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Daily and seasonal variations of soil respiration and contributions of above-and below ground litter in the rain forest of south western Cameroon in Central Africa

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Soil respiration in plots either with natural litter or without but on which was added above ground litter was examined in order to evaluate its periodic variability and the contributions of above and below-ground litter to the total soil respiration. This work was conducted within a one year period in the South western region of Cameroon. During the day, the mean soil respiration reached a seasonal peak rate ($917 \pm 19 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in May (rainy season) and a trough ($345 \pm 96 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) was observed in February (dry season) indicating a clear relation with soil moisture. The maximum diurnal values of soil respiration appeared in May between 8 and 10 am and in February between 14 and 16 pm. This evolution was proportional to air and soil temperatures. The contribution of aboveground litter to the total soil respiration was in average 34 to 43% while that of below ground litter was 57 to 66% in which is included probably about 10 to 20% of labile carbon pool. The exclusion or addition of litter to the soil surface thus modified the total soil respiration.

Key words: Tropical forest, soil respiration, variability, environmental factors, litter contribution.

INTRODUCTION

Total soil respiration is a key ecosystem process that release carbon from the soil in the form of CO_2 . It is the sum of all CO_2 produced by the respiration of both aboveground litter and soil organic matter decompositions through soil pedofauna and microbial organisms' activity and root respiration (Toutain and Brun, 1992; Raich and Tufekcioglu, 2000).

The soil organic matter is heterogenous due to decomposition of different ^{14}C signatures when comparing the various ^{14}C in soil organic matter with respired $^{14}\text{CO}_2$ (Trumbore, 2000). The soil organic matter is composed of both more rapidly and more slowly cycling components of ^{14}C . The ^{14}C signature of CO_2 is a useful indicator for

seasonal and inter-annual changes in sources of respired carbon. Soil respiration and its rate across the ecosystem play an important role in the global C as well as other nutrient cycles. It contributes to soil fertility and also defines the role of the terrestrial ecosystems in the atmospheric regulation of carbonic gas (Gunn and Trudgil 1982; Moureaux et al. 2008). The amount of soil respiration that occurs in an ecosystem is controlled by several factors such as temperature, moisture, nutrient content and level of O_2 .

Generally, soil respiration is mainly controlled by climatic differences in temperature and moisture (Rout and Gupta, 1989; Howard and Howard, 1993; Raich and Tufekcioglu, 2000; Joffre et al. 2003; Couteaux et al. 1995; Zhou et al. 2013; Xiao et al. 2014), although humidity had the greatest effect on the respiration of the soil when temperatures increases. Bai et al. (2012) found that soil respiration is more

sensitive to soil than atmospheric temperatures. The correlation between the rate of CO₂ emitted and the temperature is high when humidity is constant (Tang et al. 2005), also there exist a relationship between the amount of CO₂ emitted at the soil surface and its diffusion in the soil according to seasons. A soil whose porosity is more or less saturated with water receives little O₂ and the microbial activity decreases and also the CO₂ emitted.

Several studies on soil respiration have been carried out in the humid tropical forest zone of Latin America and the evidence of certain variations in the various organizations within the same ecosystem has been demonstrated. The various indicated values of CO₂ emitted on the soil surface are 300-400 to 1000-2000 mg CO₂ m⁻² h⁻¹ (Schulze, 1967; Gupta and Singh 1981; Kursar 1989; Kepler et al. 1990; Basu et al, 1991). The forest structure, i.e. the distribution of emergent trees with large DBH, and their belowground carbon allocation are primary factors controlling the spatial variation of soil respiration in the tropical rainforest (Katayama et al. 2009) as well as soil moisture and root biomass (Adachi et al. 2006).

A positive correlation is highlighted between both quantity and quality of residues returned to the soil surface and soil respiration. Soil respiration is greater in mature forests (Raich and Tufekcioglu, 2000) with a litter production of 7.5 to 13 t ha⁻¹ year⁻¹ (Cuevas and Medina, 1988; Schwartz, 1991; Zheng et al., 2006; GomaTchimbakala and Bernhard-Reversat, 2006). However, it is more of the combined effects of temperature, humidity and the quality of residues that control the rate of soil respiration than the vegetation types in several cases. The residues provide the energy necessary for microbial activity controlling forest productivity through the availability of nutrients (Raich and Tufekcioglu, 2000). Within the same plant formation, there is variability in the rates of soil respiration due to variations in the microclimate (Raich and Tufekcioglu 2000), light radiations that influence temperature and wet events that alter the moisture (Sotta et al 2004; Tang et al. 2005; Zimmermann et al., 2009).

The works of Wood et al. (2013) emphasize the existence of a threshold in soil moisture above which the rate of CO₂ emitted is reduced due to poor circulation of O₂ in the soil, suggesting that the texture controls soil respiration. This implies that temperature exerts a positive influence on soil respiration as long as soil moisture is not limiting (Couteaux et al., 1995). For a 24 hours period, the CO₂ emitted is highest between midday and early afternoon and lowest at night (Bai et al., 2012; Zimmermann et al., 2009). Soil respiration increases with soil humidity and the difference between day (633mg/m²/h) and night (597 mg/m²/h) was not very significant (Kursar, 1989; Gupta and Singh, 1981; Mishra and Dash, 1982).

Soil respiration consists of various sources of CO₂ emission (aboveground litter decomposition, soil organic matter decomposition, roots respiration) but the

contribution of these components are still uncertain (Rout and Gupta, 1989; Basu et al., 1991; Bowden et al., 1993; Sulzman et al., 2005; Zhou et al. 2013). Soil respiration can be influenced by deforestation and change in land use (Moureaux et al., 2008; Moghiseh et al., 2013) with respect to modification in soil organic carbon storage and global climate changes based on numerous changing factors such as the continuous increase in atmospheric CO₂, temperature and shifting precipitation patterns. In tropical areas, soil respiration is more important in pasture than in forest, clearing and plantation (Schwendenmann et al. 2007); in rainforest and secondary forest than savannah and deciduous forest (Schulze, 1967). Due to the intense contemporary changes in land use in tropical forests (Malhi, 2012) modification in litter inputs is likely to affect the rates of soil respiration consequently the relative contribution of its various components is affected.

In the tropical forests, a number of authors have been concerned with the compartmentalization of the different components of soil respiration. The aboveground litter decomposition is estimated to compose 16 to 37% of soil respiration (Zhou et al., 2013; Zimmermann et al., 2009; Valentini et al., 2008; Singh et al., 2008; Sulzman et al., 2005; Rout and Gupta, 1989). The contribution of roots respiration varies from about 38% (Pati et al. 1983) to 90% (Wang et al. 2010; Hanson et al. 2000) while microbial respiration contributes for about 60 to 62% (Kucera and Kirkham, 1971; Pati et al., 1983).

Most of the works cited in tropical areas are mostly based on South American and Asian forests. Although the tropical forests of the Congo basin in Central Africa are considered as the second lung of the world after the forests of Amazonia in South America and based on spatial variability across the ecosystem, the pattern and magnitude of soil CO₂ dynamics within these forests are still poorly documented. However, a number of investigations already exist on the production of litter, their decomposition and determination of decomposition parameters (Ibrahima et al., 2010; Goma-Tchimbakala and Bernhard-Reversat, 2006; Schwartz et al., 1991).

The main aim of this work, was to measure soil respiration in a rainforest of southwestern Cameroon in central Africa and three main objectives were undertaken. Firstly, to quantify soil respiration and its spatial variation within the site; secondly to estimate the periodic variations of soil respiration per day and its seasonal pattern including measurements of environmental factors;

and lastly, to determine the contribution of above- and belowground litter in the total soil respiration based on the amount of surface litter.

MATERIALS AND METHODS

Site description

The study was conducted in NsimiZoetele secondary forest (3°10' to 3°11' latitude N and 11°49' longitude E) located

located in the Southwestern part of Cameroon. The site, 700 m above sea level, is a secondary semi deciduous forest characterized by cesalpiniaceae; burseraceae and annonaceae (Letouzey1985). The climate consists of two dry (December to February and July to August) and two rainy (March to June and September to November) seasons. The mean annual temperature (Fig.1) is 23.5°C ranging from 18.9°C (July) to 28°C (February) with an annual precipitation average of 1633 mm with two maxima in May and October and two minima in January and July (Fig.1).

The soils at the study site are oxisols that can be more than 10 m deep with a low pH of 4.8 to 5. They consist of a litter layer of 3cm, subdivided into three layers made of firstly entire brown leaves; secondly, more humid leaves with a very fine touch; some are joined together by filaments of white rot fungi while others show a lace structure due to their extraction by soil fauna and most of the twigs crumble effortlessly on touching. The third layer is composed of fragments of leaves portions incorporated more or less into the soil where rootlets in millimeters are developed; litter is found on the organo-mineral horizon (7cm) with a dense root system of diameter one millimeter expanding horizontally to sub-horizontally.

Experimental design

To evaluate spatial and seasonal variations, five separate points were randomly chosen within a 100 m² area for the measurements of soil CO₂ efflux every two months, i.e. on May 1st, July 9th, September 15th, November 24th in 1992 and February 4th, 1993, as microclimate in the same forest could varied. These measurements were carried out in the afternoon.

Moreover, to evaluate diurnal and seasonal variations of soil respiration, measurements were carried every two hours for 24 hours at the same point and every two months as stated above.

In order to section the various contributions to soil respiration we evaluated the effect of either excluding or adding litter on the soil surface. In the previous five randomly chosen points, litter was carefully excluded just before a second measurement (S-L)a was taken. Moreover, three series (A, B, C) of three similar rectangular plots (1.5m x1m) were installed. In the first series (A) considered as control, natural litter fall was conserved at the soil surface (S+L). In the second series (B), aboveground litter was removed from the plots weekly (S-L)b from May 1st, 1992 to February 4th, 1993 and the soil laid bare during the entire experimentation period. In the third series (C), the natural litter fall was doubled (S+2L) by adding weekly litter removed from the (S-L)b plots of the B series.

All the measurements were carried out in two or three days per month in May, July, September, November 1992 and

February 1993. However, the measurements of soil respiration in the (S-L)b and (S+2L) plots started in July, two months after their installation.

Measurements of environmental factors

Within 24h, CO₂ concentration of the surrounding ambient air of the forest floor was estimated in an open circuit before each measurement of soil respiration was undertaken. Relative air humidity and temperature were also quantified using a thermohygrometer (HT-206). For spatial and seasonal variations and for the plots undergoing litter manipulation, the soil temperature was quantified with a sounding line thermometer Bioblock scientific n° 5001, 5cm deep. Also, Soil water content was determined by taking 0-10 cm deep of soil cores within the chamber immediately after CO₂ measurement; soils samples were weighed and dried at 105°C.

Soil respiration measurements

For these measurements, the apparatus used was a PVC cylinder chamber of 3mm thick of volume 50l. Generally, an area of 0,2m² of soil was covered with the cylinder chamber and with a sharp knife, the litter layer and soil were slashed and the chamber was firmly pressed and inserted 2 cm into the soil for every measurement.

The Chamber was linked using tygotubing to an infrared gas analyser AUTOCHIM-ADC of the series, R.F.D. 16129. This detector is portable and easily transported with a 5 hours autonomy after plugged to an internal electrical circuit. The flow rate of the gas towards the detector was maintained at 0.6 l per minute. A glass borosilicate gas filter was placed on the gas path to prevent dust and fine litter residues. The CO₂ reading interval was between 0 and 1000 ppm and its reading was maintained for 10mn with one reading per mn. The results of CO₂ in the ambient air of forest floor expressed in ppm and of soil respiration in mgm⁻²h⁻¹ here represented the average values of all measurements between 0 and 10mn.

A number of measurements could not be undertaken due to the problem of autonomy of the IRGA for the diurnal variations particularly in July.

The above ground litter contribution was estimated using three possibilities namely, the difference between the total soil respiration in control (S+L) and (S-L)a; the difference between soil respiration with double intake of litter (S+2L) and the control (S+L) and lastly the difference between the total soil respiration in control (S+L) and soil with litter removed every two weeks (S-L)b divided by the total respiration of the control (S+L).

The contribution of below ground litter was calculated based on two procedures involving the difference between total soil respiration (S+L) and the contribution of litter in the case of (S+2L) – (S+L) and finally, by simply consider-

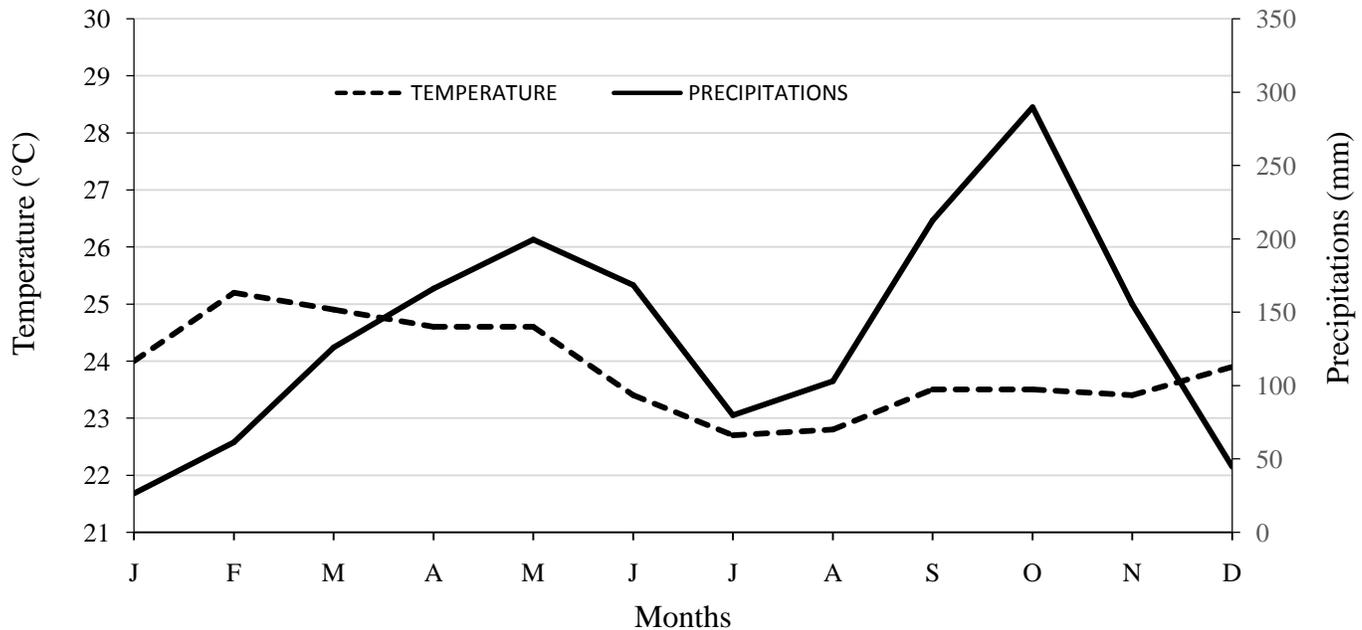


Fig 1: Monthly average temperatures and precipitations recorded at the meteorological station of Zoetele (Southwestern Cameroon)
 --- Monthly average temperatures (°C)
 ___ Monthly average precipitations (mm)

ing the contribution of the bare soil (S-L)b.

RESULTS

Variations in environmental factors on the forest floor

Diurnal variations of CO₂ content

CO₂ content in the air varied during the 24 hours period of observation and was generally greater between 18 pm-8 am considered as night period. Peaks were observed generally between 22 pm and 8 am in the night. In May, the CO₂ peaks extended from 22 pm (472 ppm), 24 am (490 ppm) to 2 am (500 ppm). In September, the peaks were observed at 24 am (346 ppm), 2 am (345 ppm), 4 am (356 ppm) and 6 - 8 am (360 ppm); while in November, they ranged from 10 am (365 ppm), 6 am (362 ppm) to 8am (372 ppm). Also, in February, they appeared between 22 - 24 pm (390 ppm), 2 am (410 ppm) and 4 - 8 am (389-390 ppm). Regarding the various seasons, (Table 1) the CO₂ content in the air in the month of May was the highest during the day (386 ± 70 ppm) and night (470.60 ± 25.40

ppm) periods. A difference of 84 ppm was observed between the CO₂ content obtained in the day and that of the night. CO₂ content in the air was lowest in September during the day (322.00 ± 16.10 ppm) as well as in the night (347.67 ± 8.55 ppm).

Air temperature on the forest floor:

Air temperatures fluctuated greatly within a 24 hours period (Fig. 2). In May, peaks were observed at 10am (24°C), 12pm (24.6°C) and 14pm (25.5°C). In September, the peaks appeared at 10 am (22.3°C), 12 pm (22.9°C), 14pm (23°C) and 16pm (25°C). In November, they were observed around 10 am (25.5°C), 12pm (26°C), 14 à 16pm (25.9°C) and 18pm (25.4°C). In February, the peaks appeared at 10 am (24.8°C), 12 pm (26.5°C) and 16 pm (25.9°C). The air temperature remains high between 10 am and 14 pm in May, 10 am and 16 pm in February and 10 am and 18 pm in November. These variations appeared to be related to sunlight.

Within the various months, the air temperature varied between 21.5 and 26.0°C in the day (8 am -18 pm) and 19.5 and 22.5°C at night (18 pm – 8 am). The lowest

Table 1: Average values of CO₂ concentration (ppm) measured in ambient forest air and evolution pattern across months at daytime and night.

	May	July	September	November	February
Day time (8-18h)	386,70 ± 34,20	366,25 ± 15,95	322,00 ± 16,10	330,33 ± 17,60	355,17 ± 18,40
Night (18-8h)	470,6 0 ± 25,40	-	347,67 ± 8,55	361,75 ± 16,50	387,83 ± 15,30

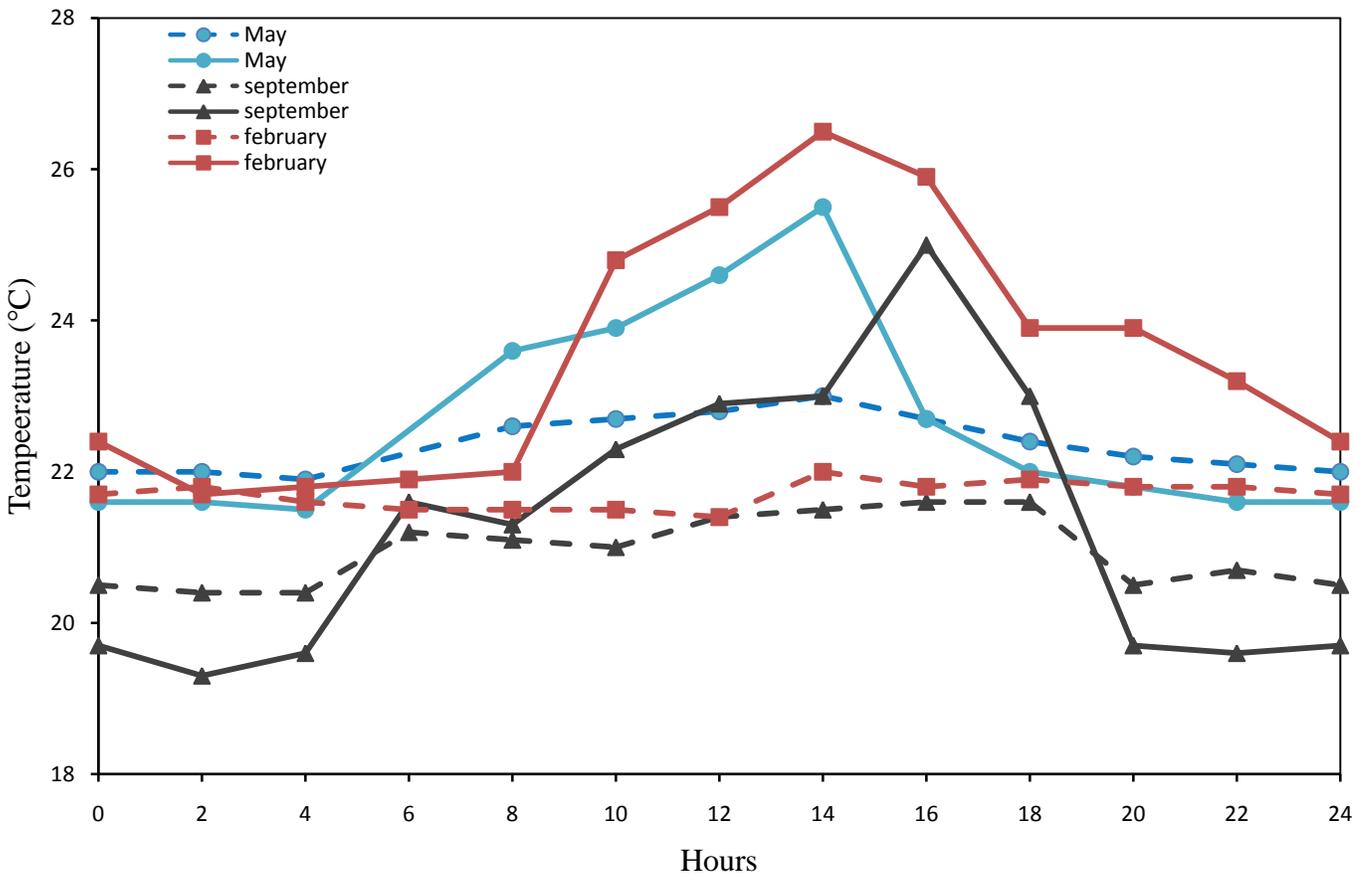


Fig 2. Variations of air temperatures and soil temperatures on the forest floor in a 24 hour periods
 _____air temperature (°C)
 -----soil temperature (°C)

temperatures were observed in September (19.3 to 25°C) and the highest temperatures at night and in the day in November (22.2 to 26°C) and February (21.7 to 26°C).

Although these measurements were punctually recorded on the floor under tree shades, the various values were in line with changes in monthly average temperatures

recorded at the meteorological station (Fig.1).

Air moisture on the forest floor

Within 24 hours, the air moisture (Fig.3) was higher at night (92 to 95%) and significantly reduced during the day. The decrease was gradual and limited from 15 to 18 pm in September (82.5 to 92.5%); it extended from 10am to 18pm

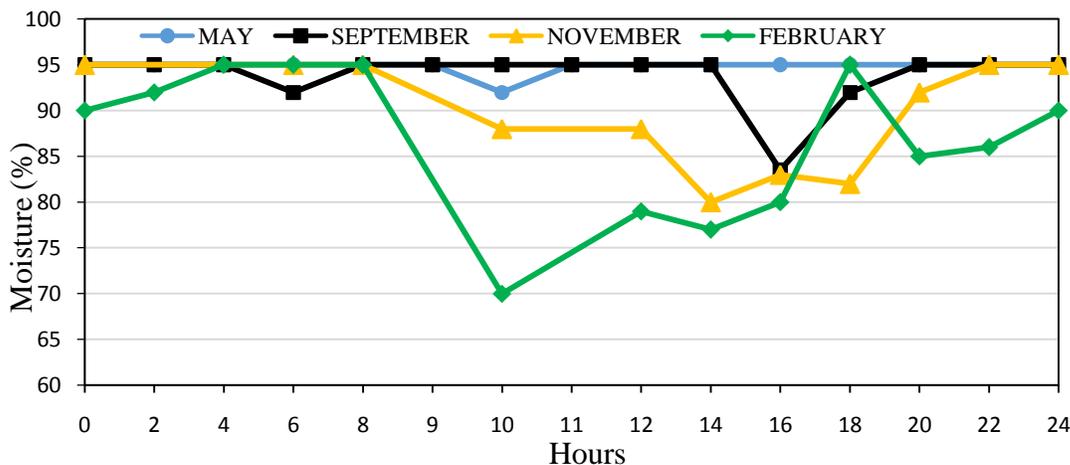


Fig 3. Variations of air moisture (%) on forest floor in a 24 hours periods

in November (80 to 88%) and 10am to 22pm in February (67 to 80%) when the most important fluctuations were observed. In the month of May, air moisture was high (95%) and constant. Air humidity is highest in May in the core of the rainy season unlike the month of February, the core of the dry season, when the air appears drier.

Diurnal variation of soil temperature:

The soil temperature (**Fig.4**) varied little in the 24-hour period. In May, temperatures were high between 8 am and 12 pm (23 to 22.4°C) and low between 18 pm and 6 am (21.9 to 22.2 °C). In September, temperatures were high between 14-18 pm (21.4 and 21.6°C) and low between 20 pm and 4 am (20.5 and 20.7°C). While in November, the soil temperature was high between 22 pm and 8 am and lower in the day. In February, the soil temperature was high between 14 pm and 2 am (22 to 21.8° C) and low between 4 am and 12 pm (21.4 and 21°C).

The soil temperature varied little within the 24 hour period between 20.5 and 23°C. Fluctuations between day and night were about 1°C in the month of May, 1.5°C in September, 2°C in November and 0.5°C in February and these were generally between 8 am-18 pm.

Compared with the ambient forest air temperatures, soil temperatures were generally low although a similar trend is observed in the day. The lowest differences are observed in the night and the highest differences within the day between 12 - 16 pm in February (4 to 4.5 ° C), between 4 pm - 6 pm in September (3.4 to 17°C) and between 12 - 14 pm in May (1.8 to 2.5°C). The highest differences were observed in the dry season in the month of February and the lowest in the rainy season in May.

Spatial and seasonal variations in soil temperature and

moisture:

In the five selected points, the soil temperature at a depth of 5 cm varied between 21.5 ± 1.36 and 22.6 ± 3.0 °C. The highest value was recorded in May (22.6 ± 3.0 °C) and the lowest in July (21.6 ± 1.26 °C) but the soil temperatures were similar in the months of September (21.6 ± 1.26 °C) and February (21.5 ± 1.36 °C). Moreover, soil moisture varied between months with the highest values (23.5 ± 3.0 %) observed in May, a rainy month and the lowest (18 ± 1.0 %) in February which is a dry month. The soil moisture in the month of May was 1.3 times higher than the soil humidity in the month of February.

Diurnal and seasonal variations of Soil respiration

Diurnal variations of soil respiration

Soil respiration fluctuated greatly within a 24 hour period (**Fig.5**) with peaks observed at 8 am ($919 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), 10 am ($968.7 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) and 12pm ($881.25 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in the month of May; then at 10 am ($412.5 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), 12 pm ($400 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in September; then 16 pm ($400 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), 18 pm ($406.5 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in November and lastly at 14 pm ($418.75 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), 16 pm ($468.75 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) and 18 pm ($393.75 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) in February. Comparing the rainy month (May) with the dry month (February), it is observed that CO₂ peaks were located between 8 and 12 am in May (mid day) and 14 to 18 pm in February (afternoon) based on the evolution of the temperature of the soil.

During the day the mean soil respiration was $798.28 \pm 158.70 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in May; $381.72 \pm 80.19 \text{ mg CO}_2 \text{ m}^{-2}$

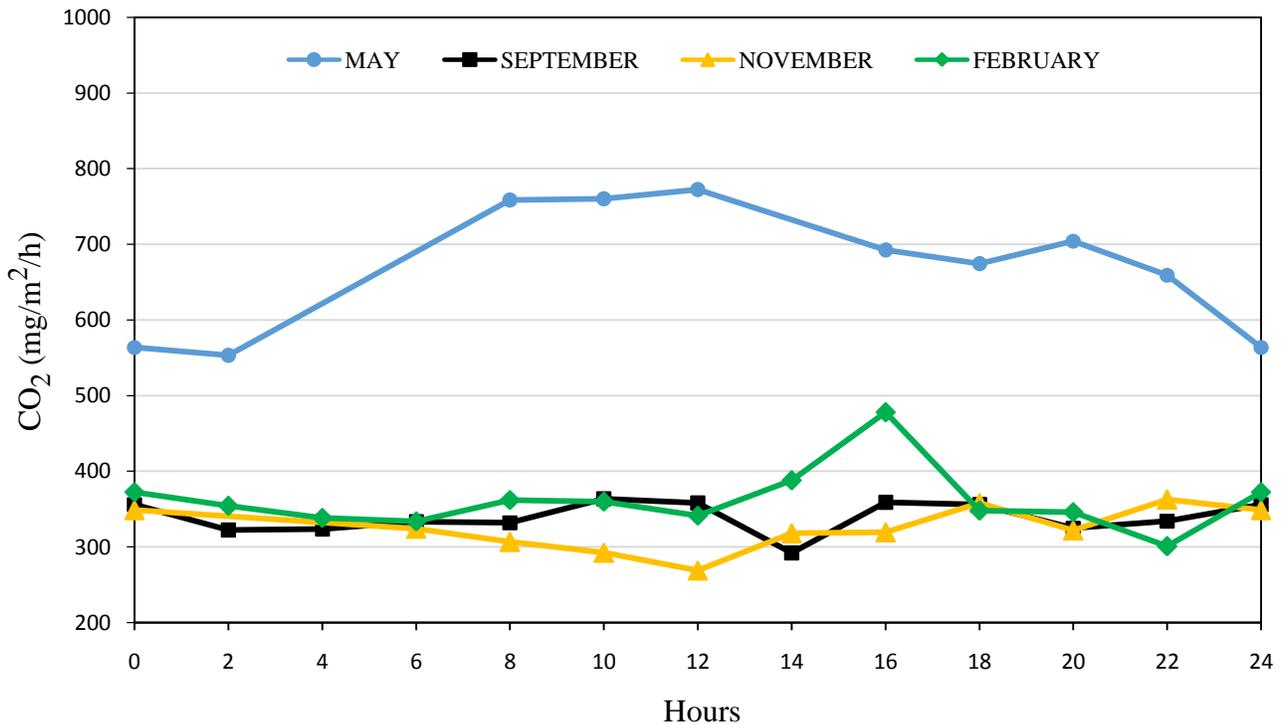


Fig 4. Daily variations of soil respiration measured in frequencies of two hours from May to February

h^{-1} in September; $352.71 \pm 74.84 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in November; and $376.82 \pm 52.65 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February. There is a relatively stable phase at night (18pm-8a m). The mean soil respiration was $629.69 \pm 96.74 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in May; $370.83 \pm 44.5 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in September; $339 \pm 17.95 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in November and $360.42 \pm 30.28 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February.

Between the various months and during the day (8 am-18 pm) and night (18 pm-8 am), average fluctuations in soil respiration were observed in September, November and February. In May, the soil respiration was high with great fluctuations during the day in relation to changes in the temperature of the air and soil.

The daily mean total respiration was $714 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in May; $376.27 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in September; $346 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in November and $355.21 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February. In general, the soil respiration was tenth to twentieth as high as the CO_2 content in the ambient air of the forest.

Seasonal and spatial variations of soil respiration

During the day, the mean soil respiration (Fig.6) of the five randomly selected points varied with seasons. The flux reached its greatest peak in May with $917.50 \pm 19 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ and was relatively low and steady in July ($550.75 \pm 104 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), September ($461.40 \pm 114 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), November ($520.31 \pm 135 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) and even

lower in February ($345.225 \pm 96 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$).

Based on the values of the standard deviations the values were less dispersed in May which is a wet month than in February, dry month. The decrease in soil respiration between these two months was about 67%.

Correlation between soil respiration and litter manipulations

With regard to the various treatments (Fig.5), i.e. the control with natural litter fall (S+L); the bare soil with litter excluded immediately (S-L)a; soil with litter removed every week throughout the experimentation (S-L)b and double litter input (S+2L), the soil respiration declined in the direction (S+2L) > (S+L) > (S-L)a > (S-L)b.

Variation of Soil respiration in S+L

Respiration in the soil (S+L) decreased (Fig.5) regularly from May ($1210 \pm 108.4 \text{ mg m}^{-2} \text{ h}^{-1}$), July ($523.44 \pm 170.27 \text{ mg m}^{-2} \text{ h}^{-1}$) and September ($474.83 \pm 157.36 \text{ mg m}^{-2} \text{ h}^{-1}$) to February ($361 \pm 141.5 \text{ mg m}^{-2} \text{ h}^{-1}$) with the exception of November ($593 \pm 154.30 \text{ mg m}^{-2} \text{ h}^{-1}$).

However, respiration remained always higher in this treatment than in soils with litter removed immediately (S-L)a or several weeks (S-L)b.

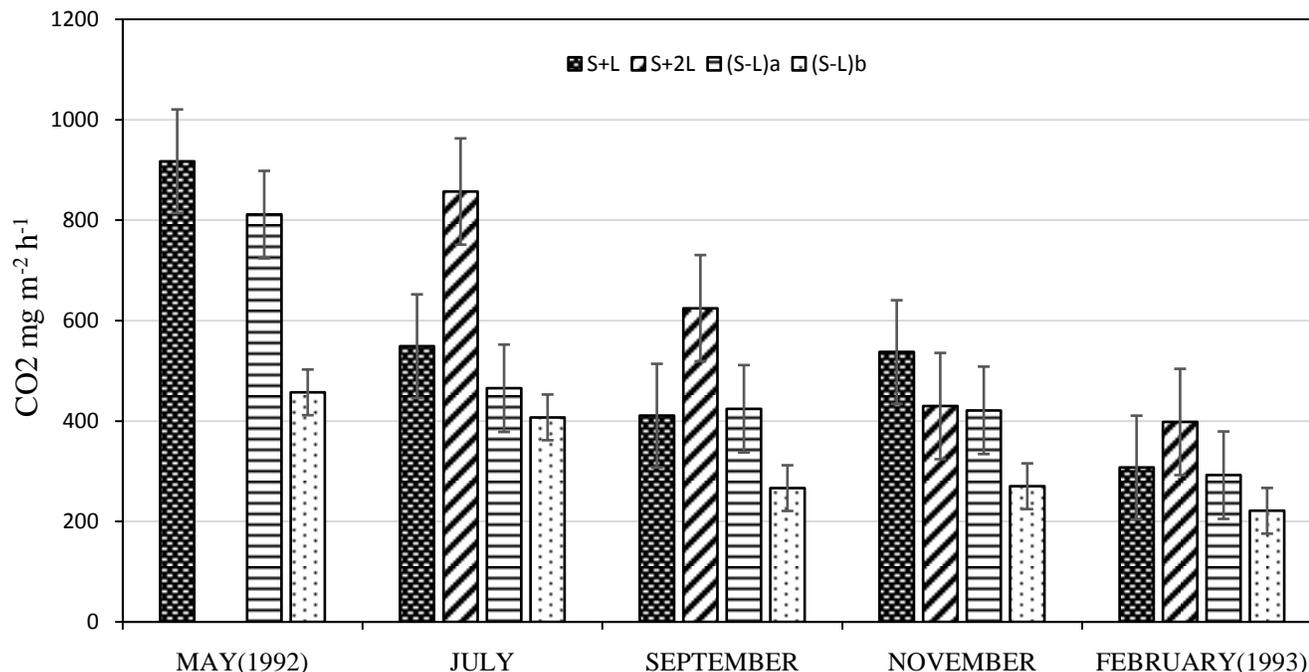


Fig 5. Seasonal and spatial variations of soil respiration with natural input (S+L) and with litter manipulated:

- (S-L)a litter removed just before the measurement was taken;
- (S-L)b litter excluded every two weeks from May to February ;
- (S+2L) litter added on the soil with natural litter taken from (S-L)b.

Variation of Soil respiration in (S-L)a and (S-L)b

The respiration of the soil (Fig.5 (S-L)a strongly decreased from May ($678.2 \pm 237.6 \text{ mg m}^{-2} \text{ h}^{-1}$) to July ($465.4 \pm 113.8 \text{ mg m}^{-2} \text{ h}^{-1}$) but varied steadily from July to September ($424.4 \pm 67.1 \text{ mg m}^{-2} \text{ h}^{-1}$), November ($421.4 \pm 123.3 \text{ mg m}^{-2} \text{ h}^{-1}$) and February ($292.2 \pm 74.27 \text{ mg m}^{-2} \text{ h}^{-1}$). These values were usually high compared to that of the soil with no litter for several weeks (S-L)b.

Soil respiration observed in bare soils (S-L)b was the lowest and decreased strongly from July ($407.4 \pm 67.2 \text{ mg m}^{-2} \text{ h}^{-1}$) to September ($266.5 \pm 41.6 \text{ mg m}^{-2} \text{ h}^{-1}$) but slightly increased from September to November ($270.26 \pm 47 \text{ mg m}^{-2} \text{ h}^{-1}$) before dropping in the month of February ($221.03 \pm 79.53 \text{ mg m}^{-2} \text{ h}^{-1}$).

The difference in soil respiration examined between (S-L)a and (S-L)b could be explained based on the amount of easily biodegradable soil organic matter that was used up over the months in the soil (S-L)b and no longer receiving more fresh organic residues on its surface for the duration of the experiment.

Variation of Soil respiration in S+2L

The CO₂ production in the soil (Fig.5) with fresh litter added (S+2L) was high and steadily decreased over the months although it remained higher than in the soil with natural

litter fall (S+L) except during the month of November in which both were similar. It was $962.5 \pm 137.5 \text{ mg m}^{-2} \text{ h}^{-1}$ in July; $620.83 \pm 133.66 \text{ mg m}^{-2} \text{ h}^{-1}$ in September; $554.17 \pm 92.14 \text{ mg m}^{-2} \text{ h}^{-1}$ in November and $554.17 \pm 56.37 \text{ mg m}^{-2} \text{ h}^{-1}$ in February. Soil respiration appears similar for November and February.

The difference observed between the two treatments (S+2L) and (S+L) seems obvious to hold based on the amount of fresh litter added to the soil (S+2L) which is a function of the litter production in the forest. This production varied in quantity and quality with the seasons (more leaves in the dry seasons i.e. December, January, February and more twigs in rainy seasons (April-May and September-October). Moreover, adding the litter modified to some extent, the microclimate at the soil surface (Fig 5). A very low difference was observed between soil respiration of (S+2L) and (S+L) in November, the end of the long rainy season with little litter covering the soil (S+L) and litter added to the soil (S+2L) is insignificant. Based on the various treatments, soil respiration showed variations between months i.e. the soil respiration in (S+L) decreased from May to February with change in soil moisture (Table2) and in (S+2L) the respiration was influenced by soil moisture and probably the quantity and quality of the litter added.

Table 2. Average values of spatial and seasonal variations of soil moisture (%) and temperature (°C) at the five randomly chosen points at daytime. * humidity of soil samples collected one hour after a heavy rain in May corresponding to the capacity of retention.

	May	July	September	November	February
Soil moisture (%)	23.5 ± 3.0 *24.8 ± 1.85	20.5 ± 1.8	18.2 ± 2.0	18.8 ± 1.2	18.0 ± 1.0
Soil temperature (°C)	22.6 ± 0.3	21.6 ± 0.4	21.6 ± 1.26	22.12 ± 0.39	21.5 ± 1.36

Contribution of above and below ground litter to total soil respiration

The above ground litter contribution to the total soil respiration(S+L) (Fig 6)

It was estimated using three possibilities namely, the difference between the total soil respiration in control (S+L) and (S-L)a; the difference between soil respiration with double intake of litter (S+2L) and the control (S+L) and lastly the difference between the total soil respiration in control (S+L) and soil with litter removed every two weeks (S-L)b divided by the total respiration of the control (S+L).

The removal of litter immediately before measurements (S-L)a slowed down the total soil respiration in the control (S+L). The contribution of litter, considered as the difference between the total soil respiration of the control (S+L) and that of the soil (S-L)a was 10 to 12% except in September when it was 2%.

The contribution of fresh above ground litters considered as the difference between soil respiration with double input of litter (S+2L) and the control (S+L) ranged between 62% in July, 41% in September, 00% in November and 38% in February of the total soil respiration.

A significant difference is observed between soil respirations of the months of February and November with quite similar soil moisture, probably due to a more intense activity carried out by soil organisms in the dry season (February).

The contribution of aboveground litter, considered as the difference between the total soil respiration of the control (S+L) and that of the bare soil (S-L)b was about 23% in July, 43% in September and November and 34% in February of the total soil respiration.

The belowground litter contribution to the total soil respiration(S+L) (Fig 6)

The contribution of below ground litter lied between 56 to 66 % in both cases except in July where in the first case this contribution was 37% and in the second case it was up to 77%.

DISCUSSION

CO₂ concentration in the ambient air of the forest

The difference between day and night in CO₂ levels is related to two important phenomena in the biosphere in which

atmospheric CO₂ is involved i.e. plant photosynthesis and respiration. During the day, atmospheric CO₂ is absorbed by plants and in the night plants respire by releasing CO₂ in the air.

The CO₂ levels recorded as the concentration in ambient air on the forest floor varied between 322 ± 16 ppm (September) and 387 ± 34.2 ppm (May) in the day and between 347 ± 8.5 ppm (September) and 470 ± 25.4 ppm (May) at night. In the month of May, high CO₂ concentrations in the air were observed both day and night but the difference between night and day was high. Within this month, the air humidity is maximum and constant (95%) throughout the 24 hour period. These results were similar to those recorded in summer in a temperate forest (Schwarzkoﬀ, 1978). Tang et al. (2005) and Zimmermann et al. (2009) highlighted the functioning of the forest based on differences in either photosynthesis or respiration intensity on a diurnal and seasonal period. In the month of May, the high CO₂ concentration is also related to the difference in temperature and rainfall which are major climatic factors during that period, producing a higher biological activity (Sotta et al. 2004) as indicated by the high air and soil humidity. In May, the active litter decomposition due to high precipitations could explain the high level of CO₂ concentration. The CO₂ content in the ambient air of the forest floor was ten to twenty times lower than the soil CO₂ efflux. Good air circulation in the forest's lower strata will generally produce a low CO₂ accumulation as suggested by Schwarzkoﬀ (1978).

Seasonal and spatial soil respiration in a secondary tropical forest

Soil respiration in tropical zone greatly varied with various plant formations, the highest values obtained in the rain forest and soil respiration was exhibited with similar seasonal variations. Values reported ranged from 300 to 459 mg CO₂ m⁻² h⁻¹ in the dry season and 681-1000 to 712-2000 mg CO₂ m⁻² h⁻¹ in the rainy season (Kursar, 1989; Kepler and al., 1990; Schulze, 1967; Rajvanshi and Gupta, 1986; Rout and Gupta, 1989; Basu et al., 1991; Valentini et al. 2008). In the present study, it has been observed that the mean soil respiration from the five randomly selected points during the day showed a yearly seasonal variation, with a low peak in February (345.225 ± 96 mg CO₂m⁻² h⁻¹),

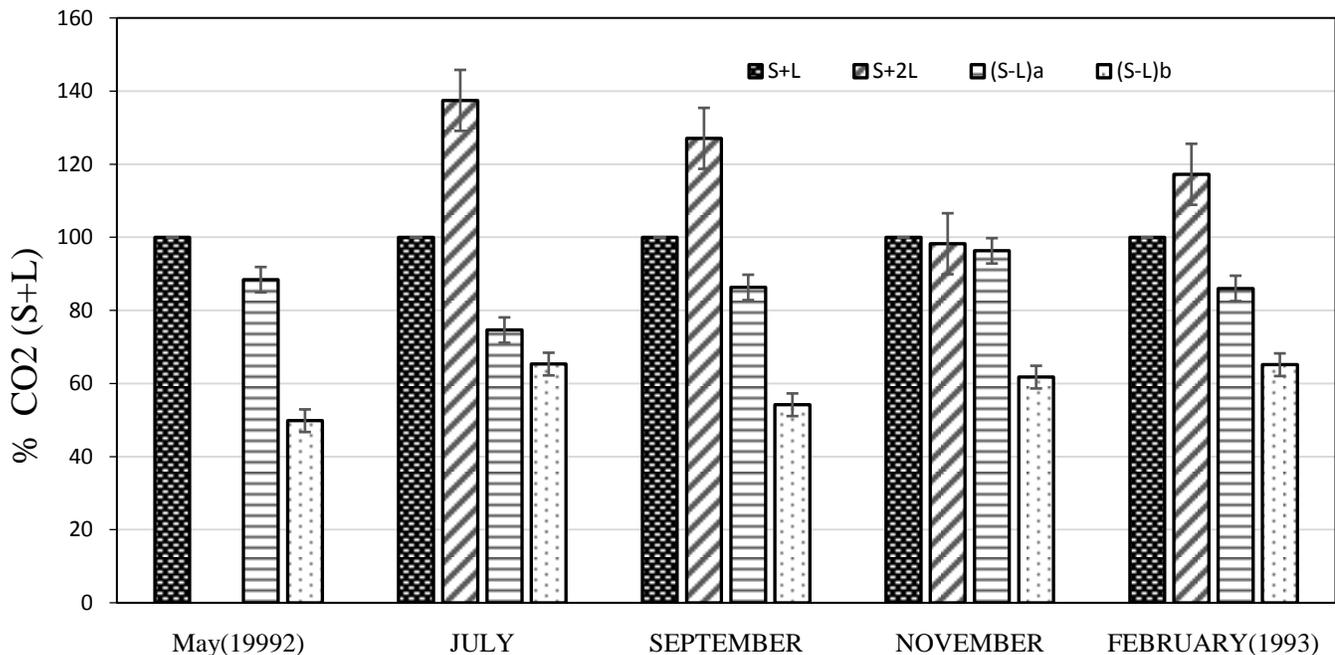


Figure 6. soil respiration with litter manipulated expressed in percent (%) of soil respiration with natural input (S+L):

- (S-L)a litter removed just before the measurement was taken;
- (S-L)b litter excluded every two weeks from May to February.
- (S+2L) litter added on the soil with natural litter taken from (S-L)b.
-

i.e. at mid long dry season and a high peak in May ($917.50 \pm 19 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), the middle of the short rainy season. The variation observed between the various plant formations within the same ecosystem in the tropical rainforest is linked to not only tree and root distribution but also to litter quality, litter microbes in the humus layer, soil type and climate seasonality (Katayama et al., 2009; Sulzman and al., 2005; Sotta et al., 2004). Other authors attribute this variability essentially to the various methodology used (Gunn and Trudgil, 1982, Basu and al., 1991, Tate and al. 1993). It is known that results obtained with the soda absorption method only represent 61.3% (Edwards and Sollins, 1973; Kucera and Kirkham, 1971) to 75% (Tate and al. 1993) of those obtained by the Infrared Gaz Analyzer. More recently, Tang et al. (2005) evoke the disturbance of air pressure in the soil and thus the concentration of CO₂ in the soil when using enclosure to measure the soil CO₂ emitted with IRGA

Within the same vegetation, a high heterogeneity in the distribution of roots and litter on the soil surface explains the spatial variation of soil CO₂ efflux (Sotta et al., 2004;

Raich and Nadelhoffer, 1989). This study indicates that there is an extent of variability in the various measuring points within the site that is low in May and high in July, September November and February. Based on measurements obtained at fixed points during the various months, the variability would be in this case related to the distribution of litterfall on the soil surface.

When comparing the soil average respiration between February and May, i.e. the dry and rainy months respectively, it is observed that the soil respiration of dry period represents 37.62% of the soil respiration of the wet period. In other words, the soil respiration during rainy period appears 2.65 times more than that of the dry period. This report is similar to the observations carried out in the Amazon (Valentini et al., 2008). The difference in the soil respiration within these same periods is of the order of 5% and that of the mean temperature of the soil is 1°C. Thus, seasonal variation of soil respiration is significantly related to soil and air temperature when water is not limited (Bai et al., 2012; Howard and Howard, 1993; Davidson and al., 2000; Fang and Moncrieff, 2001; Joffre et al., 2003; Tang

et al., 2005; Sulzman et al., 2005; Valentini et al., 2008) although some of the above authors believe that it is difficult to dissociate the effect of both factors.

From the present work, the results on the soil moisture explains better the seasonal variations of soil CO₂ efflux than soil temperature. The high CO₂ level observed in May corresponded to the rainfall peak and the soil respiration was relatively low during the months of November and February which are somehow the driest. The results indicates that the activity of soil microorganisms is limited in the dry season (February), due to the drop in soil moisture than to the temperature of the soil (Davidson et al., 2000; Fang and Moncrieff, 2001; Joffre et al., 2003; Tang et al., 2005; Sulzman et al., 2005; Valentini et al., 2008). During the various months of measurement, the temperature of the soil differs very little. The work of Wood et al. (2013) shows that there is however a tipping point of the positive effect of soil moisture on soil respiration with regard to the texture of the soil and the wet episodes enhancing soil respiration. In the temperate areas, only summer figures are comparable to those of the dry season in tropical zones (Edwards and Ross, 1983; Bowden and al., 1993).

Diurnal soil respiration in secondary tropical forest

Major variability occurs on hourly to daily basis and there is a significant positive relationship between air and soil temperatures and respiration (Sotta et al. 2004, Zimmermann et al. 2009, Wood et al.(2013).

Soil respiration fluctuated greatly within 24 hours with peaks from 8 am to 12pm in May 10am to 12pm in September 16 to 18pm in November and from 14 to 18pm in February

These fluctuations are a function of time and would correspond to an increase in both air and soil temperatures in conformity with previous work.

In the month of May, the soil respiration was high and the fluctuations during the day were also important due to the high values of air and soil temperatures, and soil moisture. Within this month, the effect of rainfall which causes pulses in soil and ecosystem respiration must be taken into account (Tang et al. 2005).

During the day, the mean soil respiration was $798.28 \pm 158.70 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in the month of May and $376.82 \pm 52.65 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February.

At night, the fluctuations in soil respiration are relatively low between 20 pm and 6 am. The mean soil respiration was $629.69 \pm 96.74 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in May and $360.42 \pm 30.28 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February.

On a daily basis, the mean total soil respiration was $714 \text{ CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in May and $355.21 \text{ CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in February. The values are lower than those collected at daytime. It appears, based on the diurnal variations of the soil, the data on seasonal soil CO₂ efflux can lead to either an over- or under estimation of the total soil respiration depending on

the time of measurement and effect of rain (Zimmermann et al. 2009).

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Effect of manipulated litter to total soil respiration

Raich and Tufekcioglu, (2000) suggest that soil respiration is greater in sites with high rates of detritus production. Several studies have investigated the contribution of aboveground litter layer and the soil below to soil respiration (Sulzman et al., 2005; Raich and Nadelhoffer, 1989; Bowden et al., 1993; Valentini et al., 2008; Tang et al., 2005; Zimmermann et al., 2009; Trumbore, 2000). The addition or the removal of fresh litter significantly increased or decreased the total soil respiration (Prevost Bouré et al., 2010; Sayer et al., 2007), thus, soil respiration was in average 20% lower when litter was removed and 43% higher when it was added. Globally, it has been observed that the relative contribution of litter to total soil respiration varies from 19% in the temperate forest (Sulzman et al., 2005) to 37% in the tropical forest (Zimmermann et al., 2009).

Contribution of above ground litter to total soil respiration

The soil respiration declined in the direction (S+2L) > S+L > (S-L)a > (S-L)b and this is similar to previous work (Prevost Bouré et al., 2010; Sayer et al., 2007). The removal of litter immediately before measurements (S-L)a slowed down the total soil respiration in the control (S+L) and the contribution of above ground litter in this case was

10 to 12% except in September when it was 2%. Based on the standard deviation, it was difficult to conclude on and to interpret the significant reduction in soil respiration as there are no more leaves covering the soil surface due to litter removal (Edwards, 1975). This removal had probably led to soil respiration overestimation due to greater respiratory activity of roots and microorganisms and a greater diffusion of gases.

Moreover, the removal of litter at the soil surface every week for months (S-L)_b also slowed down the total soil respiration. The contribution of aboveground litter, considered as the difference between the total soil respiration of the control (S+L) and that of the bare soil (S-L)_b was about 23% in July, 43% in September and November and 34% in February of the total soil respiration. Although the floor has been disturbed during the experiment in the month of May, equilibrium seemed to be attained after a few months.

The contribution of litter in this case seems to increase with time (July, September and November) and then begins to gradually decline (February). In July, and two months later, despite being bare, the soil contains probably enough tiny residues and organic matter associated with mineral material readily biodegradable equivalent to the active pool of carbon (Schwendenmann et al., 2007). Soil microorganisms will thus tackle this easily biodegradable organic matter pool and contribute to soil respiration without intake of fresh new organic material. Over the months, this labile organic matter will be used up; this justifies the continuous decrease of soil respiration from July to February, nine months after the beginning of the experiment.

According to Trumbore (2000), tropical forest soil respiration is dominated by the decomposition of organic matters soluble in bases with a quick turn over (< 1 yr) and their contribution to the total soil respiration is less than 20%. This would suggest that the contribution of above ground litter to the total soil respiration in this case would be overestimated with time since it will be part of the decomposition of the belowground litter, the secondary mineralization of humus and roots respiration.

The addition of fresh litter (S+2L) every week for months increased the total soil respiration of the control (S+L). The contribution of above ground fresh litters considered as the difference between soil respiration with double input of litter (S+2L) and the control (S+L) ranged between 62% in July, 41% in September, 00% in November and 38% in February of the total soil respiration.

In this case, the superimposition of the various litters (L) on the pre-existing litter L₁ might produce changes in the pedoclimate (luminosity, temperature, humidity and aeration) therefore water flows down from litters L stimulating the decomposition of organic matter produced from the litter next to the soil (Bowden et al 1993; Sulzman

2005). This might explain the important contribution of newly added above ground litters to total soil respiration in July, at the end of the short rainy season two months after the experiment begun. This could be a kind of booster leading to the overestimation of the litter effect (François Toutain, CNRS, Nancy-France, *pers. com.*). Finally, except in July (62%), the contribution of litter was quite comparable in both last cases and was about 34 to 43 % of the total soil respiration.

In November, soil respiration was similar on both soils i.e. the soil with double input of litter (S+2L) and the control (S+L). This could be explained based on the quantity and quality of litter at soil level. In tropical forests, drops in production are more important in dry season than in rainy periods and leaf litter production was higher during the dry season (Luizao and Schubart 1987; Schwartz 1991; Valentini et al., 2008). Thus, in the rainy seasons, the decay processes are speed up and litter accumulated during the dry season disappears within a few weeks. It was therefore obvious at the end of heavy rainy season (November), litter was almost thin or inexistent on the soil surface (Luizao et al., 1987). Thus, litter production measurements coupled with those of soil respiration with or without litter on the soil surface would allow a better interpretation of results.

Contribution of below ground litter to total soil respiration

In the temperate climate, Sulzman (2005) attributes 49 to 65% of the total soil respiration to the below ground litter of which 14 to 32% are due to rhizosphere activity. These findings corroborate that of earlier authors such as Pati et al. (1983) and Bowden et al. (1993). Moreover, Raich and Tufekcioglu (2000) estimated that the contribution of roots is very high in temperate (33-50%) and boreal (35-62%) regions. However, Raich and Nadelhoffer (1989) consider that it is hard to differentiate the contribution of the living from dead roots with regards to below ground respiration. In the humid tropical forest, Valentini et al. (2008) found that litter decomposition represents 16% of the annual soil respiration which is two times higher in the dry season, probably due to the activity of soil organisms, particularly termites.

Our work showed that the contribution of below ground litter lied between 56 to 66 % in both cases except in July where it was up to 77% and this seemed high as explained earlier, the soil (S-L)_b still contained a pool of active carbon with a rapid turnover. These values appeared acceptable according to the above cited authors. If we assumed the contribution of this pool of active carbon to be estimated by the difference between (S-L)_a, the soil exposed just before measurements were taken and (S-L)_b the soil maintained bare for months, then it would be from 13 to 33%. The difference between the contribution of (S-L)_b to soil respira-

tion (S+L) in the month of July and those from the months of September to February would probably be between 10 to 20%. These values looked more acceptable according to Trumbore (2000).

CONCLUSION

Diurnal and seasonal variations of soil respiration showed that they are influenced by the daily variation of soil temperature and seasonal variation of soil moisture respectively. This implies that the biological processes involved in the production of CO₂ on the forest floor could easily lead to the global climate change on which depend the temperature and humidity of the soil. CO₂ measurements for the assessment of the different components of total soil respiration were done with disturbance on the forest floor and the interpretation of results remained complex. Any disturbance on the forest floor will generally lead to compensation. In tropical forest, the estimations of soil respiration using cultural practices (deforestation, slash and burn, cultivation) in similar conditions of season (humidity, temperature) and time would clearly highlight the impact of litter removal and human activities on soil respiration and global climate change.

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REFERENCES

- Adachi ML, Ishida A, Bunyavejchewin S, Okuda (2009). Spatial and temporal variation in soil respiration in a seasonally dry tropical forest, Thailand, *Journal of tropical ecology*, 531-539.
- Bai C, Liang Y, GE Y, Lin X, Jia W (2012). The temporal and spatial variation of soil in pepper (*Capsicum annuum* L.), eggplant (*Solanum melongena* L.) and maize (*Zea mays* L.) agroecosystem in northwest of China. *AJCS* 6(11): 1565-1571.
- Basu S, Joshi SK, Pati D P, Behera N (1991). Soil respiration in relation to microbial biomass in a tropical deciduous forest floor from India. *Rev. Ecol. Biol.*, Vol.28, 4: 377-386.
- Bowden RD, Knute J, Nadelhoffer, Boone RD, Melillo JM, Garrison JB (1993). Contribution of aboveground litter, belowground litter and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can. J. For. Res.*, 23: 1402-1407.
- Couteaux MM, Botner P, Berg B (1995). Litter decomposition, climate and litter quality. *Tree*, 10 (2) 63-66.
- Cuevas E, Medina E (1988). Nutrient dynamics within Amazonian forests. 76: 222-235.
- Davidson EA, Verchot LV, Cattanio JH, Ackerman IL, Carvalho JEM (2000). Effects of soil water content on soil respiration in forests and cattle pastures in eastern Amazonia. *Biogeochemistry*, 48: 53-69.
- Edwards NT, Sollins P (1973). Continuous measurement of carbon dioxide evolution from partitioned forest floor components. *Ecology*, 54: 406-412.
- Edwards NT (1975). Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. *Soil Sci. Soc. Am. J.* vol.39
- Edwards NT, Ross-Todd BM (1983). Soil carbon dynamics in a mixed deciduous forest following clear-cutting with without residue removal. *Soil Sci. Soc. Am.*, 47:1014-1021.
- Fang CM, Moncrieff JB (2001). The dependence of soil CO₂ efflux on temperature, *Soil Biol. Biochem.* 33: 155-165.
- Goma-Tchimbakala J, Bernhard-Reversat F (2006). Comparison of litter dynamics in three plantations of indigenous timber-tree species (*Terminalia superba*) and a natural tropical forest in Mayombe, Congo. *Forest Ecology and Management*, 229: 304-313.
- Gunn J Cork, Trudgil ST (1982). Carbon dioxide production and concentrations in the soil atmosphere: a case study from New Zealand volcanic ash soils. *Catena*, 9: 81-94.
- GUPTA SR, SINGH JS (1981). Soil respiration in a tropical grassland. *Soil Biol. Biochem.*, 13: 261-268.
- Hanson PJ, Edwards NT, Garden CT, Andrews JA (2000). Separating root and soil microbial contribution to soil respiration. *Biogeochemistry*, 48(1): 115-146
- Howard DM, Howard JPA (1993). Relationship between CO₂ evolution, moisture content and temperature for range of soils types. *Soil Biol. Biochem.* 25(11):1537-1546
- Ibrahima A, Ntonga JC, Mvondo ZE A (2010). Leaf litter decomposition in tropical rainforest of Ebom, southwest Cameroon: comparison among guild classes, *Tropical Ecology* 51(2): 247-254.
- Joffre R, Ourdival JM, Ranbal S, Rocheteau A (2003). The key role of top soil moisture on CO₂ efflux from a Mediterranean *Quercus ilex* forest. *Ann. Forest. Science*, 60: 519-526.
- Katayama A, Kume T, Komatsu H, Ohashi M, Nakagawa M, Yamashita M, Otsuki K, Susuki M, Kumagai T (2009). Effect of forest structure on the spatial variation in soil respiration in a Bornean tropical rainforest. *Agricultural and forest meteorology*, 149: 1666-1673.
- Kepler S, Volkoff B, Cerril CC, Luizao F, Eduardo BP (1990). Respiração do solo: comparação entre áreas com mata natural, mata recem-queimada and pastagem na

- Amazonia central. *Geochim.Brasil*. 4 (2): 111-118.
- Kucera CL, Kirkham DR (1971). Soil respiration studies in tallgrass prairie in Missouri. *Ecology*, 52: 912-915.
- KURSAR TA (1989). Evaluation of soil respiration and soil CO₂ concentration in lowland moist forest in Panama. *Plant and Soil*, 113 : 21-29.
- Letouzey YR (1985). Notice de la carte phytogéographique du Cameroun au 1/500 000 - Domaine de la forêt dense. IRA, ICIV.
- Luizao FJ, Schubart HOR (1987). Litter production and decomposition in a terra-firme forest of Central Amazonia. *Experientia*, 43: 259-265.
- Malhi Y (2012). The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of Ecology*, 100: 65 -75.
- Mishra PC, Dash MC (1982). Diurnal variation in soil respiration in tropical pasture and forest sites at Sambalpur, India. *Comp. Physiol. Ecol.* 7 (2):137-140.
- Moghiseh E, Heidari A, Ghannadi M (2013). Impacts of deforestation on soil organic carbon storage and CO₂ emission. *Soil Environ.* 32(1):1-13.
- Moureaux C, Bodson B, Aubinet M (2008). Mesure des flux de CO₂ et bilan carboné de grandes cultures: état de la question et méthodologie. *Base*, 3(12): 303-315.
- Pati DP, Behera N, Bash MC (1983). Microbial and root contribution to total soil metabolism in a tropical grassland soil from Orissa (India). *Rev. Ecol. Biol. des Sols*, 20 (2): 183-190.
- Prevost-Boure NC, Soudani K, Damesin C, Lata JC, Dufrene E (2010). Increase in aboveground fresh litter quantity over-stimulates soil respiration in a temperate deciduous forest. *Applied Soil Ecology*, 46:26-36.
- Raich JW, KJ Nadelhoffer (1989). Belowground carbon allocated in forest ecosystems: global trends,. *Ecology*, 70(5): 1346-1354.
- Raich J, Tufekcioglu A (2000). Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48: 71-90.
- Rajvanshi R, Gupta SR (1986). Soil respiration and carbon balance in a tropical DalbergiaSissoo forest ecosystem, *Flora*, 178: 251-260.
- Rout SK, Gupta SR (1989). Soil respiration in relation to abiotic factors, forest floor litter, root biomass and litter quality in forest ecosystems of Siwaliks in Northern India. *ActaOecologia*, 10: 229-244.
- Sayer EJ, Powers JS, Tanner EVJ (2007). Increased litterfall in tropical forests boosts the transfer of soil CO₂ to the atmosphere; *PLoS ONE* 12: e1299.
- Schulze ED (1967). Soil respiration of tropical vegetation types. *Ecology*, 48: 652-660.
- Schwartz D (1991).- Retombées de litière, source de Zheng Z, Shanmughavel P, Sha L, CAO M, Warren M (2006). Litter Decomposition and Nutrient Release in a Tropical Seasonal Rain Forest of Xishuangbanna, Southwest China. *BIOTROPICA* 38(3): 342–347
- carbone et d'azote, in *Echange forêt – atmosphère en milieu tropical humide*. Edn. DGRST: Michel LE BERRE, pp. 141-158.
- Schwarzkoﬀ HS (1978). An open chamber technique for measurement of carbon dioxide evolution from soils. *Ecology*. 59 (5): 1062-1068.
- Schwendenmann L, Eveld Kamp, ED Sotta (2007). Effect of an induced drought on soil carbon dioxide (CO₂) efflux and soil CO₂ production in an Eastern Amazonian rainforest, Brazil. *Global change Biology*. 13: 2218-2229.
- Singh S, Amiro BD, Quideau SA (2008). Effect of forest floor organic layer and root biomass on soil respiration following boreal forest fire. *Can. J. Forest. Res.* 38: 81-95.
- Sotta ED, Meier P, Malhi Y, Nobrel AD, Hodnett M, Grace J (2004). Soil CO₂ efflux in a tropical forest in the central Amazon. *Global Change Biology*. 10:601-617.
- Sulzman EW, Brant JB, Bowden RD, Lajtha K (2005). Contribution of aboveground litter, belowground litter and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. *Biogeochemistry*, 73:231-256.
- Tang J, Misson L, Gershenson A, Cheng W (2005). Continuous measurement of soil respiration with and without roots in a ponderosa Nevada mountains, agricultural and forest meteorology. 132:212-227.
- Tate KR, Ross DJ, O'brien BJ, Kelliher FM (1993). Carbon storage and turn over and respiratory activity in the litter and soil of an old-growth southern beech forest. *Soil Biol. Bioch.* 25 (11): 1601-1612.
- Toutain F, Brun JJ (1992). Etude biodynamique des humus, éléments intégrateurs et révélateurs du fonctionnement des écosystèmes in *Les recherches en France sur les écosystèmes forestiers*. Edn. Paris: G. Landmann.
- Trumbore S (2000). Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications*, 10 (2):399-411.
- Valentini CMA, L Sanchez, SR de Paula, GL Vourlitis, J de Souza Nogueira, OB Pinto, F de Almeida L (2008). Soil respiration and aboveground litter dynamics of a tropical transitional forest in northwest MatoGrosso, Brazil. *J. of Geophys. Res.* 113: 1-11.
- Wang W, Chen WL, Wang SP. (2010). Root respiration and it's heterotrophic and autotrophic components: global patterns and responses to temperature and precipitation. *Soil Biology Biochemistry* 42: 1236 – 1244.
- Wood Tana E, Matteo Detto, Whendee L (2013). Sensitivity of soil respiration to variability in soil moisture and temperature in a humid tropical forest (Porto Rico). DOI: 10.1371/journal.Pone.0080965.
- Zhou Z, L Jiang, Edu, H HU, Y LI, D Chen, J Fang (2013). Temperature and substrate availability regulate soil respiration in the tropical mountain rainforest, Hainan island, China. *Journal of plant Ecology*, doi: 1093/jpe/-

rtt034, pp .1-10.

Xiao Hou B, LI M (2014). Rates of litter decomposition and soil respiration in relation to soil temperature and water in different-aged *Pinus massoniana* forests in the three gorges reservoir area, China. PLOS one. 9 (7):1-10.

Zimmermann M, Meir P, Bird M, Mahli Y, Ccahuana A (2009). Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. Soil Biol. and Bioch. 4: 1-3.