et al., 2016; Moyano et al., 2012, 2013). Biologically, soil moisture can affect the activity of heterotropic respiration, where low soil moisture conditions stress soil microbial communities, and autotrophic respiration (Xu and Qi, 2001; Rey et al., 2002). The latter is linked to canopy processes, where water limitation can lead to stomatal closure, limiting plant photosynthesis and thus also belowground respiratory processes (see also 4.4). One possible explanation for why the lowland soils CO_2 flux did not vary with WFPS is that the soil respiration is potentially limited by soil C availability, indicated by the similar isotope composition of litter, SOC and soil emitted CO_2 in the lowland forests (see also 4.4). Therefore, if soil respiration in lowland forests is indeed likely substrate limited, then environmental factors such as soil moisture or temperature may have less control on soil respiration (Davidson and Janssens, 2006). While soil respiration in lowland forests is most likely C-limited, respiration in montane forests seems to be more sensitive to environmental conditions and could represent a potentially large C source with climate change.

4.4 Isotopic source indicators

In this study, the link between C assimilation and soil CO_2 is evident through the distinctively different $\delta^{13}C$ signatures between lowland and montane forests along the whole cascade of carbon intake via photosynthesis, litterfall, SOC, soil CO_2 and stream dissolved CO_2. This difference holds throughout most of the year for leaf litter and soil respired CO_2 between the lowland and the montane site (Figure A2). The strongest ^{13}C enrichment of soil CO_2 was observed at the end of the dry season (September) in the montane site, likely caused by lower photosynthetic ^{13}C-CO_2 discrimination conveyed to soil respiration (Figure A2 c). Indeed, the enrichment of ^{13}C of autotrophic soil respiration resulting from stomatal closure during periods of drought has been widely documented (Ekblad, 2001; McDowell et al., 2004; Blessing et al., 2016; Salmon et al., 2019). Such distinct enrichment was presumably not detected in the lowland sites due to the absence of a prolonged dry season (Figure A2 a). A study by Ometto et al. (2002) found similar seasonal dependencies of two tropical forest of the Amazon Basin, with one site

(Santarem forest) showing a distinct seasonality of δ^{13}C signal of soil CO_2 fluxes in response to large variation in rainfall whereas the other (Manaus forest) had only little variation in rainfall and thus also little variation in δ^{13}C signal of soil CO_2 fluxes.

The δ^{13}C value of various ecosystem components (leaf litter, SOC, soil respired CO_2, and riverine CO_2) were generally enriched in the montane compared to lowland forests (Figure 3). Incrased foliar δ^{13}C values at higher altitudes are a commonly reported tendency (Körner et al., 1988; Hultine and Marshall; Chen et al., 2014). This observation is generally explained by the decrease in atmospheric pressure (and thus decreasing partial pressure of O_2 and CO_2) and decreasing temperature and its effect on partial stomatal closure and lower c_i/c_a (ratio of intercellular to ambient CO_2) (Roderick and Berry, 2001). While the decrease of O_2 partial pressure and temperature are increasing the carboxylation efficiency of the Rubisco molecule and thus declining c_i/c_a (), declining temperature also effects the viscosity of water and alter the flux of water into the plants, resulting in stomatal closure and decreasing c_i/c_a (Roderick and Berry, 2001). A decline in c_i/c_a will increase the foliar δ^{13}C value (Farquhar and Richards, 1984). Similar isotopic enrichment with altitude has been shown even within small-scale gradients in Amazonian forests (de Araújo et al., 2008). In the Amazonian study, the relatively enriched values of leaf and ecosystem respiration in the high elevation sites was explained by increased leaf-level photosynthetic capacity (higher leaf nitrogen content and leaf mass per unit area (LMA)), which is decreasing intercellular CO_2 concentrations and reducing leaf discrimination, resulting in increasing ^{13}C concentrations in the leaves (de Araújo et al., 2008). However, Bauters et al. (2017) reported decreasing leaf nitrogen content and LMA with higher elevations in tropical forests of the Congo Basin. It is more likely, that the higher δ^{13}C values in the montane forest are linked to canopy processes (photosynthesis and stomatal conductance) resulted from lower atmospheric pressure and lower temperatures. Furthermore, a shift in microbial communities due to temperature changes has been found to impact fractionation of the C isotope in heterotrophic soil respiration (enrichment of ^{13}C at lower temperatures) (Andrews et al., 2000). Overall, different δ^{13}C values in the studied ecosystem components between the two forest types might be due to a combination of different effects including temperature, canopy processes, and open vs. closed system isotope dynamics.

As C is respired and transferred down the cascade from photosynthesis to stream dissolved CO_2, it becomes more enriched with heavier isotopes when transiting from one pool to the next due to isotope fractionation (as ^{12}C tends to be preferentially consumed). This is generally a feature of 'open systems' in which reactions occur with a continuous supply of substrate, while the residual substrate and products are lost from the system. In contrast, a 'closed system' is characterized by the absence of new inputs and results in less fractionation between substrate and product (Fry, 2006). The different enrichment gradients observed between lowland and montane tropical forests indicate more closed vs. more open system dynamics, respectively. In particular, the similar isotopic signatures of litter, SOC, and emitted soil CO_2 at the lowland site indicated a more complete decomposition of the C input into the different compartments and thus relatively closed system isotope dynamics (Figure 3). However, it needs to be stated that this interpretation is somewhat speculative, as contributions of CO_2 from root respiration can vary with forest types which may confound inter-site comparison. Additional research would be needed to test for the hypothesis of the lowland forests being closed C systems. Moreover, in both systems, the highest enrichment occurs in the last step from soil to stream dissolved CO_2. A similar enrichment of stream CO_2 relative to soil respired CO_2 has also been found in the Amazon by Quay et al. (1989). However, since stream CO_2 is governed by a multitude of factors (Enrichment factors: aquatic photosynthesis, equilibration with atmosphere, outgassing, and weathering of carbonate/silicate minerals (depends on CO_2 source for SiO_2); Depletion factors: respiration of organic C, possibly photodegradation) it remains difficult to isolate a single factor causing the different isotope effects between soil CO_2 and stream dissolved CO_2 for lowland and montane forest.

5 Conclusions

Although the lowland and montane forests of the Congo Basin differed in terms of vegetation composition, climate, and edaphic conditions, there was no significant difference in annual mean soil CO_2 flux observed in this study. However, in contrast to the lowland forest, the montane forest site exhibited strong seasonality of soil CO_2 efflux, primarily driven by WFPS during the dry season. The nearly identical C isotopic signatures of soil derived CO_2, litter, and SOC in the lowland forest indicate that respiration is likely substrate limited. Substrate limitation in the lowlands would also limit the influence of environmental factors such as WFPS on the CO_2 flux rate, which corresponds well to the observed lack of correlation between soil moisture or temperature with soil CO_2 fluxes. However, this hypothesis of substrate limitation in the lowlands is highly speculative and further research would be needed to test it. Furthermore, we cannot rule out changes in soil CO_2 fluxes with changing environmental conditions given the low range in variation observed over the study period. Overall, these results fill a critical knowledge gap for soil respiration rates of major tropical forests, provide baseline flux magnitudes to better parameterize earth system models, and highlight how soil respiration in montane tropical forest soils of the Congo Basin are relatively sensitive to environmental changes and that changes in the C balance might happen in response to more erratic rainfalls and weather extremes. Further monitoring in the Congo Basin is necessary (for example eddy covariance flux towers), to set this results in context of total NEP in these ecosystems.

Data availability. All data used in this study were published at Zenodo and are available under http://doi.org/10.5281/zenodo.3757768.

Author contributions. SB, MBarthel and JS were responsible for study design. Fieldwork was conducted by SB, MBarthel, IAM, JKM, LS, and NG. Lab work was conducted by MBarthel and RAW. Data interpretation was performed by SB, MBarthel, TWD, MBauters supported by KVO, PB and JS. The manuscript was written by SB with contributions from all co-authors.

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