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Spatial and temporal variation of CO₂ efflux along a disturbance gradient in a *miombo* woodland in Western Zambia

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Received: 4 May 2010 – Accepted: 28 June 2010 – Published: 29 July 2010

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Carbon dioxide efflux from the soil surface was measured over a period of several weeks within a heterogeneous *Brachystegia* spp. dominated *miombo* woodland in Western Zambia. The objectives were to examine spatial and temporal variation of soil respiration along a disturbance gradient from a protected forest reserve to a cut, burned, and grazed area outside, and to relate the flux to various abiotic and biotic drivers. The highest daily mean fluxes (around $12 \mu\text{mol m}^{-2} \text{s}^{-1}$) were measured in the protected forest in the wet season and lowest daily mean fluxes (around $1 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the most disturbed area during the dry season. Diurnal variation of soil respiration was closely correlated with soil temperature. The combination of soil water content and soil temperature was found to be the main driving factor at seasonal time scale. There was a 75% decrease in soil CO_2 efflux during the dry season and a 20% difference in peak soil respiratory flux measured in 2008 and 2009. Spatial variation of CO_2 efflux was positively related to total soil carbon content in the undisturbed area but not at the disturbed site. Coefficients of variation of efflux rates between plots decreased towards the core zone of the protected forest reserve. Normalized soil respiration values did not vary significantly along the disturbance gradient. Spatial variation of respiration did not show a clear distinction between the disturbed and undisturbed sites and was neither explained by soil carbon nor leaf area index. In contrast, within plot variability of soil respiration was explained by soil organic carbon content.

Three different approaches to calculate total ecosystem respiration (R_{eco}) from eddy covariance measurements were compared to two bottom-up estimates of R_{eco} obtained from chambers measurements of soil- and leaf respiration which differed in the consideration of spatial heterogeneity. The consideration of spatial variability resulted only in small changes of R_{eco} when compared to simple averaging. Total ecosystem respiration at the plot scale, obtained by eddy covariance differed by up to 25% in relation to values calculated from the soil- and leaf chamber efflux measurements but without showing a clear trend.

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1 Introduction

Soil respiration is the major path by which carbon dioxide (CO₂) returns to the atmosphere after being fixed via photosynthesis by land plants. Globally this flux is estimated to be approximately 75 Pg C per year, or 10 times the emissions originating from fossil fuel combustion, and is likely to be affected by anthropogenic global warming (Schlesinger and Andrews, 2000; Bond-Lamberty and Thomson, 2010). Notwithstanding, the prediction of soil CO₂ efflux at all scales remains one of the big challenges in biogeochemical cycling, since soil respiration represents a combination of different sources, each with its own response to environmental factors and each with its own temporal variability and spatial heterogeneity (Moyano et al., 2007; Trumbore, 2006).

The factors which influence the temporal variation of soil respiration are better understood than the factors controlling its spatial heterogeneity (Buchmann, 2000; Davidson et al., 1998). Spatial patterns in soil carbon dioxide efflux have shown to be associated with heterogeneity of soil properties such as soil organic matter content or microbial biomass, but also have been explained by stand aboveground species composition and structure (Soe and Buchmann, 2005; Shibistova et al., 2002; Knohl et al., 2008). The knowledge about the sources of heterogeneity is essential for scaling soil respiration from plot measurements to ecosystem, landscape or even global level (Soegaard et al., 2000; Tang and Baldocchi, 2005). In this context, it is a great advantage that studies on the heterogeneity of soil CO₂ efflux can be conducted within the footprint area of flux towers and the up-scaled values of soil respiration can be compared to integrated fluxes from eddy covariance (EC) night-time data (Janssens et al., 2000; Aubinet et al., 2005; Kutsch et al., 2010).

Night time measurements of carbon dioxide fluxes by EC represent the total ecosystem respiration (R_{eco}) which also includes stem- and foliar respiration. Therefore, the comparison of up-scaled soil respiration to R_{eco} requires an estimation of these fluxes originating from the aboveground part of the ecosystem.

In this study, we want to investigate the spatial and temporal drivers of soil respira-

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tion, and to compare “top-down” (eddy covariance) and “bottom-up” (chambers) methods of estimating ecosystem respiration. This objective had four sub-objectives: to investigate (i) the temporal variation of soil respiration for periods of hours to years, (ii) the spatial heterogeneity of soil respiration at scales of meters to hundreds of meters, and (iii) the abiotic and biotic factors that drive this heterogeneity. In particular (iv), we wanted to know whether information of small scale heterogeneity becomes irrelevant during scaling and therefore further efforts of scaling soil respiration can be conducted by reduced sampling.

This reduction of sampling is an important goal since we conducted our research in a *miombo* woodland in Southern Africa. Measurements of soil- and ecosystem CO₂ fluxes have been made in a wide variety of ecosystems, especially forest and agricultural ecosystems in America and Europe (Borken et al., 2002; Hanson et al., 2003), but there is a paucity of similar studies from tropical ecosystems particularly in Africa (Nouvellon et al., 2008). Up to date, there is not a single study of continuous ecosystem flux measurements nor regular process measurements representing *miombo* woodlands, the most extensive (2.7 mio km²) semi-arid to sub-humid woodland formation in Southern Africa (Kanschik and Becker, 2001; Grace et al., 2006).

Miombo woodlands are the current location of the tropical deforestation and forest degradation front. The main driver is charcoal production to satisfy a growing energy demand in regional urban areas (Misana et al., 2005). After cutting for charcoal, the land is often cultivated as cropland, grazed or burned. In these cases the belowground carbon stocks in *miombo* woodlands are substantially reduced (Walker and Desanker, 2004; Chidumayo and Kwibisa, 2003; Zingore et al., 2005).

Therefore, the second (2) main objective of our work was to study the impact of disturbance. We used a gradient from a protected forest reserve to a human-disturbed derivative as an experimental platform. We hypothesized clear differences in above- as well as belowground carbon concentrations (low at the disturbed site and large in the protected reserve), aboveground biomass, soil physical variables, such as soil temperature and soil water content and associated differences in soil CO₂ efflux along

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the disturbance gradient (Fig. 1).

2 Material and methods

2.1 Site description

The *miombo* woodland studied is located within the Kataba Forest Reserve (15.43° S 23.25° E, 1084 m a.s.l.) in the Western Province of Zambia. The climate is semi-arid, having a distinct dry (May–mid October) and wet season (mid October–April). The average annual air temperature is 21.8 °C and the mean annual rainfall is 948 mm (Zambian Meteorological Department, Mongu Office, 20 km north of Kataba). Kataba Forest Reserve is a small area established in 1973 and managed by the local community in conjunction with the Zambian Forestry Department. Certain uses are permitted, including grazing and firewood collection and the forest is exposed to frequent, low-intensity ground fires. The area surrounding the forest reserve has undergone rapid and dramatic land cover change over the past decade and is severely disturbed by intense charcoal production and the conversion from woodland to agricultural land (Fig. 1). The forest is characterised by a projected canopy cover of nearly 70% (Scholes et al., 2004) and is commonly described as a “woodland”. It is intermediate in height and cover, located between the more open, lower in height savanna ecosystems to the south (e.g. Botswana) and the tall, closed tropical rainforest to the north (e.g. Democratic Republic of Congo). The dominant species are *Brachystegia spiciformis* (24.7% of total trees measured), *Brachystegia bakerana* (29.8 %), *Guibourtia coleosperma* (16.8%) and *Ochna pulchra* (24.5%). These are trees exceeding 10 m in height, mostly belonging to the non-nitrogen fixing legume family *Caesalpinaceae*. The understory is characterized by very small areas of few grasses and regular moss cover, contrary to the miombo woodlands in Mocimboa do Tempo. Open spots are often characterized by dense shrub vegetation.

In the surrounding disturbed areas, the dominant species are shrubs such as *Diospy-*

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ros batoeana (20.8 %) and *Baphia obovata* (10.4%) and large amounts of C₄ grasses that invade shortly after clear-cutting.

The soils are deep, nutrient poor Arenosols (FAO soil group). Kataba falls within the vast basin of “Kalahari sands”. For more detailed information we refer to Scholes et al. (2004) and Scanlon and Albertson (2004).

2.2 Experimental design

The study area consisted of 4 plots (each 50×50 m) located within the average 50% footprint area of a 30 m tall EC tower. Three plots were located within the protected forest and one plot was set up within the disturbed area. The disturbed plot (plot 1) outside the forest reserve had been degraded by logging and charcoal production shortly before the study was conducted. Only a few trees have remained. Grasses have invaded and regeneration has started with shrub-like trees. However, the soil has not eroded much in this early state of degradation (personal communication with the Forest Department of Zambia and personal observation, 2009).

Plot 2 and 3 were located inside Kataba forest reserve but had been subjected to small logging activities in the past with lower intensity in plot 3, which was more distant from the edge of the reserve (Fig. 1). Plot 4 was located in the core area of the forest reserve with no evidence of disturbance.

Each plot was divided into 100 subplots of 5×5 m. The ground cover in each subplot was characterised a priori to find suitable homogeneous and representative patches for soil respiration measurements using a small diameter (10 cm) chamber. The a priori characterization of the soil heterogeneity was based on the abundance of ground cover types (mosses, grasses, litter, dead wood, bare ground etc.). Each subplot was classified by its three most abundant types, e.g. EIF – litter (E), moss (I), free (F) ground (Fig. 1 and Table 1). The distribution of the collars for soil respiration measurements followed this phenomenological classification: for each class at least three collars were set in every plot and the number of repetitions per class followed its abundance. This approach guarantees a high representativeness while also accounting for rare areas

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being potential hot spots.

2.3 Soil- and leaf respiration chamber measurements

In order to ensure that each category was represented in every plot by at least 3 soil respiration measurements collars, a total of 126 locations were chosen for soil respiration measurements (21, 30, 42 and 33 collars in plots 1, 2, 3 and 4, respectively). To quantify temporal variation between the wet and the dry season, the respiration collars were sampled during three intensive field campaigns, one during the late dry season (September 2008) and two during the peak wet season, February to March 2008 and March 2009. Plastic collars (PVC – \varnothing 10 cm and 7 cm high) were inserted 1–2 cm into the mineral soil at each measurement location one week before the first sampling period and left in there for all following campaigns, to minimize the disturbance prior to the time of measurements (Soe et al., 2004). Each of the three campaigns lasted several weeks and each collar was sampled on at least 4 days during each campaign, except for the dry season measurements with fewer replicates.

Soil CO₂ efflux was measured over short periods using a closed manual chamber system with an infrared gas analyzer (LI-6400 and LI-6400-09, LiCor Inc., Lincoln, NE). After placement on a collar, the CO₂ concentration inside the chamber was reduced below ambient CO₂ and allowed to rise above ambient over time. Three measurement cycles were undertaken at each collar. They were rejected and repeated when the standard deviation was higher than 10% of the mean value. The mean of the accepted CO₂ efflux measurements calculated for all three cycles was used in further analysis. In addition, an open dynamic system, consisting of three chambers, a self-made valve switching unit and a CQP 130 portable gas exchange system (Walz, Effeltrich, Germany), was used for continuous flux measurements over diurnal periods (Kutsch et al., 2001). This system enables continuous measurements at near ambient environmental conditions, since the CO₂ concentration differences between the inside and the outside of the chamber is small and pressure fluctuations resulting from the vertical wind component, which induce a higher efflux, are transferred to the soil surface (Ray-

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ment, 2000; Janssens et al., 2000; Pumpanen et al., 2004). Each respiration chamber measurement was accompanied by measurements, adjacent to the collar, of soil water content at 5 cm soil depth (ThetaProbe, Delta-T Devices, Cambridge, UK) and soil temperature in the upper soil horizon at 5, 10 and 15 cm depth (LiCor 6400-09, LiCor Inc., Lincoln, NE, USA).

Foliage respiration was measured at several leaves of the dominant tree species in 2008 and 2009 within the inventory plots. Measurements were undertaken at dawn and during daytime using closed dark chamber attached to an infrared gas analyzer (LI-6400, LiCor Inc., Lincoln, NE, USA).

As the third process (besides soil- and leaf respiration) contributing to R_{eco} , stem respiration was calculated using plot specific values of leaf area index (LAI). Meir and Grace (2002) found an exponential increase of aboveground woody biomass respiration with rising values of LAI for tropical ecosystems. This relation was adapted for the *miombo* woodland in this study and plot and subplot specific values of LAI were used to calculate values of stem respiration instead of using a constant estimate derived from other ecosystems.

2.4 Eddy covariance measurements and data post processing

The scaffold tower was instrumented with eddy covariance equipment, as described by Aubinet et al. (2000) and Baldocchi et al. (2001), in September 2007. In brief, the system included a 3D sonic anemometer (Solent R3, Gill Instruments, Lymington, UK) and an infrared closed-path gas analyser (LI-7000 LiCor Inc., Lincoln, NE, USA). The EC system was accompanied with meteorological sensors (air temperature, humidity, net radiation, global radiation, photosynthetic active radiation, rainfall, soil water content, etc.). Soil water content in particular was measured in two vertical profiles (5, 10, 30, 50, 100 cm depth) using soil moisture probes (ThetaProbe, Delta-T Devices, Cambridge, UK).

Half-hourly flux averages were calculated and corrected using the Eddysoft software package (Kolle and Rebmann, 2007). This included spike detection in the raw data,

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transformation into physical values and calculation of the half hourly averages of CO₂ and water vapour fluxes. Thereafter the following technical and meteorological quality criteria were applied: (i) identification of data gaps caused by power failure (ii), detection of spikes in the raw data and half hour averages as shown in Papale et al. (2006), (iii) rejection of data with high variances in CO₂ and H₂O concentrations, vertical wind velocity (w) and temperature on the raw data according to Knohl et al. (2003) and (iv) application of stationarity tests and integral turbulence characteristics as given by Foken and Wichura (1996). In addition, friction velocity (u^*)-filtering at night-time was applied (lower threshold: 0.2 m s⁻², Goulden et al., 1996; Gu et al., 2005, Papale et al., 2006). Data were also filtered for an upper u^* threshold (0.7 m s⁻²) to avoid overestimation of the measured fluxes (Merbold et al., 2009b; Gu et al., 2005), resulting in a “high-quality” data set.

2.5 Gap-filling and calculation of daytime ecosystem respiration

Night-time data of net ecosystem exchange that passed the quality control filtering were used to calibrate a modified ecosystem respiration (R_{eco}) model according to Reichstein et al. (2003, Eq. 1) using soil temperature at 5 cm depth and relative plant available water in the first meter of the soil as input variables.

$$R_{\text{eco}} = R_{\text{ref}} \times f(T_{\text{soil}}, \text{RPAW}) \times g(\text{RPAW}) \quad (1)$$

where R_{eco} is the modelled respiration, R_{ref} is the respiration for a site-specific temperature for biweekly periods, f and g are functions for the influence of soil temperature (T_{soil}) and relative plant available water (RPAW) modified from the study by Reichstein et al. (2003). RPAW was calculated instead of using relative soil water content (RSWC) since RPAW affects the living tissue directly (autotrophic respiration) and the microbial biomass indirectly via the plant exudates (heterotrophic respiration). When applying RSWC instead of RPAW an overestimation of R_{eco} caused by a longer response of the autotrophic component to RSWC seems likely but is unrealistic from the biological

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point of view, since plants can only access water in the soil until a certain threshold (wilting point) depending on the soil structure.

The resulting model was used to estimate daytime respiratory fluxes from night-time measurements. The extrapolation of night-time EC measurements bears the risk of high uncertainty induced by a decrease in friction velocity, resulting from a lowering of the boundary layer at night (Moncrieff et al., 1997; Goulden et al., 1996). Furthermore, night-time fluxes measured by EC may be biased by advection (Kutsch et al., 2008). Therefore we also used a second method to approximate R_{eco} , from EC measurements, developed and explained by Lasslop et al. (2009). This method calculates R_{eco} from day-time data, as the intercept of the hyperbolic function fitted to a plot of NEE versus global radiation (i.e. the ecosystem scale light response curve). The approach takes account of the effects of vapour pressure deficit (VPD) in the light response and temperature regulates the response of the derived term for R_{eco} (Lasslop et al., 2009).

As a third approach to derive R_{eco} , the online gap-filling tool (Reichstein et al., 2005), was used. In this tool gap-filled night-time fluxes are fitted to a temperature function only (Lloyd and Taylor, 1994), ignoring the influence of soil water content, which is of crucial importance for semi-arid and arid ecosystems in Africa (Merbold et al., 2009a; Nsabimana et al., 2009; Archibald et al., 2009).

2.6 Stand structure, soil- and ecosystem-physiological parameters

Forest structure and composition measurements were made over the course of the field campaigns. For each tree within the four experimental plots we determined species, diameter at breast height (dbh) and diameter at tree base (dtb), height, damage class and precise location within the plot. Values of leaf area index (LAI) were calculated from hemispheric photographs (400 pictures in total equating 1 picture per subplot) using WinScanopy (Regent Instruments Inc., Canada).

Soil samples were collected within each subplot used for respiration measurements in 2008 and 2009 (cores 4.8 cm in diameter, 30 cm in depth). The samples were air dried in the field and shipped to a laboratory in Jena, Germany. Then, the samples

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were washed and sieved at 2 mm and 630 μm to separate coarse organic matter (primarily fine roots), particulate organic matter (mycorrhiza and charcoal) and mineral soil associated organic matter (humic substances and black carbon). Thereafter, each subsample was dried at 40 $^{\circ}\text{C}$, weighed and analyzed for total carbon and nitrogen content (VarioMax EL, Elementar Analysensysteme GmbH, Hanau, Germany).

2.7 Statistical analysis

Data analysis was performed using the statistical software package SPSS 16.0 (SPSS Inc.) and Statgraphics Centurion XV (STATPOINT Technologies, Inc., Virginia, USA). Diurnal measurements of soil CO_2 efflux were correlated with soil temperature using the exponential relationship:

$$R_{\text{soil}} = ke^{mT_{\text{soil}}}, \quad (2)$$

where R_{soil} is soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), T_{soil} is soil temperature at 5 cm depth and k and m are coefficients.

Averaged soil respiration for each categorized subplot (represented by three collars and each measured during three cycles) was fitted to soil water content with a linear function:

$$R_{\text{soil}} = a\text{SWC} + b, \quad (3)$$

where R_{soil} is soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), SWC is soil water content (volumetric %, 5 cm depth), a and b are constants derived from curve fitting (Table 2).

To study R_{soil} spatially, mean efflux rates were normalized for the overall average soil temperature (26 $^{\circ}\text{C}$) and soil water content (5.5 vol. %) using a plot specific general linear model:

$$R_{\text{snorm}} = c\text{SWC} \pm dT_{\text{soil}} \pm h\text{SWCT}_{\text{soil}} \pm i, \quad (4)$$

where R_{snorm} is the normalized soil CO_2 efflux, SWC soil water content (volumetric %), T_{soil} (soil temperature a 5 cm depth in $^{\circ}\text{C}$) and c , d , h and i are plot specific coefficients. Statistics are given in Table 3. The resulting values were correlated to the

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above mentioned stand structural, soil- and ecosystem physiological parameters using Statgraphics Centurion XV (Statpoint Technologies Inc., Virginia, USA). Differences in soil respiration fluxes and possible confounding meta-variables between the plots were tested using a Two-Way ANOVA of normalized values of soil respiration (R_{snorm}), where the plot-variable was used as a factor and the subplot-variable as a covariate.

2.8 Total ecosystem respiration (top-down vs. bottom-up approach)

To compare the top-down and bottom-up approaches of carbon efflux estimation, we calculated the EC carbon fluxes for half-hour periods on the days when soil respiration data were collected from chambers in the field. Only EC data which applied to the specific wind sectors in the direction of each of the intensive measurement plots were used (Fig. 1).

For the bottom-up approach, comprising of soil-, leaf and stem respiration, two different calculations were done. One accounted for spatial heterogeneity of soil respiration by means of an area-weighted average, based on the categories of ground cover within the plot. Furthermore, comparison was done for daytime respiration, since there were not sufficient bottom-up data for night-time soil respiration.

3 Results

3.1 Temporal variation of soil respiration

On a diurnal time scale, soil temperature was the primary driving factor associated with variations in soil respiration during both the dry season (Fig. 2a and b), and dry periods in the wet season (Fig. 2c and d) resulting in an exponential increase of soil CO₂ efflux with a rise in temperature (Fig. 2b and d). In contrast, rain events were commonly followed by a flush of carbon dioxide to the atmosphere and an increase in respiration rates thereafter but a decrease in soil temperature for several hours after

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the precipitation event (Fig. 2e). However, no significant relation between efflux rates and soil temperature could be shown for such cases (Fig. 2f). The magnitude of the increase varied with progress of the growing season and with the temporal pattern of precipitation events.

The CO₂ efflux during the dry season in 2008 was substantially less than the effluxes in the wet seasons of either 2008 and 2009. Soil respiration showed a typical seasonal pattern related to soil water content (SWC), with the maximum during the rainy season (subplot averages of 11.63 μmol m⁻² s⁻¹ in 2008 and 12.25 μmol m⁻² s⁻¹ in 2009) and the minimum during the dry season (0.94 μmol m⁻² s⁻¹ in 2008). The general pattern of soil CO₂ efflux, showing an increase with rising soil water content, was similar between and within plots. However the changes were not evenly distributed within plots as illustrated by the varying slopes of R_{soil} in Fig. 3.

The two interrelated factors (T_{soil} , SWC) influencing R_{soil} temporally were included in a general linear model to normalize the measured effluxes for further spatial analysis (Fig. 4a–d, Table 3). A linear relation between R_{soil} and T_{soil} was used, due to the small exponential increase of R_{soil} with T_{soil} , which was found for diurnal timescales.

Average wet season efflux was slightly higher in 2009 compared to 2008 for the disturbed plots (Fig. 5a) and lower for the undisturbed site (Fig. 5b) – not shown for plots 3 and 4, showing a similar picture as Fig. 5b.

3.2 Small scale spatial variation of soil respiration (within plots)

Spatial variation of respiration was based a priori on the classes of ground cover (categories). This assumption was tested for each plot separately using One-Way ANOVAs. Soil respiration varied significantly between subplots in all of the 4 plots. However, different categories in different plots were showing similar efflux rates (Fig. 6).

Parameters such as leaf area index, total soil carbon content and belowground biomass change at a lower frequency (months to years) than meteorological variables and were therefore chosen for spatial analysis of the temperature and water content normalised respiration rates (R_{snorm}). The only parameter identified in this study ex-

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plaining significant portions of the spatial variability of R_{snorm} within the undisturbed plots was soil carbon content (%) at 10 cm depth (Fig. 7d, g and j, Table 4). Leaf area index was found to be a predictor of soil respiration in only 2 of the 4 inventory plots (Fig. 7e and k) but not for the other 2 plots (Fig. 7b and h). None of the before mentioned variables explained the large variations of soil respiration in the disturbed plot (Fig. 7a, b and c).

Carbon content in the soil is commonly related to above- and belowground biomass in an ecosystem. Therefore we plotted belowground carbon content (% , 10 cm depth) against leaf area index, an indirect measure of biomass and the associated litter (and carbon) inputs. Our results show a positive relation between belowground carbon content and leaf area index (Fig. 7f, i and l) for the undisturbed plots.

3.3 Spatial variation of soil respiration along the disturbance gradient (between plots)

Measurements from all plots were available in 2009. There was no significant difference in respired carbon between the disturbed and undisturbed plots (Table 5). No trend of changes in soil respiration along the disturbance gradient was observed during the dry season 2008 (Table 5). In contrast, fluxes varied along the disturbance gradient showing a clear trend in the wet season in 2008 (data from plot 4 was not available at this time – Table 5). Coefficients of variation were always highest in the disturbed area and declined towards the most undisturbed plot for the wet season measurements (Table 5).

The variation in respiratory fluxes in 2009 was poorly explained by carbon content at a depth of 10 cm (Fig. 8a and b), showing no clear distinction between the disturbed and the undisturbed areas. No relation could be established between the large and significant differences in leaf area index between the disturbed and undisturbed sites (Fig. 8c) to the soil CO₂ efflux rates in the wet season 2009 (Table 5 and Fig. 8c).

Soil temperature was lower in the undisturbed plots than in the disturbed plot (Fig. 8d). Differences in soil carbon content (10 cm depth – Fig. 8b), soil water con-

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tent (vol. % – Fig. 8e) and charcoal content (mg, 10 cm depth – Fig. 8f) between plots were not significant.

3.4 Total daytime carbon loss

Total carbon emitted via respiration from the ecosystem to the atmosphere was highest in the wet season 2008/2009 (high values in Fig. 9) and lowest during the dry season 2008 (low values in Fig. 9). The two different bottom-up approaches differed only slightly from each other. The approach accounting for spatial heterogeneity in R_{soil} resulted in slightly less deviation from the 1:1 line (Fig. 9b) compared to simple averaging of R_{soil} (Fig. 9a). However, the variation of the top-down as well as for the bottom-up approaches was high. Assuming the chamber-based bottom-up approach provides more realistic values of the real carbon loss from the ecosystem, none of the 3 different methods for EC-based estimation matched the values from the process approach perfectly (Fig. 9a and b), but all were within the standard deviation of the process up-scaling. During the dry season in 2008 the top-down approaches underestimated the carbon loss relative to the bottom-up calculations across all plots (Fig. 9a and b).

When analyzing the results of the 3 different top-down approaches were the night time based models during all seasons (black and white dots) within a 20% range (including over- and underestimation) of the process up-scaling. The top-down approach using daytime fluxes, as described by Lasslop et al. (2009), underestimated R_{eco} by up to 25% for the different plots (grey dots in Fig. 9).

On the other hand the night-time based model including a response to soil water content and temperature clearly overestimated fluxes in the wet seasons (black dots). Generally, each model had its strengths, either for the disturbed or undisturbed plots in the dry and the wet season (not shown). Similarly each top-down approach had its weaknesses. The best fit was given by the method using night-time data and soil temperature as a predictor of R_{eco} , only (white dots).

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Portable soil chambers are well-suited to investigate spatial differences in soil CO₂ efflux, but do not allow permanent long-term observations (Soe and Buchmann, 2005). In contrast, static automatic chambers (Irvine and Law, 2002) and the understory EC method (Baldocchi and Meyers, 1991) provide continuous measurements but are often not applicable due to their complexity and expense (Pumpanen et al., 2004). In our study, the two chamber types were combined during three measuring campaigns.

We measured diurnal time-courses of soil respiration with an automatic open chamber and showed that during a day without rain, the temporal variation of soil respiration followed soil temperature. This exponential function of soil temperature has already been shown by several other studies (Evrendilek et al., 2005; Zimmermann et al., 2009). The changes in soil CO₂ efflux immediately after rainfall events, as shown in Fig. 2, confirms previous findings (Lee et al., 2004). At seasonal timescales, soil water content became the primary controlling factor. Observations similar to our results were shown by Epron et al. (2004) and Nouvellon et al. (2008) in an *Eucalyptus* plantation in Congo, which receives slightly more rain per year than Kataba, but also experiences a strong distinction between the wet and dry season. Studies in a semiarid ecosystem in the Mediterranean by Evrendilek et al. (2005) and Maestre and Cortina (2003) also showed a seasonal dependency of R_{soil} on soil water content.

Accounting for the spatial variability of R_{soil} is more difficult than accounting for temporal variations (Rayment and Jarvis, 2000; Baldocchi et al., 2006). Often, spatial variation of R_{soil} can not be explained by microclimatic variables such as soil moisture and temperature, whilst it can be explained by the variation in biological activity and soil chemistry (Law et al., 2001; Xu and Qi, 2001). For this purpose, R_{soil} is often normalized to a standard soil temperature, a standard soil moisture or both. In this study we corrected for both parameters to the overall averages measured during the campaigns, 26 °C of soil temperature and 5.5 vol. % of soil water, respectively. Several studies have found strong correlations between R_{soil} and biological factors such as the

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thickness of the moss layer (Rayment and Jarvis, 2000), root density or distance to the nearest tree (Soe and Buchmann, 2005; Tang and Baldocchi, 2005).

At Kataba forest, spatial heterogeneity of soil respiration (R_{snorm}) was explained by soil carbon content (10 cm depth) in the undisturbed plots only. Explaining this within-plot correlation between R_{snorm} and belowground carbon we hypothesized that shrubs and ground vegetation create hotspots of soil carbon, resulting in higher biological activity by sampling dry litter that is moved around by the wind particularly during the dry season. We observed thick litter layers and higher carbon content in the mineral soil under *Copaifera baumiana* and *Xylopia odoratissima* shrubs that seem to create micro-zones of decreased turbulence near the forest floor. Hence, the appearing higher litter deposition at these micro-sites will increase abundance and turnover of belowground biomass and attract roots and mycorrhiza (King et al., 2001). Leaf area index, an indirect measure for biomass (Churkina et al., 2003) and therefore also associated with carbon content (Fig. 7) was only a poor predictor for the spatial variation of soil respiratory efflux. Referring to the above mentioned hot spots of soil carbon we assume an underestimation of the presented LAI values at these hot spots, caused by the method applied. Leaf area index was calculated from hemispheric photographs which were taken at a height of 1 m and therefore mostly above the sparse grass layer.

None of the before mentioned variables explained the within-plot variation of R_{snorm} in the disturbed plot, neither did other biotic and abiotic parameters such as belowground biomass or charcoal content as proposed by other studies (Salimon et al., 2004; Maestre and Cortina, 2003). The highly variable flux estimates and heterogeneity observed in the disturbed area may be explained by the disturbance itself. First of all, regular disturbance such as tree logging was still occurring at the site, resulting in changes in the aboveground biomass resulting in less organic compounds being transported to the root system. Secondly, remnants of charcoal kilns besides very grassy patches (occurring after clearing) and contrary to deserted patches resulted in a large heterogeneity aboveground as well as belowground without showing clear trends in respiration rates.

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The hypothesized disturbance gradient was given by different magnitudes of disturbance in the four different plots, where plot 1 was highly disturbed with few trees left ($n_1=48$), plots 2 and 3 showing decreasing amounts of logging and an increasing number of trees ($n_2=98$, $n_3=178$) and plot 4 showing no sign of disturbance or charcoal production with a total number of 364 trees (>1.3 m in height and >2 cm in diameter).

Along the gradient from plot one in the North to plot four in the South of the study area (Fig. 1) respiratory carbon fluxes from the soil did not show a significant trend in 2009 as hypothesized, neither did soil carbon content. Decreases in soil temperatures were found towards the undisturbed plots, whereas values for soil water content and charcoal content did not vary significantly. The only variable showing a strong distinction between the disturbed and undisturbed areas was leaf area index. Once again we explain an underestimation of LAI with the method applied to derive estimates, particularly in the disturbed plot. Our estimates of LAI only accounted for tree and shrub LAI, but not for grass LAI, a possible explanation for not having found a correlation between CO_2 efflux rates and LAI along the disturbance gradient.

The hypothesis of an increase in soil respiration, soil carbon content and soil water from the disturbed plot towards the undisturbed area were falsified. Similar efflux rates in the different plots were described by equal amounts of belowground carbon. Logging for charcoal production leads to a significant reduction in aboveground tree biomass, but no change in the belowground carbon (Chidumayo and Kwibisa, 2003; Chidumayo, 1991). Such decreases may have only been found if the site was transformed into an agricultural field (Zingore et al., 2005). Analogue values of soil water content along the gradient were explained by several measurements of high values of soil water in the disturbed area particularly above remnant charcoal kilns. The specific structure of charcoal is known for its high water holding capacity (DeLuca and Aplet, 2008) and therefore resulted in similar amounts of soil water.

Generally, values for carbon concentrations found in the top soils in our study (0.69%–3.33%) are in the same order of magnitude as those found by Walker and Desanker (2004) for comparable *miombo* woodlands in Malawi (1.2%–3.7%). Differ-

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ences in belowground carbon concentrations between intact and disturbed sites reported by Walker and Desanker (2004) could not be shown for Kataba forest. As suggested previously, an explanation may be the post-logging land management that allowed tree regeneration and grass invasion, whereas conversion to agricultural land causes extremely fast losses of soil organic matter as shown by Zignore et al. (2005) in Zimbabwe.

The expected decrease in charcoal content towards the undisturbed sites could not be shown, even though different amounts (not significant) of charcoal were found in the four plots. The observed charcoal concentration in the undisturbed area may be a result of the history of the site. Low intensity ground fires are common for *miombo* woodlands and important to sustain the forest structure (Kikula, 1986) resulting in the occurrence of charcoal in all plots.

The results of the soil respiration study were compared to EC measurements since the simultaneous application of several methods is a more robust way to estimate the carbon dynamics of an ecosystem (Knohl et al., 2008; Wang et al., 2010). Continuous flux measurements using the eddy covariance technique (Baldocchi and Meyers, 1998; Aubinet et al., 2000) have become one of the widely accepted tools amongst others e.g. biomass inventories (e.g. Mund et al., 2002), atmospheric inversions (e.g. House et al., 2003) and up-scaling of process measurements (e.g. Nouvellon et al., 2008; Kutsch et al., 2001) to study ecosystem carbon budgets.

In this study we evaluated respired carbon only. For our comparison between the bottom-up and top-down methods, we calculated R_{eco} by summing-up soil respiration, stem respiration (calculated from adjacent measures of LAI) and leaf respiration of the dominant species within the 50% fetch of the EC tower, along wind sectors associated with the measurement plots (Fig. 1). When discussing possible measurements errors in leaf area index before, we must stress that these errors may only be relevant for the vegetation below 1 m height and we do not expect large differences in leaf respiration between the C_4 -grasses and the C_3 -trees (Byrd et al., 1992).

Chamber measurements were conducted during daytime hours. Therefore we had to

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calculate daytime respiration from EC. For this purpose we used the same methods that are usually applied for the partitioning of EC fluxes into R_{eco} and gross photosynthesis (Reichstein et al., 2005; Papale et al., 2006; Lasslop et al., 2009), which are based on the temperature response curve of night-time respiration or the light response curve of NEE. Their drawback is that night-time EC measurements are very uncertain (Aubinet, 2008; Goulden et al., 1996; Moncrieff et al., 1997; Van Gorsel et al., 2007). However, since the topography of the area is very flat and due to the thorough quality filtering criteria we used prior to our data analysis, we assume that the night-time data we used are reliable.

R_{eco} values obtained from EC flux partitioning were within the standard deviation of the up-scaled process measurements during the two wet seasons. We found the best matching between the top-down approach (Fig. 9a and b – white dots) following Reichstein et al. (2005) and the bottom-up approach that accounted for spatial heterogeneity (Fig. 9b). The modified Reichstein et al. (2003) approach and the Lasslop et al. (2009) approach over- and underestimated up-scaled R_{eco} . Since these approaches only consider soil temperature as a modifier, we conclude that the strong influence of soil water content needs to be included in arid and semi-arid ecosystems (Epron et al., 2004) as is done in method 1. Remaining differences between the top-down and the bottom-up values may be explained by biweekly parameterization of the model, and the short term complexity of R_{soil} to rain pulses, as recently shown by Williams et al. (2009) for a savanna in South Africa, as well as by uncertainties in the up-scaling procedure of the bottom-up model.

5 Conclusions

A wide variety of variables were found to influence the temporal and spatial variation in soil respiration. We have shown that in order to evaluate temporal variation at a plot scale, models of R_{soil} in semi-arid ecosystems need to at least include soil water content and soil temperature.

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When comparing plots of different degrees of disturbance spatial heterogeneity was found to depend on soil properties such as carbon content. At high disturbance levels, plot-internal heterogeneity in R_{soil} depended on the disturbance itself, in particular on position and impact of charcoal kilns. To the contrary, lower disturbance resulted in a different pattern, with soil organic carbon content being the main driver. We assume that disturbance at high levels modified natural processes and increased heterogeneity. In the densest plot 4 with lowest disturbance spatial, heterogeneity was small.

Accounting for spatial heterogeneity up-scaling resulted in slightly but not significantly lower values for average plot efflux. The comparisons between top-down derived values for R_{eco} (EC technique) were within the range of bottom-up derived values (chamber up-scaling). Nonetheless, a considerable under- and overestimation was found in flux partitioning methods that used over-simple temperature models to extrapolate night-time fluxes to daytime, or using the daytime light response curve to estimate respiration. We suggest that both top-down methods and bottom-up methods should be applied in order to improve confidence of results obtained in future studies.

Appendix A

Abbreviations

CO ₂	carbon dioxide
LAI	leaf area index
R_{eco}	total ecosystem respiration
EC	eddy covariance
NEE	net ecosystem exchange
GPP	gross primary production
RPAW	relative plant available water
RSWC	relative soil water content
VPD	water vapour pressure deficit

SWC	soil water content
ANOVA	analysis of variance
R_{soil}	soil respiration
R_{leaf}	leaf respiration
R_{stem}	stem respiration
R_{snorm}	normalized soil respiration
T_{soil}	soil temperature
dbh	diameter at breast height
dtb	diameter at tree base

Acknowledgements. This study was funded as part of the CarboAfrica Initiative (EU, Contract No: 037132). We thank Manyando and Lumbala, the incredible strong helping hands in the field, the Max-Planck Institute for Biogeochemistry, in particular the field experiments group, Olaf Kolle, Martin Hertel, Kerstin Hippler and Karl Kübler for help during the setup and regular maintenance, technical knowledge and additional instruments installed at the site in Mongu, Zambia. E.-D. Schulze for providing additional institutional funding. We are thankful to Corinna Rebmann for assistance during EC data processing and comments while preparing the manuscript as well as Gitta Lasslop for running the data through a different algorithm to flux partition EC data. Comments of 3 anonymous reviewers helped severely to improve an earlier version of the manuscript.

The service charges for this open access publication have been covered by the Max Planck Society.

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Table 1. Description for the different codes of ground cover and the combination of the 3 most abundant ground cover types for each subplot and the finally used ground cover categories that were finally chosen. Several categories can be found in each plot, others are specific for a single plot, e.g. CFG in plot 4.

single code classification	single code description	categories	description of categories	occurrence (Plot No.)
A	tree	ECl	litter, grasses, moss	2,3,4
B	shrubs	EBI	litter, shrubs, moss	2,3,4
C	grasses	EBF	litter, shrubs, free ground	1,2,3,4
D	dead wood	EAB	litter, trees, shrubs	2,3,4
E	litter	EBC	litter, shrubs, grasses	1,2,3,4
F	free ground	ECF	litter, grasses, free ground	1,2,3,4
G	charcoal	EFI	litter, free ground, moss	2,3,4
H	herbs (local mats)	EAD	litter, trees, dead wood	2,3,4
I	moss	EAI	litter, trees, moss	2,3,4
		EBD	litter, shrubs, dead wood	3,4
		EDI	litter, dead wood, moss	3,4
		EAC	litter, trees, grasses	3
		ECD	litter, grasses, dead wood	3
		EAF	litter, trees, free ground	2
		ECH	litter, grass, herbs	1
		CHF	grasses, herbs, free ground	1
		EFH	litter, free ground, herbs	1
		CFG	grasses, free ground, charcoal	1

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Table 2. Categories for each of the 4 plots and the statistical results of the curve fits of soil respiration (R_{soil}) to soil water content (SWC) within each subplot. “**” indicate significant correlations between R_{soil} and SWC. Strong correlations were found for plot 4 where significance levels were not reached caused by insufficient amounts of data (2009 measurements only). Grey highlighted areas visualize the disturbed plot.

Site	Category	Categorial No.	Slope (a)	Intercept (b)	r^2	n	P
MTP1	FHE	1	0.79	1.46	0.58	7	0.02*
	CBE	2	0.64	-1.74	0.51	3	0.32
	HCF	3	0.38	1.44	0.4	7	0.07
	HCE	4	0.28	4.13	0.19	6	0.37
	CFE	5	0.55	2.6	0.61	6	0.04*
	EBF	6	0.36	2.9	0.18	6	0.39
	GCF	7	0.39	3.09	0.55	7	0.05*
MTP2	ECI	1	0.82	4.09	0.47	7	0.05*
	EBI	2	0.34	2.27	0.16	7	0.19
	EBF	3	0.67	3.22	0.41	7	0.09
	EAB	4	0.52	2.23	0.81	7	0.003*
	EBC	5	0.7	2.65	0.51	7	0.04*
	ECF	6	0.72	1.82	0.8	7	0.003*
	FIE	7	0.62	1.41	0.53	7	0.03*
	EAD	8	0.11	3.6	0.06	7	0.53
	FEA	9	0.79	2.41	0.57	7	0.02*
	EIA	10	0.89	1.04	0.85	7	0.0007*

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Table 2. Continued.

Site	Category	Categorical No.	Slope (a)	Intercept (b)	r^2	n	P
MTP3	ECI	1	0.36	2.46	0.29	8	0.09
	EBI	2	0.2	2.18	0.1	8	0.22
	EBF	3	0.47	2.97	0.33	8	0.1
	EAB	4	0.8	1.79	0.84	8	0.0008*
	EBC	5	0.88	2.34	0.86	7	0.0015*
	ECF	6	0.51	3.15	0.7	8	0.0054*
	FIE	7	0.62	2.99	0.61	8	0.01*
	EAD	8	0.55	2.1	0.69	8	0.0063*
	EIA	9	0.13	4.93	0.04	7	0.65
	DBE	10	0.64	2.75	0.28	8	0.09
	DIE	11	0.47	2.79	0.57	8	0.01*
	ACE	12	0.51	2.57	0.52	8	0.02*
	DEC	13	0.67	3.12	0.54	8	0.02*
MTP4	ABE	1	0.33	4.41	0.87	3	0.15
	ADE	2	0.06	4.05	0.98	3	0.06
	EBF	3	0.14	3.26	0.95	3	0.09
	EDI	4	-0.01	5.63	0.09	3	0.79
	EBF	5	0.23	4.76	0.89	3	0.14
	IEB	6	-0.04	6.18	0.33	3	0.6
	CBE	7	0.14	4.91	0.11	3	0.46
	IEA	8	0.11	4.6	0.84	3	0.18
	BED	9	0.1	5.43	0.99	3	0.01*
	FCE	10	0.22	5.26	0.98	3	0.05*
	ICE	11	0.42	5.06	0.96	3	0.07
MTP1 All Averaged			0.43	2.41	0.55	41	<0.0001*
MTP2 All Averaged			0.79	1.67	0.69	79	<0.0001*
MTP3 All Averaged			0.53	2.82	0.51	107	<0.0001*
MTP4 All Averaged			0.12	4.97	0.18	33	0.007*

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Table 3. Statistics and coefficients of the general linear model, including soil temperature and soil water content as primary factors influencing soil respiration on temporal time scales are given. n gives the amount of data available for each plot, p the significance level and c , d , h and i the plot specific coefficients. Grey highlighted is the disturbed plot.

Plot	n	r^2	p	c	d	h	i
1	173	0.34	0.000***	-0.43	-0.21	0.03	8.91
2	213	0.53	0.000***	-0.36	-0.19	0.04	7.54
3	325	0.47	0.000***	-0.28	-0.0006	0.03	2.85
4	108	0.09 ^a	0.01**	0.24	0.19	-0.005	0.33

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Table 4. Statistics for the various correlations between soil respiration and environmental variables are presented (see also Fig. 7). This includes correlation coefficients (r^2), significance levels (p) and amount of data used (n) as well as slope and intercept for significant relations. n.s. = not significant, n.a. = not available, grey highlighted areas visualize the disturbed plot.

Plot	Regression Variables	r^2	p	n	slope	intercept
1	R_{snorm} vs. C	n.a.	n.s.	91	n.a.	n.a.
	R_{snorm} vs. LAI	n.a.	n.s.	91	n.a.	n.a.
	C vs. LAI	n.a.	n.s.	91	n.a.	n.a.
2	R_{snorm} vs. C	0.27	0.000***	92	4.19	4.05
	R_{snorm} vs. LAI	0.14	0.000***	92	3.86	0.21
	C vs LAI	0.19	0.000***	92	0.58	-0.43
3	R_{snorm} vs. C	0.03	0.03*	115	1.32	5.03
	R_{snorm} vs. LAI	n.a.	n.s.	115	0.18	5.34
	C vs LAI	n.a.	n.s.	115	0.23	0.14
4	R_{snorm} vs. C	0.08	0.0028**	108	3.18	4.7
	R_{snorm} vs. LAI	0.03	0.049*	108	1.72	3.35
	C vs LAI	0.33	0.000***	108	0.5	-0.36

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Table 5. Descriptive and ANOVA statistics are shown for soil respiration values along the disturbance gradient. The grey highlighted lines show the disturbed plot where the non-highlighted values represent the undisturbed plots. Differences in average plot respiration were significant in 2008 without showing a clear trend. Plot 4 was observed in 2009 only.

Year/Season	Plot	average R_{snorm} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	standard deviation	coefficient of variation (%)	ANOVA p-Value
2008/Wet	1	4.94	1.31	26.51	0.000***
	2	6.54	2.00	30.59	
	3	6.53	1.85	28.38	
	4	n.a.	n.a.	n.a.	
2008/Dry	1	2.93	1.26	42.96	0.000***
	2	5.64	2.02	35.87	
	3	2.46	0.38	15.65	
	4	n.a.	n.a.	n.a.	
2009/Wet	1	5.80	2.54	43.88	0.26
	2	6.00	1.69	28.20	
	3	5.59	1.43	25.66	
	4	6.01	1.43	23.87	



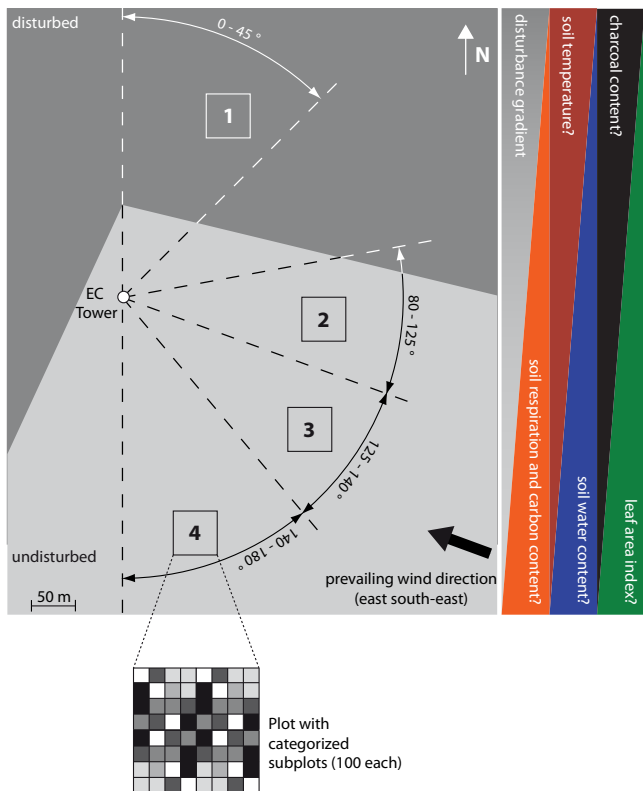


Fig. 1. Scheme of the site and experimental setup in Mongu (Zambia). The dark grey area represents the disturbed area driven by deforestation, burning and grazing. The light grey area represents the north western corner of Kataba forest reserve, established in 1973. The measurement plots, divided into subplots of different ground cover, were established along a disturbance gradient from North to South, with plot 1 being highly disturbed, 2 and 3 being slightly disturbed (edge effects) and 4 undisturbed in the core area of the forest reserve. The prevailing wind direction was east-southeast. All plots were located within the 50% fetch of the eddy covariance tower. Wind sectors in the direction of the inventory plots, used for the comparison of eddy covariance measurements to chamber measurements are shown. Coloured triangles are given to visualize hypothesized trends of the most important abiotic and biotic factors.

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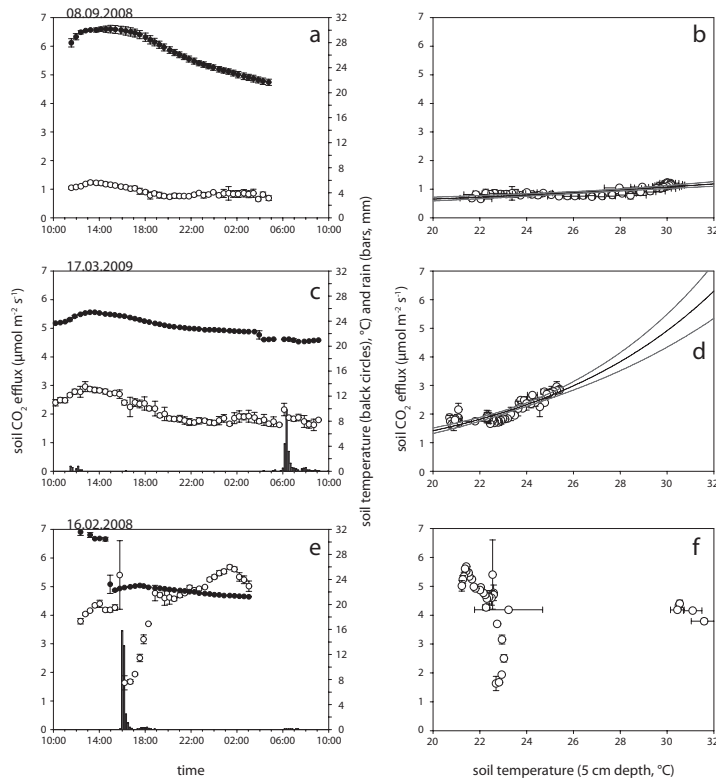


Fig. 2. Diurnal variation of soil respiration (R_{soil} , white circles \pm SD of three replicates) and soil temperature (T_{soil} , black circles \pm SD of three replicates) during the wet seasons 2008 **(a)** and 2009 **(c)** and the dry season 2008 **(b)** shown for a single subplot located in plot 2. Vertical bars show the occurrence and magnitude of rain events. The right panel shows the exponential response of R_{soil} to soil temperature (T_{soil}) at 5 cm depth. **(b)** 2008 Dry: $R_{\text{soil}} = 0.2449 \times e^{0.0493T_{\text{soil}}}$, $r^2 = 0.60$, $p < 0.0001^{***}$, $n = 41$; **(d)** 2009 Wet: $R_{\text{soil}} = 0.118 \times e^{0.1243T_{\text{soil}}}$, $r^2 = 0.78$, $p < 0.0001^{***}$, $n = 53$.

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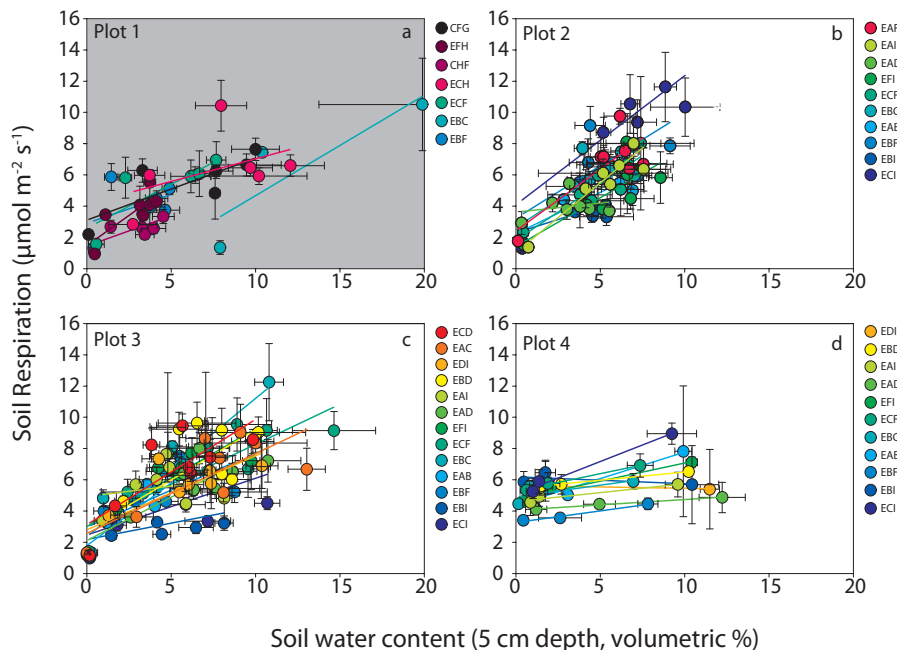


Fig. 3. Relation of R_{soil} , measured during the field campaigns 2008 and 2009, plotted against soil water content (SWC) at a depth of 5 cm along the disturbance gradient for each subplot (coloured) and plot. Detailed information on categorized subplots and statistics are given in Tables 1 and 2.

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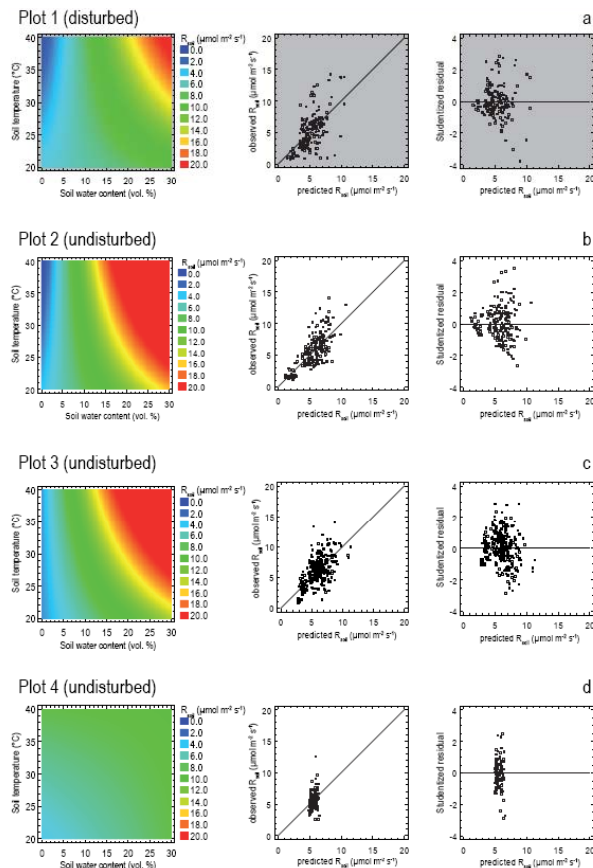


Fig. 4. General linear models explaining soil respiration using soil temperature and soil water content as predictors. **(a–d)** represent the 4 inventory plots. The first column shows the response of R_{soil} in relation to T_{soil} and SWC. The second column the predicted versus the observed respiratory values and the third column the associated residual plots. Plot 4 is slightly underrepresented due to a lack of data for the wet and dry season 2008.

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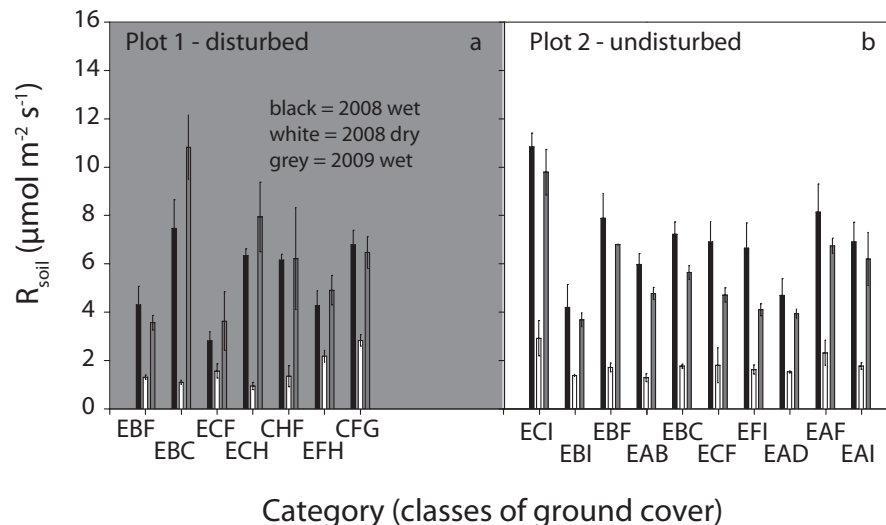


Fig. 5. Differences in averaged soil respiration are shown for subplots for the different years and seasons. Data for only 2 of the inventory plots are given, where **(a)** (grey highlighted) represents the disturbed area showing higher values of R_{soil} in 2009 (grey bars) compared to 2008 (black bars) and **(b)** represents the undisturbed area showing the exactly opposite result. Smallest efflux rates were always observed during the dry season (white bars). Categories are given according to Tables 1 and 2.

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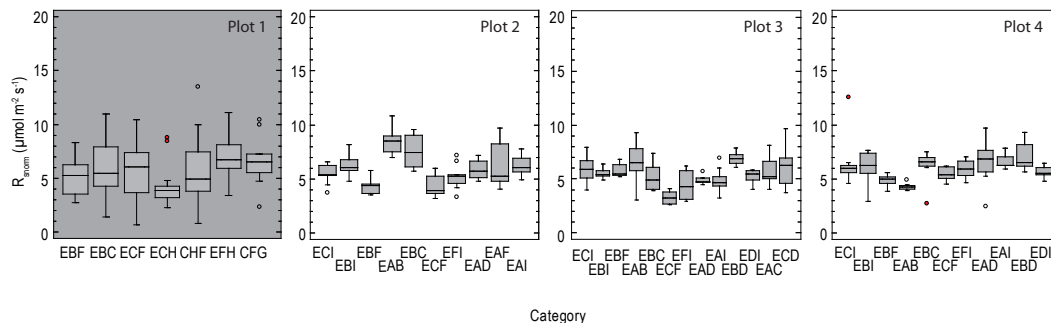


Fig. 6. Differences in subplot efflux rates in 2009 shown for each inventory plot (a–d representing plot 1–4). Average efflux rates deviated strongly between subplots. On the contrary, efflux rates of different subplots between plots showed similar values and vice versa. Variation in subplot specific efflux rates was highest in the disturbed plot 1 (a). Categories are given according to Tables 1 and 2.

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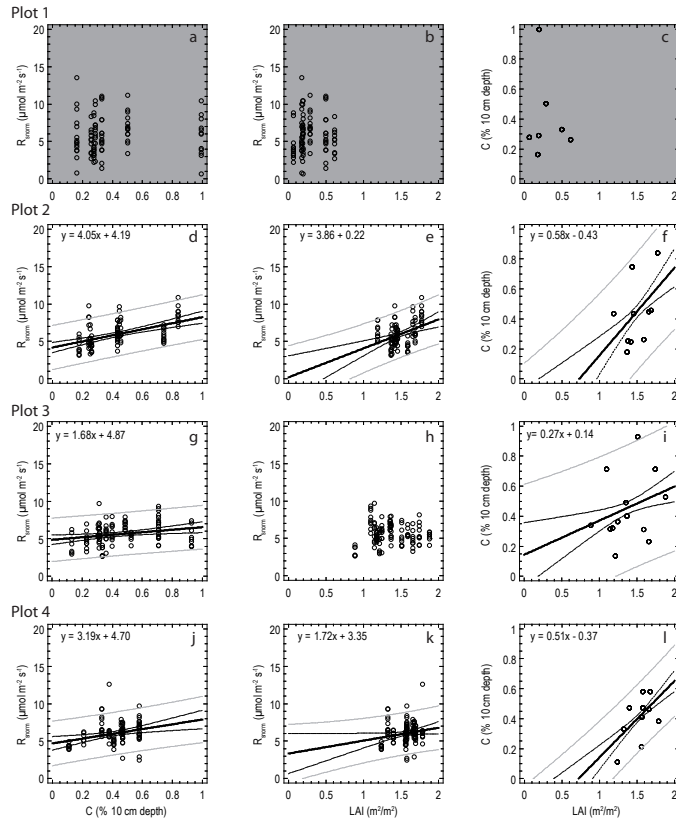


Fig. 7. The figure shows the relations between normalized soil respiration (R_{snorm}) and soil carbon content (10 cm depth) and leaf area index within each of the 4 inventory plots. Thick black lines represent the regression after applying a linear curve fit (statistics are given in Table 4). Thin black lines show the according 95% confidence intervals and grey thin lines represent the 95% prediction bands. No correlation was found for the disturbed plot 1. The last column shows the relation between belowground carbon content (10 cm depth) and leaf area index, respectively.

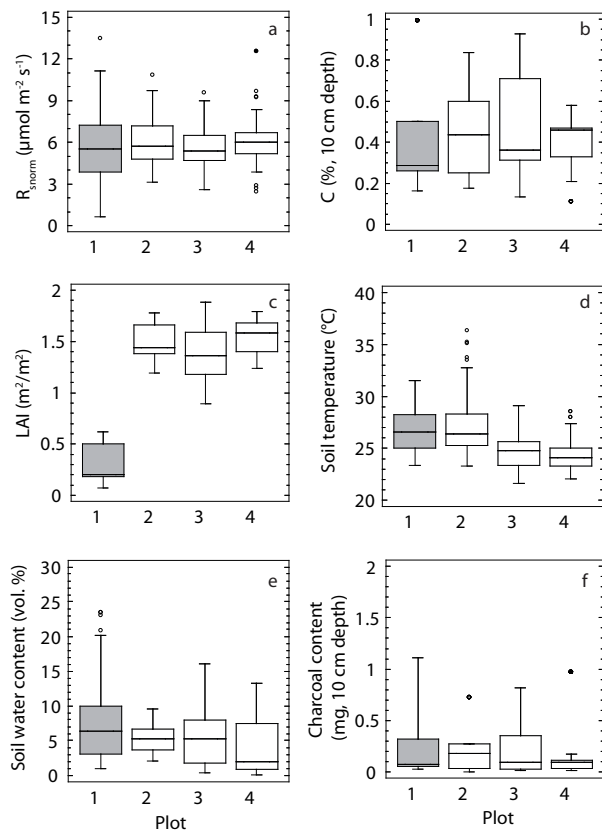


Fig. 8. Plot specific values for normalized soil respiration **(a)** and several biotic **(b and c)** and abiotic parameters **(d, e and f)** are shown to visualize between plot differences – 2009 only. Average values of the various variables in plot 1 (disturbed) did not deviate significantly from values derived for the three other plots (2–4, undisturbed). The only exception was shown for values of leaf area index. Filled dots represent outliers.

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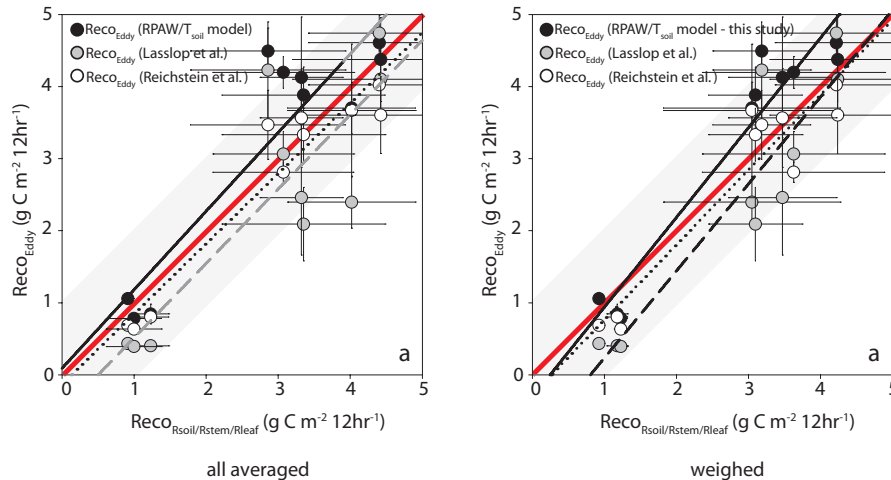


Fig. 9. Total carbon loss (g C m^{-2}) during 12 daytime hours (06:00 a.m.–06:00 p.m.) for each plot during the different seasons (wet season=high values, dry season=smaller values). Three different approaches were used to calculate daytime ecosystem respiration from eddy covariance data: 1: (black dots, black solid regression) a model, including the response of R_{eco} to relative plant available water (0–100 m) and soil temperature (5 cm depth) parameterized bi-weekly from high quality nocturnal data; 2: (grey dots, grey solid regression) a model recently developed by Lasslop et al. (2009); 3: (white dots, black dotted regression) were values of R_{eco} received from a gapfilling – and fluxpartitioning tool (Reichstein et al., 2003). Two different methods were used for the bottom-up approach (a) averaging all measurements of soil- and leaf respiration plus the calculated values of stem respiration and (b) accounting for spatial heterogeneity by the categorized soil CO_2 efflux plus leaf- and stem respiration. All bars are given \pm SD. The red line shows the 1:1 line, the grey highlighted area show the 20% deviation from the 1:1 line.

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