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Response of CO$_2$ fluxes and productivity to water availability in two contrasting ecosystems in northern Benin (West Africa)

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Abstract

· **Key message** CO$_2$ fluxes were measured during 18 months in a forest and a savannah in northern Benin. Higher values of carbon fluxes were found during the wet season at each site. A strong dependency of carbon fluxes on water relations was found in two contrasting sites. The forest sequestered 640 ± 50 and the savannah 190 ± 40 g C m^{-2} year^{-1}.

· **Context** In West Africa, the main mechanisms or factors governing the dynamics of ecosystems, especially the dynamics of the carbon fluxes and productivity, still remain less known. This study reports the carbon fluxes over two contrasting ecosystems, notably a protected forest (lat 9.79°N, long 1.72°E, alt 414 m) and a cultivated savannah (lat 9.74°N, long 1.60°E, alt 449 m) in northern Benin. The two sites were among those equipped by the AMMA-CATCH observatory and Ouémé 2025 project.

· **Aims** Flux data were analyzed at the daily and seasonal scales in order to understand their controlling variables. We discussed the patterns of CO$_2$ fluxes and the characteristics of the two ecosystems. The study also focused on the different water usage strategies developed by the two ecosystems since the alternation between dry and wet seasons highly influenced the seasonal dynamics. Finally, the annual carbon sequestration was estimated together with its uncertainty.

· **Methods** The carbon fluxes were measured during 18 months (July 2008–December 2009) by an eddy-covariance system over two contrasting sites in northern Benin. Fluxes data were computed following the standard procedure. The responses of CO$_2$ fluxes to the principal climatic and edaphic factors, and the canopy conductance were studied.

· **Results** A clear CO$_2$ fluxes response to main environmental factors was observed, however with difference according to the seasons and vegetation types. The ecosystem respiration showed the highest values during the wet season and a progressive decrease from wet to dry periods. Also, the carbon uptake values were high during the wet period, but

Contribution of the co-authors Expédit Evariste Ago conducted mainly the data analysis and prepared the manuscript with contributions from all co-authors. The field work with the eddy-covariance technique was carried out by Jean-Martial Cohard and Sylvie Galle who processed the raw data of fluxes. Marc Aubinet and Euloge Kossi Agbossou assisted in the data analyses. All authors read and approved the final manuscript which was submitted.

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low during the dry period. However, the CO_2 fluxes for the protected forest were always higher than that for the cultivated savannah within each defined period. This was due to the seasonal changes not only in phenology and physiology but also to the acclimation to environmental conditions, especially to the soil water availability. The water use efficiency was influenced by VPD during the day conditions for two ecosystems. However, the VPD response curve of water usage was relatively constant for the protected forest during the transitional and wet seasons. In contrary, for the cultivated savannah the VPD response decreased about 46 % from transitional dry-wet to wet seasons and remained relatively constant until transitional wet-dry season. The close relationships between the net CO_2 assimilation and the canopy conductance were found for the two ecosystems. This suggests a regulation of the stomata by a partial stomatal closure besides the radiation control. Finally, the forest sequestered at the annual scale 640 ± 50 and the savannah 190 ± 40 g C m^{-2} year^{-1}.

• **Conclusion** We conclude with a strong relation between the carbon fluxes and water in the two investigated ecosystems. Apart from the radiation control, the stomata also play an important role in the regulation of the CO_2 assimilation in the two ecosystems.

1 Introduction

In West Africa, the long drought period during the 1970s and 1980s had led to a significant decrease in the annual averages of precipitation which reached 20–40 % of those in previous years (Nicholson 2013; Panthou et al. 2014). This high hydric deficit, which was never known in West Africa in the past, had severe impacts on agricultural activities and vegetation development due likely to its spatial extent and temporal continuity (IPCC 2013). In the West Africa region, the climate is strongly controlled by the West African Monsoon (WAM), but with significant differences related to the variability of precipitation between Sahelian and Sudanian regions as reported by several authors (Lebel et al. 2009; Nicholson 2013). Consequently, most ecosystems (anthropogenic and natural) may be significantly modified in the context of climate change and high population growth in West Africa (IPCC 2013; Ajonina et al. 2014). Few recent networks underlined that the knowledge of carbon exchanges between atmosphere and ecosystems remains very limited in West Africa (Bombelli et al. 2009; Valentini et al. 2014; Grace et al. 2014). In this context, the analyses of photosynthesis and

respiration of terrestrial ecosystems could be important to better understand vegetation responses to extreme climatic events as severe droughts or delayed rains. Thus, some investigations on responses of CO_2 fluxes and ecosystems properties to main meteorological, physiological, ecological, and anthropogenic factors are necessary. In addition, only a few studies have been reported on long-term CO_2 fluxes and carbon sequestrations in West Africa by several frameworks such as CarboAfrica project and AMMA-CATCH "African Monsoon Multidisciplinary Analysis" and "Couplage de l'Atmosphère Tropicale et du Cycle Hydrologique" observatory, which contributes significantly to the FluxNet network database (http://fluxnet.ornl.gov) (Brümmer et al. 2008; Ago et al. 2014, 2015; Tagesson et al. 2015; Quansah et al. 2015). Our study analyzed the CO_2 fluxes that were measured over a cultivated savannah and a protected forest under a Sudanian climate in northern Benin. These two sites were installed by the national Ouémé 2025 project and the AMMA-CATCH observatory.

The carbon fluxes were analyzed in terms of the net ecosystem exchange (NEE), ecosystem respiration (ER), and gross primary productivity (GPP). In particular, their different responses to the environmental changes were investigated from July 2008 to December 2009 in the two ecosystems in northern Benin. We discussed the patterns of carbon fluxes, productivity, water relations, and the main factors characterizing the two sites period by period. In doing so, the following questions were addressed: (a) How did carbon fluxes (NEE, GPP, ER) for the two contrasting ecosystems vary from daily to seasonal time-scales? (b) How did the main differences in the physiological, phenological, climatic, and edaphic factors contribute to their temporal and spatial variabilities? (c) What was the annual carbon sequestration of each site with its uncertainty?

2 Materials and methods

2.1 Two sites' description

The two contrasting sites are located at the Nalohou and Bellefoungou villages in Djougou district in northern Benin (Fig. 1). Specifically, they were a cultivated savannah (9.74°N, 1.60°E, 449 m) and a protected forest (9.79°N, 1.72°E, 414 m). Figure 2 displays some views of the two sites during the dry and wet seasons. The regional annual rainfall ranges between 1100 and 1500 mm from 1950 to 2009, with an average of 1303 mm (Guyot et al. 2012) and more than 75 % concentrated from May to September (Fig. 3). However, on the basis of the cumulated amounts, the rainfall regime is characterized not only by a distribution along seasons but also by a significant inter-annual variability. During 2009, while
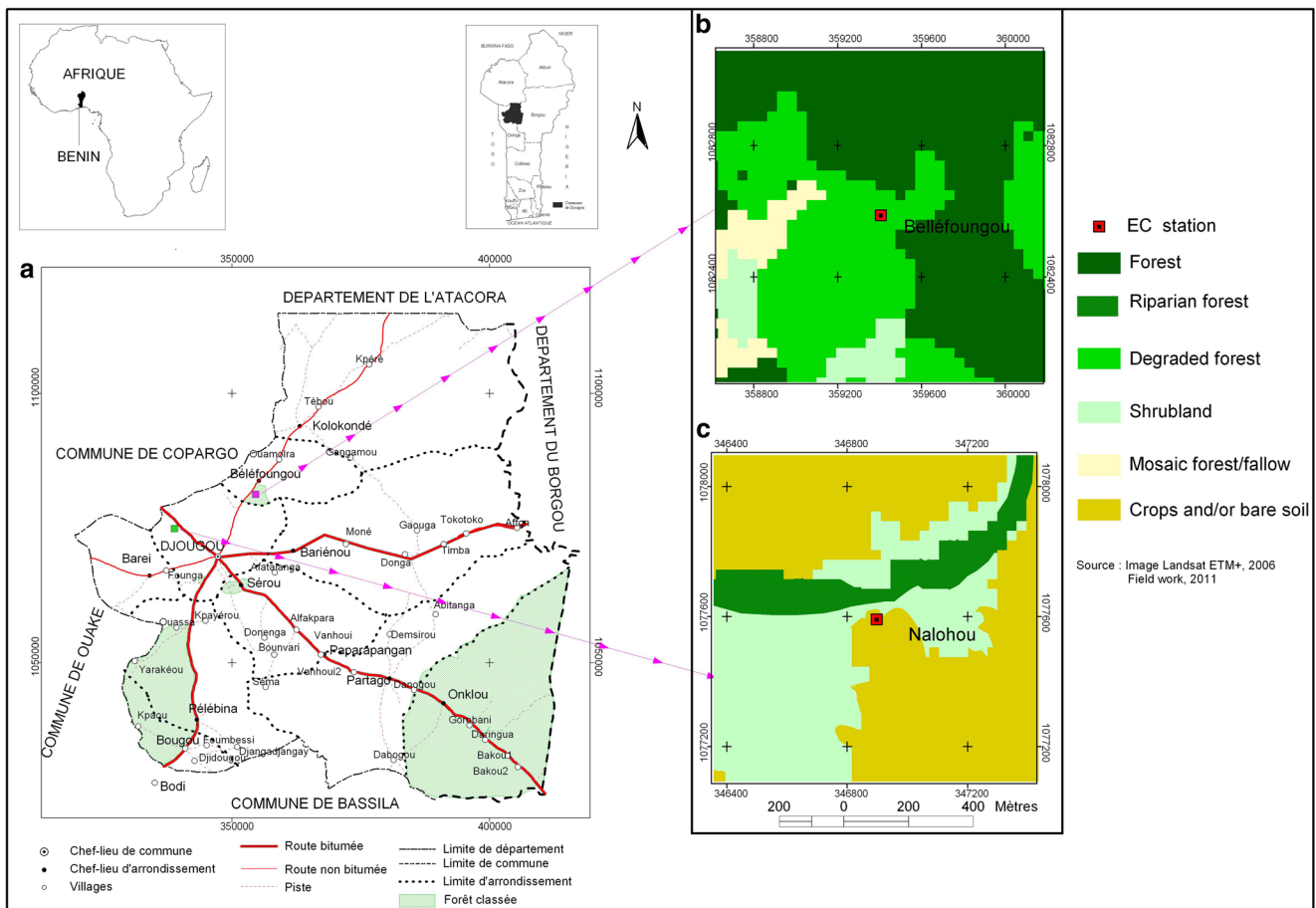
Fig. 1 Location of the two studied eddy-covariance sites and their land use distributions on a 1-km^2 area around the tower **a** in West Africa, **b** forest (Bellefoungou), and **c** savannah (Nalohou)

the forest site received 1625 mm of precipitation, an average of 1495 mm of the rain was recorded at the savannah site. Near the surface soils of the two sites are a Luvisol skeleta chromic (FAO classification) composed of 4–6 % clay, 20–22 % sand, and 74–75 % silt (Youssouf and Lawani 2000).

However, a large variability of the soils was observed in the deeper layers within each site covering all the ranges between loamy-sandy to clay soils. In Djougou district, a surface layer of 1–3 m was vertically observed followed by an alterite zone of 10–20 m (Faure and Volkoff 1998). For the two sites,
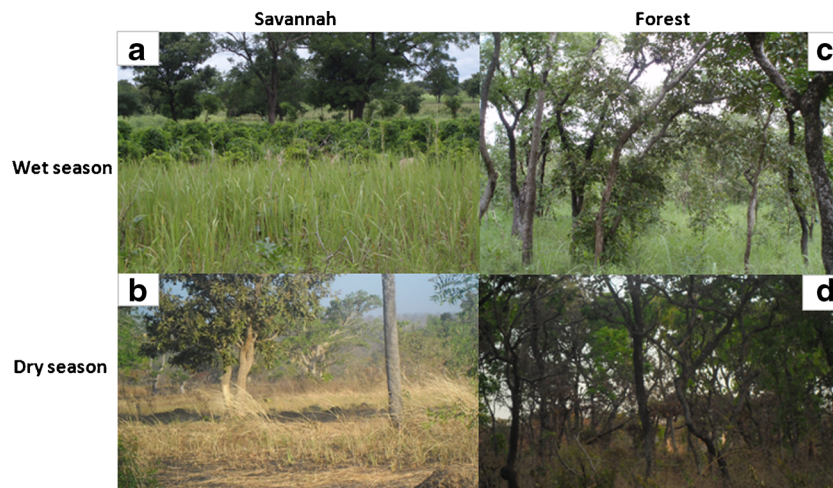
Fig. 2 View of both ecosystems during the dry (below) and wet seasons (above): savannah (**a**, **b**) and forest (**c**, **d**)
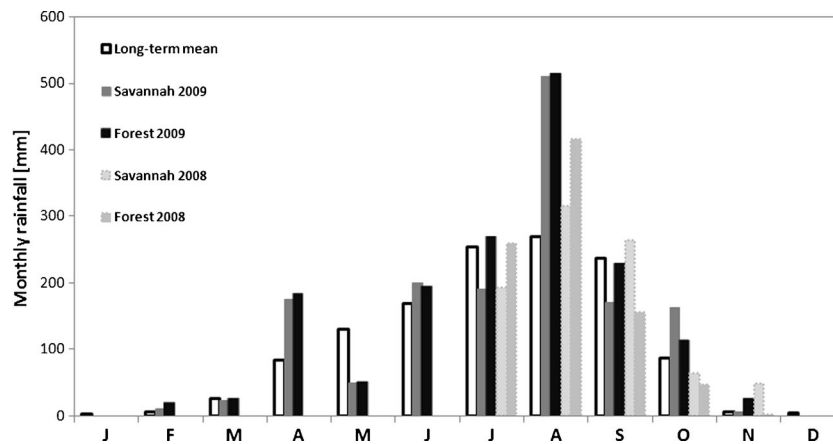
Fig. 3 Long-term monthly averages of the rainfall at Djougou district in northern Benin and those during 2008/2009 years at both investigated sites

during the wet season, the water table closes always from the ground surface (2–3 m), but does not exceed a depth of 6–10 m during the dry season (Séguis et al. 2011). The savannah site vegetation is relatively heterogeneous. This heterogeneity can have an impact on the seasonal variability of the carbon fluxes. Indeed, the contrasted seasonal climatic conditions seem to correspond to different wind directions and then to different footprints (Ago et al. 2014). However, the wind speeds rarely exceed 3 m s^{-1} at the two sites. The two sites have been studied by several authors: Ago et al. (2014) analyzed the carbon fluxes over the cultivated savannah, while Mamadou et al. (2014) and (Guyot et al. 2009, 2012) studied the energy and water vapor fluxes. For the protected forest site, only the fluxes of the energy and water vapor have been investigated by Mamadou (2014).

For the cultivated savannah site, the tree density was specifically low (~40 trees/ha) with 13.6 m as the average tree height. First, the trees that were in the footprint areas were located further than 100 m. Fifty-six (56) dominant vegetation species were identified in the wet season (September 2010) around the flux tower on 1 km^2 area for the herbs (mostly C4 plants), the trees (mostly C3 plants), and the crops (C3 and C4 plants). During the dry seasons, while the net CO_2 fluxes were mainly covered in the daytime by the sparse crops and few perennial herbs (96 %) with weakly sparse woody species (4 %), in the nighttime, the impact of the savannah area was more important on the measured fluxes (43 %) and that of the bare soil with sparse crops that were 57 % (Ago et al. 2014). During the wet periods, the CO_2 fluxes were largely affected mainly by the crops and herbs (77 %) and the sparse shrubs/trees (23 %). The slope was 2 % in a south–north direction.

The protected forest vegetation has also been described by other authors such as Blanchard et al. (2007) and Houéto et al. (2013). In fact, its total area was estimated at 709 ha while it was 1300 ha in 1943 when the

"reserve" status was given. The ecosystem was composed of 159 species identified (trees, shrubs, and herbs), and the woody strata was mostly dominated by species such as *Isoberlinia* spp. and *Vitellaria paradoxa* (Houéto et al. 2013). The average tree density (of diameter at breast height, i.e., dbh > 10 cm) was found between 321 and 338 trees/ha. The highest tree was 15 m high with the canopy covering approximately 60–80 % of the total soil area (Ago et al., personal communication). Four main vegetation types were identified on the basis of the Landsat TM scenes acquired in 2006 (Fig. 1b): forest (56 %), degraded forest (29 %), shrubland (7 %), and mosaic forest/fallow (8 %). Nevertheless, the measured fluxes were always affected by the trees and shrubs (mostly C3 plants) within the forest during the wet and dry seasons. In recent years, the site has been more and more subjected to strong human pressures. The slope was 2.5 % in a west–east direction.

2.2 Measurement system

2.2.1 CO_2 flux measurements

Continuous CO_2 flux measurements were performed using an eddy-covariance system installed above the protected forest and cultivated savannah. The two sites are located approximately 15 km apart from each other. The wind velocity was measured with a tridimensional sonic anemometer (CSAT-3; Campbell Scientific Instruments, Logan, Utah, USA) placed above the canopy at a height of 18 and 4.95 m above the ground for the forest and savannah sites, respectively. The sonic anemometer was coupled with an infrared gas analyzer open path (Licor 7500, Inc., Lincoln, Nebraska, USA) which measured the H_2O and CO_2 concentrations. The two gas analyzers were factory calibrated every 2 years. More information on this setup can be found in Ago et al. (2014). The CO_2 fluxes

which were treated in this study were measured during 18 months, from 1st July 2008 to 31st December 2009.

2.2.2 Climatic and environmental measurements

A meteorological station was also installed since 2005 and measured the atmospheric pressure, wind speed, wind direction, air temperature, and humidity (Vaisala WXT 510 weather station, Vaisala Oyp, Helsinki, Finland) at 5 and 2 m height at the forest and savannah, respectively. Some extra-temperature (HMP45C, Vaisala) and wind measurements (Vaisala wind monitor) were available at 18 m height at the forest site. Other variables like soil temperature (107 Temperature Probe; Campbell Scientific Instruments (CSI), Logan, Utah, USA) were also measured at 10 and 30 cm depth, four-component radiation (CNR1 radiometer Kipp and Zonen, Delft, The Netherlands) at a height of 2 m (savannah) and 18 m (forest), and soil moisture at 10 and 30 cm depth vertically (CS616 probes, Volumetric water reflectometer; Campbell Scientific Instruments, Logan, Utah, USA). The rainfall (weighing precipitation gauge, OTT; Hydrometry Ltd., Dublin, Ireland) was recorded at a height of 1.2 m. All these variables were sampled at 30 s time step and were averaged at half hour scale. The photosynthetic photon flux density (Q, μmol m^{-2} s^{-1}) was estimated as twice the global radiation (R_g, W m^{-2}) (Scanlon and Albertson 2004; Boulain et al. 2009; Ago et al. 2014, 2015). The CO₂ fluxes and meteorological conditions data were also available during 18 months, from 1st July 2008 to 31st December 2009. Annually, the radiation sensors were calibrated by a comparison with the standard sensors (CGR4 and CMP21 Kipp and Zonen, Delft, The Netherlands).

Main species dominating vegetation were inventoried on a 1-km^2 area around the two flux towers during the wet season with the height of the herbs monitored only at the savannah site. The dominant species were defined as those most abundant in coverage and density. The leaf area index (LAI) time series was obtained by a combination of the satellite LAI products (SEVIRI) and in situ measurements. More details on the LAI estimation method can be found in Ago et al. (2014) and Mamadou et al. (2014).

2.3 Data treatment, analysis, and uncertainty evaluation

Half-hourly corrected flux NEE were calculated by Eq. (1) below as the algebraic sum of the turbulent flux (F_{CO2}) measured by the eddy-covariance system and the CO₂ storage flux change in the air below the measurement point, considering the additional terms negligible (Aubinet et al. 2001). The storage flux was computed using a single measurement point of the CO₂ concentration at a height of 18 m (forest) and 4.95 m (savannah) as applied in several studies in the Africa region by

several authors (Archibald et al. 2009; Merbold et al. 2009; Ago et al. 2014, 2015).

$$NEE = F_{CO_2} + \frac{1000 * \Delta CO_2 * h_m}{\Delta t} \qquad (1)$$

where F_{CO_2} is the flux measured by the eddy-covariance system (μmol m^{-2} s^{-1}), ΔCO_2 is the difference in the CO₂ concentrations (mmol m^{-3}) measured between time t_0 and t_1, Δt is the time step of 1800 s, h_m is the sonic anemometer height, and the factor 1000 converts 1 mmol into micromoles.

All these data were computed following the standard Carboeurope procedure of the treatment of the eddy-covariance fluxes (Aubinet et al. 2012) with the classical corrections (despiking, high frequency losses, double rotation, WPL). Flux data recorded during the rainy events and the half-hour following the rains were excluded from the analysis. The stationary tests (Foken and Wichura 1996) were applied following three quality levels as Ago et al. (2014). In order to remove the nighttime fluxes during the periods of the low turbulence, the u_* -filtering criterion was applied as in several studies (Aubinet et al. 2012). We used the evolution of the averages nighttime fluxes following the u_* classes (Merbold et al. 2009; Ago et al. 2014). For $u_* <0.1$ m s^{-1}, the nighttime fluxes were rejected because they depended on the turbulence and led to an underestimation. For $u_* >0.1$ m s^{-1}, the nighttime fluxes were stable and the threshold of 0.10 m s^{-1} was fixed for the two sites as per other authors for similar African sites (Archibald et al. 2009; Boulain et al. 2009; Merbold et al. 2009; Ago et al. 2014, 2015).

In the following development, we will consider that a negative net ecosystem exchange (NEE) expresses that the fluxes are downward (i.e., dominated by the photosynthesis) while the positive values correspond to the upward exchanges (i.e., respiration is dominating).

In order to firstly obtain the seasonal and annual cumulated estimates of the net CO₂ exchanges and to secondly discriminate ER and GPP, the half-hour net fluxes were gap-filled. We used the parameterizations to describe the fluxes responses to the main meteorological and edaphic driving factors as applied by several authors in Africa (Merbold et al. 2009; Ago et al. 2014, 2015; Tagesson et al. 2015; Quansah et al. 2015). They were different for the daytime and nighttime fluxes. For the measurement period, the amount of the gaps due to the eddy-covariance technique failures or weather conditions was 49 and 45 % for forest and savannah, respectively. These amounts of the data gap-filled were higher than 39 and 41 % found on the half-hourly data by Sjöström et al. (2009) and Archibald et al. (2009), respectively. However, Papale et al. (2006) underlined that 20–60 % of the data measured by an eddy-covariance technique was rejected by the different quality filters applied. We used the Misterlich equation, Eq. (2), to describe the daytime fluxes responses as a function of the

photosynthetic photon flux density (Q) (Aubinet et al. 2001) taking into account the SWC influence through a simple linear function expressed by Eq. (3) as obtained by Ago et al. (2014):

$$NEE = -[A_{max} + ER_d]*\left[1-exp\left\{\frac{-\alpha Q}{(A_{max} + ER_d)}\right\}\right] + ER_d \qquad (2)$$

where NEE is the net ecosystem exchange (μmol m^{-2} s^{-1}), Q is the photosynthetic photon flux density (μmol m^{-2} s^{-1}) with three parameters characterizing the model: ER_d, the dark respiration (μmol m^{-2} s^{-1}); α, the quantum light efficiency (μmol μmol^{-1}); and A_{max}, the NEE at the light saturation (μmol m^{-2} s^{-1}). The latter varies with the soil water content (SWC) (m^3 m^{-3}) following Eq. (3) where A_o is a constant (μmol m^{-2} s^{-1}) related to the light-response characteristics of the vegetation.

$$A_{max} = A_o * SWC \qquad (3)$$

These parameters were deduced monthly from the data by fitting the non-linear equation, Eq. (2), using the Levenberg-Marquardt algorithm with Matlab software (R2010b version; the Mathworks, Natick, USA). This Eq. (2) saturates at higher Q and leads to more realistic values of the net CO_2 uptake at the light saturation compared to the classical rectangular hyperbola one (Michaelis and Menten 1913). Therefore, Aubinet et al. (2001) did not recommend the classical equation of Michaelis-Menten underlining that the deduced values of NEE at the light saturation and quantum light efficiency by the latter were higher of 30 and 20 %, respectively, than those given by Eq. (2), while the estimated values for ER_d were not found to be significantly different.

As the range variability of the daily average temperature for the two sites was relatively low (<10 °C) and the seasonality of the dry periods was clearly marked, ER was not expected to depend on the temperature. We used therefore only SWC at 10 cm depth to predict the ecosystem respiration (nighttime and daytime) at half-hour scales for both ecosystems (Williams and Albertson 2004; Curiel Yuste et al. 2007; Williams et al. 2009). This dependence with the SWC at 10 cm depth was fitted for the two sites using the half-hourly nighttime fluxes measured ($u_* > 0.1$ m s^{-1}) by Eq. (4) which expresses a sigmoidal function proposed by Ago et al. (2014):

$$ER = a*\left[1-Exp\left(-b*(SWC)^2\right)\right] \qquad (4)$$

where a is the maximal ER (μmol m^{-2} s^{-1}), b is a parameter characterizing the site controlling the sigmoid slope, and ER is the ecosystem respiration measured at half-hour scale (μmol m^{-2} s^{-1}). These two parameters were determined fitting

the Eq. (4) using the whole nighttime fluxes data filtered for the whole measurement period.

The leaf stomata play an important role in the exchanges atmosphere-vegetation by a physiological control (Collatz et al. 1991). Therefore, in order to analyze the main factors affecting the transfers atmosphere-ecosystems of the CO_2 and water vapor, the canopy conductance, g_c (mm s^{-1}) was estimated assuming the big-leaf hypothesis (Monteith and Unsworth 2013) and the inverting Penman-Monteith equation (Eq. 5) for the whole dry days at radiation saturation conditions ($Q > 1000$ μmol m^{-2} s^{-1}) during the entire flux measurements period as described by Aubinet et al. (2001):

$$g_c = \left[r_a\left(\frac{\Delta}{\gamma}\left(\frac{(R_n-G)}{LE}-1\right)-1\right) + \frac{\rho_a(VPD)\varepsilon}{E}\right]^{-1} \qquad (5)$$

where Δ is the slope of the saturation curve (Pa K^{-1}), γ is the psychrometer constant (Pa K^{-1}), ρ_a is the air density (kg m^{-3}), VPD is the vapor pressure deficit (kPa), ε is the ratio of the molecular weights of water and dry air, Pa is the atmospheric pressure (kPa), LE is the latent heat flux (W m^{-2}), R_n is the net radiation (W m^{-2}), G is the ground heat flux (W m^{-2}), E is the water vapor flux (kg m^{-2} s^{-1}), and r_a is the aerodynamic resistance (s m^{-1}).

The aerodynamic resistance was deduced from the turbulence measurements by Eq. (6) below as obtained by Mamadou et al. (2014) and Mamadou (2014) for the two investigated sites:

$$r_a = \frac{u}{u*^2}\frac{\varphi m}{\varphi H} \qquad (6)$$

where u is the average wind speed (m s^{-1}), $u*$ is the friction velocity (m s^{-1}), and φm and φH are the Businger-Dyer stability functions (Businger et al. 1971).The ground heat flux was derived from the soil temperature and soil water content profiles using the harmonic method for these two studied sites as per other authors (Guyot et al. 2009; Mamadou et al. 2014; Mamadou 2014). This approach is based on the heat diffusion coefficient estimated from the soil temperature at two depths. The thermal conductivity was computed by using the measured soil water content and the volumetric heat capacity of the soil and water. More details for this method can be found in Guyot et al. (2009).

In drier tropical regions, the water availability appeared primary for the growth or survival of the plants, and better assessing the ecological responses to the global changes (Seghieri et al. 2009; Walther 2010). At the leaf level, the instantaneous water use efficiency (WUE) quantifies the rate of the carbon uptake per unit of the water lost. At the field scale, it appears difficult to measure directly the photosynthesis and transpiration rates for the whole canopy or ecosystem (Baldocchi 1994). Therefore, the estimated WUE was defined in this study as the ratio of the

absolute value of the net carbon uptake *NEE* and the net evapotranspiration *E* as used in other studies by several authors worldwide (Baldocchi et al. 1985; Baldocchi 1994; Verhoef et al. 1996; Moncrieff et al. 1997; Scanlon and Albertson 2004; Boulain et al. 2009; Keenan et al. 2013; Ago et al. 2014, 2015). Especially, the WUE was used here for better understanding and comparison of the water status of the two contrasting ecosystems during the photosynthetic carbon uptake (Williams and Albertson 2004; Yang et al. 2010; Medlyn and De Kauwe 2013). The sensitivity to the dry periods of the water usage was evaluated using a VPD-curve response to the WUE within each of the four defined periods following the non-linear equation, Eq. (7):

$$WUE = WUE_{max}*(1 + w*VPD)^{-1} \qquad (7)$$

Where WUE_{max} is a theoretical maximum WUE [mmol C (mol H₂O)$^{-1}$] occurring when the VPD (kPa) is zero and *w* is an empirical coefficient measuring the sensitivity of the WUE to VPD. Both parameters depend on the characteristics of the vegetation. In this study, the WUE_{max} was fixed to 8 mmol C [mol (H₂O)$^{-1}$] for the two ecosystems in order to determine the coefficient *w* and make a relevant comparison. The seasonal course of *w* was used to compare the WUE responses for the two ecosystems to the environmental conditions changes, notably the drought.

The daytime fluxes gaps were filled using Eqs. (2) and (3) as applied by Ago et al. (2014). *NEE* was partitioned into its two main components, gross primary productivity (GPP) and ecosystem respiration (ER). The Reichstein et al. (2005) approach was used and the total uncertainty was computed as per Ago et al. (2014).

2.4 Different periods considered

The comparison of the two sites was mainly based on the annual vegetation development in response to the climatic and edaphic conditions changing, themselves depending on two main seasons (dry and wet). In this study, we preferred to use four periods as proposed by Franquin (1969) within the inter-tropical regions which were based on the water balance. In addition, most annual herbs appear usually in May, grow during the wet season, and reach their yearly maximum height in October when they are also senescent. In order to take into account this physiological pattern of the annual herbs, we defined the four following periods for making a relevant comparison between two sites:

–   Period I : from December to March (dry period) of 121 days;
–   Period II: from April to May (transition dry to wet period) of 61 days;

–   Period III: from June to September (wet period) of 122 days;
–   Period IV: from October to November (transition wet to dry period) of 61 days.

3 Results

3.1 Micro-meteorological conditions

The mean climatic conditions at the two sites are summarized in Table 1 and Fig. 4. Overall, period I and II were characterized by higher radiation (*Q*), higher air temperature (*T*$_A$), higher vapor pressure deficit (VPD), and lower soil water content (SWC) at 10 cm depth. Compared to period II, the relative lower radiation during period I can be mostly explained by an available radiation in the atmosphere top and peaks are associated with Harmattan events which transport the aerosols to the West Africa region (Nicholson 2013; Mamadou et al. 2014; Quansah et al. 2015). During the drought periods (I and II), the isolated rainy events occurred (first one of April), and ~20 % of the rainy days were observed with more or less 17–18 % of the 2009 annual rainfall (Tables 1 and 4). Period III was marked by the lowest *Q*, lowest *T*$_A$, lowest VPD, and highest SWC (Table 1). Most of the rainfall was usually concentrated during this period (>70 % of the annual amount) with ~66 % of the total rainy days. During period IV, a significant increase was observed in *T*$_A$ and VPD time series which corresponds to the severe decrease of the rainfall and SWC that indicates the installation of the next dry season. The daily SWC average at 10 cm depth remained below 0.03–0.05 m³ m^{-3} until the end of March (Fig. 4c).

Main particularities between the two sites were observed and concerned mostly precipitation and SWC at 10 cm depth. During 2009, a difference of 129 mm was found, forest and savannah sites having received 1624 and 1495 mm, respectively. The rainy days number was 134 for the savannah, but relatively higher than 124 of the forest (Table 4). The seasonal dynamic of the SWC seems similar at the two sites, but the SWC values at 10 cm depth for the forest were always slightly higher than those for the savannah with significant differences during the wet than the dry periods (Fig. 4d; Table 1). This was probably due to the differences between the soil evaporation rates, soil characteristics, deeps infiltration, and importance of the runoffs in relation with the vegetation types at the two sites. These results were in accordance with other findings reported between some sites more and less near each other in West Africa by other authors, especially concerning the rainfall regimes (Ago et al. 2005; Boulain et al. 2009; Seghieri et al. 2009; Merbold et al. 2009; Quansah et al. 2015). It

Table 1 Evolution of the average meteorological variables: air temperature (T_A), photosynthetic photon flux density (Q), vapor pressure deficit (VPD), soil temperature (T_S), soil water content (SWC) at 10 cm depth, leaf index area (LAI), and cumulated rainfall during each period of vegetation growth at two sites

Ecosystems	T_A (°C)		Rainfall (mm)		Q (μmol m⁻² s⁻¹)		VPD (kPa)		T_S (°C)		SWC (m³ m⁻³)		LAI (m² m⁻²)	
	F	S	F	S	F	S	F	S	F	S	F	S	F	S
Period I	27.6±0.3	26.3±0.3	46.8	32.7	411.0±8.2	424.9±9.0	2.7±0.1	2.4±0.1	29.8±0.3	30.0±0.5	0.05±0.00	0.05±0.00	1.1±0.1	0.5±0.0
Period II	27.1±0.3	26.8±0.4	234.4	224.1	462.2±21.6	496.1±22.3	1.3±0.1	1.4±0.1	30.6±0.4	32.2±0.5	0.10±0.01	0.07±0.01	1.9±0.1	0.8±0.1
Period III	24.1±0.2	23.8±0.2	1203.5	1069.3	349.3±13.8	387.4±13.9	0.6±0.0	0.6±0.0	26.9±0.2	27.3±0.2	0.14±0.00	0.11±0.00	2.6±0.1	2.2±0.1
Period IV	25.6±02	24.5±0.2	139.5	169.2	420.8±11.8	446.3±10.4	1.5±0.1	1.3±0.1	27.7±0.2	26.6±0.1	0.09±0.01	0.08±0.01	2.5±0.1	2.0±0.1

The uncertainties are the 95 % confidence intervals

T_A air temperature, T_S soil temperature, VPD vapor pressure deficit, SWC soil water content at 10 cm depth, LAI leaf area index, F forest, S savannah

appears reasonable to consider both meteorological conditions at the two sites as similar overall.

3.2 Diurnal patterns of CO₂ fluxes and driving factors

The diurnal patterns of NEE during the four periods defined for the two sites (not shown) present a clear classical behavior with the CO_2 assimilation dominating during the day conditions and the respiration occurring only during the night. The net CO_2 uptake was constantly higher at the forest than at the savannah sites. During the dry seasons, the net CO_2 uptake was limited for the savannah and reduced for the forest due to the plant species which were present in the footprint and their own densities for each of the two sites (Ago et al. 2014). The forest respiration was always higher than that of the savannah during the year. For the two sites, the net CO_2 assimilation remained more important during the wet compared to the dry seasons, which was supported by the seasonal evolutions of the LAI values (Fig. 4a; Table 1). A dissymmetry was observed in the diurnal courses of NEE not only during the dry season but also during the wet season. This suggests a significant impact of other environmental factors, notably temperature, humidity, or vapor pressure deficit. However, this impact can be limited because of the weakness of the dissymmetry. Finally, the maximum values of the daytime averages of NEE within the four defined periods varied from 20.3 ± 0.8 to 28.2 ± 1.2 μmol m⁻² s⁻¹ for the forest and from 2.6 ± 0.2 to 17.6 ± 0.8 μmol m⁻² s⁻¹ for the savannah.

The response of ER to the temperature was analyzed for the two sites by plotting the nighttime NEE against the soil temperature (T_S) measured at 10 cm depth (Fig. 5). Within the four periods, no clear relationship was observed between the nighttime NEE and T_S. This lack of relationship with the temperature could be due to numerous reasons. Firstly, the ER could be insensitive to the range of the temperature variability at the two sites, especially because the variation of the daily temperature average was low (<10 °C). Secondly, within a given ecosystem, there are several sources of the CO_2 emissions, each of them having its own controlling factors (Davidson et al. 2006a). Thirdly, the seasonality of the dry periods was clearly marked and therefore the ER relationship with the temperature could be masked by the response to the SWC (Curiel Yuste et al. 2007). Moreover, a highly positive significant correlation was found between the nighttime NEE and the soil water content at both sites (Fig. 6): forest ($R^2 = 0.77$, $p < 0.0001$) and savannah ($R^2 = 0.75$, $p < 0.0001$). This suggests that the ER was mainly controlled by the soil water availability at the two sites as reported for similar ecosystems in Africa by other authors (Williams and Albertson 2004; Williams et al. 2009; Ago et al. 2014). In contrast, other studies reported for several dry West African sites (annual sum rainfall < 1000 mm) that the ER was primarily driven by the temperature and additionally by the soil water content (Brümmer et al. 2008; Merbold et al. 2009; Quansah et al. 2015).
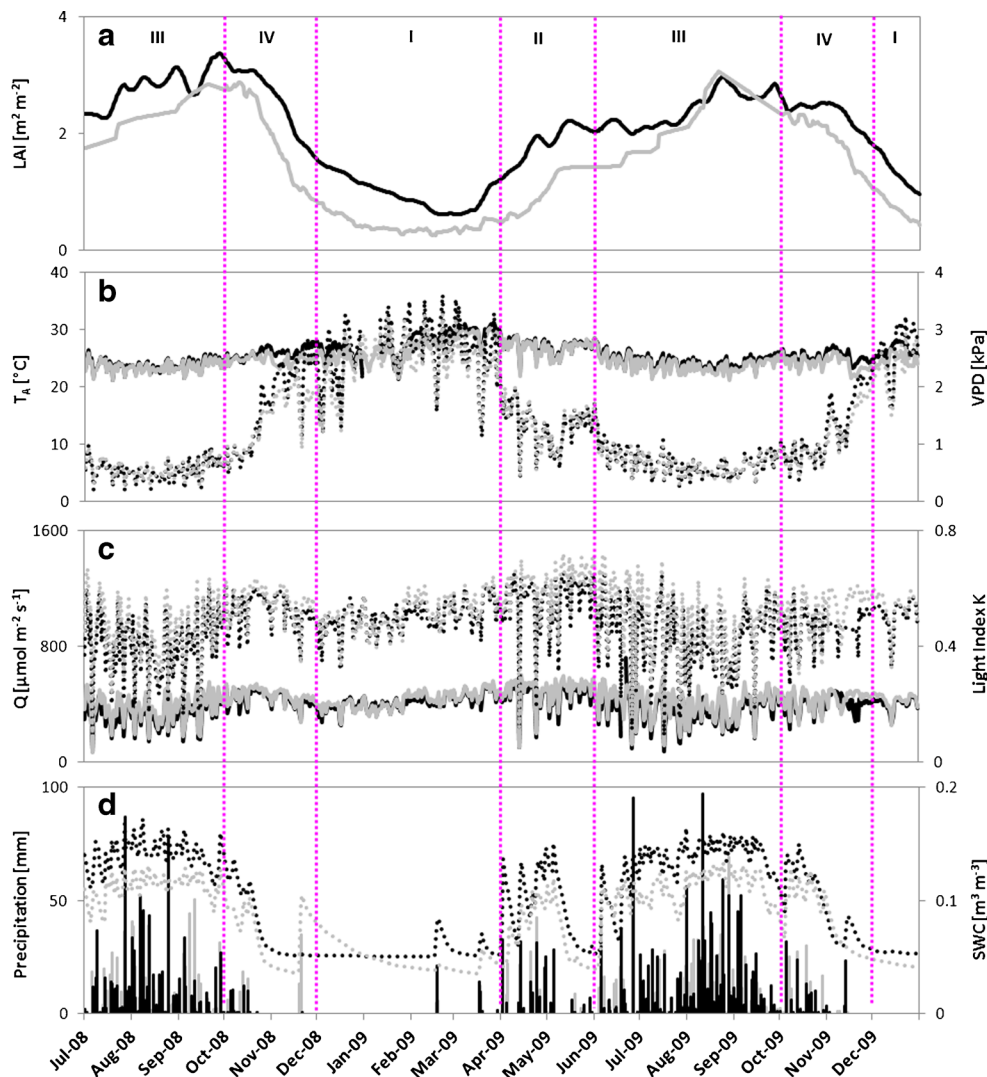
Fig. 4 Seasonal variation of the relevant meteorological variables with the vegetation growth from 1st July 2008 to 31st December 2009 at both sites: daily averages of **a** leaf area index (LAI), **b** vapor pressure deficit (VPD), air temperature (T_A), **c** photosynthetic photon flux density (Q) and light index (K), and **d** precipitation and soil water content (SWC) at 10 cm depth. Forest (*black color*) and savannah (*gray color*). The *vertical pink discontinuous line* indicates the periods I to IV

The peak seasonal average of the nighttime respiration based on Eq. (4) was 5.4 ± 0.1 μmol m^{-2} s^{-1} for the savannah which was lower than 8.2 ± 0.2 μmol m^{-2} s^{-1} for the forest (Table 2) while within each period, the dark respirations which were deduced from Eq. (2) ranged from 1.0 ± 0.4 to 6.8 ± 1.1 μmol m^{-2} s^{-1} for the savannah and from 4.4 ± 1.5 to 8.8 ± 1.5 μmol m^{-2} s^{-1} for the forest. However, during the year, the ER of the forest was always higher than that of the savannah within the four periods (Figs. 8 and 9; Table 3). The comparison of these results and values supports well the robustness of the validity not only of higher ER during the wet than dry periods but also of higher ER magnitude found for the forest. However, the differences between the values were due to the differences in the methods, fluxes, models, and periods used for the different estimations.

### 3.3 Seasonal courses of CO₂ and carbon fluxes in the two sites with their own characteristics

The NEE data corresponding to criterion ($Q > 1000$ μmol m^{-2} s^{-1}) was plotted against g_c within each period in order to better understand the influences of each vegetation type considering the ecosystems/atmosphere exchanges (Fig. 7). Except during the dry period, a slightly curvilinear dependency of the CO₂ assimilation with the canopy conductance was observed for the two sites. Overall, the decrease in NEE (in absolute value) following decreasing g_c was clear, especially during the wet period over the two sites. This suggests a limitation of the leaf CO₂ assimilation at higher canopy conductance. The thresholds can be identified around 15 and 10 mm s^{-1} for the forest and savannah sites, respectively. During the dry periods, g_c did almost never exceed the
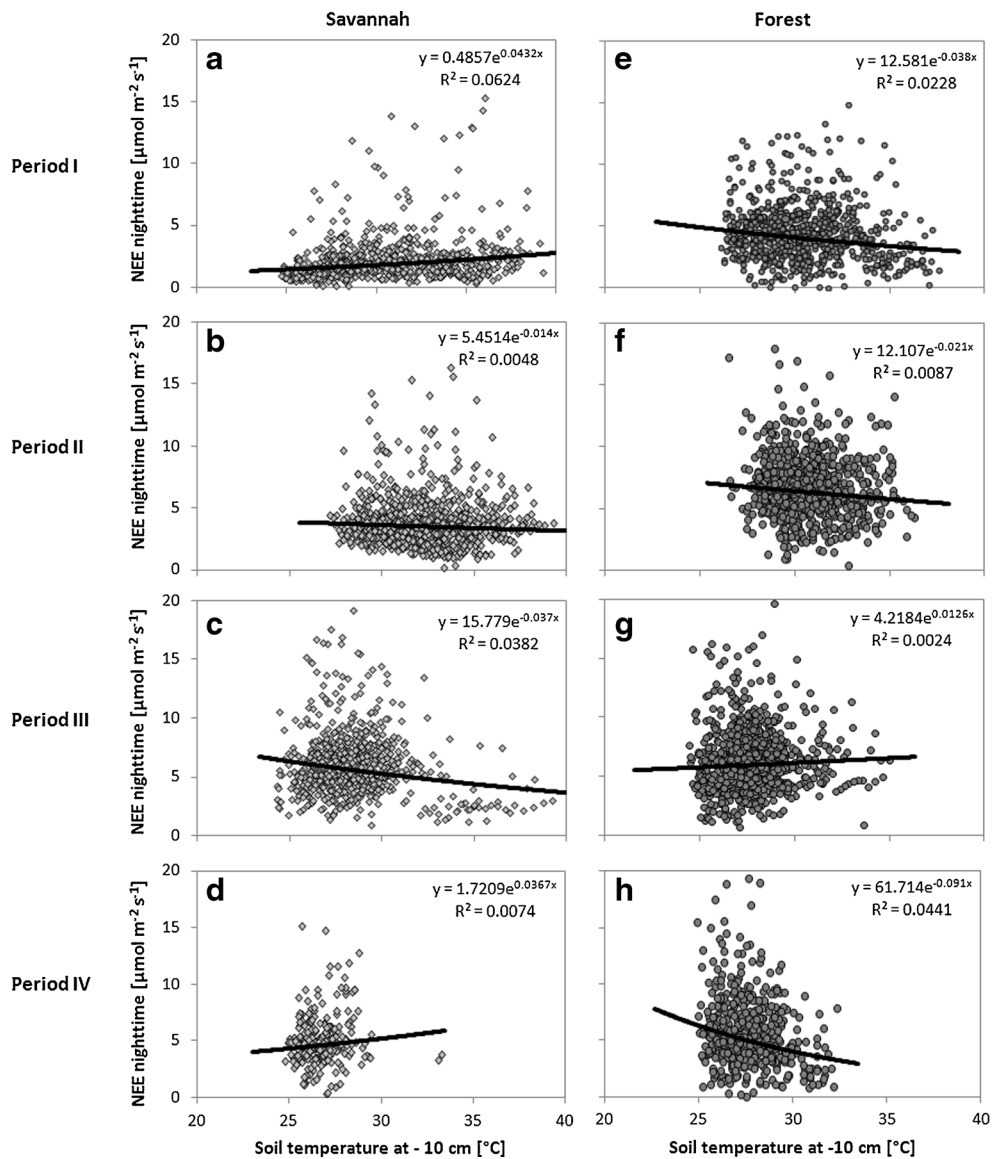
Fig. 5 Relationships between the nighttime NEE and soil temperature at 10 cm depth at both sites during periods I to IV: Savannah (**a–d**) and forest (**e–h**). Data were filtered

threshold and only few net CO_2 assimilation were observed. The clear decrease in the CO_2 uptake following a decrease in the canopy conductance suggests a partial stomatal regulation in the two ecosystems besides the radiation control. Similar

close relationships were also reported for several African ecosystems between the net CO_2 uptake and the canopy conductance both at the spatial (Merbold et al. 2009) and temporal scales (Kutsch et al. 2008).
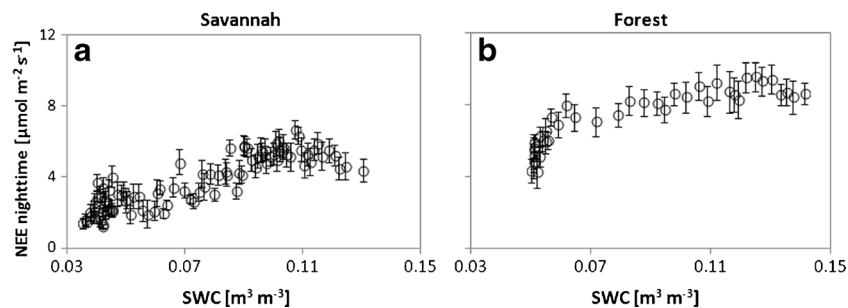
Fig. 6 Relationships between the nighttime NEE and soil water content at 10 cm depth at both sites during the year: savannah (**a**) and forest (**b**). Filtered data were used. Data points are bin averages of 25 measurements. *Error bars* are 95 % confidence intervals

Table 2 Sigmoidal fit results and statistics of the nighttime fluxes versus SWC at 10 cm depth for forest and savannah sites

Parameters	Forest	Savannah
a (μmol m^{-2} s^{-1})	8.2 ± 0.16	5.4 ± 0.14
b (μmol m^{-2} s^{-1})	403.0 ± 26.12	268 ± 20.00
r^2 (%)	39	40
RMSE (μmol m^{-2} s^{-1})	1.55	1.54

The uncertainties are the 95 % confidence intervals

RMSE root mean squared error, r^2 root square (coefficient of determination)

The seasonal evolution of the important parameters characteristics of the two sites during the four periods is summarized in Fig. 8 and reveals likely how vegetation acclimate to the changes in the main environmental conditions. At the seasonal scale, both $A_{\max}$ and α were higher within each period for the forest than savannah, indicating higher radiation-use efficiency for the forest than savannah. This could be due to the differences between the canopy structures: at the savannah, plants (mostly crops and herbs) have narrow and elongated canopies while the forest (mostly trees and shrubs) has a top and open canopy that is able to intercept an important radiation. Also, the photosynthetic capacity of the green leaves can play an important role in the radiation-use efficiency for the forest. Moreover, the two parameters ($A_{\max}$ and α) increased following increasing g_c, then following the growth of the vegetation for the two sites which was confirmed by LAI seasonal courses (Fig. 4a; Table 1). From the wet to dry periods, these two parameters decreased.

Overall, the coefficient w was relatively constant from April to November for the forest, showing a constant sensitivity of its water use to the seasonal VPD variations. For the savannah, the values of w were high within period II, decreased from periods II to III, and then remained relatively constant until period IV. This suggests that for the savannah, the water use was more sensitive to the VPD variations during period II than III, but showed a relatively constant sensitivity from periods III to IV. On the contrary, the water use for the forest showed a relatively constant sensitivity from period II to IV (from April to November). However, the whole seasonal behavior of each of these ecosystems corresponded to an average response of a large number of plant species. Each plant can individually respond differently to the changes in the main environmental conditions such as drought.

The seasonal variations of the carbon fluxes were also analyzed for the two sites (Fig. 9). During periods I and II, the forest sequestered the carbon while the savannah emitted it clearly (Fig. 9c). For the savannah site, this behavior was due to the absence of the vegetation practically in the footprint areas and the vegetation growth beginning with the rains. However, the cumulated fluxes were relatively high at the two sites (Fig. 9a–c) due mainly to this period length that was more significant (121 days). During period III, both sites sequestered the carbon because of the full growth of the vegetation (shrubs, trees, herbs, crops) due to the best seasonal environmental conditions. Typically, the cumulated GPP reached 41 and 56 % of the total annual with the ER of 40 and 44 % for the forest and savannah, respectively, because of the long growth timing of the vegetation (Table 4). However, the GPP and ER were always lower for the savannah than forest both at the daily and seasonal scales with the absolute values of the ER/GPP ratio around 69–71 % (Fig. 9f). Period IV was marked by a weak radiation increase if it was compared to the wet period, and both sites sequestered the carbon considering the daily and cumulated carbon fluxes (GPP, ER) decreasing (Fig. 9; Table 3). These results were due to a significant decrease in the soil water content and green biomass amounts (crop harvest, desiccation, senescence) as shown in the LAI values (Fig. 4; Table 1). The decrease in the daily cumulated ER and GPP appeared more significant for the savannah (20 and 39 %, respectively) than for the forest (only 15 and 17 %, respectively) due to the differences between most species composing both sites concerning their physiologies, phenologies, or canopy structures (Seghieri et al. 2009; Houéto et al. 2013). The absolute value of ER/GPP ratio increased greatly compared to that of 24 % during period III for the savannah while it increased only by 2 % for the forest (Fig. 9f).

Table 3 The daily means of the carbon fluxes (NEE, GPP, ER) during each period for forest and savannah sites

Ecosystems	NEE [g C m^{-2}d^{-1}]		GPP [g C m^{-2}d^{-1}]		ER [g C m^{-2}d^{-1}]	
	Forest	Savannah	Forest	Savannah	Forest	Savannah
Period I	-1.59 ± 0.16	0.80 ± 0.10	-6.01 ± 0.14	-1.82 ± 0.06	4.43 ± 0.69	2.72 ± 0.12
Period II	-1.56 ± 0.32	0.26 ± 0.19	-7.71 ± 0.30	-3.79 ± 0.36	6.15 ± 0.21	3.89 ± 0.26
Period III	-2.76 ± 0.20	-2.18 ± 0.21	-9.52 ± 0.20	-7.60 ± 0.24	6.77 ± 0.55	5.24 ± 0.75
Period IV	-2.19 ± 0.13	-0.47 ± 0.34	-7.94 ± 0.26	-4.62 ± 0.48	5.75 ± 0.19	4.21 ± 0.23

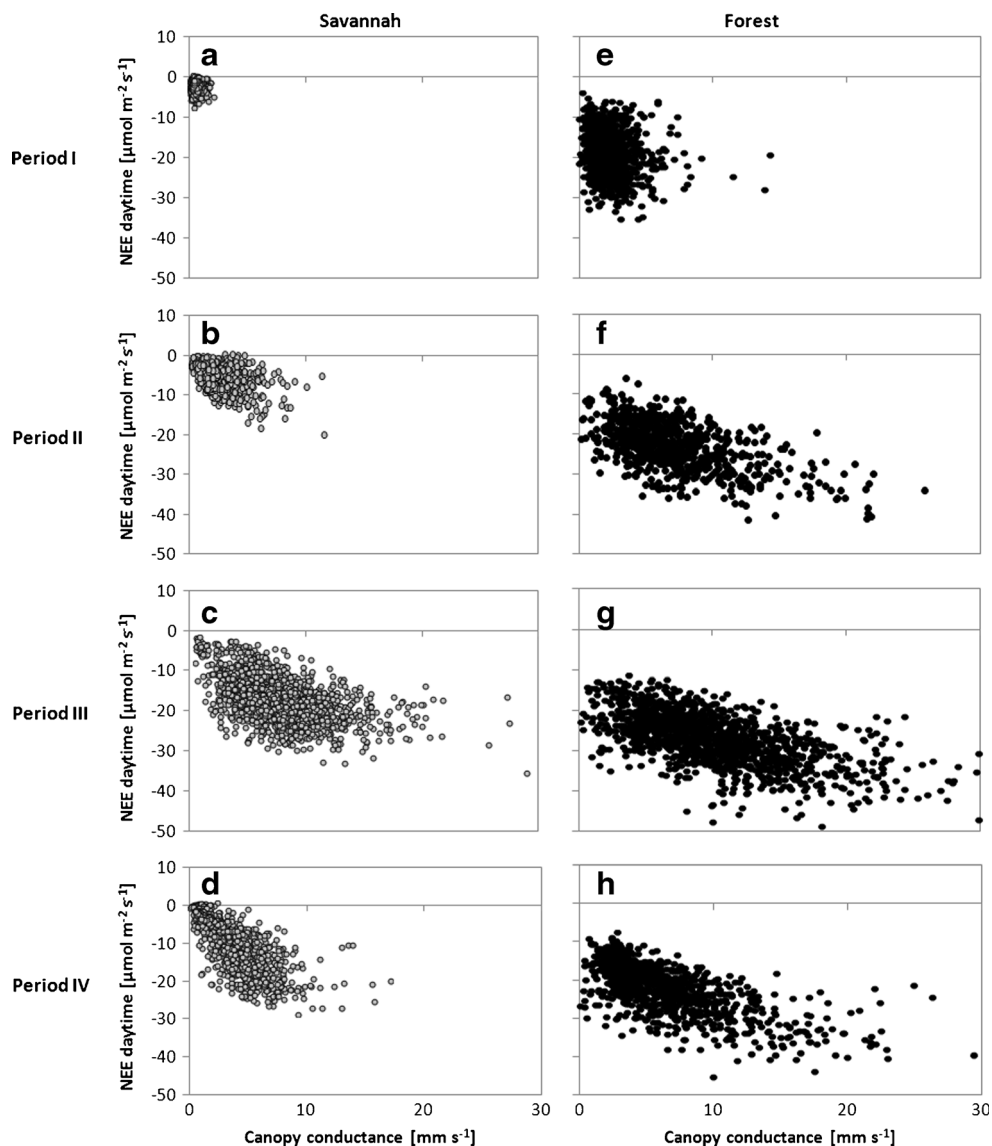The uncertainties are the 95 % confidence intervals

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Fig. 7 Net CO_2 assimilation ($Q > 1000$ μmol m^{-2} s^{-1}) response to the canopy conductance during periods I to IV. Savannah (**a–d**) and forest (**e–h**)

### 3.4 Annual carbon sequestration of the two sites

At the annual scale, the cumulated NEE indicated during the measurement period a clear carbon sequestration with the average values of 190 ± 40 and 640 ± 50 g C m^{-2} for the savannah and forest sites, respectively. In West Africa, similar results were reported for some similar ecosystems using the eddy-covariance measurements (Brümmer et al. 2008; Ago et al. 2014; Tagesson et al. 2015; Quansah et al. 2015). However, other sites were in equilibrium (Hanan et al. 1998; Ago et al. 2015) or carbon emitters (Quansah et al. 2015). The variability of the ecosystem patterns was probably due to several factors as the drought (low annual precipitation), types of vegetation, anthropogenic pressures, or environmental conditions (Ago et al. 2016). On the model basis, Bombelli et al. (2009) found that the "Northern Savanna Belt" region

including the whole West African ecosystem was a net carbon sequester of 248 ± 50 g C m^{-2} at the annual scale.

4 Discussion

4.1 Larger ecosystem respiration (ER) for the forest than savannah

The average of the CO_2 nighttime fluxes reported for the tropical forests and woodlands ranged from 3 to 8.5 μmol m^{-2} s^{-1}, with little seasonal variability (Vourlitis et al. 2001; Loescher et al. 2003; Merbold et al. 2009; Longdoz et al. 2010; Ago et al. 2015). It varied between 1 and 6 μmol m^{-2} s^{-1} for the savannah sites in West Africa (Brümmer et al. 2008; Merbold et al. 2009; Ago et al. 2014; Tagesson et al. 2015; Quansah
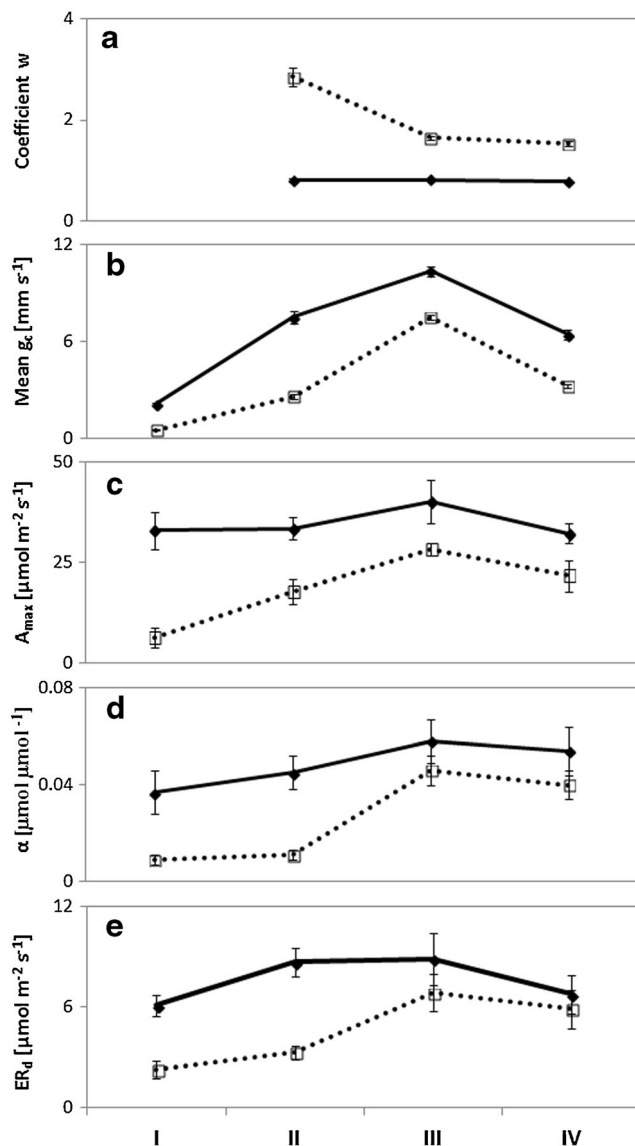
Fig. 8 Seasonal courses of the parameters characterizing both ecosystems during the four periods: **a** the coefficient *w* describing the WUE sensitivity to VPD; **b** the average canopy conductance (g_c); **c** NEE at the light saturation, A_{max}; **d** the quantum efficiency, α; and **e** the dark respiration, ER_d. Savannah (*dark discontinuous line*) and forest (*dark continuous line*). The lack of data during period I was due to the selection criterion of NEE and E in the WUE calculation. *Error bars* are 95 % confidence intervals and very low for g_c and *w*

et al. 2015). Unsurprisingly, a large increase of the ER was observed for the two sites from the dry to wet periods (Figs. 8 and 9; Table 3) with the highest values of the ER occurring during the wet periods due mainly to the full vegetation growth and the best environmental conditions. These ER values and magnitudes were consistent with those reported for the forest and savannah by other authors in the tropical regions, and were mainly explained by the significant seasonal variabilities of the autotrophic and heterotrophic respirations. During the dry periods, a decrease of ER_d to 4.4 ±1.5 μmol m^{-2} s^{-1} was observed for the forest, which was

closer to ER_d values reported for the savannah during the wet periods (Fig. 8e). Between 2001 and 2002, Mulindabigwi (2005) used the soil chambers EGM-2 to measure the soil respirations in similar ecosystems located in Djougou district and near our two studied sites. These authors found the averages of the soil respiration ranging from 5.1 to 12.2 for the semi-deciduous forest, 3.2 to 7.8 for the woodland, and 2.5 to 7.7 μmol m^{-2} s^{-1} for the fallow. Of course, these soil respiration values cannot be directly compared to those of the ER obtained using an eddy-covariance system for similar sites because the latter includes the aerial vegetation respiration. However, as the soil respiration is generally the major component of ER (Aubinet et al. 2001; Davidson et al. 2006b), it appears relevant that a high soil respiration leads also to a high ER measured by an eddy-covariance technique and therefore a higher ER_d found for the two investigated sites, especially during the wet season (Figs. 8e and 9b–e).

The ER, which includes the heterotrophic (HR) and autotrophic respirations (AR), is generally known to depend strongly on the temperature, soil water status, vegetation dynamics, and land-use regime (Hanan et al. 1998; Curiel Yuste et al. 2007; Archibald et al. 2009; Williams et al. 2009; Merbold et al. 2009; Ago et al. 2014, 2015). For both sites, the ER was found mainly controlled by the soil water content with similar seasonal dynamics and differences in their values between the periods (Figs. 8e and 9b–e; Table 3). This dependency was likely due to the enhancement of two ER components, i.e., AR and HR, by a high soil water availability from dry to wet seasons as reported for other West African sites (Hanan et al. 1998; Brümmer et al. 2008; Ago et al. 2014, 2015; Quansah et al. 2015), though an increase in the green vegetation density, litter and organic matter amounts, and microorganism activities is also strongly influenced by rainfall regimes. Indeed, the soil moistening induces an activation of HR by an increase of the dissolved organic carbon or by a stimulation of the microorganism activities (Williams et al. 2009). In the two sites' region, the litter amount was usually its seasonal maximum level at the end of the dry season (Mulindabigwi 2005). Also, the rain leads to an increase of the AR by a great growth of the vegetation during the wet season as reported elsewhere in Africa (Hanan et al. 1998; Archibald et al. 2009). At the daily scale, for the two sites, a highly significant correlation was found between the ER and the net CO₂ assimilation ($p < 0.0001$, $R^2 = 0.38$ and $R^2 = 0.56$ for the forest and savannah, respectively). This suggests an important influence of the seasonal ER variability by that of the AR and therefore by the vegetation development for the forest than savannah. Larger ER values observed at the daily and seasonal scales for the forest compared to savannah (Figs. 8e and 9b–e) could be due to the relative great contribution of the AR to ER for the forest than savannah. The differences in the ER between the two sites were significant
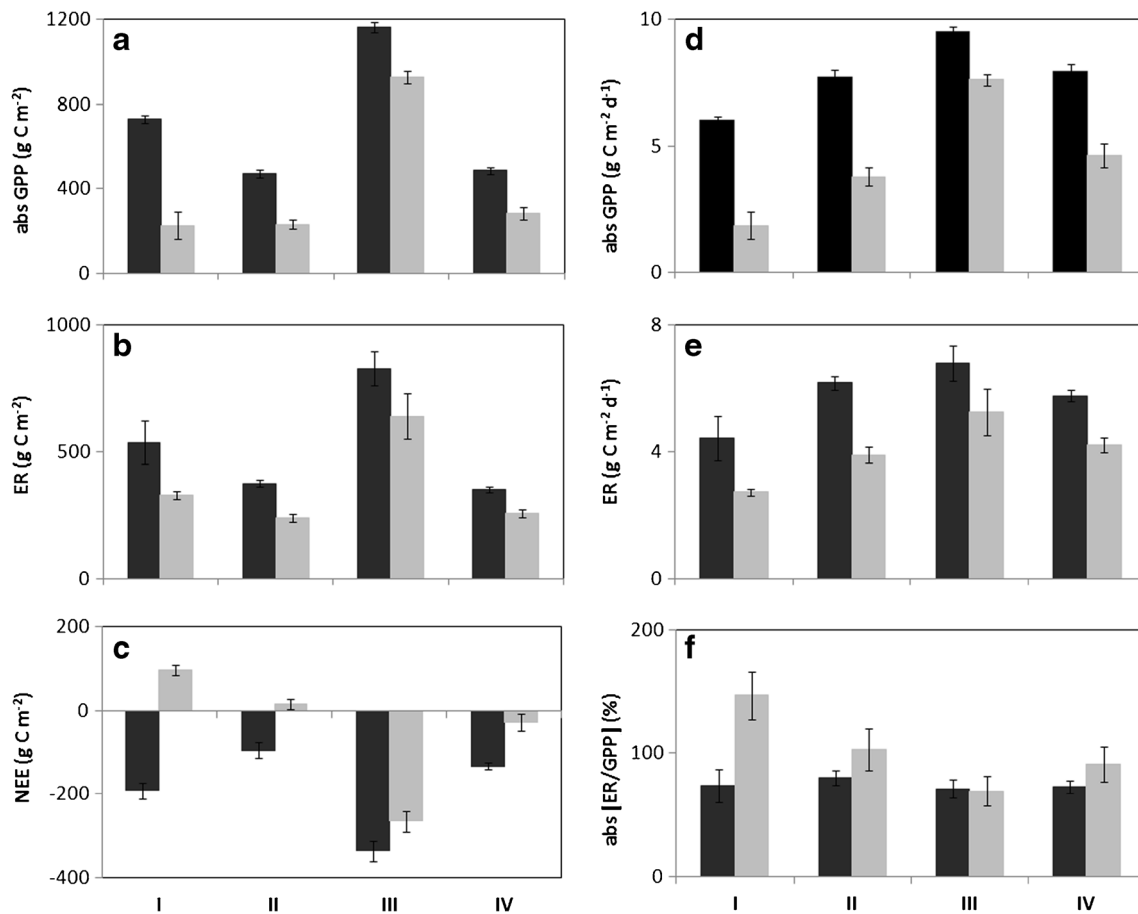
Fig. 9 Seasonal evolution of the carbon fluxes for both sites during the four periods. Forest (*dark color*) and savannah (*gray color*): **a** the absolute value (abs) of the cumulated GPP, **b** the cumulated ER, **c** the cumulated NEE, **d** the absolute value (abs) of the daily GPP, **e** the daily ER, and **f** the absolute value (abs) of the daily ER/GPP ratio. *Error bars* are 95 % confidence intervals

during the dry periods rather than during the wet one. Moreover, the AR that depends mainly on the growth vegetation (Chambers et al. 2004) may be significantly affected by the drier conditions. Indeed, during dry periods (lack of rain, soil, and air drought conditions), the vegetation growth was reduced due mainly to the senescence and desiccation processes leading to the reduced density of the active leaves, but in different proportions according to the ecosystem types (savannah or forest). In particular, the wind was mainly from the northeast and no herbaceous cover is present between the sparse trees or shrubs at the savannah site. Thereby, for a given ecosystem when the vegetation growth is limited, the AR may be also expected to be limited and leads, therefore, to a significant reduction of the ER. This was probably the case for the savannah site during the dry periods with the ER value remarkably lower than that of the forest, the HR resulting mainly from the dissolved organic carbon or stimulation of the microorganism activities of the soil, surface litter amount, and soil organic matter pool (Vourlitis et al. 2001; Davidson et al. 2006a; Williams et al. 2009).

Table 4 Day numbers during each period of rains and vegetation growth

Ecosystems	Total length (days)	Rainy length (days)		Rainy/total rainy length (%)	
	–	Forest	Savannah	Forest	Savannah
Period I	121	5	5	4	4
Period II	61	20	19	16	14
Period III	122	80	88	65	66
Period IV	61	19	22	15	16
Total	365	124	134	100	100

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4.2 Differences in NEE and GPP values between the two sites: a combination of phenological and physiological factors

As ER, the seasonal dynamics of the GPP differed between the four periods at the two sites, but with similar seasonal evolutions (Fig. 9). This GPP dynamic was phased with the annual growth of the vegetation in Sudanian and Sahelian regions (Seghieri et al. 2009; Guyot et al. 2012; Mamadou 2014; Ago et al. 2014, 2015). The similar seasonal trend in GPP for the two sites was likely related to similar meteorological conditions rather than other factors at the whole Djougou district. However, the GPP was always higher within each period for the forest than savannah and needs to be discussed considering the floristic compositions, root systems, canopy structures or green leaf densities, photosynthetic capacities, and edaphic conditions. During the wet periods, the savannah was mainly composed by the herbs and crops (mostly C4) with a few trees (mostly C3) while the forest was mainly formed by the trees (mostly C3) with few herbs (mostly C4) for the underlying strata. During the dry seasons, similar plant species (essentially shrubs and trees), soil water content, and climatic conditions were observed at the two sites, but a significant difference in their densities was found and confirmed by the LAI evolution (Fig. 4). The forest showed a less clear behavior in the seasonal variations of A_{max} and α compared to the savannah (Fig. 8c, d). This suggests that the CO$_2$ assimilation at saturation and quantum efficiency were less sensitive to the dry season for forest compared to savannah. This higher radiation conversion by the forest than the savannah could be favored by a higher physiological performance of the trees/shrubs and their canopy structures that were generally more efficient in terms of the radiation interception as reported by several authors for similar African sites (Williams and Albertson 2004; Merbold et al. 2009; Longdoz et al. 2010; Fisher et al. 2013; Sjöström et al. 2013). Indeed, the trees are generally able to use the water from the deep soil during the dry periods through their root system to satisfy the atmospheric demand and maintain their photosynthesis activities. Canadell et al. (1996) found that the maximum rooting depth of the trees in the tropical regions ranged from 3.7 ± 0.5 to 15.0 ± 5.4 m. In particular, the deep roots system of the main tree species in the Sudanian region is generally located in the first layers of the soil, up to 2 m depth or more (Bationo et al. 2001, 2005; Dourma et al. 2006). As a result, the deep roots of the shrubs and trees in the Sudanian region are also able to use the water from the deep layers during the drought periods for the satisfying of the atmospheric demand and the photosynthesis. Therefore, the main differences in the patterns of the CO$_2$ assimilation during the dry seasons between our two sites could be better explained by the differences between the vegetation types (species, green biomass amounts, canopy structures) as observed in Africa (Williams and Albertson 2005). Jenerette et al. (2009) found over 3 years

at San Pedro River in Southern Arizona, USA that the GPP values were consistently higher and less variable for the woodland than for grassland with some distinct rates and variability during the growing seasons.

During the year, while the absolute ER/GPP ratio was relatively constant (71–80 %) for the forest, it was highly variable (69–157 %) for the savannah (Fig. 9f). This clearly showed that the forest was more stable within and among the four periods than savannah. The absolute ER/GPP ratio was lesser than 100 % for the forest as the GPP dominated always ER at the daily and seasonal scales (Fig. 9d–f; Table 3). Houéto et al. (2013) concluded the stability for this forest using the data of the dendrometric measurements. For the savannah, the daily GPP was lower than ER during the dry periods and at the beginning of rains, confirming that the first precipitations were not sufficient to induce continuously the leaf initiation and thus increase the GPP. However, the GPP becomes higher than ER from June to October when the soil water availability reaches a sufficient level, suggesting continuous growth of the vegetation inducing an absolute ER/GPP ratio lower than 100 % (Fig. 9d–f; Table 3).

4.3 Sensitivity to water usage

During the day, a VPD-curve response to the WUE was observed within each period. WUE was high during the morning due to both the low radiation and low VPD. From morning to afternoon, the WUE decreases continuously (not shown), while VPD increases and reaches its maximal value around 15:00 before decreasing until sunset (Verhoef et al. 1996; Moncrieff et al. 1997; Williams and Albertson 2004). This daily course suggests an influence of the VPD on the WUE, notably a partial stomatal closure impact besides the control by the radiation (Yang et al. 2010). In Africa, similar daytime WUE courses were found for similar Sudano-Sahelian sites (Verhoef et al. 1996; Moncrieff et al. 1997; Friborg et al. 1997; Boulain et al. 2009; Ago et al. 2014, 2015). The two ecosystems were more efficient during morning and wet period than during afternoon and dry period. The daytime WUE values were in the same order to those reported for similar sites in West Africa varying from 0.04 ± 0.09 to 8.25 ± 1.94 mmol C (mol H$_2$O)$^{-1}$ (Verhoef et al. 1996; Moncrieff et al. 1997; Friborg et al. 1997; Boulain et al. 2009; Ago et al. 2014, 2015).

At the seasonal scale, the WUE was also influenced by the drought conditions, but the sensitivity to the water usage did not vary for the forest. In contrast, the sensitivity for the savannah decreased about 46 % from April–May to June and then remained constant until October–November. The difference observed between the two ecosystems' sensitivity was mainly due to the vegetation types and the acclimation of the plant growth within each period with the main environmental condition changes. Overall, the forest sensitivity of the water usage was always lower than that for the savannah.

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5 Conclusion

The main objective of this study was to highlight the patterns of the carbon fluxes, the driving variables, especially the responses of carbon fluxes to water in the two contrasting sites in northern Benin (West Africa). The data revealed the strong influences of water on CO_2 fluxes in the two contrasting ecosystems investigated. To our knowledge, this study remains the first comparison between savannah and forest ecosystems in the Sudano-Sahelian region using a long-term eddy-covariance dataset.

In particular, it showed that the carbon fluxes were subjected to a large seasonal variability in the two ecosystems, depending on the variability of the environmental factors, especially between the dry and wet seasons. While the meteorological conditions were similar in this region, the flux values were consistently lower (in absolute value) for the savannah than for the forest. This was due to the differences in physiological and phenological characteristics of plant species at the two sites. However, a larger ecosystem respiration was observed during the wet periods, expressing not only a significant litter amount but also greater intensity of the microorganism's activity. At daily and seasonal scales, the relationships were close between the CO_2 uptake and canopy conductance.

The forest showed a relatively constant sensitivity towards water usage from April to November. On the contrary, the savannah sensitivity was highly variable between dry and wet periods. However, the forest was always less sensitive than the savannah within a given period.

The forest sequestered the carbon during the four periods, while the savannah sequestered only during the wet and transitional wet to dry periods. Finally, the forest was more stable during the year, while the savannah was clearly variable following the periods. At the annual scale, the forest sequestered 640 ± 50 g C m^{-2} and the savannah 190 ± 40 g C m^{-2}.

Compliance with ethical standards

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