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REGULAR ARTICLE

Functional traits drive the difference in soil respiration between *Gilbertiodendron dewevrei* monodominant forests patches and *Scorodophloeus zenkeri* mixed forests patches in the Central Congo basin.

Benoît Cassart · Albert Angbonga Basia · Mathieu Jonard · Quentin Ponette

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Abstract
Aims In tropical rainforests, soil respiration accounts for the major part of ecosystem respiration, yet a deep understanding of the influence of forest type and species composition is still lacking. We therefore selected patches of the rainforest in the Central Congo basin differing in their species composition, some patches under the *Scorodophloeus zenkeri* Harms mixed forests (MIF) and others in the *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF). We measured daily soil respiration over a one-year period.
Methods By fitting a simple conceptual model of soil respiration, including fine root biomass, soil organic C stocks and ground climate measurements (soil moisture and temperature), we attempted to distinguish autotrophic and heterotrophic soil respiration, and to better understand the drivers behind total soil respiration.
Results On an annual basis, soil respiration was 10% higher under MOF (22.10 Mg C ha^{-1} y^{-1}) compared to MIF (20.01 Mg C ha^{-1} y^{-1}) ($p < 10^{-3}$). While the estimated autotrophic and heterotrophic soil respiration contributed about equally to soil respiration in MOF, autotrophic soil respiration slightly dominated (59%) in MIF. In both forests, the combined contribution of litterfall inputs and fine roots productivity was lower than the heterotrophic flux, with the largest difference observed under MOF (−6.16 Mg C ha^{-1} $year^{-1}$) compared to MIF (−2.62 Mg C ha^{-1} $year^{-1}$). The sensitivity analysis of the model showed that the higher heterotrophic soil respiration under MOF was driven by the twofold C accumulation in MOF topsoil compared to MIF. Soil moisture was a major driver of temporal changes in soil respiration, but hardly impacted the differences in annual soil respiration between forests.
Conclusion While the difference in SOC accumulation between forests was driven by the low nutrient to C ratios of *Gilbertiodendron dewevrei* tissues, additional research is needed to identify the causes behind the unbalanced C budget.

Keywords Simple conceptual model · Tropical rainforest · Fine root · Soil moisture · Autotrophic respiration · Heterotrophic respiration · Compositional effects

BC and QP conceived and designed the experiments. ABA and BC performed the experiments. BC, MJ and QP analysed the data

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B. Cassart · M. Jonard · Q. Ponette
UCLouvain-ELI, Earth and Life Institute, Université catholique de Louvain, Croix du Sud 2, L7.05.09, BE-1348 Louvain-la-Neuve, Belgium

B. Cassart (✉)
ERAIFT, Ecole Régionale Post-universitaire d'Aménagement et de Gestion Intégrés des Forêts et Territoires Tropicaux, Kinshasa, Democratic Republic of the Congo
e-mail: cassartb@gmail.com

A. Angbonga Basia
Institut Facultaire des Sciences Agronomiques de Yangambi, Yangambi/Kisangani, Democratic Republic of the Congo

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Introduction

In the context of increasing CO_2 concentration in the atmosphere and associated climate change, understanding biophysical controls on carbon (C) fluxes and stocks in terrestrial ecosystems is of major importance. C sequestration in forest ecosystems is the result of a balance between uptake (photosynthetic carbon fixation) and loss (ecosystem respiration) (Malhi et al. 1999; Chen et al. 2013). In tropical forests, soil respiration accounts for more than 70% of total ecosystem respiration (Malhi et al. 1999). In addition, tropical forests have the highest soil respiration rates globally (Luyssaert et al. 2007; Hashimoto et al. 2015). Despite their key role in the global C cycle, the tropical forests have been less studied and their C budget, sources vs sinks of carbon, is still controversial (Clark 2004).

Soil respiration results from the activity of roots, mycorrhizal hyphae and the associated microbes (autotrophic component) and from the decomposition of organic materials from aboveground and belowground litter by micro-organisms (heterotrophic component) (Subke et al. 2006). Both autotrophic and heterotrophic soil respirations involve various biological and ecological processes and are highly variable at all spatial (from respiration chamber to forest stand) and temporal (hours to years) scales (Luo and Zhou 2006). Therefore, their response to change in environmental conditions may differ (Subke et al. 2006; Epron 2009). However, contrasting results reported in numerous studies in tropical forests highlight the poor mechanistic understanding of these processes (Holland et al. 2000; Wei et al. 2010; Cavaleri et al. 2015).

At local scale, ground climate conditions through soil moisture and, to a lesser extent, soil temperature, are recognized as the most influential environmental factors controlling the temporal variation in soil respiration and its components in tropical rainforests (Davidson et al. 2000; Wood et al. 2013; Tan et al. 2013; Rubio and Detto 2017). The size of the soil organic C pool, the quality of organic matter inputs (above and belowground), the abundance of roots and the distance and the size of the surrounding trees have been shown to affect soil respiration and its components (autotrophic vs. heterotrophic) over small spatial scales (Epron et al. 2004; Bréchet et al. 2011; Hopkins et al. 2013). Since all these variables are influenced by the forest cover (De Deyn et al. 2008), soil respiration and its components should be largely impacted by forest composition under similar conditions of macroclimate, topography and soil.

Tree species identity impact on soil respiration is linked to functional traits that drive C assimilation, transfer and respiration as well as litter decomposition through their impact on litter quality and ground climate conditions which control the activity of heterotrophs (De Deyn et al. 2008). Indeed, tree species identity may affect soil CO_2 efflux through a variety of mechanisms, mainly by controlling the quantity and the quality of aboveground and belowground litter production in one hand, and root-derived respiration (root respiration and root exudates) on the other hand (Metcalfe et al. 2011).

Heterotrophic soil respiration is the product of the microbial decomposition of soil organic matter and is directly affected, among other factors, by litter quantity and quality (e.g. C:N ratio, lignin and nutrient concentrations), via the alteration of the microbial communities and the decomposition rates (Keller et al. 2013; Bréchet et al. 2017). Higher litter inputs lead to potential greater availability of labile C components and nutrients and thus to increased OM decomposition (Liu et al. 2009).

Autotrophic soil respiration is defined to include all processes occurring in the rhizosphere, hence root respiration is a combination of root growth and activity as well as microbial activity in the rhizosphere. Although coarse roots (> 2 mm) are the most important contributor to root biomass, variability in autotrophic soil respiration has been shown to be mainly explained by changes in fine roots (≤ 2 mm) biomass (Hopkins et al. 2013). In addition to belowground process, Högberg et al. (2001) have shown that respiration from roots and their fungal symbionts were also considerably coupled to photosynthetic activity. Therefore, changes in light availability through reduced allocation of photosynthate to roots could lead to important change in autotrophic soil respiration (Wofsy et al. 1988).

Many factors affect both autotrophic and heterotrophic soil respirations which interact with each other and mutually affect soil respiration. For example, an increase in N availability may not only promotes heterotrophic soil respiration by stimulating the OM decomposition rate but also enhances N nutrition increasing photosynthesis and maintenance respiration and stimulating thereby autotrophic soil respiration (Wang et al. 2010; Hopkins et al. 2013).

Tropical rainforests comprise a large range of tree species composition and diversity, from highly diverse

forests with up to 300 tree species per ha (Sullivan et al. 2017) to ecosystems where nearly one single tree species dominates in the upper canopy layer (Connell and Lowman 1989; Peh et al. 2011). Whereas such contrasts in species composition and diversity may potentially lead to substantial changes in soil respiration and its components (Raich and Tufekciogul 2000; Bréchet et al. 2009; Metcalfe et al. 2011; Raich 2017), the influence of forest type and diversity on soil respiration remains largely unknown.

Here we investigate R_T in selected patches located into two major forest types of the Central Congo basin, in DR Congo: the *Scorodophloeus zenkeri* Harms mixed forests (MIF) and the evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF). These two forest types cover extensive areas in the zone, where they frequently co-occur on similar ecological conditions (Hart et al. 1989; Kearsley et al. 2017; Cassart et al. 2017). The specific objectives of this paper were: (i) to quantify the autotrophic and heterotrophic components of soil respiration; (ii) and to investigate the drivers behind the spatial and temporal variation of soil respiration and its components for the two forest types.

To that end, we measured soil respiration monthly during a one-year period in selected patches (clusters made of three trees) within MIF and MOF, and fitted a simple conceptual model that attempts to separate soil respiration into autotrophic and heterotrophic components using measured environmental variables: soil organic C stocks (forest floor and 0-10 cm mineral soil layer), pedoclimatic variables (soil temperature and moisture) and fine roots biomass.

Materials and methods

Site description

Our investigations were carried out in 2012 and 2013 in the Yoko Forest Reserve in the Tshopo province (Democratic Republic of Congo, DRC). The reserve is located on a sandy plateau at about 28 km south of Kisangani (00 19′12” N, 25 17′43″ E; 450 m above sea level) and covers an area of 6975 ha. Vegetation within the reserve consists of pristine moist semi-deciduous rainforest mixed with variable patches of moist evergreen rainforests. Few transition forests and slash-and-burn agriculture areas are found on the west side of the reserve.

Based on the meteorological data collected from the Yangambi station (located 100 km to the west of Kisangani) between 1961 and 2009, the annual precipitation averages 1780 (±230) mm with two distinct rainy seasons (March–June and August–December), and a cumulated dry season length of *ca* 3 months (January–February and July) with monthly precipitation lower than 60 mm. The mean annual air temperature is 24.8 °C with minimal variation across the year. The dominant soil type is classified as Xanthic Ferralsol (Van Ranst et al. 2010) mostly composed of quartz sand, with low content of kaolinite clay and hydrated iron oxides.

A preliminary survey allowed us to select areas of the Reserve dominated either by semi-deciduous *Scorodophloeus zenkeri* Harms mixed forests (MIF) or by evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF), in otherwise similar climatic, topographic and edaphic conditions. As reported by Cassart et al. (2017) the well-drained soils under MIF and MOF had similar chemical and physical soil properties. They were highly weathered and acidic ($pH < 4.8$), with a coarse sandy texture that slightly decreased with depth.

As shown in Table 1, the dendrometric characteristics were not significantly different between the two forest types while species composition and diversity strongly differed. Species diversity quantified by the Shannon Diversity Index was much higher in MIF compared to MOF. While *S. zenkeri* accounted for 28.2% of the total basal area in MIF, the contribution of *G. dewevrei* to total basal area amounted to 73.1% in MOF allowing this forest to be classified as monodominant (Connell and Lowman 1989). Additional information on site and stand characteristics may be found in Cassart et al. (2017).

Measurements and sampling

Sampling zone

One hundred and six 40 × 40 m plots were established (77 and 29 in MIF and MOF, respectively) within an area of 2 km^2 (Fig. 1a). Based on the higher species diversity under MIF compared to MOF, we expected a higher variability of soil respiration in MIF. Therefore, we installed a higher number of plots in MIF.

Each plot was centred on a tree cluster which comprised three mature trees of the canopy layer forming a triangle with the trees. The cluster centres were located at a distance from the trees ranging from 2.5 to 9.3 m (Fig. 1b-c). Four types of clusters were chosen for investigation: monospecific clusters (each cluster tree belongs to the corresponding dominant tree species, ie *S. zenkeri* and *G. dewevrei* in MIF and MOF, respectively), two-species clusters including the dominant tree species, three-species clusters including the dominant tree species and three-species clusters without the dominant tree species (see Supplementary material 1 for the distribution of the 106 plots between these four types of clusters). Because of its lower species diversity (Table 1), only mono- and two-species clusters were established in MOF. In each plot, all living trees with a diameter at breast height > 10 cm were measured and identified to species level, and all trees with diameter at breast height > 16 cm were mapped to determine local stand characteristics.

Measurements of litterfall, soil respiration, temperature and water content

Within each cluster, 1 m^2 circular litter traps (1.3 m high) were installed in the centre of the cluster (Fig. 1c) and litterfall was collected monthly from May 2012 to April 2013. Coarse woody debris with a diameter > 1 cm were discarded and the remaining litter was sorted into two fractions (leaves and fine woody debris). Both litterfall fractions were dried at 70 °C during 48 h and weighed. For each litterfall fraction, C and N concentrations were determined by the dry combustion method (Thermo Finnigan Flash EA 1112 elemental analyser) on composite samples pooled per cluster over three months (May to July, Aug. to Oct., Nov. to Jan. and Feb. to April), and multiplied by the corresponding biomass. Those four quarterly contributions were then summed up to obtain annual C litterfall inputs as leaves and fine woody debris per cluster.

In addition, total daily soil respiration was measured monthly from May 2012 to April 2013 in each cluster using the soda lime technique as described in Keith and Wong (2006). Following those authors, this method has been shown to yield measurement of CO_2 efflux that are quantitatively similar and unbiased with respect to an IRGA method.

The measurements were conducted at the same locations during the study year. Briefly, CO_2 emitted from the soil was absorbed for 24 h in 60 g of predried soda lime granules in inert glass petri dish placed on wire stands suspended above the litter surface to avoid obstructing CO_2 efflux from the soil. The chambers consisted of white polyethylene plastic buckets with the base cut off (25 cm tall, 30 cm diameter and inserted 3 cm in the soil 4 weeks prior to the start of the measurements) and a heavy lid that adequately sealed the chamber during measurement. Every chamber was kept free of seedlings and woody debris throughout the whole measurement period. Four blanks per forest type were used to account for CO_2 absorption during handling and drying.

In order to assess the forest floor contribution to soil respiration, a second respiration chamber was set up in each monospecific cluster ($n = 16$ and $n = 13$ in MIF and MOF, respectively; Supplementary Material 1; Fig. 1c). Four weeks prior to the start of the soil respiration measurements, the litter layer (holorganic layers, $O_L + O_F + O_H$) was carefully removed from each of these chambers without damaging the superficial root mat, placed on a removable device made from metal mesh and reinstalled in the respiration chamber. This apparatus allowed us to measure soil respiration monthly from May 2012 through April 2013 without forest floor contribution (R_{WF}) by removing the litter layer only during the measurement day while keeping it during the rest of the period to keep disturbance to a minimum. Litter contribution was then estimated by subtracting CO_2 efflux in the chamber with periodic litter removal from the respiration in the control chamber. However, as the litter removal experiment gave unplausible and contradictory results, the latter were only reported and discussed in Supplementary materials 2.

The soil temperature at 5 cm depth was simultaneously monitored adjacent to each chamber using a digital thermometer (Fig. 1d). Soil moisture (volumetric water content) was determined on two 0–10 cm deep soil cores (2×100 cm^3) in undisturbed areas directly adjacent to the chamber immediately after CO_2 measurement; soil samples were weighed and oven-dried at 105 °C for 48 h. Due to important power supply issues during the oven drying of the soil samples, soil moisture is only available from July 2012.

Table 1 Summary of forest, soil characteristics (soil climate and organic carbon stocks) and fine roots biomass in the forest floor and in the upper 0–10 cm mineral soil for the mixed (MIF) and monodominant (MOF) forests (averages ± standard errors). Repeated measurements of soil climate, soil organic C stocks and fine roots biomass have been averaged over the sampling period. The five most abundant species selected based on their basal area ratio (%) are presented. Species abbreviations for Scorodophloeus zenkeri, Cynometra hankei, Julbernardia seretii, Prioria oxyphylla, Polyalthia suaveolens, Gilbertiodendron dewevrei, Cola griseiflora, Panda oleosa. Different letters in a row indicate significant difference between forests ($p \leq 0.05$). Stand characteristics and species diversity were derived from stand inventories as described by Cassart et al. (2017)

	MIF	MOF
Stand characteristics		
Stand density (tree.ha^{-1})	392 ± 9 ^{a}	405 ± 20 ^{a}
Total basal area (m^2.ha^{-1})	31.4 ± 1.9 ^{a}	34.9 ± 4.6 ^{a}
Species diversity		
Shannon index	3.12 ± 0.04 ^{a}	1.49 ± 0.01 ^{b}
Five most abundant species	*S. zenkeri* (23.3%)	*G. dewevrei* (73.1%)
	C. hankei (6.7%)	*S. zenkeri* (7.8%)
	P. suavolens (5.5%)	*P. oxyphylla* (6.0%)
	A. mannii (4.2%)	*C. griseiflora* (1.8%)
	P. oxyphylla (4.0%)	*P. oleosa* (1.6%)
Soil climate (0–10 mineral soil layer)		
Annual mean soil moisture (m^3 m^{-3})	0.33 ± 0.01 ^{a}	0.38 ± 0.01 ^{b}
Annual mean soil temperature (°C)	23.64 ± 0.02 ^{a}	23.78 ± 0.03 ^{b}
Soil organic C (Mg C ha^{-1})		
Litter component layer (O_L)	1.13 ± 0.05 ^{a}	2.85 ± 0.19 ^{b}
Decomposed organic matter layer ($O_F + O_H$)	1.43 ± 0.08 ^{a}	3.83 ± 0.35 ^{b}
0–10 cm mineral soil layer	13.62 ± 0.32 ^{a}	22.24 ± 1.15 ^{b}
Fine roots biomass (Mg C ha^{-1})		
Fine root in forest floor	0.34 ± 0.01 ^{a}	0.33 ± 0.01 ^{a}
Fine root in the upper 0–10 cm mineral soil	0.82 ± 0.03 ^{a}	0.75 ± 0.04 ^{b}

Forest floor, fine roots and soil sampling

The forest floor was sampled every two months from May 2012 to March 2013 in two opposite selected points around each chamber (cf. Fig. 1d), using a 20 × 20 cm metal frame. For each sample, the litter component (O_L) and the decomposed organic matter ($O_F + O_H$) were separated. Briefly, the litter component layer was described as non-decomposed fallen plant material and the decomposed organic matter layer as partly or strongly decomposed organic material (see van Delft et al. (2006)). Roots were removed using a tweezer and forest floor samples were then pooled per cluster for determination of oven-dry mass (70 °C during 48 h). Forest floor samples from the July collection period were grinded for C and N analyses.

Fine roots (roots ≤2 mm in diameter) were sampled every two months from July 2012 to March 2013 from the upper 0–10 cm mineral soil layer in two opposite selected points around each respiration chamber (cf. Fig. 1), using Kopecky cylinders (250 cm^3). Roots were removed from the soil by wet sieving. Roots from the forest floor and the upper 0–10 cm mineral soil were separated into fine (≤ 2 mm) and coarse roots using a vernier scale. Samples were then pooled per cluster for determination of oven-dry mass (70 °C during 48 h). Root C and N concentrations were determined on a subset of 16 and 30 root samples selected across the entire collection period and cluster types, in MOF and MIF respectively.

Mineral soil samples (0–10 cm depth) were collected in May 2012 at four locations per cluster, using an

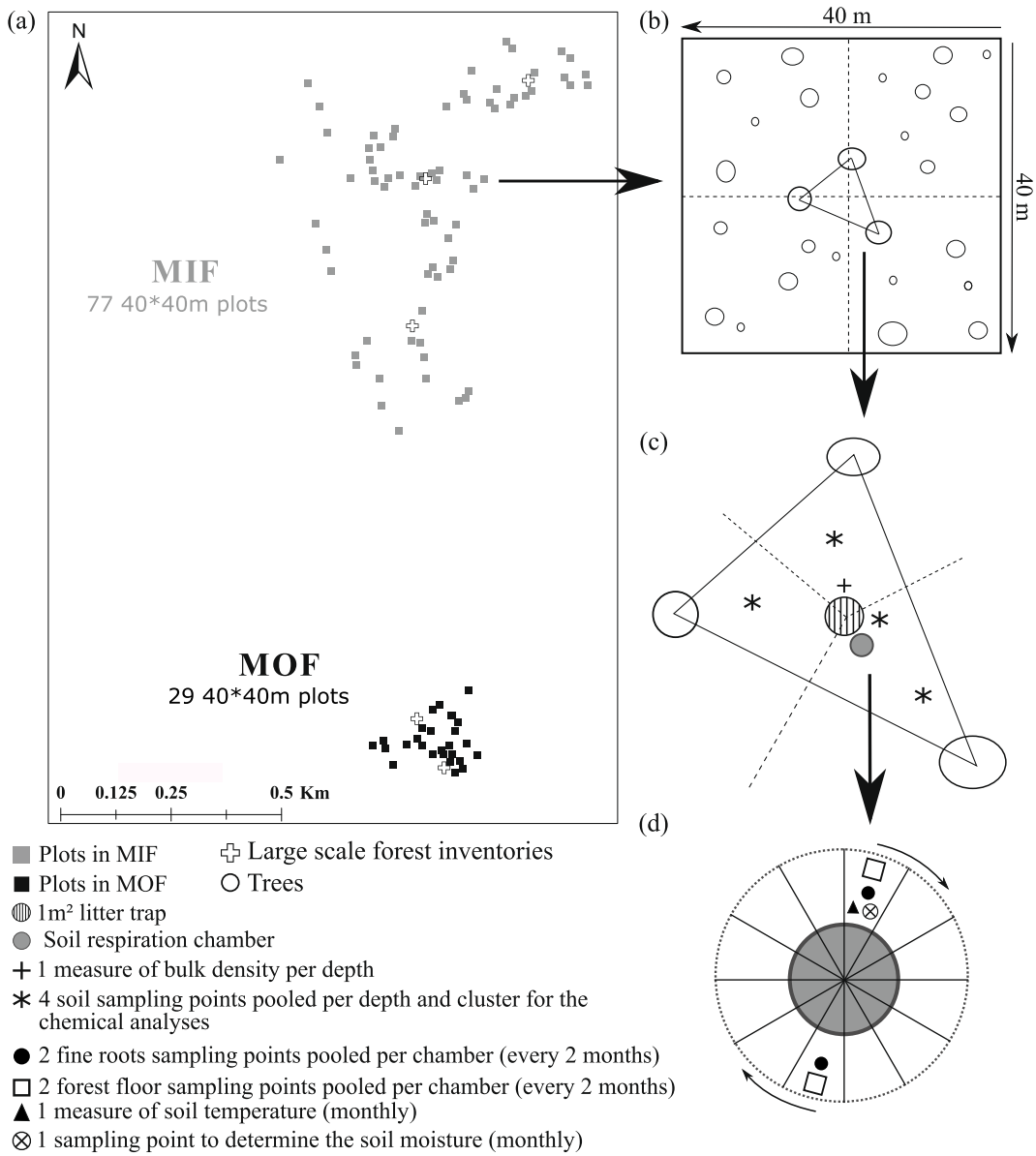

Fig. 1 Sampling plan and sampled locations in MIF and MOF. **a** Study area, indicating the location of the plots in MIF and MOF. **b** Configuration of the cluster within the plot. **c** Measurement of soil respiration and sampling of litterfall, mineral soil and soil bulk density within a cluster area. **d** Sketch showing the shift in sampling/measurement location for soil temperature, soil moisture, fine roots and forest floor around the chamber over time during the study period

Edelman auger sand-type. No coarse fragments were found in mineral soil samples; similarly, we did not detect any charcoal presence. Samples were then pooled into one sample per cluster, air-dried, sieved at 2 mm and milled for C and N analyses. Bulk density was determined at one location per cluster, using Kopecky cylinders (100 cm^3) after sieving at 2 mm and oven-drying at 105 °C. Soil pH was determined potentiometrically in 0.01 M $CaCl_2$ (1:5 soil:solution ratio).

In order to assess the decay rate of soil organic C in the upper 0–10 cm mineral soil, we carried out a laboratory incubation experiment. Mineral soil samples from monospecific and 2-species clusters ($n = 36$ and 29 respectively in MIF and MOF) were sieved at 2 mm and moistened at field capacity with deionized water. The soil samples (30 g equivalent dry soil) were then incubated during 91 days in 500 ml hermetic plastic jars containing a 30 ml vial filled with NaOH solution. The

CO_2 trapped in NaOH solution was determined every week by measuring the changes in electrical conductivity according to the method of Rodella and Saboya (1999). Experiment was conducted in duplicate per cluster in a temperature-controlled dark room at 20 °C. Six blanks (plastic jars without soil samples) were used to account for CO_2 absorption during the experimental procedure. The water content was kept at field capacity by weighing and spraying deionized water at the soil surface during conductivity measurements, so that soil moisture did not limit microbial activity. Prior to incubation, subsamples were taken and milled for C analyses. Cumulated decay rates of the upper 0–10 cm mineral soil from incubation (k_{inc}, gC-CO_2 gC_{MS}^{-1} day^{-1}) were calculated by dividing the amount of C-CO_2 absorbed by NaOH solution by the initial C stocks of the incubated sample and by the corresponding number of days.

Simple soil respiration model

We developed a simple soil respiration model that simulates the production of CO_2 in soil (forest floor plus the upper 0–10 cm mineral soil). In the model, the total soil CO_2 efflux (R_T, g C day^{-1} m^{-2}) is the result of microbial respiration from organic matter decomposition (R_H) and the growth and maintenance respiration of roots (R_A):

$$R_T = \sum_{i=1}^{3} RH_i + \sum_{i=1}^{2} RA_i \quad (1)$$

The heterotrophic respiration is related to organic matter decomposition which is proportional to the amount of C in soil pool (SOC_i, g C m^{-2}). In this model, the soil is divided into three layers (subscript *i*) assumed to exhibit contrasted maximum decay rates ($k_{F,i}$, day^{-1}): O_L, $O_F + O_H$ and 0–10 cm mineral soil layer. For each considered pool, the maximum decay rate ($k_{F,\ i}$) is modulated by the soil temperature at 5 cm depth (T, °C) using a Q_{10} function and by the square root of the soil moisture (m^3 m^{-3}) (Eq. 2). Cassart et al. (2017) highlighted strong differences in the quality of organic matter inputs between MIF and MOF leading to contrasted carbon accumulation; therefore, we allowed the coefficient k to vary by forest type (subscript *F*) and by soil layers (subscript *i*).

$$RH_i = k_{F,i} \times SOC_i \times \sqrt{\text{soil moisture}} \times Q_{10}^{(T-Tmax)/10} \quad (2)$$

As shown by Eq. 3, growth and maintenance respiration of roots (autotrophic component) is modelled as a function of the root biomass (B, g m^{-2}) and the maximum specific respiration rates of roots (α, gC-CO_2 g^{-1} day^{-1}) regulated by T and soil moisture, similarly to heterotrophic soil respiration (see Eq. 2). In this study we focus on the fine roots (≤ 2 mm) biomass, the strongest contributing pool to autotrophic soil respiration while coarse roots represent the largest proportion of root mass (Raich and Nadelhoffer 1989; Makita et al. 2012). Higher fine roots productivity was reported in the forest floor compared to mineral soil under tropical forests (John 1983; Cuevas and Medina 1988). Therefore, in this model, fine roots biomass is divided between forest floor and mineral soil (subscript *i*).

$$RA_i = \alpha_i \times B_i \times \sqrt{\text{soil moisture}} \times Q_{10}^{(T-Tmax)/10} \quad (3)$$

Given the limited range of observed soil temperatures (22.5–25.5 °C; Fig. 4b), the limited sensitivity of soil respiration to T in tropical rain forests in general (Davidson et al. 2000; Bréchet et al. 2018) and in our data set in particular (Fig. 4b), the strong collinearity between k and Q_{10}, and the risk of overparameterizing the model, we considered one single, average, Q_{10} value. This value was fixed at 1.8, as this minimized the Akaike information criteria (AIC) of the model; in addition, it is within the range reported for tropical forests (Zhou et al. 2009; Hashimoto et al. 2015). For both heterotrophic and autotrophic soil respirations, we used a monotonically increasing function to describe the relationship between soil respiration rate and soil water content as no clear inflection point could be observed within the range of soil moisture measurements (Fig. 4a).

This soil respiration model was fitted on a total of 1272 data points using a weighted mixed procedure with the cluster and the date of measurement both nested in forest type as random effects. Residuals were weighted by a power function of soil moisture to account for heteroscedasticity. The type of clusters was considered as random effect but explained no significant additional variation in soil respiration. We assumed that the upper 0–10 cm mineral soil C stocks and the C concentrations of the litter component, the decomposed organic matter

and mineral soil layers remained constant during the respiration measurements. Root biomass and forest floor C stocks not measured in August, October, December and February, were estimated based on measurements made in adjacent dates. The validity of the soil respiration model was assessed by comparing the predicted annual respiration rates with the observed annual respiration rates (see next section). Based on the soil respiration model predictions, the forest floor contribution to annual soil respiration was obtained by summing the CO_2 efflux of both the litter component and the decomposed organic matter layers derived from Eq. 2.

To further explore the drivers behind the difference in estimated soil respiration fluxes between MIF and MOF, we performed a one-at-a-time sensitivity analysis (Hamby 1994; Cariboni et al. 2007) of the soil respiration model. This method consists in repeatedly modifying one (group of) variable(s)/parameter(s) at a time while keeping the others fixed (e.g. to the average). In our case, we focused our sensitivity analysis on the heterotrophic respiration flux as only this flux proved to be significantly different between forests (see the Results section), and considered the following three groups of variables/parameters: maximum decay rates (k_{OL}, k_{OF+OH}, $k_{Mineral\ Soil}$), soil microclimate (soil water content and soil temperature), and soil organic C stocks (combined C stocks of the forest floor and upper 0–10 cm mineral soil). For each group, we ran two different sets of simulations for each forest type: one using the forest-specific values for all parameters and variables, which served as a reference for comparison; the other, using average values across both forests for all variables, except that targeted by the sensitivity analysis. The difference between forests obtained by changing only one group of variables at a time was then divided by the reference difference to obtain an estimate of its relative contribution.

Calculations and statistical analysis

Spatial variation analysis

Using the daily respiration data (total soil respiration) measured monthly from May 2012 to April 2013, annual soil CO_2 efflux (AR_T, Mg C ha^{-1} $year^{-1}$) was estimated with eq. 4, where $R_{T,m}$ is the daily mean soil respiration measured during the m-month and D_m the number of days of the m-month.

$$AR_T = \frac{\sum_{i=1}^{12} R_{T,m} \times D_m}{100} \quad (4)$$

Annual autotrophic and heterotrophic soil respirations were estimated similarly from autotrophic and heterotrophic soil respirations predicted by the soil respiration model. In order to explore the possible drivers behind the spatial variability of annual soil respiration across forest types, we used linear regression through bidirectional stepwise elimination based on the AIC using a set of explanatory variables. These variables were classified into the following four categories: (i) leaf litterfall quantity (Mg C ha^{-1} y^{-1}), (ii) fine root production (Mg C ha^{-1} y^{-1}), (iii) stand parameters (forest type, total basal area (m^2) and weighted basal area (m^2) in a radius of 20 m, and distance to the nearest tree) and (iv) soil parameters (C:N ratios, C and N stocks in both the upper 0–10 cm mineral soil and forest floor, pH of the 0–10 cm mineral soil layer). Fine root production in the forest floor and in the upper 0–10 cm mineral soil was calculated with the 'Maximum-Minimum' formula described by Brunner et al. (2013), by subtracting the lowest biomass from the highest biomass value obtained with the sequential coring. Although fine roots turnover measured by the maximum-minimum method might be underestimated, it still provides reliable comparison between MIF and MOF. For the weighted basal area (BA_W) estimation, each trunk cross section (S_i, m^2) was weighted by the ratio between the distance of the tree from the cluster centre (r_i, m) and its diameter at breast height (DBH, m) according to Eq. 5 (Bréchet et al. 2011):

$$BA_W = \frac{\sum_{i=1}^{n} S_i \times \left(1 - \left(\frac{r_i}{20}\right)^2\right)}{\pi \times 20^2} \quad (5)$$

Statistical analysis

The significance of the differences in forest patches characteristics (density, total basal area and shannon index), C stocks (forest floor, mineral soil and fine root), C fluxes (annual litterfall, fine roots production and soil respiration) and environmental conditions (soil moisture and temperature) between forest types was tested using Student's t test. Before performing statistical analyses, the normality of all variables was tested by skewness and kurtosis normality tests. All statistical analyses were performed in R version 3.2.2.

Results

Ground climate

On average, the significant difference ($p < 0.05$) in soil moisture between forest types during the measurement period (0.33 ± 0.01 and 0.38 ± 0.01 m^3 m^{-3}, mean ± standard error, in MIF and MOF, respectively) did not exceed 13% (Table 1). Soil moisture displayed a strong seasonal pattern (Fig. 2a). In both forests, soil moisture values peaked during both rainy seasons: Oct-Dec and Mar-Apr (Fig. 2a). However, the increase started a month earlier in MIF and the maximum soil moisture during the main wet season was almost 50% lower in MIF (0.33 ± 0.01 m^3 m^{-3}) compared to MOF (0.46 ± 0.01 m^3 m^{-3}). Although significant ($p < 0.05$), the average difference in soil temperature between MIF and MOF was lower than 1% all along the year (mean soil T: 23.64 ± 0.02 and 23.78 ± 0.03 °C in MIF and MOF, respectively). Despite a weak increase in February, no clear seasonal variation in soil temperature was observed in any of the forest types (Fig. 2b).

Soil carbon stocks, litter and fine root production

As shown in Table 2 and Fig. 3, annual foliar litterfall did not significantly differ between MIF (2.86 ± 0.06 Mg C ha^{-1} $year^{-1}$) and MOF (2.79 ± 0.13 Mg C ha^{-1} $year^{-1}$). Monthly leaf litterfall showed two peaks of production (Fig. 2c): in January–February (long dry season) on the one hand, and from August to September on the other (beginning of the main rainy season with strong winds). Similarly, annual fine woody debris litterfall was comparable in both forest types (1.75 ± 0.05 and 1.80 ± 0.12 Mg C ha^{-1} $year^{-1}$ in MIF and MOF, respectively) and accounted for less than 40% in weight of total annual litterfall (leaves + fine woody debris).

MIF exhibited higher ($p < 0.05$) fine root biomass in the upper 0–10 cm mineral soil compared to MOF (0.82 ± 0.03 and 0.75 ± 0.04 Mg C ha^{-1} in MIF and MOF, respectively). Similar fine root biomass in forest floor were reported in MIF (0.34 ± 0.01 Mg C ha^{-1}) and MOF (0.33 ± 0.01 Mg C ha^{-1}). Fine root biomass in the forest floor and the upper 0–10 cm mineral soil exhibited slight increases in November, following the highest monthly precipitation (Fig. 2d). Whereas fine root biomass in the forest floor did not differ significantly between forest types, a higher ($p < 0.05$) annual fine root production in the forest floor was observed under MOF (0.55 ± 0.02 and 0.66 ± 0.04 Mg C y^{-1} ha^{-1} in MIF and MOF, respectively; Table 2). For both MIF and MOF, fine root biomass in the upper 0–10 cm mineral soil was two times higher compared to forest floor (Table 1, Figs. 2d and 3) in contrast to annual fine root production which was highest in the forest floor (Table 2, Fig. 3).

The soil organic C stock in the forest floor plus the 0–10 cm mineral soil layer was significantly higher ($p < 10^{-3}$) under MOF (28.83 ± 0.71 Mg C ha^{-1}) compared to MIF (16.22 ± 0.52 Mg C ha^{-1}). However, this difference between forest types was higher in the forest floor (62%) compared to the upper mineral soil (39%) (Table 1, Fig. 3). As shown in Figs. 2f-3 and Table 1, the forest floor C stocks were about three times higher in MOF (6.68 ± 0.43 Mg C ha^{-1}) compared to MIF (2.55 ± 0.09 Mg C ha^{-1}); the litter component layer accounted for 45% of the total forest floor in both forest types.

Soil respiration

On average, the daily soil respiration was slightly but significantly ($p < 10^{-5}$) higher in MOF (6.08 ± 0.13 g C m^{-2} day^{-1}) compared to MIF (5.48 ± 0.10 g C m^{-2} day^{-1}). Similarly to soil moisture, soil respiration exhibited strong increases in rainy seasons (Fig. 2e) and the maximum of soil respiration during the main wet season (November) in MIF (5.43 ± 0.11 g C m^{-2} day^{-1}) was almost twice lower compared to MOF (8.94 ± 0.50 g C m^{-2} day^{-1}). At annual scale (Table 2, Fig. 3), the difference in soil respiration between forest types led to a significantly 10% higher annual soil respiration under MOF (22.1 ± 0.5 Mg C ha^{-1} $year^{-1}$) compared to MIF (20.0 ± 0.3 Mg C ha^{-1} $year^{-1}$).

Stepwise regression was carried out to assess the potential drivers of the spatial variation of annual soil respiration. This analysis indicated that 29% ($p < 10^{-5}$) of the spatial variation in annual soil respiration within MIF and MOF could be accounted for by combinations of fine root production in forest floor, weighted basal area, C stocks and pH of the 0–10 cm mineral soil layer (Table 3). Fine root production in forest floor, weighted basal area, C stocks of the 0–10 cm mineral soil layer were positively and significantly related to annual soil respiration whereas pH of the 0–10 cm mineral soil layer exhibited negative relationship with annual soil respiration.

Based on the soil respiration model estimates (Table 2), the estimated annual heterotrophic soil respiration was nearly 30% higher under MOF compared to MIF (11.65 ± 0.48 and 8.62 ± 0.18 Mg C ha^{-1} $year^{-1}$ in MOF and MIF, respectively; $p < 10^{-7}$) whereas the estimated

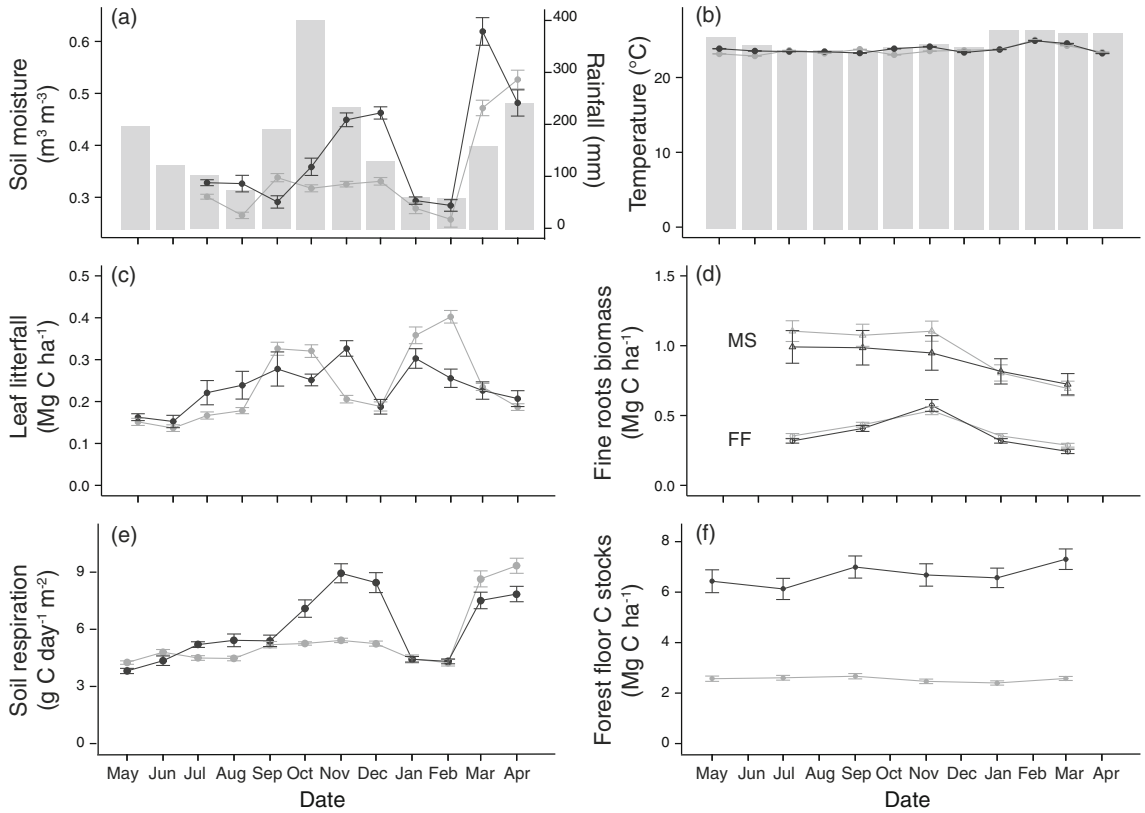

Fig. 2 Seasonal pattern of (**a**) precipitation (mm month^{-1}, grey bars) and volumetric water content of the 0–10 cm soil layer (m^3 m^{-3}), **b** air (grey bars) and soil temperature in the 0–10 cm layer (°C), **c** leaf litterfall (Mg C ha^{-1} month^{-1}), **d** fine roots biomass in the 0–10 cm soil layer (white triangle) and in the forest floor-FF (white circle) (Mg ha^{-1}), **e** total soil respiration (g C day^{-1} m^{-2}) and f) forest floor C stocks (Mg C ha^{-1}) measured from May 2012 to April 2013 in the mixed (MIF, in grey) and monodominant (MOF, in black) forests (averages±standard errors)

autotrophic components were similar in both forest types (12.57 ± 0.22 and 12.14 ± 0.23 Mg C ha^{-1} year^{-1} in MOF and MIF, respectively; $p = 0.18$). For both forest types, the sum of estimated heterotrophic and autotrophic soil respiration was included within the confidence interval of annual soil respiration. In addition, the heterotrophic respiration flux associated with the forest floor amounted to 2.16 ± 0.08 and 2.91 ± 0.28 Mg C ha^{-1} year^{-1} under MIF and MOF, respectively.

The soil respiration model explained about two thirds ($R^2 = 0.64$) of the temporal variation in soil respiration (Table 4). Regressions between observed and fitted soil respiration in both forest types were not significantly different ($p > 0.05$) from the 1:1 line.

Estimated fine root respiration rates (Table 4) were significantly higher in the forest floor (5.49×10^{-2} gC g^{-1} day^{-1}) compared to the 0–10 cm mineral soil layer (0.37×10^{-2} gC g^{-1} day^{-1}). The maximum decay rates (k) values fitted for each layer (litter component, decomposed organic matter, and 0–10 cm mineral soil layers) were higher under MIF compared to MOF (Table 4). The biggest contrast between forest types was shown for the litter component layer (O_L) which was approximatively one hundred times higher under MIF (2.00×10^{-3} day^{-1}) compared to MOF (0.02×10^{-3} day^{-1}). In both MIF and MOF, highest k values were exhibited by the decomposed organic layer ($O_F + O_H$).

Discussion

Annual soil C-CO_2 fluxes and their variations in time and space

Annual soil C-CO_2 fluxes

Annual soil respiration under MIF (20.0 ± 0.3 Mg C ha^{-1} year^{-1}) and MOF (22.1 ± 0.5 Mg C ha^{-1} year^{-1}) are

Table 2 Aboveground annual litterfall, annual fine root production in the forest floor and in the 0–10 cm mineral soil layer, and annual soil respiration for the mixed (MIF) and monodominant (MOF) forests (averages ± standard errors). Different upper letters in a row indicate significant difference between forests ($p \leq 0.05$). Contributions of the autotrophic and heterotrophic components were estimated using the fitted soil respiration model

	MIF	MOF
Aboveground annual litterfall (Mg C ha^{-1} y^{-1})		
Leaf	2.86 ± 0.06 [a]	2.79 ± 0.13 [a]
Fine woody debris	1.75 ± 0.05 [a]	1.80 ± 0.12 [a]
Total	4.63 ± 0.09 [a]	4.57 ± 0.20 [a]
Annual fine roots production (Mg C ha^{-1} y^{-1})		
Forest floor	0.55 ± 0.02 [a]	0.66 ± 0.04 [b]
Mineral soil	0.32 ± 0.03 [a]	0.26 ± 0.02 [a]
Total	0.94 ± 0.22 [a]	0.89 ± 0.10 [a]
Annual soil respiration (Mg C ha^{-1} y^{-1})		
Annual soil respiration	20.01 ± 0.34 [a]	22.10 ± 0.46 [b]
Annual heterotrophic soil respiration	8.62 ± 0.18 [a]	11.65 ± 0.48 [b]
Annual autotrophic soil respiration	12.14 ± 0.23 [a]	12.57 ± 0.22 [a]

within the 16.2 to 24.4 Mg C ha^{-1} $year^{-1}$ range reported for old-growth tropical forests (Davidson et al. 2000; Sotta et al. 2004; Epron et al. 2006). According to Litton et al. (2007), between 30 and 60%, even more, of the C assimilated by photosynthesis in forested ecosystems is allocated to roots as total belowground C allocation (TBCA). For soils that are near steady state with respect to total organic C storage, Raich and Nadelhoffer (1989) showed that TBCA can be estimated at annual scale as soil-surface CO_2 efflux minus aboveground fine litterfall (leaf + fine wood litterfall). On this basis, slightly higher TBCA values ($p < 10^{-2}$) were found for MOF (17.23 ± 0.48 Mg C ha^{-1} $year^{-1}$) than for MIF (15.37 ± 0.34 Mg C ha^{-1} $year^{-1}$). Though those values are close to the range of 13.40 to 15.20 Mg C ha^{-1} $year^{-1}$ reported for tropical primary forests in the Amazon (Davidson et al. 2002), they might overestimate effective TBCAs due to non-steady state conditions as discussed under discussion section 3.

Temporal and spatial variations of R_T

Seasonal pattern of soil respiration In both forest types, soil respiration exhibited a strong relationship with soil moisture (Fig. 4) with the highest rates of soil respiration during rainy seasons (Fig. 2a and e). These observations emphasized the well-known relationships between soil respiration and soil moisture in tropical forests (Davidson et al. 2000). In both MIF and MOF, the square root curve used to model soil respiration in function of soil moisture (Fig. 4, $R_T = -5.27 + 18.99 \times \sqrt{\text{soil moisture}}$, $R^2 = 0.54$) highlighted the monotonic increase in soil respiration with soil moisture. Whereas soil moisture above field capacity may reduce soil respiration in tropical forest (Sotta et al. 2006; Wood et al. 2013), no such effect was observed in this study, probably because in our case, soil moisture exceeded 0.5 m^3 m^{-3} in only 8% of cases in the well-drained soils under MIF and MOF.

Through its implication on microbial and root activity as well gas diffusion, soil temperature is often identified as the dominant factor in controlling temporal variation of soil CO_2 efflux in boreal and temperate ecosystems (Lloyd and Taylor 1994; Vargas et al. 2010). In MIF and MOF, where soil temperatures are high and relatively constant over the year (Fig. 2b), the absence of relationship between soil respiration and soil temperature is not surprising (Fig. 4b) as previously reported by Davidson et al. (2000).

In addition to soil climatic variables, the seasonal trend in soil respiration and its components is strongly influenced by net primary productivity through above- and belowground litter production. Due to the addition of easily-decomposable organic compounds to the soil, increased litter inputs may accelerate decomposition mainly by stimulating decomposers activity (Leff et al. 2012). Increases in soil respiration reported in November and December after the peak in litterfall and fine root biomass may reflect this priming effect (Fig. 2). However, net primary productivity is largely determined by rainfall and temperature, which makes it difficult to separate the individual contribution of each factor.

Spatial variability of soil respiration In both forest types, annual soil respiration was highly variable from place to place, ranging from 14.36 to 28.03 Mg C ha^{-1} yr^{-1} and from 17.49 to 28.68 Mg C ha^{-1} $year^{-1}$ in MIF and MOF, respectively. The most critical variable explaining the spatial variation of annual soil respiration was weighted basal area (Table 3). This suggests that soil respiration is the result of a large set of biological processes related to the surrounding trees (Luo and Zhou 2006; Katayama et al. 2009). Trees are involved, either directly (root respiration) or indirectly (root derived rhizosphere respiration, production of carbon substrates for microbial respiration), in most of

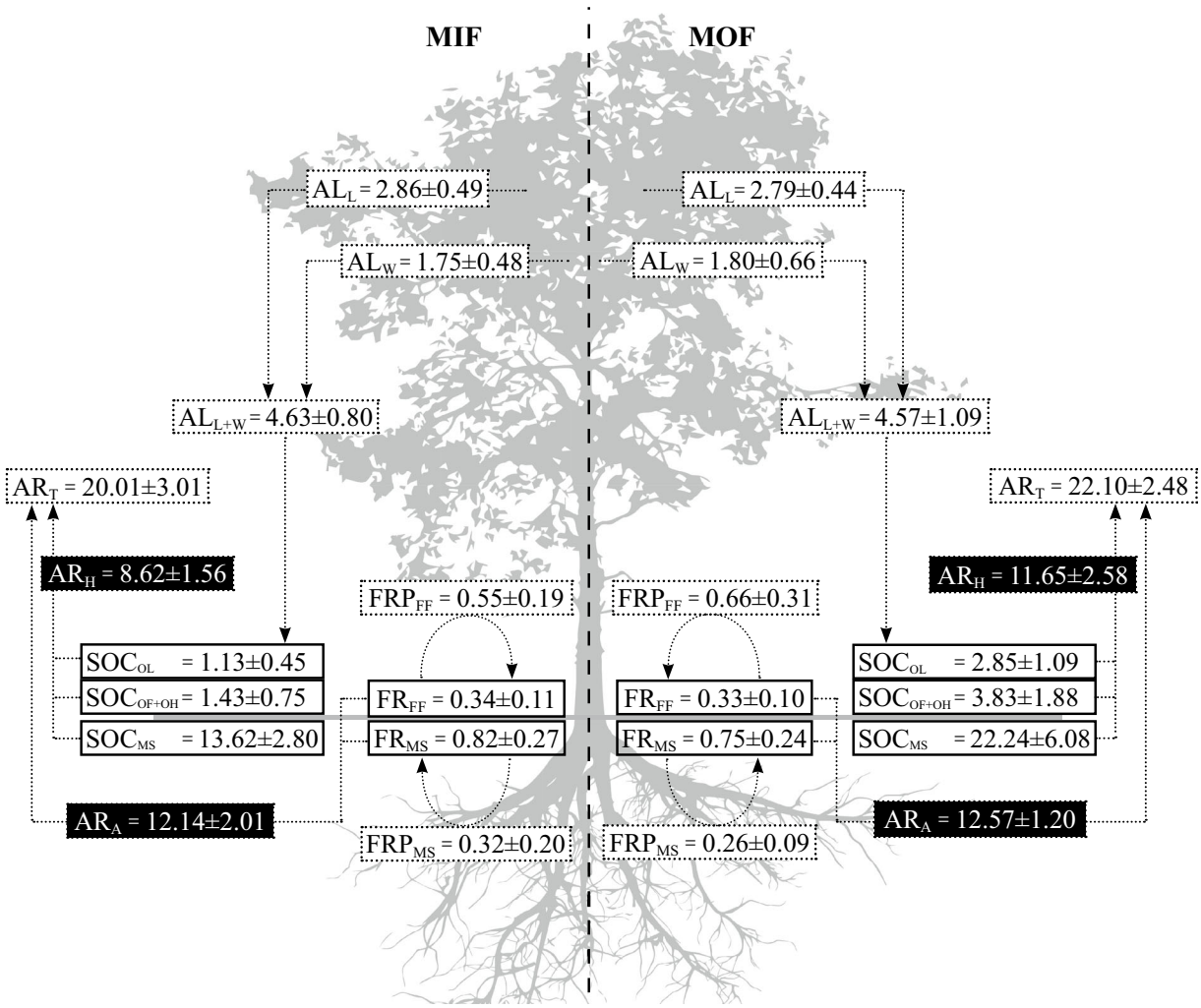

Fig. 3 Main C stocks and fluxes in MIF and MOF, in the Yoko Reserve. Stocks - Soil organic carbon stocks (litter component layer-SOC_{OL}, decomposed organic matter layer-SOC_{OF+OH} and 0–10 cm mineral soil layer C stocks-SOC_{MS}); fine roots C stocks (forest floor-FR_{FF} and 0–10 cm mineral soil layer-FR_{MS}). Annual fluxes - litterfall (leaf-AL_L, woody debris-AL_W and total fine, AL_{L+W}); fine roots production (forest floor-FRP_{FF} and 0–10 cm mineral soil layer-FRP_{MS}); soil respiration (heterotrophic-AR_H, autotrophic-AR_A and total-AR_T). All units are Mg C ha^{-1} $year^{-1}$ and Mg C ha^{-1} for C fluxes and stocks, respectively. C fluxes and stocks in white boxes have been measured and C fluxes in black boxes have been estimated from the soil respiration model

these processes. Among them, increased root density and biomass associated with greater basal area would enhance photosynthesis and the flux of current assimilates to roots, promoting autotrophic respiration (Högberg et al. 2001; Bréchet et al. 2011). In the same time, as increased total basal area is expected to reduce soil temperature and soil moisture due to greater interception of solar radiation and precipitation (Perot et al. 2017), and hence soil respiration, stand structure would have a relatively limited impact on the pedoclimatic conditions compared to its effects on other physical and biotic drivers of soil respiration. In agreement with our soil respiration model, the stepwise regression highlighted the major role of the soil organic C stocks in explaining the variation in soil respiration. Through increase in availability of C substrates for microorganisms, soil organic C in the upper 0–10 cm mineral soil significantly enhanced annual soil respiration (Raich and Tufekciogul 2000). Fine root production was also strongly linked to annual soil respiration spatial variation, reflecting a major source of belowground C inputs (Finér et al. 2011); the selection of the forest floor component over the upper mineral soil one is consistent with the higher fine root production in the holorganic

Table 3 Variables that best explain the spatial variability of annual soil C-CO_2 efflux according to a stepwise multiple regression procedure (model $R^2 = 0.29$ and $p < 10^{-5}$). The parameter estimates and the associated standard error are provided as well as the partial R^2. The candidate variables were: (i) leaf litter quantity (annual C inputs as leaf litterfall), (ii) fine root production in the forest floor or in the upper 0–10 cm mineral soil, (iii) stand parameters (forest type, total basal area and weighted basal area, and distance to the nearest tree) and (iv) soil parameters (the upper 0–10 cm mineral soil and forest floor C:N ratios, the upper 0–10 cm mineral soil and forest floor C or N stocks, pH of the 0–10 cm mineral soil layer). *, **, *** denote a significant coefficient at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$

Selected variables		Parameters (SE)	Partial R^2
Intercept		30.99*** (7.06)	na
Fine root production	Fine root production in the forest floor	3.20* (1.45)	15%
Stand parameters	Weighted basal area	14.05*** (3.91)	37%
Soil parameters	Soil organic C in the mineral soil	0.11** (0.03)	27%
	pH in the mineral soil	−3.31 (2.36)	21%

layers for both forest types (Table 2, Fig. 3). A negative relationship was found between pH of the 0–10 mineral soil layer and annual soil respiration which is surprising as higher pH values have generally a positive effect on the growth and activity of microbes and thus on heterotrophic soil respiration (Motavalli et al. 1995; Luo and Zhou 2006). Negative effect of pH on soil respiration may be the result of the strong negative relationship between soil pH and the upper 0–10 cm mineral soil C stocks in both forest types also reported by Cassart et al. (2017) in MIF and MOF.

All four selected variables accounted for the difference between MIF and MOF forests, as no additional forest type effect could be selected by the stepwise regression procedure. Among them, the soil organic C in the upper 0–10 cm mineral soil is expected to integrate the biggest part of the forest type effect, given its much higher accumulation under MOF compared to MIF (Table 1); by contrast, the difference between MIF and MOF were much more limited for the other variables (weighted basal area, pH in mineral soil and fine root production in forest floor).

On the other hand, none of the four major drivers behind the spatial variability in annual soil respiration varied significantly with cluster types, in any of the forests (ANOVA, $p > 0.10$); this finding explains why cluster type was found to be not significant when fitting the soil respiration model (eqs. 1 to 3).

Parametrization of the soil respiration model

Our modelling approach assumes the autotrophic soil respiration to be proportional to the fine root biomass (Eq. 3). As the mycorrhizae biomass is also expected to be proportional to the fine root biomass (Nilsson et al. 2005), our estimates of autotrophic respiration would include the contributions of both fine roots and associated fungi. Higher respiration rates of fine roots (α) in the litter layer compared to the upper 0–10 cm mineral soil are consistent with their higher annual productivity

Table 4 Parameter estimates (mean ± standard error) of the soil respiration model (Eq. 1 to 3) fitted based on the soil C-CO_2 efflux under MIF and MOF. α (gC-CO_2 g^{-1} day^{-1}): respiration rates per biomass unit of fine roots in the forest floor (α_{FF}) and the upper 0–10 cm mineral soil (α_{MS}); k (day^{-1}): maximum decomposition rates of organic C in the litter component layer (k_{OL}), the decomposed organic matter layer (k_{OF+OH})and the upper 0–10 cm mineral soil layer (k_{MS}). *, **, *** denote a parameter significantly different from 0 at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$

Parameters		MIF	MOF
Autotrophic soil respiration	α_{FF}	$(5.49 \pm 0.45^{***}) \times 10^{-2}$	
	α_{MS}	$(0.37 \pm 0.17^{*}) \times 10^{-2}$	
Heterotrophic soil respiration	k_{OL}	$(2.00 \pm 2.52) \times 10^{-3}$	$(0.02 \pm 1.99) \times 10^{-3}$
	k_{OF+OH}	$(4.04 \pm 1.60^{*}) \times 10^{-3}$	$(3.17 \pm 1.06^{***}) \times 10^{-3}$
	k_{MS}	$(2.25 \pm 0.37^{***}) \times 10^{-3}$	$(1.63 \pm 0.28^{***}) \times 10^{-3}$

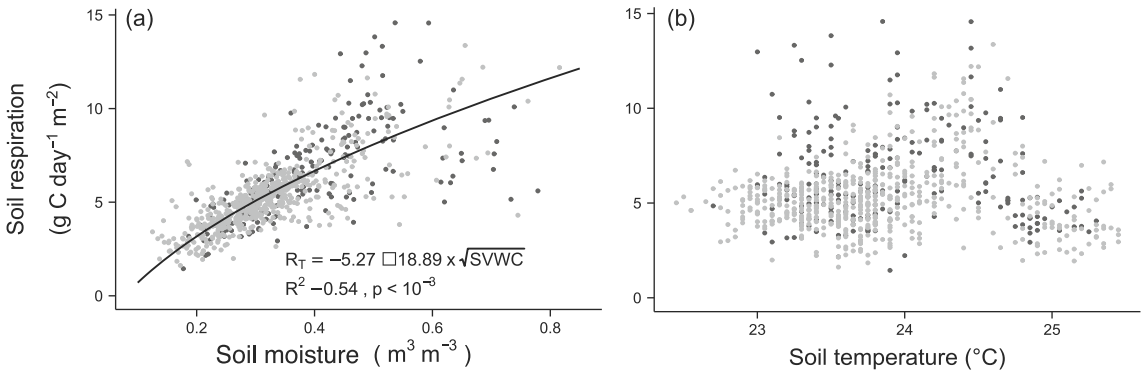

Fig. 4 Relationships between total soil respiration and soil moisture (**a**) or soil temperature (**b**) in the mixed (MIF, grey dots) and monodominant (MOF, black dots) forests

suggesting higher activity (Table 2, Fig. 3). Indeed, although the litter layer exhibited a fine root biomass two times lower compared to the upper 0–10 cm mineral soil in both MIF and MOF, fine root production in forest floor was approximatively 50% higher. The hypothesis of a higher fine root activity in forest floor compared to the upper 0–10 cm mineral soil is also supported by the selection of fine root production in forest floor, not fine root production in the upper 0–10 cm mineral soil, in the stepwise regression procedure used to explain the spatial variations of annual soil respiration (Table 3). Previous studies of superficial root mat in Amazonian forest have shown higher root production in the litter layer (John 1983; Cuevas and Medina 1988). Maintenance of a superficial root mat into freshly fallen litter enables the trees to catch efficiently the flux of nutrients brought by throughfall or released during litter decay (Laclau et al. 2004). In addition, compared to mineral soil, the forest floor frequently exhibits an increased aeration and water infiltration, a reduced soil compaction, and is thus a better environment for root penetration and growth (Dexter 2004).

As modelled by Eq. 3, the amount of CO_2 produced through root respiration is determined by the root biomass and specific root respiration (α), regulated by soil temperature and moisture. In fact, α may also be influenced by root morphology (e.g. tissue density, diameter and specific root length), age and N concentration (Makita et al. 2012). Nevertheless, scaling the direction and magnitude of the relationships between α and this set of biotic influencing factors is problematic because of a lack of experimental data for tropical rainforests (Luo and Zhou 2006; Hopkins et al. 2013). Therefore, our soil respiration model only considered the most important factors (fine root biomass, soil temperature and soil moisture) reported for these ecosystems.

The maximum decomposition rates (k) fitted by the soil respiration model (Table 4) for the forest floor ranged from 0.02×10^{-3} to 4.04×10^{-3} day^{-1}. Those estimates are consistent with the mean k of 6.10×10^{-3} (from 0.80×10^{-3} to 12.00×10^{-3} day^{-1}) reported for the litter layer in tropical forest (Hättenschwiler et al. 2011); they are also in agreement with decay rates obtained from the ratio of annual litter production (leaf + fine wood litterfall) to steady-state accumulation of forest floor (forest floor C stocks) (Olson 1963) which amounted to 5.34×10^{-3} and 2.12×10^{-3} day^{-1} in MIF and MOF, respectively.

Regarding the mineral soil layer, the k values (Table 4) were comparable to the initial decay rates values from the laboratory incubation experiment (k_{inc}) for MIF ($2.70 \pm 0.10 \times 10^{-3}$ day^{-1}) and MOF ($1.82 \pm 0.09 \times 10^{-3}$ day^{-1}) (see Supplementary material 3). Although k_{inc} strongly decreased with time, the difference of k_{inc} between forest types (in average $31.2 \pm 0.4\%$) remained constant during the experiment and are consistent with the difference of fitted k values between forest types reported for the soil respiration model (17.8%).

Though the differences were not significant, the lower k values for the litter component, the decomposed organic matter and the mineral soil layers in MOF compared to MIF are consistent with the greatest C accumulation in soil (forest floor + mineral topsoil) under MOF reported in this study for otherwise comparable aboveground (4.63 and 4.57 Mg C ha^{-1} y^{-1}) and belowground C inputs (0.94 and 0.89 Mg C ha^{-1} y^{-1}). They are also in agreement with the limited organic

matter decomposition under *G. dewevrei* previously reported by Torti et al. (2001) and Peh et al. (2012).

Autotrophic and heterotrophic components of soil respiration under MIF and MOF

For both forests, the estimates of the autotrophic and heterotrophic C-CO_2 fluxes, as well as of their contributions to total soil respiration, are comparable to those previously reported for tropical forests (Hashimoto et al. 2015; Tian et al. 2015). Whereas the difference in annual autotrophic soil respiration between forest types was not significant, the heterotrophic soil respiration was found to be about 30% higher under MOF compared to MIF (Table 2, Fig. 3). As the heterotrophic respiration fluxes associated with the forest floor were very close in both forests, most of the difference in heterotrophic respiration between MIF and MOF should be related to the mineral soils.

Based on the sensitivity analysis (Table 5), the difference in annual heterotrophic soil respiration between forests appeared to be mostly related to the much larger C accumulation in the forest floor + mineral topsoil under MOF (28.83 ± 1.16 Mg C ha^{-1}) compared to MIF (16.22 ± 0.32 Mg C ha^{-1}). As neither the aboveground annual litterfall nor the annual fine roots production differs significantly between the forest types (Table 2, Fig. 3), the much higher C storage in the holorganic layers and upper mineral soil under MOF compared to MIF should be attributed to a difference in organic matter decomposition. A previous litterbag decomposition study carried out in the same forests indeed showed that the difference in leaf decomposition was tightly related to a multivariate measure of initial litter quality including 11 functional traits (Cassart et al. 2020). In particular, the leaf litter from *G. dewevrei*, which dominates the litterfall under the monodominant forest (Cassart et al. 2017), was characterized by high lignin and low nutrient (N, P, Ca) concentrations, as opposed to correspondingly low lignin and high nutrient concentrations for the *S. zenkeri* leaf litter. This is also consistent with the lower, yet not significantly, *k* values fitted for all layers in MOF compared to MIF with our soil respiration model (Table 4).

Though the contrasting quality of organic matter inputs undoubtedly drives the difference in C storage between MIF and MOF, it is not expected to explain the difference in heterotrophic fluxes between forests under equilibrium conditions. In both forests, however, the combined contribution of litterfall inputs and fine roots productivity was lower than the heterotrophic flux (Table 2; Fig. 3), with the largest difference observed under the monodominant-forest (−6.16 Mg C ha^{-1} $year^{-1}$) compared to the mixed-forest (−2.62 Mg C ha^{-1} $year^{-1}$). Although rhizosphere carbon flux (including exudation, rhizodeposition and allocation to extra-matrical hyphae) may be an important contributor to soil C budget under forested ecosystems (Jones et al. 2004), only fine root production has been considered in this study. Those components have been shown to represent from 1 to 10% of the total carbon (C) assimilated during photosynthesis (Jones et al. 2004; Phillips et al. 2008; Yin et al. 2014). Therefore, an important part of this unbalance could be explained by differences in these unmeasured rhizodeposits between MIF and MOF.

The magnitude between the observed and expected input - output C fluxes budget could also indicate a non-equilibrium situation. This hypothesis is compatible with the time series of precipitation data available from the nearby Yangambi meteorological station, which shows that our measurement period corresponds to consistently higher precipitation inputs in comparison to those recorded over the past 10 years (Supplementary Material 4). In those conditions, we might expect the heterotrophic flux to be enhanced in proportion to the C accumulation in the soil, which is agreement with the results of the sensitivity analysis referred to above (Table 5).

Table 5 Results of the sensitivity analysis of the model showing the influence of selected parameters (maximum decay rates: k_{OL}, k_{OF+OH}, k_{MS}) and variables (soil microclimate: soil water content and soil temperature; combined C stocks of the forest floor and upper 0–10 cm mineral soil) on the difference in heterotrophic soil respiration between forest types. Negative values indicate that the difference in respiration related to the considered driver is opposite to the observed difference

Maximum decay rates		−114.8%
Variables	Pedoclimatic (soil moisture and temperature)	23.8%
	soil organic C (forest floor, upper 0–10 cm mineral soil)	189.2%

Difference in mycorrhizal types has been reported between the two forests, with predominantly ectomycorrhizal fungi under MOF (Phillips et al. 2013; Frey 2019), and mostly arbuscular fungi under MIF (Onguene and Kuyper 2001), both with impacts on OM decay yet through varying mechanisms (Wurzburger and Brookshire 2017; Frey 2019; Hall et al. 2020). While their contribution to the observed difference in heterotrophic respiration under non equilibrium situation may not be excluded, the difference in mycorrhizal associates should not impact the heterotrophic respiration fluxes under steady-state conditions.

Finally, the difference in pedoclimatic conditions only marginally affected annual heterotrophic soil respiration by accentuating the difference in soil C-CO_2 efflux among forests by only 23.8% (Table 5).

Extrapolating our results from the patch level to the whole forest

To judge the relevance of the results we obtained at the patch level for the whole forest, we compared the distribution of means for the 10 m radius weighted basal areas obtained through simulation ($n = 100$) by randomly sampling each forest using the sample size of the corresponding clusters (i.e. $n = 29$ for MOF; $n = 77$ for MIF) in inventory plots set up previously (Cassart et al. 2017), to the distribution observed in the clusters. While the cumulated distributions revealed the lower weighted BA range (< 1.5–2 m^2 ha^{-1}) was under-sampled in the clusters, the observed average values fell within the 95% confidence intervals associated with the random sampling for each forest type (see Supplementary material 5). So, although our sampling was designed to capture the stocks and fluxes at the patch level, our results may still be considered as giving a reliable insight when extrapolated at the whole forest level, for each of the two forests under study.

Conclusions and perspectives

Despite a difference in total soil respiration between forest types that did not exceed 10%, the heterotrophic respiration was ca. 30% higher under MOF compared to MIF. The difference in annual heterotrophic soil respiration was mostly related to the much larger soil organic C storage under MOF, reflecting the higher recalcitrance of organic matter inputs under MOF reported by previous comparative decomposition studies (Cassart et al. 2020) and further highlighted by the estimated maximum decomposition rates. By contrast, we found no difference in organic C input through litterfall and fine root production between forests. Difference in heterotrophic C-CO_2 fluxes could be related to differences in unmeasured rhizodeposits, or to non-equilibrium conditions which would then boost the decomposition process in proportion to the carbon stocks. Further work would however be needed to confirm these hypotheses, by carefully investigating additional input-output C fluxes.

Whereas the spatial variation in annual soil CO_2 efflux across forest patches was mostly related to local weighted basal area, soil organic C in the mineral soil, pH in the mineral soil and fine root production in the forest floor, seasonal trends were largely driven by soil moisture.

Our sampling was designed to capture the stocks and fluxes at the patch level, and additional studies are needed to confirm their reliability at the whole forest scale.

Finally, as MIF and MOF co-exist on a large range of soils (Hart et al. 1989), it remains to determine whether the control of those biotic and abiotic factors over the seasonal and spatial variations of soil respiration and its components would be similar in different ecological conditions.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-020-04808-6.

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