Biogeosciences, 7, 3459–3471, 2010
www.biogeosciences.net/7/3459/2010/
doi:10.5194/bg-7-3459-2010


Biogeosciences

# $CO_2$, $CH_4$ and $N_2O$ fluxes from soil of a burned grassland in Central Africa

**S. Castaldi**[1,5], **A. de Grandcourt**[2,6], **A. Rasile**[1], **U. Skiba**[3], **and R. Valentini**[4,5]

[1]Dipartimento di Scienze Ambientali, Seconda Università di Napoli, via Vivaldi 43, 81100 Caserta, Italy
[2]Centre de Cooperation Internationale en Recherche Agronomique pour le Developpement (CIRAD), Persyst, UPR80, TA B-80/D, 34398 Montpellier Cedex 5, France
[3]Centre for Ecology and Hydrology, Edinburgh, Bush Estate, Penicuik, Midlothian EH26 QB, UK
[4]Dept. of Forest Environment and Resources (DISAFRI), University of Tuscia, via S. Camillo de Lellis, 01100 Viterbo, Italy
[5]Euro Mediterranean Center for Climate Change, via Augusto Imperatore 16, 73100, Lecce, Italy
[6]Centre de Recherche sur la Durabilité et la Productivité des Plantations Industrielles, BP 1291, Pointe Noire, Republic of Congo

Received: 17 April 2010 – Published in Biogeosciences Discuss.: 1 June 2010
Revised: 24 October 2010 – Accepted: 25 October 2010 – Published: 8 November 2010

**Abstract.** The impact of fire on soil fluxes of $CO_2$, $CH_4$ and $N_2O$ was investigated in a tropical grassland in Congo Brazzaville during two field campaigns in 2007–2008. The first campaign was conducted in the middle of the dry season and the second at the end of the growing season, respectively one and eight months after burning. Gas fluxes and several soil parameters were measured in each campaign from burned plots and from a close-by control area preserved from fire. Rain events were simulated at each campaign to evaluate the magnitude and duration of the generated gas flux pulses. In laboratory experiments, soil samples from field plots were analysed for microbial biomass, net N mineralization, net nitrification, $N_2O$, NO and $CO_2$ emissions under different water and temperature soil regimes. One month after burning, field $CO_2$ emissions were significantly lower in burned plots than in the control plots, the average daily $CH_4$ flux shifted from net emission in the unburned area to net consumption in burned plots, no significant effect of fire was observed on soil $N_2O$ fluxes. Eight months after burning, the average daily fluxes of $CO_2$, $CH_4$ and $N_2O$ measured in control and burned plots were not significantly different. In laboratory, $N_2O$ fluxes from soil of burned plots were significantly higher than fluxes from soil of unburned plots only above 70% of maximum soil water holding capacity; this was never attained in the field even after rain simulation. Higher NO emissions were measured in the lab in soil from burned plots at both 10% and 50% of maximum soil water holding capacity. Increasing the incubation temperature from 25 °C to 37 °C negatively affected microbial growth, mineralization and nitrification activities but enhanced $N_2O$ and $CO_2$ production. Results indicate that fire did not increase post-burning soil GHG emissions in this tropical grasslands characterized by acidic, well drained and nutrient-poor soil.

*Correspondence to:* S. Castaldi
(simona.castaldi@unina2.it)

## 1 Introduction

Fire is a widespread phenomenon in the African continent. Its occurrence varies from "natural" events, based entirely on lightning as ignition source, to actively applied fires, based on rangeland management (Bothma and Du, 1996; Trollope, 1990). African savannas, which represent approximately half of the African land surface (Scholes and Walker, 2004), are mostly characterized by the co-dominance of trees and grasses (Sankaran et al., 2005) and are distributed in areas characterized by alternating dry and rainy seasons (Huntley and Walker, 1982; Scholes and Hall, 1996). Mean annual precipitation, duration of dry season, soil fertility and disturbance (fire, herbivory and cutting) are the key factors that determine the density of grasses, trees and shrubs (Sankaran et al., 2005; Bond, 2008). When the density of trees is below 10% of the total surface cover, the savanna environments are generally classified as tropical grasslands (Scholes and Hall,

1996). Sub-Saharan Africa grasslands occupy approximately 14.5 millions of $km^2$ and most of this area is affected by fire (White et al., 2000). Fire influences nutrient cycling patterns by modifying plant cover and biodiversity (Menault, 1977; Swaine et al., 1992; Sankaran et al., 2005) and by directly altering chemical, biological and physical properties of soil (Menaut et al., 1993; Andersson et al., 2004a, b). Enhanced rates of mineralization and nitrification have been reported in burned savannas at the beginning of the rainy season (Adedejii, 1983; Singh et al, 1991). Soil $NH_4^+$concentration was found to increase in savanna and shrubland soils after burning (Christensen, 1973; Singh, 1994; Castaldi and Aragosa, 2002) in consequence of organic matter combustion and heath-induced release from organo-mineral soil complexes (Raison, 1979; Kovacic et al., 1986; Prieto-Fernandez et al., 2004 ). Andersson et al. (2004b) measured increased values of $NH_4^+$ and dissolved organic N and C in savanna soil after burning, resulting in higher rates of mineralization and nitrification when soil water content enabled microbial activation. This generally occurs in the event of rain in seasonally-dry ecosystems and is often accompanied by pulses of $NO_x$, $N_2O$, $CO_2$ emissions (Davidson et al., 1993; Breuer et al., 2000; Garcia-Montiel et al., 2003; Butterbach-Bahl et al., 2004; van Haren et al., 2005). Duration and magnitude of these gas pulses vary in relation to frequency and intensity of fire occurrence, plant cover, soil nutrient status and soil matrix potential (Pinto et al., 2002; Rees et al., 2006; Williams et al., 2009). Gas emissions are generally enhanced by wetting-drying cycles (Davidson et al., 1993; Mills and Fey, 2004; van Haren et al., 2005; Jenerette et al., 2008).

Fire may influence the rate of soil $CO_2$ efflux by changing the contribution of autotrophic respiration to total soil $CO_2$ emissions and by modifying the amount of soil organic matter in the top soil. Burning of grasslands often results in earlier growth of grass in the growing season, increasing the length of the biomass growth period (Ojima et al., 1994). On the one hand, by maintaining the dominance of grasses over shrubs and trees, fire-based management of grassland increases the detritus in the upper soil centimetres as grasses have a shallower rooting system as compared to shrubs and trees (Ansley et al., 2002). On the other hand, frequent fires (yearly to once every three years) have been reported to lead to a decline in soil C, as a result of fire combustion of above-ground biomass, leaf litter and soil organic matter in the upper few centimetres (Fynn et al., 2003; Knicker, 2007). Furthermore, fire might influence gas diffusivity by changing soil porosity and water balance (Snyman, 2003; Knicker, 2007), which affects soil potential for $CH_4$ oxidation. Most of the available studies on tropical seasonally-dry ecosystems indicate that fire increases the net consumption of $CH_4$ (Castaldi et al., 2006).

Savannas are generally regarded as modest carbon sinks (per surface unit area) (Bombelli et al., 2009), or, where fire frequency is high, they are considered to have an almost neutral carbon balance (Saarnak, 2001, Bombelli et al. 2009). However, data on post burning variations of soil greenhouse gas fluxes in tropical environments are relatively scarce and do not give a clear and univocal answer (Levine et al., 1996; Zepp et al., 1996; Andersson et al., 2004b; Michelsen et al., 2004, Castaldi et al., 2006). The present work investigates the impact of fire on post-burning fluxes of $CO_2$, $CH_4$ and $N_2O$ from a grassland ecosystem of central-western Africa. Specific objectives were to verify (a) whether burning increases the availability of extractable N substrates and stimulates microbial growth, microbial activity, $CO_2$, $N_2O$ and NO production, (b) how simulated rain events affect fluxes of $CO_2$ and $N_2O$ in burned soils, and (c) whether fire enhances soil $CH_4$ sink.

For this purpose, gas fluxes were measured in the field one month and eight months after an induced fire. A rain simulation experiment was also carried out in burned and unburned plots. Lab experiments were performed with soil from experimental plots, incubated at different soil water contents and temperatures. The study site was in Congo Brazzaville in view of the presence of extended grassland areas subjected to frequent (yearly) man induced fires.

## 2 Materials and methods

### 2.1 Study site

The research site is located in the littoral region of Congo, close to Tchizalamou (4°17′20.61″13 S and 11°39′22.78″ E, Kouilou district, 82 m a.s.l). The region is covered by a forest-savanna mosaic situated between the coastline and the Mayombe forest (Favier et al., 2004). The present grass and shrub savannas result from two interacting factors: seasonally-dry climate and expansion of populations practising savanna burning. The climate of the Tchizalamou area is a two-season transition equatorial type, characterized by a long dry and cloudy season from mid-May to mid-October, followed by a rainy season from mid-October to mid-May. An optional short dry season may occur around mid-February to mid-March. The mean annual rainfall is about 1200 mm and the annual temperature about 25 °C, with seasonal variations of ca. 5 °C (Pointe Noire airport meteorological station 1982–2001). The herbaceous layer in grasslands is dominated by taller Poaceae such as *Loudetia simplex*, *Loudetia arundinacea*, or *Andropogon shirensis* with some occurrence of short Poaceae, Joncaceae and Cyperaceae (e.g., *Ctenium newtonii*, *Bulbostylis laniceps*). *Loudetia simplex* makes up more than 50% of the above-ground biomass, that reached about 3.8 Mg $ha^{-1}$ of dry matter at the end of the rainy season in 2008 (de Grandcourt et al., in preparation). Some shrubs of 1–2 m height are present, in particular *Annona arenaria* (less than 5 individuals $ha^{-1}$). The soils are Ferralic Arenosols (FAO classification), homogeneous in the landscape in terms of colour (greyish in upper soil layers to ochre in deep layers), texture (the sand

content is >85%), structure (always distinctive), and chemical composition (CEC $<0.5\,cmol_c\,kg^{-1}$ whatever the soil layer). These soils have a low clay content, are poor in nutrients and therefore unsuitable for agricultural purposes. Similar soil characteristics are found in most of the coastal region of central Africa (Kouilou region in Republic of Congo, coastal Gabon). The studied area is subjected to extensive fires every year, between mid-June and mid-July; fires may also occur during the short dry season in February. Fire generally spreads very rapidly and with low intensity. No agriculture or cattle grazing are conducted in the grasslands; the only human activity that occurs is the mushroom harvest at the beginning of the wet season. The soil in the study site presents a bulk density of $1.43\,g\,cm^{-3}$ and a water-holding capacity of 20%.

### 2.2 Experimental design

Two intensive experimental campaigns were organized, one starting one month after the day of burning (11 June 2007), during the dry season, and the other eight months after burning, in February 2008. This latter period corresponded to a particularly severe "short dry season", between mid-January to mid-April during a period generally regarded as the "wet season". At the moment of burning the grassland still had approximately 20% of green biomass. As the area is subjected every year to big fires, an area of about 1/2 hectare was isolated from fire by burning preventively a perimeter of vegetation around it, in order to create an "unburned treatment".

To simulate dry-wet cycle events, a $20\,m^2$ area was rain-sheltered with a transparent plastic tent, mounted at a height of two meters (to limit sun shading and temperature increase) in each treatment (unburned and burned). The purpose of the tent was to partially limit the input of rain on the plots in the 15 days before the beginning of gas sampling. Rain simulation was performed with 30 mm of water (tap water taken in the laboratory just before use). This amount of water corresponds to a typical large rain event, based on the analysis of rain events occurring at the station in the two previous years. Each rain-sheltered area, was divided into 4 plots ($2\,m \times 2.5\,m$), three of which were watered in different moments before the starting of gas sampling (15, 7, 1 day before gas sampling). One subplot in each treatment under the tent was left unwatered. In order to verify the influence of the tent on gas fluxes and on some key soil characteristics (water content and temperature), another subplot outside the tent was left unwatered.

### 2.3 Field GHG flux sampling and measurements

$CO_2$, $N_2O$ and $CH_4$ fluxes were measured from each plot on 4 replicates. In order to measure $N_2O$ and $CH_4$ fluxes, we used closed static chambers (Hutchinson and Mosier, 1981; Smith et al., 1995). These were made of PVC collars (7 cm high with a diameter of 15 cm), inserted in the soil to about 5 cm depth in a slot previously dug by a metal cutting ring, and chamber lids (20 cm high with a diameter of 15 cm) provided with a 2-way stopcock sampling port. To determine $N_2O$ and $CH_4$ fluxes, gas (20 ml) was sampled from 9 a.m. to 12 a.m., using gas-tight syringes, from the chamber headspace at 0, 20 and 60 min after closure; it was immediately stored in pre-evacuated gas-tight vials, which were sealed with thermal glue and shipped within a month from gas sampling to the Department of Environmental Sciences (DSA-SUN,ITALY) for gas chromatographic analysis. Flux rates were determined via linear regression of the three sampling points (0, 20, 60 min) for each chamber and by applying a temperature and pressure correction. The minimum detectable flux over a period of 60 min was $0.10\,mg\,N_2O\,m^{-2}\,d^{-1}$ and $0.07\,mg\,CH_4\,m^{-2}\,d^{-1}$. The analytical precision of the GC for standards at ambient concentration was approximately 1.5%, using one standard deviation as a measure of mean error. Any flux below these reported detection limits was assigned a value of zero. Soil temperature (HI93510 thermometer, Hanna Instruments Canada Inc., Laval, Quebec) and soil water content (ThetaProbe ML2, Delta-T Device Ltd, Cambridge, UK) were measured in correspondence of each chamber (0–10 cm depth), 5 cm from the chamber edge, at each sampling date.

Soil respiration (Rs) was measured using the Li 8100 soil respiration infrared gas analyzer system with a 8 cm-diameter chamber (LiCor Inc, Lincoln, NE, USA) which was placed on collars (7 cm high, 4 collars per each plot) inserted in the soil to a depth of 5 cm inside the PVC collars used for $N_2O$ and $CH_4$ fluxes measurements. The increase of the $CO_2$ concentration was measured over an interval of 2 minutes (including a dead band of 30 seconds) starting at the ambient $CO_2$ concentration. Soil temperature at 0-40 cm depth was monitored simultaneously with soil $CO_2$ efflux using a thermocouple penetration probe (Li6000-09 TC, LiCor Inc) in the vicinity of the soil respiration chamber. This temperature value was used to normalize soil respiration values at 25 °C, using the temperature function: $R_{(T)} = R_{(25°)} \cdot Q_{10}^{\frac{(T-25)}{10}}$, with a $Q_{10}$ value equal to 2.78, determined from a dataset of soil respiration measured on the site since 2006 (Caquet et al., in preparation). This normalization was used to compare the effect of wetting treatments independently from temperature effects on soil respiration. In fact, soil respiration was measured during different hours of the day depending on the daily experimental load with a variation of soil temperature in a range of 4.2 °C (measured from from 9 a.m. to 5 p.m.) in the first campaign and 2.7 °C (measured from from 9 a.m. to 1 p.m.) in the second campaign. The volumetric soil water content in the topsoil layer (0–6 cm) was monitored just after respiration measurements at 5 cm from chamber edge.

Gas fluxes were measured at least five times within two weeks in all plots (unburned and burned; unwatered, and watered 1, 7 and 15 days before starting).

### 2.4 Soil sampling

Soil was sampled at 0–10 cm depth at the end of the two campaign periods from unburned and burned control plots (unwatered) by taking 4 soil cores from each plot. The soil samples were immediately sieved (2 mm mesh), air-dried (2 day max required) and shipped to DSA-SUN and the Centre for Ecology and Hydrology (CEH, UK) for subsequent analyses.

### 2.5 Laboratory incubations

Two laboratory experiments were set up. In the first (at DSA-SUN), soil samples from the two treatments were analysed for microbial biomass, net N mineralization, net nitrification, $N_2O$, NO and $CO_2$ emissions under different soil water and soil temperature regimes. For this purpose, 50 g of sieved soil samples were repacked into columns (10 cm height, 5.5 cm inner diameter, the volume occupied by the soil about 50 $cm^3$, bulk density $1.00 \pm 0.07$ and $1.03 \pm 0.1\,g\,cm^{-3}$, for unburned and burned soil, respectively) that were incubated in half-litre flasks (on triplicate). Soils were incubated for 15 days at 0, 25%, 50%, 100% of maximum water-holding capacity, $WHC_{max}$, ($WHC_{max}$ 33% for burned and 37% for unburned soil measured on repacked sieved soil columns) and at two temperatures (25 °C and 37 °C). In order to observe the pulse effect of water addition on dry soil, pre-incubation was omitted. The flasks were kept open and water loss was corrected every day by gravimetrical determination. Gas fluxes were measured on days 0, 1, 3, 10 and 15, by closing the flasks with air-tight lids and sampling gas at $t_0$ and after 24 h. At the beginning and at the end of the incubation (15 days), soil mineral N was determined to quantify mineralization and nitrification net rates; soil microbial biomass was quantified at the end of the experiment.

For the second incubation experiment (at Centre for Ecology and Hydrology, Edinburgh), sieved soil samples (100 g on triplicate) repacked into clear Perspex columns (20 cm height, 5.5 cm inner diameter, volume occupied by soil around 100 $cm^3$) were incubated at 25 °C at 10% and 50% of $WHC_{max}$. NO emissions were measured one hour, 5 days and 7 days after water addition, using a gas flow-through system described in details by Dick et al. (2001). NO was analysed by chemiluminescence (42C model, Thermo-Environmental Instrument) and $O_3$ by UV absorption (427 model, Thermo-Environmental Instrument). $N_2O$ fluxes were determined in the same day (30 min after NO flux determination) closing the columns for 30 minutes and sampling 20 ml of gas from the column headspace at $t_0$ and $t_{30}$ min. $N_2O$ concentration in the samples was determined by gas chromatography. Soil cores were left uncapped in between gas sampling events and losses of water were corrected everyday by gravimetrical determination

### 2.6 Analytical technique

Soil mineral N was extracted with 0.5 M $K_2SO_4$ (1:4 soil extractant v/v) and filtered with Whatman filter no. 42. $NH_4^+$ and $NO_3^-$ were then determined on extracts by potentiometric analysis using specific electrodes for $NH_4^+$ (Model Orion 9512) and $NO_3^-$ (Model Orion 9707). Soil total carbon and nitrogen content were determined on homogenized soil sample by flash combustion-gas chromatography on a NCS-soil Thermo FlashEA 1112. Net N mineralization and net nitrification rates over 15 days were calculated respectively as the difference between total mineral N ($NH_4^+$ + $NO_3^-$) or nitric N, measured after 15-day incubation and at $t_0$. The spectrophotometric ninhydrin method developed by Moore and Stein (1954) was used to quantify $\alpha$-amino-N in soil extracts (soil: extract 1:5) using 0.5 M $K_2SO_4$. This procedure enables the quantification of soluble proteins, aminoacids and molecules containing $\alpha$-amino-groups. A fumigation-extraction method was used in order to estimate the $\alpha$-amino-N fraction associated with soil microbial biomass. Soil (5 g) was fumigated for 24 h with chloroform. The fraction of the cell constituents, made available by fumigation, was extracted by shaking the soil with 20 ml of 0.5 M $K_2SO_4$ for 1 h and filtering the suspension with paper filter (Whatman no. 42). The ninhydrin-N deriving from the biomass was calculated as µg ninhydrin-N $g^{-1}$ dry soil of the fumigated samples minus the µg ninhydrin-N $g^{-1}$ dry soil of the unfumigated samples. By using this value, the µg biomass N $g^{-1}$ was calculated using a conversion factor of 62 (Ocio and Brookes, 1990).

$CH_4$, $N_2O$ and $CO_2$ determinations on field and laboratory gas samples were made at DSA-SUN using a gas chromatograph (Fison series 800) equipped with an electron capture detector (ECD) maintained at 280 °C and a flame ionization detector (FID) set up to analyse the three gases on the same sample, using a frontflush and a backflush system (Castaldi et al., 2004). Column and precolumn were stainless steel packed with Porapak Q, both maintained at 60 °C. $N_2$ was used as carrier gas (flow rate 40 $cm^3\,min^{-1}$). The injection port was provided with a 2-ml loop. $N_2O$ analysis at CEH were done using a gas chromatograph (Hewlett Packard, 5890) equipped with an electron capture detector kept a 320 °C, columns were stainless steel packed with Porapak Q (oven 60 °C) and Ar/$CH_4$ was used as carrier at a flow rate of 40 ml $min^{-1}$. Standards were injected every 20 samples to allow for GC drift.

### 2.7 Statistical analyses

As the same site was sampled over consecutive days, a two-way "repeated measurements" analysis of variance (ANOVA) was used to determine differences in gas fluxes, considering treatment and season as sources of variation. When the difference was significant ($P < 0.05$) an "all pairwise" comparison was carried out using the "Student

**Table 1.** A selection of soil chemical characteristics of the unburned and burned plot soils measured during the first (one month after burning) and second field campaign (eight months after burning) for the top 10 cm of soil. Different superscript letters indicate significant differences (two-Way ANOVA, $P < 0.005$) among values in the same row.

| | 1st campaign | | 2nd campaign | |
|---|---|---|---|---|
| | Unburned | Burned | Unburned | Burned |
| Bulk density | $1.43 \pm 0.10$ | | | |
| pH | $3.65^{a} \pm 0.03$ | $3.73^{a} \pm 0.01$ | | |
| Total soil C (%) | $0.95^{a} \pm 0.07$ | $1.17^{a,b} \pm 0.99$ | $1.53^{b} \pm 0.22$ | $2.03^{b} \pm 0.30$ |
| Total soil N(%) | $0.06^{b} \pm 0.01$ | $0.08^{b} \pm 0.01$ | $0.02^{a} \pm 0.03$ | $0.26^{c} \pm 0.11$ |
| $\mu g\, NH_4^+$-N $g^{-1}$ d.s. | $2.72^{b} \pm 0.01$ | $3.44^{b} \pm 0.70$ | $0.14^{a} \pm 0.19$ | $5.41^{c} \pm 0.23$ |
| $\mu g\, NO_3$-N $g^{-1}$ d.s. | $0.34^{a,b} \pm 0.07$ | $0.38^{b,c} \pm 0.04$ | $0.18^{a} \pm 0.10$ | $0.58^{c} \pm 0.16$ |
| a-amino-N $\mu g$ N $g^{-1}$ d.s. | $13.50^{a} \pm 5.92$ | $26.42^{c} \pm 1.64$ | $21.71^{b} \pm 0.28$ | $27.68^{c} \pm 0.92$ |
| Volumetric water content (%)* | $3.6^{a,b} \pm 0.2$ | $3.9^{b} \pm 0.2$ | $3.8^{a,b} \pm 0.1$ | $2.8^{a} \pm 0.2$ |
| Soil temperature °C* | $26.7^{a} \pm 1.2$ | $26.5^{a} \pm 1.2$ | $26.7^{a} \pm 1.2$ | $26.9^{a} \pm 0.6$ |

* average of 5 days of field measurements taken during 2 weeks of campaign

Newman-Keul test". When normality test failed, a Kruskal-Wallis ANOVA on ranks was performed. Simple linear regressions, multiple linear regression and non- linear regression analysis were performed to find the relationship between independent and dependent variables (Sigma Stat, Jandel Scientific). To test for significant differences between slopes and intercepts of two different linear regressions, an analysis of covariance (ANCOVA) by the GLM procedure was performed using SAS/STAT 9.00 (SAS Institute Inc, Cary, NC, USA). Significant differences were at the $P < 0.05$ level.

## 3 Results

### 3.1 Soil parameters

The analysed soil was characterized by an acidic pH, slightly higher in the burned plots, and relatively low content of total C and N (Table 1). Total C increased in both treatments after eight months but no significant difference was observed between burned and unburned plots. Total N was significantly higher after eight months in burned plots, while one month after burning it was equally low in both treatments (Table 1). $NH_4^+$-N was the dominant form of soil mineral N in both sampling campaigns (Table 1), and it was slightly higher in burned plots than in controls (Table 1). The soil content of extractable organic N, measured as $\alpha$-amino-N (aminoacids, peptides, proteins, etc), was much higher than mineral N in both sampling periods, and it was significantly higher in burned plots (Table 1). Soil water content (average of five sampling days over 2 weeks of campaign) measured in unwatered plots was extremely low during both campaigns and, as also observed for soil temperature, did not change significantly between treatments (Table 1, Fig. 1). The rain-sheltering tent did not significantly influence soil water content and temperature in both campaigns, as no significant difference ($P > 0.05$ two-way ANOVA) between datasets obtained outside and inside the tent was observed for these two variables

When the rain event was simulated, the maximum soil water-filled pore space (WFPS), measured in the top 10 soil centimetres, was approximately 42.8% during the first campaign and 51% during the second campaign (Fig. 1). Soil WFPS decreased rapidly after water addition, going back to values comparable to the control plots within 10 days, in the first campaign, and 7 days, in the second campaign (Fig. 1), with no significant difference between burned and unburned treatments (Fig. 1).

### 3.2 Soil respiration

As no difference between $CO_2$ effluxes measured from unwatered controls outside and inside the tent was found, average daily fluxes of soil respiration were calculated using all the replicates from unwatered plots. The average daily soil respiration, not normalized for temperature, was $7.8 \pm 0.3$ mg of $CO_2\, m^{-2}\, d^{-1}$ (unburned) and $5.6 \pm 0.1$ (burned) mg of $CO_2\, m^{-2}\, d^{-1}$ (calculated from 12 days of measurements) one month after burning. Eight months after burning average daily soil respiration was $11.2 \pm 0.6$ mg of $CO_2\, m^{-2}\, d^{-1}$ (unburned) and $11.8 \pm 0.9$ (burned) mg of $CO_2\, m^{-2}\, d^{-1}$ (calculated from 6 days of measurements). The increase in soil respiration observed after eight months, for both treatments, was statistically significant ($P < 0.05$ using a two-way ANOVA). The difference between treatments was statistically significant ($P < 0.05$ using a two-way ANOVA) one month after burning (first campaign) but not after eight months. Watering induced a pulse of $CO_2$ emission, which peaked in the first day after water addition and decreased afterwards, getting back to control (unwatered) levels within 10 days and 7 days in the 1st and 2nd campaign, respectively, following the same pattern observed for

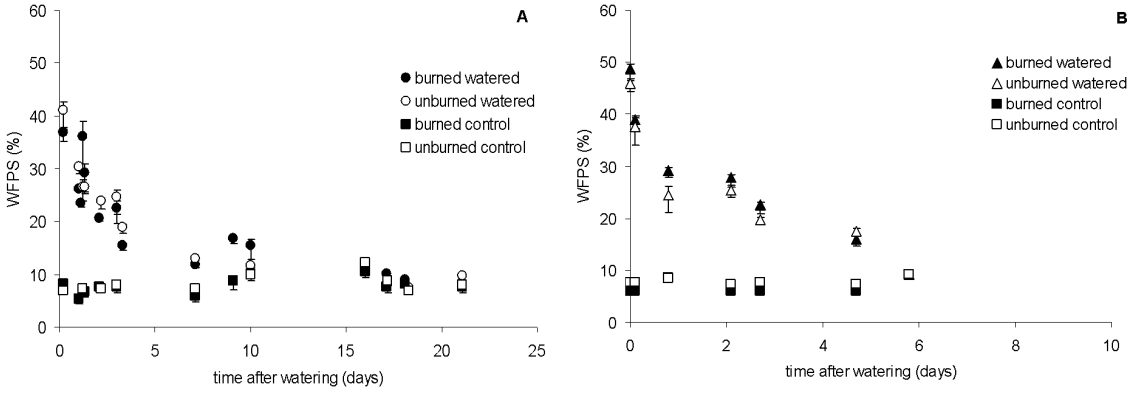


**Fig. 1.** Soil water filled pore space (%) (0–10 cm soil depth) in function of time after watering (days) during the 1st campaign **(A)** one month after burning and the 2nd campaign **(B)** eight months after burning. The vertical bars correspond to one standard error ($n = 3$ to 12).

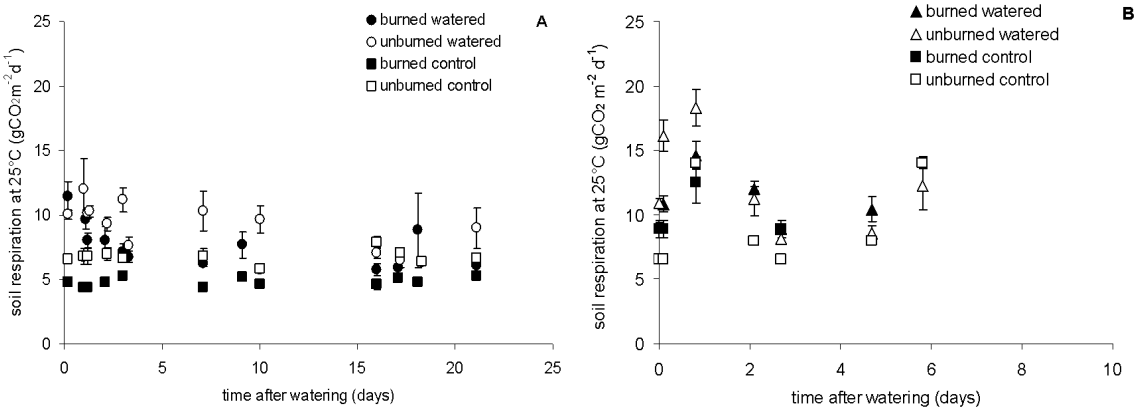


**Fig. 2.** Soil respiration normalized at 25 °C, using a $Q_{10}$ of 2.78 ($g\,CO_2\,m^{-2}\,d^{-1}$) in function of time after watering during the 1st campaign **(A)** one month after burning and the 2nd campaign **(B)** eight months after burning. The vertical bars correspond to one standard error ($n = 3$ to 9).

soil WFPS (Figs. 1 and 2). Comparing data sampled in the same days shows that $CO_2$ emissions from unburned watered plots were usually significantly higher than emissions from burned watered plots one month after burning (Fig. 2a).

The normalized soil respiration increased linearly with the increase in soil water-filled pore space (WFPS) in both campaigns (Fig. 3). The slopes of the regression lines, which fitted the data from burned and unburned plots (equations reported in Fig. 3), were not significantly different ($P > 0.05$, ANCOVA) in either campaigns, whereas the y-axis intercept was significantly higher in unburned than in burned plots ($P < 0.0001$, ANCOVA) in both campaigns. In the present study, the applied normalization to soil respiration data, using $Q_{10}$ correction, did not affect the result. In fact, both normalized and raw data of soil respiration increased linearly with increasing soil WFPS, moreover, the normalization did not significantly alter differences in slopes and intercepts between burned and unburned plots.

No significant difference was observed between the frequency distribution of soil respiration values for unburned and burned treatments in both campaigns, and the data were normally distributed (Kolmogorov-Smirnov test)

### 3.3 Methane fluxes

$CH_4$ flux in unwatered plots (average of data from outside and inside the tent) one month after burning (1st campaign) resulted in a net emission in unburned plots ($0.70 \pm 0.62\,mg\,CH_4\,m^{-2}\,d^{-1}$) and in a net, although weak, sink in burned plots ($-0.34 \pm 0.27\,mg\,CH_4\,m^{-2}\,d^{-1}$).The difference was statistically significant ($P < 0.05$). Eight months after burning (second campaign), the site acted as a weak net $CH_4$ sink in both unburned ($-0.40 \pm 0.57\,mg\,CH_4\,m^{-2}\,d^{-1}$) and burned ($-0.75 \pm 0.75\,mg\,CH_4\,m^{-2}\,d^{-1}$) plots, with no significant difference between treatments. $CH_4$ fluxes were highly variable, as indicated by the flux distribution reported in Fig. 4. A significant difference in the distribution of $CH_4$ fluxes, among flux-size classes, was observed for the two treatments one month after burning (Fig. 4). In fact, a clear reduction in

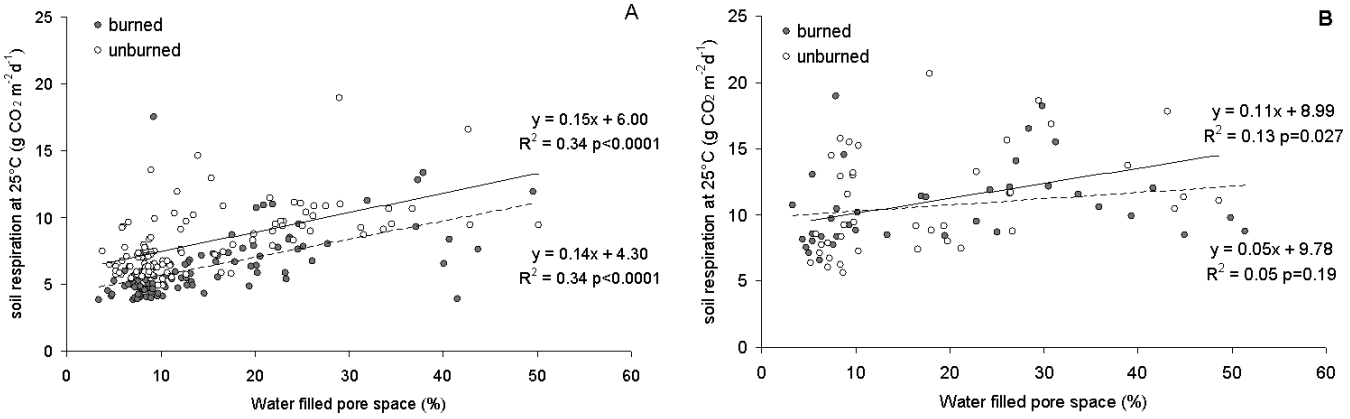


**Fig. 3.** Soil respiration normalized at 25 °C, using a $Q_{10}$ of 2.78 ($g\,CO_2\,m^{-2}\,d^{-1}$) in function of water filled pores space (%) during the 1st campaign (A) one month after burning and the 2nd campaign (B) eight months after burning. Each point refers to one single chamber measurement. Lines (continuous unburned, dotted burned) represent linear regressions indicated by the correspondent equations.

the frequency of fluxes above 0.80 mg $CH_4\,m^{-2}\,d^{-1}$ and an increase of fluxes below 0 mg $CH_4\,m^{-2}\,d^{-1}$ was observed in burned plots (Fig. 4). Eight months after burning, the frequency distributions in the two treatments were similar (Fig. 4). Analysing the relationship between soil water-filled pore space and $CH_4$ fluxes, obtained including the watered plots (Fig. 5), we observe that in the first month after burning most of the fluxes were positive (net emission) in unburned plots and negative (net consumption) in burned plots for values of WFPS below 15%. Most of the measured fluxes were positive in both treatments above this threshold. Eight months after burning there was no clear difference between fluxes measured in either treatment. In contrast to what observed in the first campaign, the increase in soil WFPS did not induce a clear shift from net $CH_4$ sink to net $CH_4$ source in the second campaign, although above 10% of WFPS the frequency of net $CH_4$ emissions increased (Fig. 5).

### 3.4 Nitrous oxide fluxes

Nitrous oxide fluxes were low, and in the second campaign many of the analyzed fluxes were below the detection limit of the technique used. The daily average $N_2O$ flux, calculated from 5 days of measurements in both campaigns, was $0.02 \pm 0.13$ mg of $N_2O\,m^{-2}\,d^{-1}$ in unburned plots (range $-0.7$ to 0.6) and $0.02 \pm 0.10$ mg of $N_2O\,m^{-2}\,d^{-1}$ in burned plots (range $-0.4$ to 0.5) one month after burning; $-0.03 \pm 0.11$ mg of $N_2O\,m^{-2}\,d^{-1}$ in unburned plots (range $-0.6$ to 0.0) and $0.0 \pm 0.4$ mg of $N_2O\,m^{-2}\,d^{-1}$ in burned plots (range $-0.1$ to 0.2) eight months after burning. A slight shift of flux frequency distribution towards more positive (emission) fluxes was observed in burned plots, compared with unburned ones (Fig. 6). The average flux in the two treatments, however, was not significantly different. Water addition produced no detectable increase of $N_2O$ emissions (data not shown) in both unburned or burned plots.

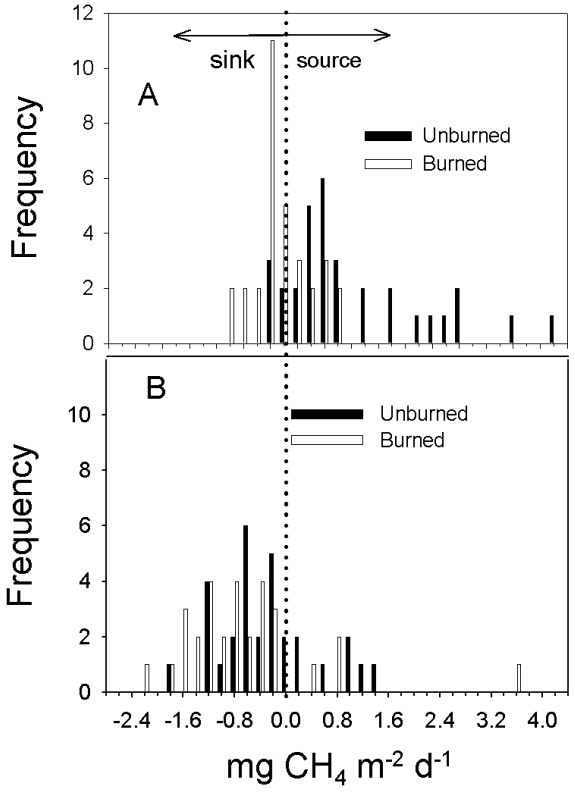


**Fig. 4.** The frequency distribution of single-chamber estimates of $CH_4$ fluxes ($mg\,CH_4\,m^{-2}\,d^{-1}$) measured in unburned and burned plots (no water treatment) during the 1st campaign (A) one month after burning ($n = 32$) and the 2nd campaign (B) eight months after burning ($n = 30$). The range of each size class interval is 0.2 mg $CH_4\,m^{-2}\,d^{-1}$.

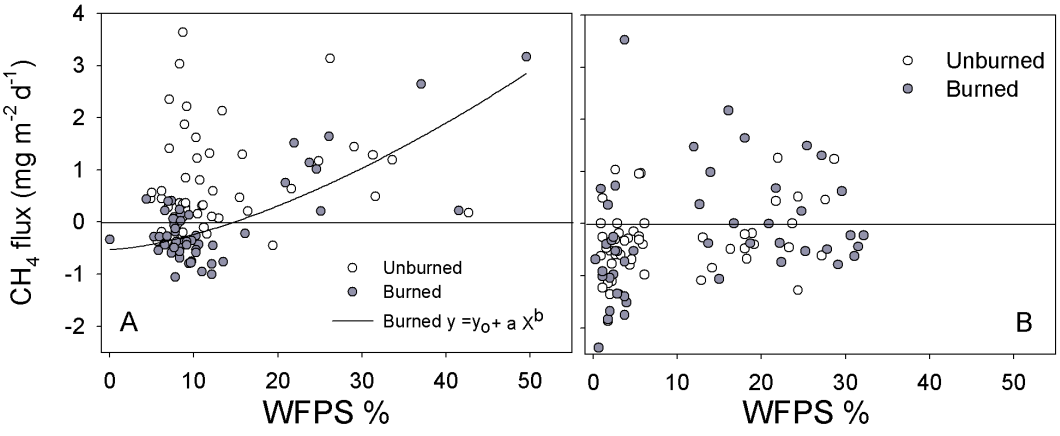


**Fig. 5.** Single chamber $CH_4$ fluxes (mg $CH_4$ $m^{-2}$ $d^{-1}$) plotted versus soil water filled pore space (%) reported for the 1st campaign (A) one month after burning and the 2nd campaign (B) eight months after burning. In graph A line represents the fit of data from burned plots ($y_0$= −0.53; a = 0.008; b = 1.54; $R^2 = 0.76$).

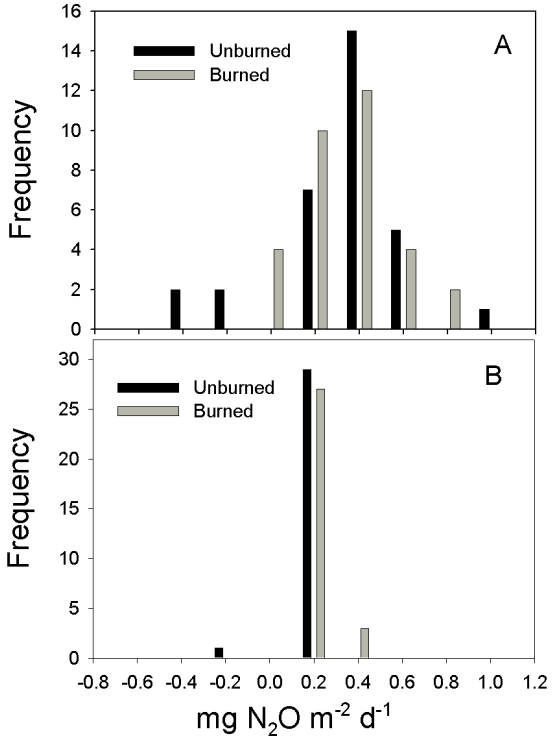


**Fig. 6.** The frequency distribution of single-chambers estimates of $N_2O$ fluxes (mg $N_2O$-N $m^{-2}$ $d^{-1}$) measured in unburned and burned plots (no water treatment) during the 1st campaign (A) one month after burning ($n = 32$) and the 2nd campaign (B) eight months after burning ($n = 30$). The range of each size class interval is 0.2 mg $N_2O$-N $m^{-2}$ $d^{-1}$.

### 3.5 Laboratory incubations

In the first incubation experiment, 92% of $N_2O$ production occurred within the first day after water addition; thereafter $N_2O$ fluxes decreased exponentially (data not shown). $N_2O$ emission was significantly enhanced in soil from burned plots but differences with soil from unburned plots were found only above 50% of $WHC_{max}$ (Fig. 7). $N_2O$ fluxes rose exponentially with increasing water content, with a faster rate in soil from burned plots (Fig. 7, insert). Rising the temperature from 25 to 37 °C had no significant effect on $N_2O$ emissions even at 100% of $WHC_{max}$. The pulse of $CO_2$ peaked the first day after water addition, accounting for about 50% of total cumulative $CO_2$ emission over about 15 days. At the end of the incubation (day 15), $CO_2$ emissions from watered soil (25, 50 and 100% of $WHC_{max}$) were still significantly higher than from unwatered soil (0% $WHC_{max}$) (data not shown). Figure 7, reporting the cumulative $CO_2$ emissions at day 1, 2, 3, 4, 5, 7 and 15 of incubation, shows that respiration was significantly stimulated by water addition at 25% of $WHC_{max}$. Further water addition induced no further significant change in the rate of $CO_2$ production. The increase of incubation temperature from 25 °C to 37 °C significantly stimulated $CO_2$ production. The highest respiration rates were found in watered soil from burned plots (Fig. 7). Microbial biomass N, net N mineralization and net nitrification were lower at 37 °C than at 25 °C (Fig. 8). Net nitrification was close to zero for all tested soil water contents at 37 °C. At 25 °C both nitrification and microbial biomass showed a maximum between 25 and 50% of $WHC_{max}$; at 100% of $WHC_{max}$, biomass growth was significantly reduced and no net nitrification was observed. Net N mineralization increased with increasing soil water content up to 100% of $WHC_{max}$ (Figs. 7 and 8), following the same pattern as for $N_2O$ production. Rates of net N mineralization and values of microbial biomass N were slightly higher in soil from burned plots. Higher NO emission were measured in soil from burned plots compared with that from unburned plots and NO fluxes were significantly higher at 10% of $WHC_{max}$ compared with 50% $WHC_{max}$, for both treatments (Fig. 9). The NO pulse induced by water addition (zero flux

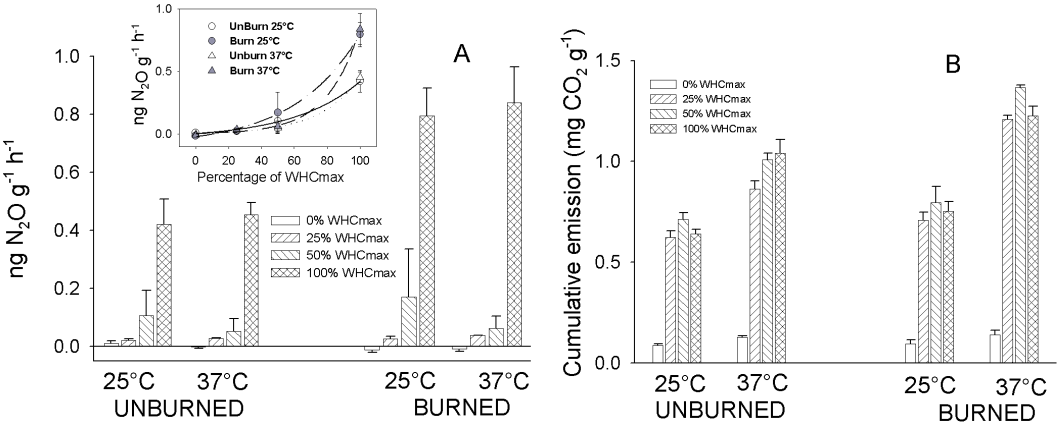


**Fig. 7.** (A) Emissions of $N_2O$ (ng $N_2O$ $g^{-1}$ soil dry weight $h^{-1}$) measured during the day of maximal $N_2O$ production after water addition (day 1) and (B) cumulative $CO_2$ emissions (mg $CO_2$ $g^{-1}$ soil dry weight) over 15 days from soil of burned and unburned plots incubated at 0, 25, 50 and 100% of maximal water holding capacity saturation ($WHC_{max}$) and at two temperatures (25 °C or 37 °C). In the small insert is $N_2O$ emissions (ng $N_2O$ $g^{-1}$ soil dry weight $h^{-1}$) vs. % of $WHC_{max}$. Bars are one standard deviation.

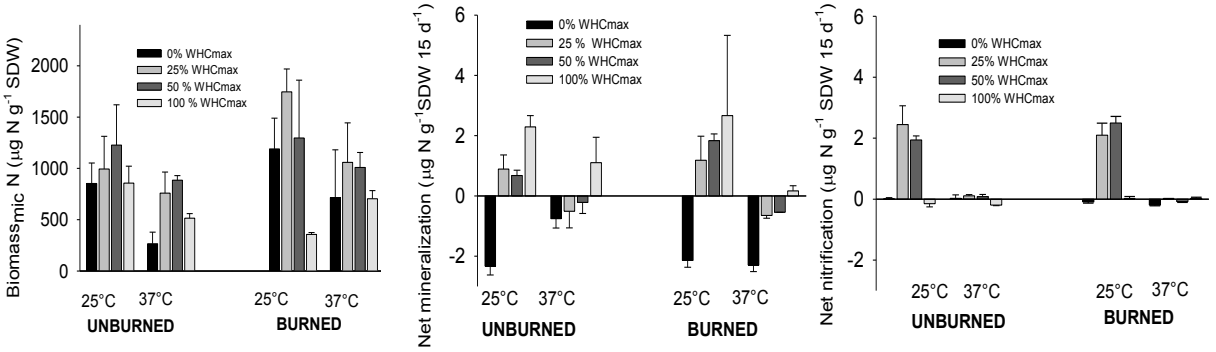


**Fig. 8.** Microbial biomass N (µg N $g^{-1}$ soil dry weight) and rates of net N mineralization (µg N $g^{-1}$ soil dry weight) and net nitrification (µg N $g^{-1}$ soil dry weight) measured after 2 weeks of incubation in soil from burned and unburned plots incubated at 0, 25, 50 and 100% of $WHC_{max}$ and at two temperatures (25 °C or 37 °C).

at time zero, 1 h before watering, data not shown) decreased significantly after 5 days of incubation. At 10% $WHC_{max}$ no $N_2O$ production was detected whereas at 50% of $WHC_{max}$ $N_2O$ emissions never exceeded 0.10 ng N $g^{-1}$ $h^{-1}$.

## 4 Discussion

### 4.1 Soil respiration

Results indicate that fire had a transient effect on soil respiration in the studied savanna grassland. Burned plots emitted significantly less $CO_2$ than unburned plots during the first campaign (one month after burning, dry season); however, this difference was no longer detectable eight months after burning (growing season). A first explanation for the observed difference in $CO_2$ emissions, one month after burning, is that fire destroyed the above-ground vegetation, which partly contributed to the maintenance activity of grass roots. Thus, fire reduced the autotrophic component of the soil respiration in burned plots. A second explanation is that fire reduced the heterotrophic component of soil respiration by consuming the litter, which represent a source of C for microbes, or by killing part of soil microflora directly. Indeed, a higher content of extractable $\alpha$-amino-N was found in burned soil one month after fire. Andersson et al. (2004b) reported an increase of dissolved organic C in savanna soils immediately after burning and suggested that this may partly derive from peptides and proteins released from the microbial biomass killed by heating. However, laboratory data do not indicate a reduction of microbial biomass and activity in the soil from burned plots. Moreover, a comparable amount of $CO_2$ was released at 25 °C from the soil sampled in burned and unburned plots (25–100% $WHC_{max}$) and, at 37 °C, $CO_2$ production was significantly higher in the soil from burned plots (Fig. 7). Hence, we expect that microbial activity was not impaired by fire in the field. However, our experimental

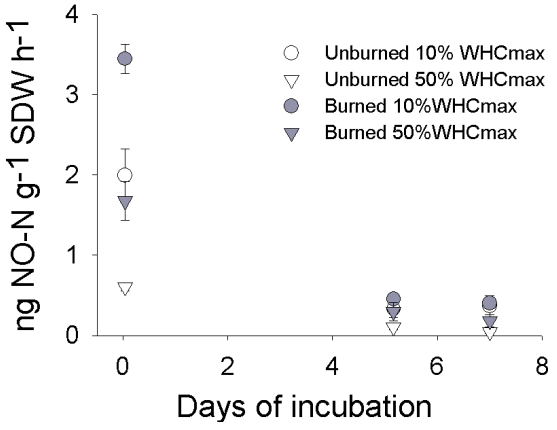


**Fig. 9.** Emissions of NO (ng NO-N $g^{-1}$ soil dry weight $h^{-1}$) measured from soil of burned and unburned plots incubated at 10% and 50% of $WHC_{max}$.

design did not enable us to establish a conclusive partitioning of the $CO_2$ flux between autotrophic and heterotrophic sources. Both laboratory and field data showed that no less than 10 days were necessary to extinguish the $CO_2$ pulse generated by water addition in the dry season, and that the maximum emission occurred within a day after water addition. Several authors reported a quick response of ecosystem respiration to rain pulses under dry conditions (Jenerette et al., 2008; Xu and Baldocchi, 2004; Williams et al., 2009), but pulses generally came to an end within one to three days. Eight months after burning, the pulse peak of $CO_2$ was comparable to the pulse obtained in the first campaign, but its lifetime was shorter (7 days) and the background (unwatered) rate of soil respiration was higher. During this period, both treatments presented similar plant cover density and grass height, and the soil showed a higher content of total C and $\alpha$-amino N, probably reflecting higher C and N inputs associated to root growth, turnover and exudation. These conditions might have stimulated microbial growth and activity, thereby resulting in higher rates of soil respiration but also in a faster consuming of substrates made available by water addition (shorter pulse lifetime).

Previous studies in Nigeria, Venezuela and South Africa showed no difference in soil $CO_2$ emissions between burned and unburned savannas (Adedeji, 1983; Hao et al., 1988; Zepp et al., 1996). A slight stimulating effect of fire on soil respiration was found in Brazilian cerrado, but only after watering of the soil (Poth et al., 1995). Michelsen et al. (2004) found higher soil respiration in forest and woodland subject to sporadic burning compared with frequently burned grasslands. In line with the results obtained in the present study, lower soil respiration rates were found in burned grassland savannah areas in Ethiopia compared with unburned areas (Andersson et al., 2004a).

### 4.2 Methane fluxes

The very low soil water content at the time of measurements and its loose structure, mainly dominated by sand, are likely to create favourable conditions for significant methanotrophic activity (Striegl et al., 1992; Potter et al., 1996; Castaldi and Fierro, 2005; Castaldi et al., 2006). However, our data showed that the unburned grassland plots were a $CH_4$ source or a weak sink. Similar results were also reported for some tropical ecosystems (Hao et al., 1988; Poth et al., 1995; Scharffe et al., 1990; Sanhueza et al., 1994; Zepp et al., 1996: Castaldi et al., 2004; Brümmer et al., 2009). In the present study we observed net $CH_4$ emissions even at 7% of WFPS, hence at very dry conditions, which makes it quite unlikely that $CH_4$ derives from anaerobic hotspots of microbial activity, as hypothesised in other studies (Castaldi et al., 2004; Verchot et al., 2000). A more probable source of $CH_4$ might be termite activity, also considering that the study site presented an extremely high abundance of termite nests. Although great care was taken at the moment of sampling to keep distant from termite nests. It is known that termite activity can affect the soil several meters far from the nest and the pattern of this source is difficult to predict. Fire significantly reduced the frequency of net $CH_4$ emissions, and this was particularly evident one month after burning. We could hypothesise that fire temporarily reduced termite activity outside the nest. Indeed, even $CH_4$ production inside the termite nests was significantly reduced in the first months after burning (Castaldi and de Grandcourt, in preparation). Other authors have obtained evidence that clearance of savanna soil surface (grasses and litter) by burning produces a significant reduction of methane emission from the soil-grass system (Poth et al., 1995; Zepp et al., 1996). Indeed, with the destruction of most of the litter, burning reduces the amount of palatable substrate that termites can use, either directly as litter or as soil organic matter. Soil-feeding termites, such as those belonging to the genus *Cubitermes* or those feeding on litter such as *Nasutitermes*, both present in the site, may be affected by substrate reduction due to fire. As observed for $CO_2$ fluxes, the effect of fire on $CH_4$ fluxes was transient. In fact, eight months after burning the frequency distribution of $CH_4$ fluxes in the two treatments showed no significant difference.

### 4.3 Nitrous oxide emissions

As typical of savannas with acidic and nutrient-poor soils (Scholes et al., 1997; Andersson et al., 2004a, b: Castaldi et al., 2006), the grassland ecosystem analysed in this study was characterized by low $N_2O$ fluxes. The range of fluxes reported for undisturbed savanna ecosystems is quite narrow, going from small uptake values to emissions of few mg $N_2O$-N $m^{-2}$ $d^{-1}$ (Castaldi et al., 2006), except if the soil receives significant amount of fertilizer (Brümmer et al., 2008). Higher $N_2O$ fluxes in undisturbed savannas were found only

in isolated patches of nutrient-rich soil (Otter and Scholes, 2000) or in savannas areas located in valleys characterized by higher soil water retention and accumulation of organic matter (Sanhueza et al., 1990). Higher $N_2O$ fluxes in seasonally dry tropical environments are reported only for forests (Sanhueza et al., 1990; Verchot et al., 1999, Castaldi et al., 2006). A combination of environmental factors contribute to keep $N_2O$ fluxes low: good soil drainage, low pH and low nutrient status (Castaldi et al., 2006). During the dry season the low soil water content is a major controlling factor, which limits the possibility of development of anaerobic microsites, where $N_2O$ production could take place (Firestone and Davidson, 1989; Smith, 1990). In the studied site, the water-filled pore space (WFPS %) was always below 51%, thus below the level at which $O_2$ diffusion is sufficiently low to enable a sharp increase of $N_2O$ production (60% – 90% of WFPS) (Davidson, 1991). Laboratory incubations indicated that a significant increase in $N_2O$ production is to be expected only above 75% of $WHC_{max}$. This water content was much higher than the content required to stimulate $CO_2$ production. N availability is also an important limiting factor for $N_2O$ production. During the dry season, mineralization and nitrification activity would probably produce low amounts of mineral N, as demonstrated by laboratory data. At the onset of the rainy season, the increase of soil water content might significantly stimulate mineralization activity leading to an increase of mineral N availability. This would favour the occurrence of pulses of NO and $N_2O$, although the resprouting of shrubs and growth of herbaceous plants may lead to competition for mineral N between plants and microbes (Bate, 1981). The manipulation rain experiments proposed in this and other studies are probably not sufficient to simulate the conditions occurring at the onset of the rainy season, both in terms of soil water content and mineral N availability. Thus, the response of $N_2O$ production to water addition observed in this study cannot be taken as representative of the $N_2O$ pulse which would be generated at the onset of the rainy season. Laboratory data indicated that one small rain event was sufficient to treble NO emission in burned plots, although the pulse was relatively short-lived. Similar results were shown in Brasilian cerrado by Poth et al. (1995) who measured NO fluxes in watered burned sites (1 day or 1 month after fire event) up to three times higher than fluxes from unburned sites. In accordance with our results, Levine et al. (1996) and Johansson et al. (1988) provided evidence that N gaseous emissions in burned savannas and tropical grassland are mostly dominated by NO.

## 5 Conclusions

Fire increased the availability of extractable N substrates in the soil; it is likely that this fostered higher rates of NO emissions measured in the soil from burned plots. Laboratory incubation experiments provided evidence that when soil water condition were optimal, $N_2O$ production was significantly higher in soil from burned plots. However, in the field, soil water content limited $N_2O$ production, even after rain simulation; thus no difference of $N_2O$ emission between burned and unburned plots was observed. Burning did not enhance soil $CO_2$ emissions; on the contrary, a transient detrimental effect on soil respiration was observed immediately after burning. The studied soil was not, as expected, a $CH_4$ sink, but during part of the year it was a slight $CH_4$ source, even in very dry conditions. Fire seemed to affect the net $CH_4$ flux, shifting $CH_4$ flux distribution towards more negative values (consumption). Overall, this preliminary data show that fire did not increase post-burning soil GHG emissions in the studied site. However, in order to generalize these findings a wider study would be needed to cover spatial variability of the African landscape mosaic in terms of vegetation, soil characteristics, termites abundance and biodiversity, possibly in the frame of a wider temporal window.

*Acknowledgements.* Acknowledgements. Financial support for this scientific research was provided by the European Commission through funding of the project "CarboAfrica" (GOCE, 037132) under the VI Framework Programme (FP6).

Edited by: M. Bahn

## References

Adedeji, F. O.: Effect of fire on soil microbial activity in Nigerian southern Guinea savanna, Rev. Ecol. Biol. Sol, 20, 483–492, 1983.

Andersson, M., Michelsen, A., Jensen, M., and Kjoller, A.: Tropical savannah woodland: effects of experimental fire on soil microorganisms and soil emissions of carbon dioxide, Soil Biol. Biochem., 36, 849–858, 2004a.

Andersson, M., Michelsen, A., Jensen, M., Kjoller, A., and Gashew, M.: Carbon stock, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems, Soil Biol. Biochem., 36, 1707–1717, 2004b.

Ansley, R. J., Dugas, W. A., Heuer, M. L., and Kramp, B. A.: Bowen ratio/energy balance and scaled leaf measurements of $CO_2$ flux over burned Prosopsis savanna, Ecol. Appl., 12, 948–961, 2002.

Bate, G. C.: Nitrogen cycling in savanna ecosystems, in: Terrestrial Nitrogen Cycles, edited by: Clark, F. E. and Rosswall, T., Ecological Bulletin (Stockholm), 33, 463–475, 1981.

Bombelli, A., Henry, M., Castaldi, S., Adu-Bredu, S., Arneth, A., de Grandcourt, A., Grieco, E., Kutsch, W. L., Lehsten, V., Rasile, A., Reichstein, M., Tansey, K., Weber, U., and Valentini, R.: An outlook on the Sub-Saharan Africa carbon balance, Biogeosciences, 6, 2193–2205, doi:10.5194/bg-6-2193-2009, 2009.

Bond, W. J.: What Limits Trees in C4 Grasslands and Savannas? Annu. Rev. Ecol. Evol. S, 39, 641–659, 2008.

Bothma, J. and Du, P.: Game counts, edited by: Du, P. and Bothma, J. Game Ranch Management, National Book Printers, Western Cape, 1996.

Breuer, L., Papen, H., and Butterbach-Bahl, K.: $N_2O$ emission from tropical forest soils of Australia, J. Geophys. Res., 105, 26353–26367, 2000.

Brümmer, C., Brüggemann, N., Butterbach-Bahl, K., Falk, U., Szarzynski, J., Vielhauer, K., Wassmann, R., and Papen, H.: Soil-Atmosphere Exchange of $N_2O$ and NO in Near-Natural Savanna and Agricultural Land in Burkina Faso (W. Africa), Ecosystems, 11, 582–600, 2008.

Brümmer, C., Papen, H., Wassmann, R., and Brüggemann, N.: Fluxes of $CH_4$ and $CO_2$ from soil and termite mounds in south Sudanian savanna of Burkina Faso (West Africa), Global Biogeochem. Cy., 23, GB1001, doi:10.1029/2008GB003237, 2009.

Butterbach-Bahl, K., Kock, M., Willibald, G. Hewett, B., Buhagiar, S., Papen, H., and Kiese, R.: Temporal variations of fluxes of NO, $NO_2$, $N_2O$, $CO_2$, and $CH_4$ in a tropical rain forest ecosystem, Global Biogeochem. Cy., 18, GB3012, doi:10.1029/2004GB002243, 2004.

Caquet, B., de Grandcourt, A., Thongo Mbou, A., Kinana, A., Epron, D., Saint-André, L., and Nouvellon, Y.: Soil respiration and belowground carbon allocation in a tropical savanna, Plant Soil, in prep., 2010.

Castaldi, S., Ermice, A., Strumia, S.: Fluxes of $N_2O$ and $CH_4$ from soils of savannas and seasonally-dry ecosystems, J. Biogeogr., 33, 401–415, 2006.

Castaldi, S. and Fierro, A.: Soil – atmosphere methane exchange in undisturbed and burned Mediterranean shrubland of Southern Italy, Ecosystems, 8(2), 182–190, 2005.

Castaldi, S., De Pascale, R. A., Grace, J., Montes, R., and San José, J.: Nitrous oxide and Methane fluxes from soil of Orinoco savanna under different land use, Global Change Biol., 10, 1947–1960. 2004.

Castaldi, S. and Aragosta, D.: Factors influencing nitrification and denitrification variability in a natural and fire disturbed Mediterranean shrubland, Soil Biol. Fertil., 36, 418–425, 2002.

Castaldi, S. and de Grandcourt A.: $CH_4$ fluxes from termite activity in African grassland savanna and its influence on the $CH_4$ flux budget at site, Ecosystems, in prep., 2010.

Christensen, N. L.: Fire and the nitrogen cycle in California chaparral, Science, 181, 66–68, 1973.

Davidson, E. A.: Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in: Microbial production and consumption of greenhouse gases: Methane, nitrogen oxides and halomethanes, edited by: Rogers, J. E. and Whitman, W. B., 219–235, American Society for Microbiology, Washington, D.C., 1991.

Davidson, E. A., Matson, P. A., Vitousek, P. M., Riley, R., Dunkin, K., Garcia-Mendez, G., and Maass, J. M.: Processes regulating soil emission of NO and $N_2O$ in a seasonally dry tropical forest, Ecology, 74, 130–139, 1993.

de Grandcourt, A., Thongo Mbou, A., Kinana, A., Ngoyi, S., Minzele, C., Caquet, B., Nouvellon, Y., and Saint-André, L.: Vegetation dynamics, aboveground and belowground productions in tropical grassland in Congo, J. Tropical Ecol., in prep., 2010.

Dick, J., Skiba, U., and Wilson, J.: The effect of rainfall on NO and $N_2O$ emissions from Ugandan agroforest soils, Phyton – Ann. Rei. Bota. A, 41, 73–80, 2001.

Favier, C., de Namur, C., and Dubois, M. A.: Forest progression modes in littoral Congo, Central Atlantic Africa, J. Biogeogr., 31, 1445–1461, 2004.

Firestone, M. K. and Davidson, E. A.: Microbiological basis of NO and $N_2O$ production and consumption in soil, in: Exchange of trace gases between terrestrial ecosystems and the atmosphere, edited by: Andreae, M. O. and Schimel, D. S., 7–21, John Wiley & Sons, New York, USA, 1989.

Fynn, R. W. S., Haynes, R. J., and O'Connor, T. G.: Burning causes long-term changes in soil organic matter content of a South African grassland, Soil Biol. Biochem., 35, 677–687, 2003.

Garcia-Montiel, D. C., Steudler, P. A., Piccolo, M., Neill, C., Melillo, J. M., and Cerri, C. C.: Nitrogen oxide emissions following wetting of dry soils in forest and pastures in Rondonia, Brazil, Biogeochemistry, 64, 319–336, 2003.

Hao, W. M., Scharffe, D., Crutzen, P. J., and Sanhueza, E.: Production of $N_2O$, $CH_4$ and $CO_2$ from soils in the tropical savannah during the dry season, J. Atmos. Chem., 7, 93–105, 1988.

Hutchinson, G. L. and Mosier, A. R.: Improved soil cover method for field measurements of nitrous oxide fluxes, Soil Sci. Soc. Am. J., 45, 311–316, 1981.

Huntley, B. J. and Walker, B. H.: Ecology of tropical savannas, Berlin, Springer-Verlag, 1982.

Jenerette, G. D., Scott, R. L., and Huxman, T. E.: Whole ecosystem metabolic pulses following precipitation events, Funct. Ecol., 22, 924–930, 2008.

Johansson, C., Rodhe, H., and Sanhueza, E.: Emissions of NO in tropical savanna and a cloud forest during the dry season, J. Geophys. Res.-Atmos, 93, 7180–7192, 1988.

Knicker, H.: How does fire affect the nature and stability of soil organic nitrogen and carbon? A review, Biogeochemistry, 85, 91–118, 2007.

Kovacic, D. A. D., Swift, M., Ellis, J. E., and Hakonson, T. E.: Immediate effects of prescribed burning on mineral soil nitrogen in ponderosa pine of New Mexico, Soil Science, 141, 71–76, 1986

Levine, J. S., Winstead, E. L., Parsons, D. A. B., Scholes, M. C., Scholes, R. J., Cofer, W. R., Cahoon, D. R., and Sebacher D. I.: Biogenic soil emissions of nitric oxide (NO) and nitrous oxide ($N_2O$) from savannas in South Africa: The impact of wetting and burning, J. Geophys. Res.-Atmos, 101(D19), 23689–23697, 1996.

Menault, J. C.: Evolution of plots protected from fire since 13 years in a guinea savanna of Ivory Coast, 4th Symp. Tropical Ecology, Panama, 1977.

Menaut, J. C., Abbadie, L., and Vitousek, P. M.: Nutrient and organic matter dynamics in tropical ecosystems, in: Fire in the Environment: The Ecological, Atmospheric and Climatic Importance of Vegetation Fires, edited by: Crutzen, P. J. and Goldammer, J. G., Wiley, Chichester, 215–231, 1993.

Michelsen, A., Andersson, M., Jensen, M., Kjøller, A., and Gashew, M.: Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems, Soil Biol. Biochem., 36, 1707–1717, 2004.

Mills, A. J. and Fey, M. V.: Frequent fires intensify soil crusting: Physico-chemical feedback in the pedoderm of long-term burn experiments in South Africa, Geoderma, 121, 45–64, 2004.

Moore, S. and Stein, W. H.: A modified ninhydrin reagent for the photometric determination of amino acids and related compounds, J. Biol. Chem., 211, 907–913, 1954.

Ocio, J. A. and Brooks, P. C.: An evaluation of methods for mea-

suring the microbial biomass in soils following recent additions of wheat straw and the characterization of the biomass that develops, Soil Biol. Biochem., 22, 685–694, 1990.

Ojima, D., Schimel, D. S., Parton, W. J., and Owensby, C. E.: Long and short-term effects of fire on nitrogen cycling in tallgrass prairie, Biogeochemistry, 24, 67–84, 1994.

Otter, L. B. and Scholes, M. C.: Methane sources and sinks in a periodically flooded South African savanna, Global Biogeochem. Cy., 14, 97–111, 2000.

Pinto, A. S., Bustamante, M. M. C, Kisselle, K., Burke, R., Zepp, R., Viana, L. T., Varella, R. F., and Molina, M.: Soil emissions of $N_2O$, NO, and $CO_2$ in Brazilian savannas: Effects of vegetation type, seasonality, and prescribed fires, J. Geophys. Res., 107(D20), 8089, doi:10.1029/2001JD000342, 2002.

Poth., M., Anderson, I. C., Miranda, H. S., Miranda, A. C., and Riggan, P. G.: The magnitude and persistence of soil NO, $N_2O$, $CH_4$ and $CO_2$ fluxes from burned tropical savanna in Brasil, Global Biogeochem. Cy., 9, 503–513, 1995.

Potter, C. S., Davidson, E. A., and Verchot, L. V.: Estimation of global biogeochemical controls and seasonality in soil methane consumption, Chemosphere, 32, 2219–2246, 1996.

Prieto-Fernandez, A., Carballas, M., and Carballas, T.: Inorganic and organic N pools in soils burned or heated: immediate alteration and evolution after forest wildfires, Geoderma, 121, 291–306, 2004.

Raison, R. J.: Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review, Plant Soil 51, 73–108, 1979.

Rees, R. M., Wuta, M., Furley, P. A., and Li, C.: Nitrous oxide fluxes from savanna (miombo) woodlands in Zimbabwe, J. Biogeogr., 33, 424–437, 2006.

Saarnak, C. F.: A shift from natural to human-driven fire regime: implications for trace-gas emissions, Holocene, 11, 373–375, 2001.

Sanhueza, E., Cardenas, L., Donoso, L., and Santana, M.: Effect of plowing on $CO_2$, CO, $CH_4$, $N_2O$ and NO fluxes from tropical savannah soils, J. Geophys. Res., 99(D8), 16429–16434, 1994.

Sanhueza, E., Hao, W. M., Scharffe, D., Donoso, L., and Crutzen, P. J.: $N_2O$ and NO emissions from soils of the Northern Part of the Guayana Shield, Venezuela, J. Geophys. Res., 95, 22481–22488, 1990.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., February, E. C., Frost, P. G. H., Hiernaux, P., Hrabar, H., Metzger, K. L., Prins, H. H. T., Ringrose, S., Sea, W., Tews, J., Worden, J., and Zambatis, N.: Determinants of woody cover in African savannas, Nature, 438, 846–849, 2005.

Scharffe, D., Hao, W. M., Donoso, L., Crutzen, P. J., and Sanhueza, E.: Soil fluxes and atmospheric concentration of CO and $CH_4$ in the northern part of the Guayana Shield, Venezuela, J. Geophys. Res., 95, 22475–22480, 1990.

Scholes, M. C., Martin, R., Scholes, R. J., Parsons, D., and Winstead, E:. NO and $N_2O$ emissions from savanna soils following the first simulated rains of the season, Nutr. Cycl. Agroecosys., 48, 115–122, 1997.

Scholes, R. J. and Hall, D. O.: The carbon budget of tropicals savannas, woodlands and grasslands, in: Global Change: Effects on Coniferous Forest and Grasslands, edited by: Breymeyer, A. I., Hall, D. O., Melillo, J. M., and Agren, G. I., SCOPE, 56, 69–100, 1996.

Scholes, R. J. and Walker, B. H.: An African Savanna: Synthesis of the Nylsvley Study, Cambridge Studies in Applied Ecology and Resources Management, Cambridge University Press, pp. 300, 2004.

Singh, R. S., Raghubanshi, A. S., and Singh, J. S.: Nitrogen-mineralization in dry tropical savanna: effects of burning and grazing, Soil Biol. Biochem., 23, 269–273, 1991.

Singh, R. S.: Changes in soil nutrients following burning of dry tropical savanna, Int. J. Wildland Fire, 4, 187–194, 1994.

Smith, K. A.: Anaerobic zones and denitrification in soil: modelling and measurements, in: Denitrification in Soil and Sediment, edited by: Revsboech, N. P. and Sørensen, J., Plenum Press, New York, 228–240, 1990.

Smith, K. A., Clayton, H., McTaggart, I. P., Thomson, P. E., Arah, J. R. M., and Scott, A.: The measurement of nitrous oxide emissions from soil by using chambers, Phil. Trans. R. Soc. Lond. 351, 327–338, 1995.

Snyman, H. A.: Short-term response of rangeland following an unplanned fire in terms of soil characteristics in a semi-arid climate of South Africa, J. Arid. Environ., 55, 160–180, 2003.

Striegl, R. G., McConnaughey, T. A., Thorstenson, D. C., Weeks, E. P., and Woodward, J. C.: Consumption of atmospheric methane by desert soils, Nature, 357, 145–147, 1992.

Swaine, M. D., Hawthorne, W. D., and Orgle, T. K.: The effects of fire exclusion on savanna vegetation at Kpong, Ghana, Biotropica, 24, 166–172, 1992.

Trollope, W. S. W.: Veld management with specific reference to game ranching in the grassland and savanna areas of South Africa, Koedoe, 33, 77–86, 1990.

van Haren, J. L. M., Handley, L. L., Biel, K. Y., Kudeyarov, V. N., McLain, J. E. T., Martens, D. A., and Colodner, D. C.: Drought-induced nitrous oxide flux dynamics in an enclosed tropical forest, Glob. Change Biol., 11, 1247–1257, 2005.

Verchot, L. V., Davidson, E. A., Cattânio, J. H., and Ackerman, I. L.: Land use change and biogeochemical controls of methane fluxes in soils of Eastern Amazonia, Ecosystems, 3, 41–56, 2000.

Verchot, L. V., Davidson, E. A., Cattânio, J. H., Ackerman, I. L., Erickson, H. E., and Keller, M.: Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia, Global Biogeochem. Cy., 13, 31–46, 1999.

White, R. P., Murray, S., and Rohweder, M.: Pilot Analysis of Global Ecosystems (PAGE): Grasslands, World Resources Institute, Washington D.C., pp. 70, 2000.

Williams, C. A., Hanan, N., Scholes, R. J., and Kutsch, W.: Complexity in water and carbon dioxide fluxes following rain pulses in an Africa savanna, Oecologia, 161, 469–480, 2009.

Xu, L. K. and Baldocchi, D. D.: Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California, Agric. For. Meteorol., 123, 79–96, 2004.

Zepp, R. G., Miller, W. L., Burke, R. A., Dirk, A., Parsons, B., and Scholes, M. C.: Effects of moisture and burning on soil-atmosphere exchange of trace carbon gases in a southern African savanna, J. Geophys. Res., 101, 23699–23706, 1996.