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Precipitation as driver of carbon fluxes in 11 African ecosystems

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Abstract

This study reports carbon and water fluxes between the land surface and atmosphere in eleven different ecosystems types in Sub-Saharan Africa, as measured using eddy covariance (EC) technology in the first two years of the CarboAfrica network operation.

5 The ecosystems for which data were available ranged in mean annual rainfall from 320 mm (Sudan) to 1150 mm (The Republic of Congo) and include a spectrum of vegetation types (or land cover) (open savannas, woodlands, croplands and grasslands). Given the shortness of the record, the EC data were analysed across the network rather than longitudinally at sites, in order to understand the driving factors for ecosystem respiration and carbon assimilation, and to reveal the different water use strategies in these highly seasonal environments.

10 Values for maximum net carbon assimilation rates (photosynthesis) ranged from $12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in a dry, open Acacia savanna (C_3 -plants) up to $40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for a tropical moist grassland. Maximum carbon assimilation rates were highly correlated with mean annual rainfall ($R^2=0.89$). Maximum photosynthetic uptake rates were positively related to satellite-derived f_{APAR} . Ecosystem respiration was dependent on temperature at all sites, and was additionally dependent on soil water content at sites receiving less than 1000 mm of rain per year. All included ecosystems, except the Congolese grassland, showed a strong decrease in 30-min
20 assimilation rates with increasing water vapour pressure deficit above 2.0 kPa.

1 Introduction

Information about Africa's role in the global carbon cycle is sparse. It remains unknown whether Africa, as a whole, represents a net sink or source of atmospheric carbon, and how carbon exchange varies temporally and spatially at the continental scale (Williams
25 et al., 2007). Africa supports a large variety of terrestrial ecosystem types, reflecting differences in climate, geology, and species composition, as well as land use and land

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use change taking place all over the continent.

Three important approaches have been applied recently to understand the variations of structure and function of African ecosystems in space and time as well as their drivers. The first focused on the biocomplexity of savannas (Sankaran et al., 2005,
5 2008; Bucini and Hanan, 2007) and followed a long tradition of ground-based ecophysiological research trying to understand the role of water, nutrients, herbivory and fire in savanna dynamics, and in particular on tree-grass interactions (Walter, 1939, 1971; Scholes and Walker, 1993; Scholes and Archer, 1997; Jeltsch et al., 2000; Scholes et al., 2004; Bond and Keeley, 2005; Bond et al., 2005).

10 The second approach has used remote sensing to reveal large-scale environmental control of vegetation patterns. The “eye in the sky” provides indices that can be used to extrapolate in time and space process-oriented knowledge derived by the studies using the first. For example, Archibald and Scholes (2007) demonstrated that it is possible to use a knowledge of the different life history strategies of trees and grasses to “unmix”
15 their phenologies in low resolution satellite imagery, which is an important step forward towards modelling of carbon and water fluxes at a regional scale.

The third approach, recently summarized by Lloyd et al. (2008), is to develop continental-scale mass balances, constrained by isotope measurements. Williams et al. (2007) reviewed what these studies reveal about Africa. This approach is of
20 particular importance for the partitioning between ocean-atmosphere exchanges and land-atmosphere exchanges in global carbon cycle studies, because the relatively low natural photosynthetic discrimination (Δ) of C_4 grasses is similar to that accompanying air-to-sea CO_2 exchange (Lloyd and Farquhar, 1994).

25 These approaches suggest that the most important pattern driving structure and function of African ecosystems is rainfall (Williams et al., 2007), but a number of additional processes, like fire, herbivory and soil fertility, need also to be taken into consideration.

We suggest that analysis of variation in ecosystem-atmosphere exchange of carbon dioxide and water, at the hours-to-years timescale, as measured by eddy covari-

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ance, can be a fourth approach to understanding the structure and function of African ecosystems and unravelling the role of Africa in the global carbon cycle. To date, such information has been scarce. A limited number of eddy covariance-based analyses of seasonal variation of ecosystem-atmosphere carbon exchange have been published over the last few years, describing single ecosystem types such as Mopane woodlands (*Colophospermum mopane*), broad-leaved deciduous Combretum-dominated savannas, fine-leaved Acacia-dominated savannas, as well as plantations of clonal Eucalypt in tropical Africa (Goutorbe et al., 1997; Nouvellon et al., 2000; Epron et al., 2004, 2006; Veenendaal et al., 2004; Arneth et al., 2006; Archibald et al., 2008, this issue; Bruemmer et al., 2008; Kutsch et al., 2008, this issue). Some studies that seek to provide a broader integration over latitude or along rainfall gradients have been based on short-term campaign measurements (Dolman et al., 1997, 2003; Scanlon and Albertson, 2004; Scholes et al., 2004; Shugart et al., 2004; Schuttemeyer et al., 2006). However, brief field campaigns always lack information on seasonality, which is essential for understanding such highly seasonal environments.

Here we compare the observed seasonality across a range of vegetation types and climate zones. We focus specifically on the flux response to variations in moisture inputs, in terms of annual precipitation and as caused by changes from wet to dry season and vice versa. We specifically seek to test whether precipitation and soil moisture are not only a principle determinant of the distribution of vegetation types in Africa, but also the overriding environmental controls on the seasonal variation in Net Ecosystem Exchange of carbon (NEE). Furthermore, we investigate whether NEE-soil moisture relationships known from observations in drought-stressed temperate (Mediterranean) or boreal ecosystem that contain only C_3 species are also found in tropical ecosystems with their variable mix of C_3 and C_4 photosynthetic systems, and rainfall rather than temperature-controlled seasonality.

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1.1 Material and methods

1.1.1 Study sites

Eddy covariance data for at least a full year were available for eleven sites, distributed over Sub-Saharan Africa. These sites are either part of or associated with the CarboAfrica network (a newly-established part of the global Fluxnet community, with strong affiliations to the CarboEurope network). Associated sites have been parts of other internationally or nationally funded projects that are listed in the Acknowledgements.

The Sub-Saharan region is that part of Africa south of the Sahara desert, including the grasslands, shrublands and savannas of western and eastern and southern Africa, and the forests and woodlands of central Africa (Hudman and Jackson, 2002), as well as a range of derived land uses such as croplands and tree plantations. The study covers ecosystems from the very dry Sahel (Sudan, Mali and Niger), to the semi-arid and sub-humid regions in Southern Africa (Botswana, Zambia and South Africa) (Scholes et al., 2004), to humid environments towards the equator (The Republic of Congo, see Fig. 1 and Table 1 for details). The study areas differ in ecosystem type, seasonality and mean annual rainfall. The most extensive ecosystem types in Sub-Saharan Africa, as Mopane woodlands (*Colosphermum mopane*), Miombo woodlands (*Brachystegia spiciformis*), fine-leaved Acacia savanna (e.g. *Acacia senegal*, *Acacia nigrescens*), broad-leaved Combretum savanna (*Combretum apiculatum*) and a typical grassland in the Republic of Congo (*Loudetia* sp., *Ctenium newtonii*), as well as a eucalyptus plantation (*Eucalyptus* sp. clone) are represented in this study.

1.2 Technical setup and data post-processing

All sites were equipped with eddy covariance equipment (Aubinet et al., 2000; Baldocchi et al., 2000, 2001a) (Table 2). Roughly, each system included a 3-D sonic anemometer (Solent R3, Gill Instruments, Lymington, UK; Csat sonic anemometer, Campbell Scientific, Logan, UT, USA; Young 81000V, R. M. Young Company, MI, USA)

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and an infrared gas analyser (LI-6262/7000/7500, LiCor Inc., Lincoln, NE, USA). Eight sites used an open path system and three used a closed path system. Disadvantages of the open path system (Webb et al., 1980; Webb, 1982; Leuning and Moncrieff, 1990; Leuning, 2007; Serrano-Ortiz et al., 2008) were balanced by its low power consumption, a great advantage in remote regions. At all sites the EC system was complemented with meteorological sensors (air temperature, humidity, radiation, rainfall, soil water content etc.). Tower height ranged from 3.8 m (grassland in the Republic of Congo) up to 30 m (woodland in Zambia). A total equivalent to 22 years of EC data was used for this synthesis. The data were all collected between the years 1999 and 2008. Some years only contained a few weeks of usable data. Nevertheless, each site was represented by data from the dry as well as the wet season (Nouvellon et al., 2000; Veenendaal et al., 2004; Epron et al., 2006).

Half hour flux averages were calculated using various software packages (EddyRe, Eddysoft, Ecoflux and Eddy_PPC). Even though standardized quality criteria (Papale et al., 2006; Kolle and Rebmann, 2007) were applied by each site coordinator, data sets were again screened and filtered for missing and uncertain values. In addition, u^* -filtering was applied at nighttime (Goulden et al., 1996; Zamolodchikov et al., 2003; Papale et al., 2006). Data were also filtered for an upper u^* threshold (Fig. 2) to avoid overestimation of the measured fluxes (Zamolodchikov et al., 2003; Merbold et al., in review). All thresholds are given in Table 2.

1.3 Flux partitioning and ecosystem-physiological parameters

Soil water content and temperature are important variables controlling ecosystem respiration (Anthoni et al., 2004; Reichstein et al., 2005; Trumbore, 2006). To analyse the response of ecosystem respiration (ER) to these factors, daily averaged night time fluxes were used to represent ER. For all sites, except the two Congolese sites, data were normalized to a reference temperature of 20°C using a fixed Q_{10} of 2 (Eq. 1), and

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thereafter analysed for soil moisture influences (Eq. 2):

$$ER_{20} = Q_{10} ER^{(\frac{20-T}{10})} \quad (1)$$

where ER_{20} is the normalized respiration at 20°C, ER is the measured ecosystem respiration in $\mu\text{mol m}^{-2} \text{s}^{-1}$, T the soil temperature in °C (depth 5 cm) at the given time.

$$ER_{20} = aSWC + b \quad (2)$$

where SWC represents soil water content in % at a depth of 0.05 to 0.5 m (depending on which depth gave the best correlation), a the slope of the regression and b the intercept. Data from the two Congolese sites, receiving more than 1000 mm of annual rainfall, were statistically analysed for temperature using an exponential growth function (Eq. 3):

$$ER = me^{(T-d \cdot T_a)} \quad (3)$$

where T_a is the air temperature in °C, m and d are coefficients and shown in Table 3.

Daytime ecosystem respiration was calculated by Eqs. (1), (2) and (3). Gross primary production (GPP) was calculated by subtracting calculated respiration from measured values of net ecosystem exchange (NEE, Eq. 4):

$$NEE = GPP^* + ER \quad (4)$$

Gross primary production was then fitted to a hyperbolic response function of measured global (ie direct plus diffuse) radiation (5) using quantile regression (Cade et al., 2005; Kutsch et al., 2008, this issue) to derive an envelope for each site. The envelope function was defined to include 95% of the observations:

$$GPP = \left[Fp_{\max} * \tanh \left(e^{\frac{R_g}{Fp_{\max}}} \right) \right] * (-1) \quad (5)$$

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where R_g represents global radiation (W m^{-2}), $Fp_{\max}$ the maximum photosynthetic capacity, and e is a coefficient controlling the slope of the function. These ecosystem-scale light response curves were derived using all available daytime data, without distinguishing between dry and wet season.

- 5 Canopy conductance for water vapour exchange with the atmosphere was calculated as proposed by Herbst et al. (2002) and Jensen and Hummelshoj (1995). For a more detailed description of the method, see Kutsch et al. (2008, this issue).

1.4 Supplemental data

- 10 In order to make the measured data available for higher integration some key values were expressed relative to the fraction of absorbed photosynthetic radiation (f_{APAR}), a satellite-derived product calculated by the Joint Research Centre (<http://fapar.jrc.it/>). We used averaged peak growing season 10 day averages at 1 pixel ($1 \text{ km} \times 1 \text{ km}$) resolution for each site.

2 Results

- 15 2.1 Basic data comparison

- Like most parts of Sub-Saharan Africa, the ecosystems under consideration are characterised by a strong seasonality in moisture inputs. For the eleven sites studied, the dry season ranged from 5 months (The Republic of Congo) up to 7 months in Sudan. The Congo sites usually experience two wet seasons and two dry seasons per year, caused by the movement of the Inter-tropical Convergence Zone (ITC).

- 20 All study sites have similar long-term annual temperatures, ranging from $22\text{--}29^\circ\text{C}$. In many other respects the sites differ greatly, for instance in soil, vegetation type and land use (Table 1).

- 25 The main flux results from the sites are compiled in Figs. 3–7. Figure 3 shows the moisture response of ecosystem respiration for all sites with annual rainfall lower

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than 1000 mm and the temperature response for sites with annual rainfall higher than 1000 mm. Light (Fig. 4), water vapour pressure deficit of the air (VPD, Fig. 5) and temperature (Fig. 6) responses of canopy photosynthesis (Fp) are shown in the following figures. VPD response of canopy conductance for water vapour (Fig. 7) is shown next.

- 5 Temperature has an influence on ecosystem respiration (ER) at all sites. However, for the drought-prone sites (receiving less than 1000 mm of annual precipitation), the main driving factor for ER was soil water content. Therefore all values were normalized to 20°C (R_{20}), using soil temperature at a depth of 5 cm. Coefficients for the linear soil moisture response of R_{20} are shown in Table 3. Only the sites in the Republic of Congo were primarily driven by temperature (Fig. 3j and k), while soil water content did not show a convincing correlation for these sites. The lowest respiration rate was observed at Agoufou, Mali with an overall daily average value of $1.35 \mu\text{mol m}^{-2} \text{ s}^{-1}$. In contrast, the highest efflux rates were observed in Tchizalamou, the Republic of Congo, with an overall average of $3.19 \mu\text{mol m}^{-2} \text{ s}^{-1}$, while peaks in respiration of 10 to $20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ are not unusual, in particular after rain events.

- 15 The maximum canopy-scale photosynthetic rates ($Fp_{\max}$) of the various ecosystems ranged from $-12 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in the Niger (Wankama Millet) to $-40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at Tchizalamou, the Republic of Congo (Fig. 4). Fp was found to decrease with increasing vapour pressure deficit (VPD) at all sites experiencing values of VPD higher than 2.0 kPa (Fig. 5). In addition, some ecosystems showed a strong relationship between canopy photosynthesis and temperature, under light saturation and VPD <20 mbar (Fig. 6).

At sites within a notable range of VPD over the year, canopy conductance decreased with increasing values of VPD (>2.0 kPa) (Fig. 7).

- 25 2.2 Integration of key values and comparison to remote sensing data

Key variables such as $Fp_{\max}$ and $Gs_{\max}$ (here defined as conductance at $Fp_{\max}$) were calculated analysed in relation to mean annual rainfall in the next step. The following patterns were observed:

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- Within the range of the study (300–1200 mm) we found strong correlation between mean annual rainfall and maximum photosynthetic uptake ($Fp_{\max}$) that could be best described by an exponential growth function ($r^2=0.89$, Fig. 8a). Note, that the Kelma site (Mali), experiencing additional water inputs from the surrounding areas, was not included.
 - Maximum photosynthetic uptake is strongly related to $Gs_{\max}$ (Fig. 8b). The high standard deviation in this graph results from the way we analysed the data: for all values of $Fp_{\max}$ out of each dataset that were higher than 90% of the $Fp_{\max}$ calculated by quantile regression (see Fig. 4), $Fp_{\max}$ and canopy conductance were averaged. These data may contain measurements just after rainfall with high interception and soil evaporation as well as data just at the beginning of a dry period when water vapour is predominantly transported through the stomata. We used this procedure, since it is impossible to define the exact situation for deriving $Gs_{\max}$ according to Schulze et al. (1994).
- In the next step the key values of the different sites were compared to f_{APAR} data from satellite observations. For this comparison, we distinguished between purely or almost purely grass-dominated lands on one hand and mixed or tree-dominated (further only called “tree dominated”) ecosystems on the other. The following correlations were found:
- f_{APAR} increased with mean annual rainfall for both groups of ecosystems (Fig. 8c): However, the envelope curves we found for the two groups of ecosystems differed: the curve for tree-dominated ecosystems had a steeper increase at low rainfall and leveled off around 800 mm, whilst the curve for the grass-dominated lands increased more smoothly but did not level off within the observed rainfall gradient.
 - $Fp_{\max}$ and f_{APAR} correlated linearly without leveling off within the observed range of rainfall (Fig. 8d). $Fp_{\max}$ increase was steeper for grass-dominated ecosystems than for tree-dominated, which may be also related to differences in the photosynthetic pathways of trees (C_3) and grasses (C_4).

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3 Discussion

The study combines results of eddy-covariance measurements along a rainfall gradient and through different ecosystems of Sub-Saharan Africa. Savanna ecosystems, which predominate in Africa, are thought to be a key source of variability in the global terrestrial cycles of water and carbon (Williams et al., 2007; Weber et al., 2008). Moreover, all African ecosystems will likely experience increasing climate-change-driven and human pressure in the future (Fuller and Prince, 1996; Williams et al., 2007). Improved quantification of their atmospheric carbon exchange across vegetation types thus provides fundamental information that can, for instance, be used to evaluate the performance of current terrestrial carbon cycle models in terms of their capacity to reproduce the response to the seasonal and inter-annual variation in weather conditions. Obviously, eleven study sites cannot by themselves provide representative continental coverage, but this preliminary synthesis represents a significant advance given the paucity of information to date. We note that the examples presented here include some of the most typical natural and anthropogenic vegetation types in Sub-Saharan Africa. However, the tropical rainforests of Central Africa remain unrepresented. Measurements within the humid forests of the Congo basin will be an important future challenge.

The strong correlation discovered between maximum photosynthetic uptake ($Fp_{\max}$) and mean annual precipitation (Fig. 8a) poses the question whether this result was achieved by chance, due to amounts precipitation in the year of measurement being similar to the long-term averages, or whether $Fp_{\max}$ indeed reflects an adaptation of the ecosystem to the long-term mean of water availability (Shugart et al., 2004). The explanation for the latter hypothesis could be the fact that tree coverage and consequently the tree contribution to $Fp_{\max}$ is stronger related to mean annual rainfall (Sankaran et al., 2005) and should be relatively constant inter-annually, whereas the grass layer may respond more variably to inter-annual changes in precipitation in terms of biomass, leaf area and contribution to $Fp_{\max}$. Analyses by Scanlon et al. (2006) and Archibald and Scholes (2007) showed that inter-annual variation in integrated NDVI (NPP) was almost

entirely determined by the grass layer: i.e. the higher the tree cover at a site, the more consistent the phenological signal from year to year. The relatively constant leaf area of the tree layer during the growing season may explain the high correlation between $Fp_{\max}$ and mean annual precipitation even if the rainfall did not match the long-term average in the year under consideration.

The relationship between annual rainfall and $Fp_{\max}$ increased exponentially in our study. We assume that it would eventually saturate, forming a s-shaped curve, if sites with higher precipitation were included. Tree cover fraction reaches a maximum between 650 and 1200 mm of rainfall (depending on the statistics used, Sankaran et al., 2005 and Bucini and Hanan, 2007) whereas studies on annual litterfall show a saturation of foliage production with mean annual precipitation only beyond 4000 mm (Liu et al., 2004). Annual gross primary production rises with mean annual precipitation up to at least 3000 mm (Luyssaert et al., 2007). This shows that tree cover may only be a weak predictor of productivity of a site.

Canopy photosynthetic capacity was strongly correlated to maximum surface conductance ($Gs_{\max}$ at $Fp_{\max}$, Fig. 8b). This was predicted by Schulze et al. (1994) in a theoretical study scaling knowledge from leaf level measurements. The eddy covariance method is well suited to test these predictions. The results match the predictions by Schulze et al. (1994) very well and confirm the close relationship between canopy conductance and $Fp_{\max}$ being constant over space (this study) and time (Kutsch et al. 2008, this issue). This seems to be relevant for scaling processes from leaf to ecosystem level and even to higher scales.

Since scaling is often combined with remote sensing and water and carbon fluxes depend highly on leaf area (Schulze et al., 1994; Baldocchi et al., 2001b; Nouvellon et al., 2001) we used satellite derived f_{APAR} in order to further analyse our results. Fensholt et al. (2004) showed the strong connection between leaf area index (LAI), f_{APAR} and normalized difference vegetation index (NDVI). We prefer f_{APAR} for this purpose because it avoids the problems of saturating NDVI at high values, and the canopy architecture assumptions that need to be made when estimating LAI from satellite data.

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Plotting f_{APAR} against mean annual rainfall shows a pattern that is similar to the pattern shown for tree cover versus mean annual rainfall by Sankaran et al. (2005). Grass-dominated sites showed a lower slope than the more wooded systems (Fig. 8c) but may reach a similar f_{APAR} at higher mean annual rainfall.

This was the rationale for distinguishing between tree- (predominantly C_3) and grass-dominated (predominately C_4) ecosystems when plotting $Fp_{\max}$ against f_{APAR} . Sites mainly consisting of C_4 plants (grassland and croplands) showed a stronger increase in $Fp_{\max}$ with f_{APAR} than C_3 dominated sites (Fig. 8d). The Sudan site, which is sparsely covered with C_3 Acacia trees (less than 30%) with an understory of C_4 grasses contributing the majority of the measured fluxes, was treated as a C_4 dominated ecosystem. The Kelma site (Mali) was not included in the linear regression of C_3 dominated ecosystems because it represents a severe outlier. This may depend on the geometry of the site – if it is surrounded by large stands of the same type or is it a small grove just next to a large bare area that is dominating the f_{APAR} signal – and therefore may show the limitations of remote sensing in heterogeneous areas.

4 Conclusion and outlook

In this study, we present a first integration of water and carbon fluxes in African ecosystems. Within a rainfall gradient between 320–1150 mm the data showed a strong dependency of carbon fluxes on water relations. In particular, the strong correlation between maximum canopy photosynthetic capacity and mean annual rainfall revealed valuable insights in ecosystem functioning in semi-arid environments. However, we could only speculate about the eco-physiological mechanisms underlying our observations, even though we matched theoretical predictions based on global eco-physiological knowledge. We suggest that more ground-based measurements should be combined with modelling approaches related to optimality theory.

The combination of eddy covariance measurements with remote sensing resulted in important findings for scaling to regional or even continental level. It could be shown

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that f_{APAR} provides a good measure for the spatial distribution of canopy photosynthetic capacity. We expect that further tests with additional indices (e.g. photochemical reflectance index, PRI) will provide also better descriptions of seasonal dynamics (Sjöström et al., 2008).

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Table 1. Basic site information, including location, altitude in m, mean annual air temperature (MAT), mean annual rainfall (MAP), ecosystem type with the dominant species, information about C3/C4 distribution, protective state and soil classification.

Site and publication (No in Fig. 1)	Country	Coordinates	Altitude	MAT in m	MAP in °C	Ecosystem in mm	Dominant	C ₃ /C ₄ species	Protective state	Soil type
Demokeya (4) Sjöström et al. (2008) this issue	Sudan	13.2829 N 30.4783 E	500	26	320	Sparse acacia savanna	<i>Acacia</i> spp., <i>Aristida pallida</i> , <i>Eragrostis tremula</i> and <i>Cenchrus biflorus</i>	30/70	Protected but not fenced	Cambic Arenosol
Agoufou (10)	Mali	15.34322 N 1.48067 W	290	29.7	350	Open woody savanna	<i>Combretum glutinosum</i> , <i>Acacia</i> spp.	25/75	unprotected, high cattle grazing	Sandy loam
Kelma (11)	Mali	15.22370 N 1.56620 W	273	29.6	350	Open acacia woodland	<i>Acacia seyal</i>	90/10	unprotected, grazing occasional cattle	Clayey soils
Maun (2) Veenendaal et al. (2004)	Botswana	19.9275 S 23.5672 E	950	22	464	Mopane woodland	<i>Colospermum mopane</i>	80/20	Unprotected, cattle grazing, fire wood	Kalahari sands
Skukuza (1) Kutsch et al. (2008) this issue	South Africa	25.0197 S 31.4969 E	359	21.9	547	Broadleaved and fineleaved savanna	<i>Combretum</i> sp. <i>Acacia</i> sp.	30/70	Kruger National Park	Sandy clay loam
Wankama (8) (Millet) Boulain et al. in review, 2008	Niger	13.6474 N 2.6298 E	244	28.5	560	Millet crop	<i>Pennisetum glaucum</i>	10/90	Crop field	Arenosol
Wankama (9) (Fallow) Ramier et al. in review, 2008	Niger	12.6475 N 2.6336 E	235	29.5	560	Fallow bush	<i>Guiera senegalensis</i> , <i>Zornia glochidiata</i>	80/20	Fallow bush	Sandy ferruginous Arenosol
Bontoli (7) Bruemmer et al. (2008)	Burkina Faso	10.18222 N 3.67277 W	293	29.5	926	Grass- and shrubland	<i>Andropogon ayanus</i> , <i>Loudetiopsis kerstingii</i>	70/30	Nature reserve	Sandy loam
Mongu (3) Scanlon and Albertson (2004)	Zambia	15.4377 S 23.2527 E	1053	24.6	945	Miombo woodland	<i>Brachystegia bakeriana</i> , <i>Brachystegia spiciformis</i>	95/5	Protected forest reserve	Kalahari sands
Kissoko (5) Marsden et al. (2008)	The Rep. of Congo	4.7914 S 11.9822 E	108	23.5	1076	Clonal Eucalyptus plantation	<i>Urograndis</i> (<i>E. urophylla</i> x <i>E. grandis</i>)	100/0	Plantation	Ferralic Arenosol
Tchizalamou (6)	The Rep. of Congo	4.2892 S 11.6564 E	82	25.7	1150	Grassland	<i>Loudetia</i> sp., <i>Ctenium newtonii</i>	0/100	unprotected	Ferralic arenosol

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Table 2. Shows information about the different Eddy covariance setups, as well as the amount of data relevant for analysis (number of night and day time values) and lower/upper thresholds of friction velocity u^* .

Site	Measuring height in m	Gas analyzer	Sonic anemometer	Years of measurements	Thresholds of friction velocity u^* (low/up)	Number of 30 min data – Total (night/day)
Demokeya	9	LiCor 7500	GILL R3	2005–2007	0.15/0.5	6924 (2190/4734)
Agoufou	4.2	LiCor 7500	Csat (Campbell)	2007	0.15/0.4	3408 (2041/1367)
Kelma	12	LiCor 7500	Csat (Campbell)	2007–2008	0.05/0.6	1578 (1195/383)
Maun	13.5	LiCor 6262	GILL R3	1999–2001	0.15/0.65	16 114 (6507/9607)
Skukuza	16	LiCor 6262	Csat (Campbell)	2003	0.15/0.65	4011 (1234/2777)
Wankama						
Millet	5.1	LiCor 7500	Csat (Campbell)	2005–2006	0.1/0.55	9101 (4441/4660)
Wankama						
Fallow	4.95	LiCor 7500	Csat (Campbell)	2005–2006	0.05/0.5	8922 (4124/4798)
Bontoli	2.65	LiCor 7500	Csat (Campbell)	2004–2006	0.05/0.45	5506 (2771/3735)
Mongu	19.5	LiCor 7000	GILL R3	2007–2008	0.2/0.7	1500 (590/910)
Kissoko	23.25	LiCor 7500	Young 81000V	2005–2006	0.15/0.5	24 088 (11 044/13 044)
Tchizalamou	3.8 changing	LiCor 7500	Young 81000V	2006–2007	0.05/0.3	16 053 (7642/8411)

4093

Table 3. Coefficients determined for analysis (Eqs. 1–3, see also Fig. 3). Coefficients m and d are given for the two Congolese sites, where an exponential relationship with air temperature was found. Values for $F_{p_{\max}}$ were fitted by quantile regression to derive an envelope (95%) for each site – see material and methods, data post-processing. Photosynthetic flux at $R_g=0$ is assumed to be 0.

Site	Ecosystem respiration (daily data)	Slope a/m	Intercept b/d	r^2	n	p	Gross primary production	$F_{p_{\max}}$	Coefficient θ	n	f_{APAR} by JRC (10 day averages, 1 pixel, peak growing season)
Demokeya		0.29	−0.176	0.42	144	<0.0001		14	0.09	2579	0.11
Agoufou		0.40	−6.42	0.47	172	<0.0001		15	0.05	1068	0.045
Kelma		0.09	−1.05	0.65	111	<0.0001		31	0.2	383	0.026
Maun		0.48	1.28	0.31	514	<0.0001		16	0.08	9607	0.31
Skukuza		0.18	0.25	0.30	511	<0.0001		17	0.05	2777	0.29
Wankama											
Millet		0.18	1.38	0.08	210	<0.001		12	0.03	4660	0.08
Wankama											
Fallow		0.42	0.41	0.30	219	<0.0001		20	0.05	4798	0.4
Bontoli		0.095	0.45	0.51	300	<0.0001		27	0.07	3735	0.45
Mongu		0.95	2.27	0.40	126	<0.0001		24	0.1	909	0.408
Kissoko		$m=0.36$	$d=0.10$	0.16	119	<0.001		32	0.18	13 049	0.51
Tchizalamou		$m=0.0026$	$d=0.30$	0.46	473	<0.0001		40	0.15	6291	0.318

4094

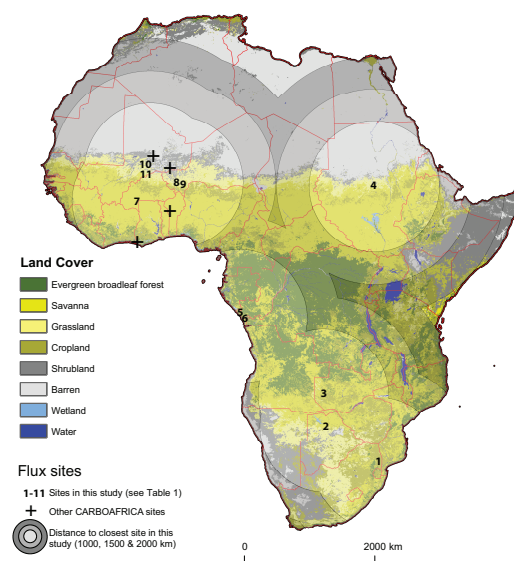


Fig. 1. The most common land cover types in Africa and the locations of eddy-covariance towers integrated in this study. “1–11” indicate sites included in this study (for more information see Table 1), while other CarboAfrica sites are shown as “+”. (Data from Global Land Cover Characterisation <http://edcsns17.cr.usgs.gov/glcc/glcc.html>).

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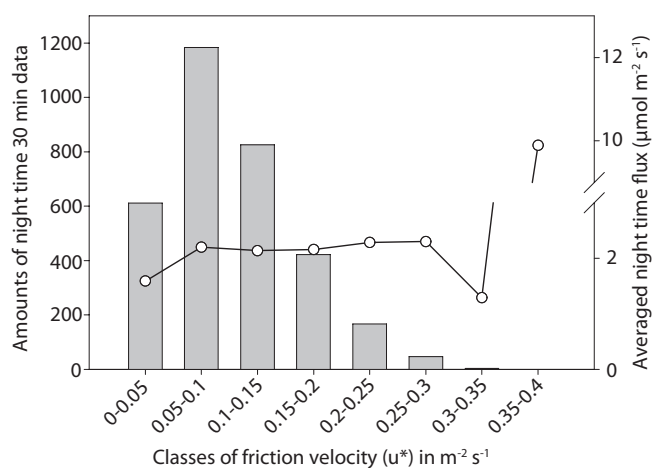


Fig. 2. An example, showing how u^* thresholds were defined, from grassland site at Tchizalamou, the Republic of Congo. The left y-axis shows the number of 30 min intervals for each u^* class and the right y-axis shows the averaged flux for each class. For $u^* < 0.05$, the average flux is depressed. We rejected these data as they lead to underestimation. For $0.05 < u^* < 0.3$ the average flux is stable and used in the analysis. For $u^* > 0.3$ averaged fluxes are exaggerated, leading to overestimation, and were rejected.

4096

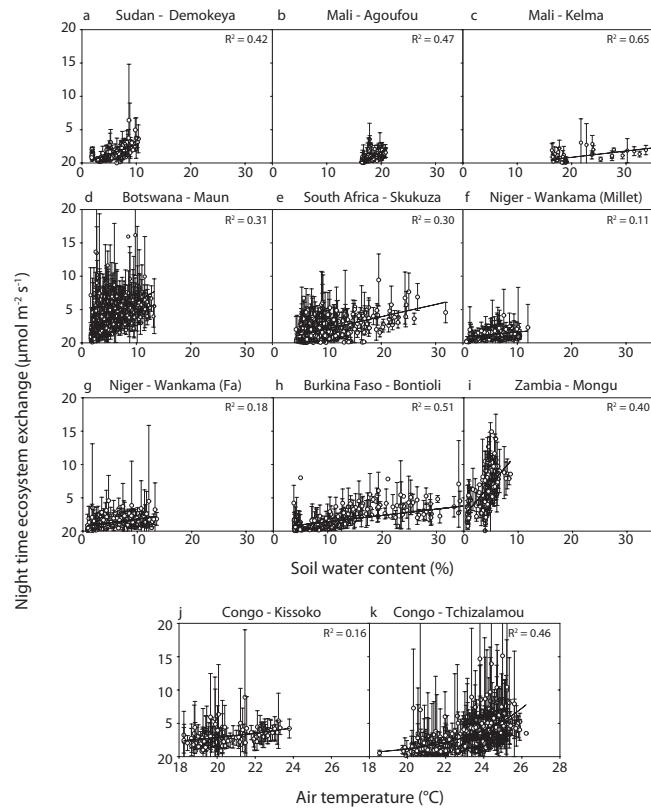


Fig. 3. Daily averaged night time flux (ecosystem respiration) versus soil water content (for sites with rainfall less than 1000 mm) or air temperature (Congolese sites with rain > 1000 mm).

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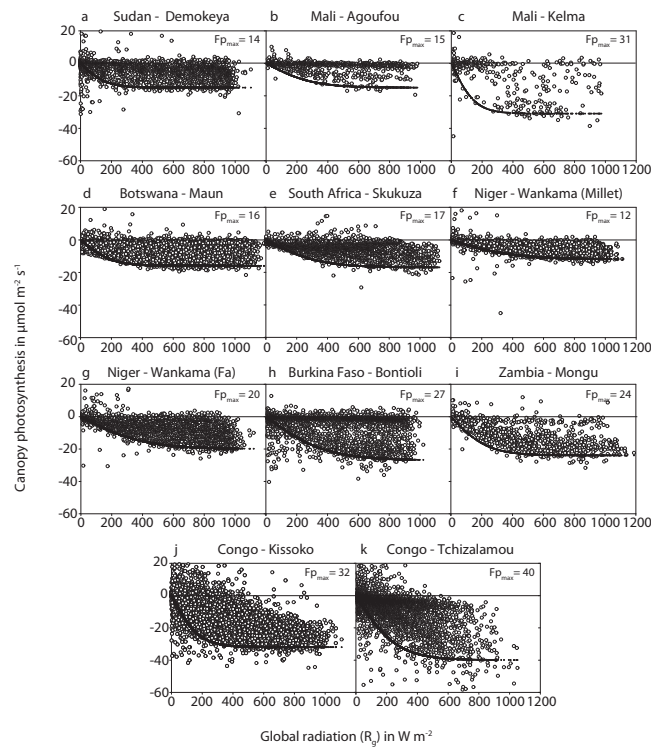


Fig. 4. Photosynthetic fluxes (F_p) versus global radiation allowing the estimation of the maximum uptake rate ($F_{p,max}$).

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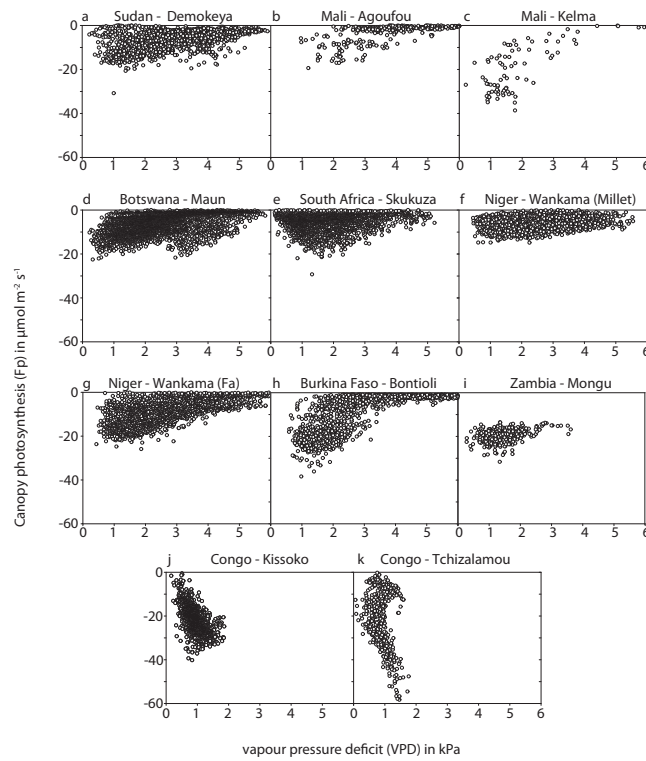


Fig. 5. The response of light-saturated photosynthetic flux ($R_g > 500 \text{ W m}^{-2}$) to water vapour pressure deficit in kPa (VPD). A strong decrease in F_p where VPD exceeds 2.0 kPa can be seen for several sites.

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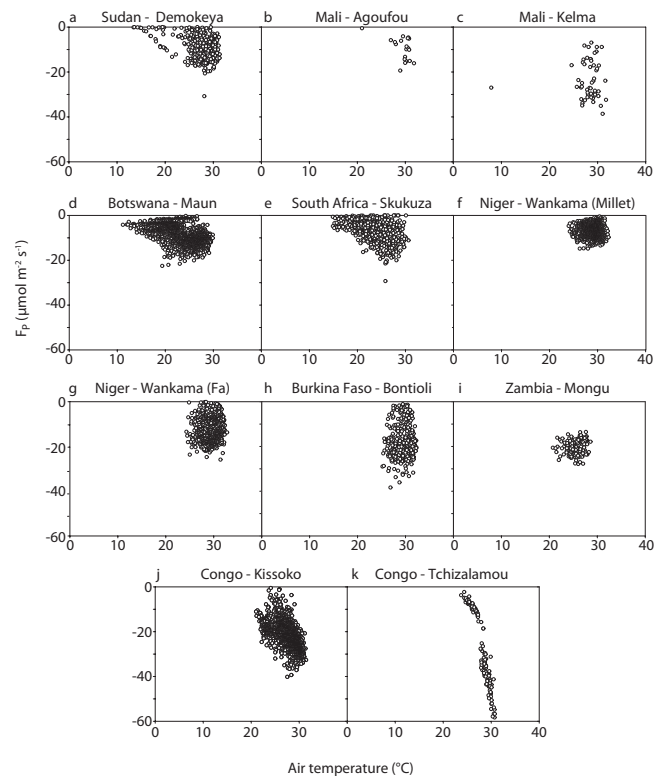


Fig. 6. The response of light-saturated photosynthetic flux ($R_g > 500 \text{ W m}^{-2}$) and water vapour pressure deficit (VPD) smaller than 2.0 kPa to air temperature showing a strong relation for some sites.

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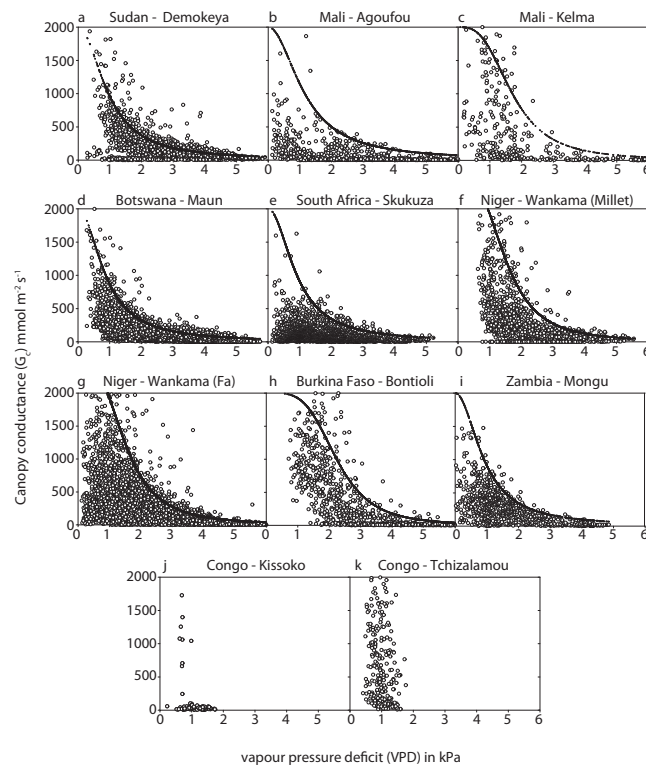


Fig. 7. The relationship between canopy conductance and VPD. Canopy conductance decreases with increasing values of VPD.

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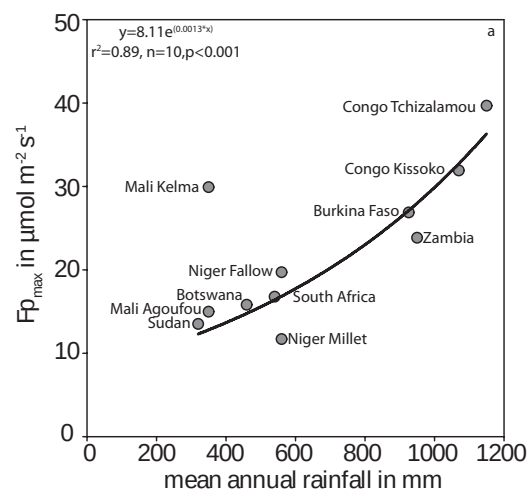


Fig. 8a. $Fp_{\max}$ versus mean annual rainfall for 10 African ecosystems (Mali-Kelma was excluded due to artificial water run-on). The best-fit relationship was exponential ($r^2=0.89$, $y=8.11 e^{(0.0013x)}$, $p<0.0001$, $n=10$).

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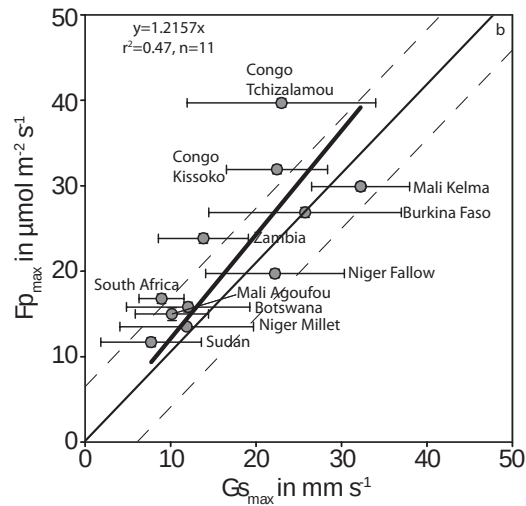


Fig. 8b. Canopy conductance ($G_{s_{max}}$) versus maximum photosynthetic uptake rate (both shown ± 1 SD, hardly visible for $F_{p_{max}}$). The thin solid line (with the 1 SD limits dashed) shows the global relationship of $F_{p_{max}}$ and conductance found by Schulze et al. (1994) and the thick solid regression line shows the regression for the eleven African sites. ($r^2=0.47$, $y=1.2157x$, $n=11$).

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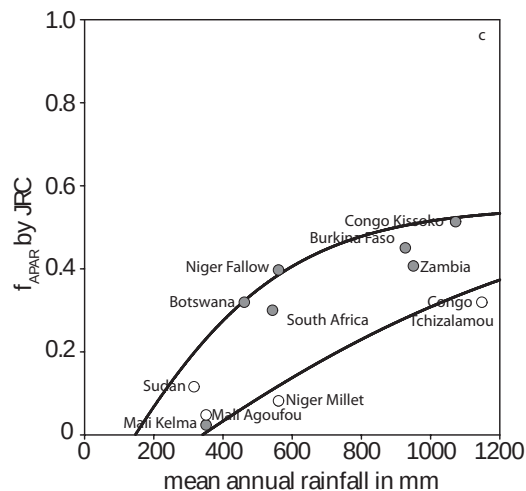


Fig. 8c. The relationship of satellite-derived f_{APAR} to mean annual rainfall for the analysed sites. The tree dominated ecosystem ($n=6$, grey, Mali-Kelma excluded) lie along the capacity curve, levelling off at 800 mm of rainfall ($y=0.75 \cdot \tanh(x \cdot 0.0014/0.75) - 0.2$) and the grasslands ($n=4$, white) are explained by the curve below ($y=0.8 \cdot \tanh(x \cdot 0.0006/0.8) - 0.2$).

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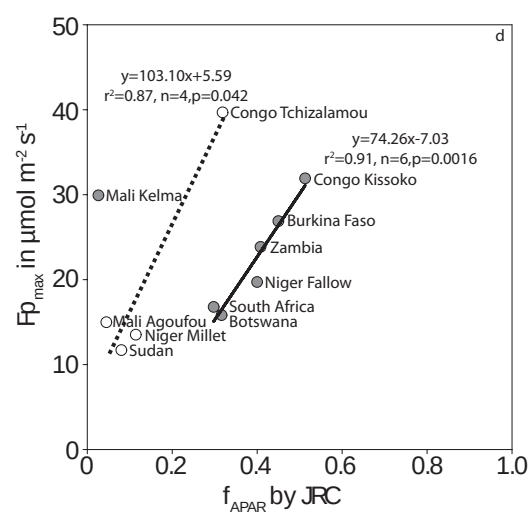


Fig. 8d. The relationship between Fp_{max} and f_{APAR} for the African sites. Sites dominated by C_3 (grey) trees have a different slope to those dominated by C_4 grasses (white). (C_3 : $r^2=0.91$, $y=74.26x-7.03$, $p=0.0016$, $n=6$, Mali-Kelma excluded; C_4 : $r^2=0.87$, $y=103.10x+5.59$, $p=0.042$, $n=4$).