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Effect of the replacement of a native savanna by an African *Brachiaria decumbens* pasture on the CO_2 exchange in the Orinoco lowlands, Venezuela

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Abstract

In the Orinoco lowlands, savannas have been often replaced by pastures composed of the C_4 grass, *Brachiaria decumbens* Stapf. We addressed following questions: (*1*) How does the replacement of the native vegetation affect CO_2 exchange on seasonal and annual scales? (*2*) How do biophysical constraints change when the landscape is transformed? To assess how these changes affect carbon exchange, we determined simultaneously the CO_2 fluxes by eddy covariance, and the soil CO_2 efflux by a chamber-based system in *B. decumbens* and herbaceous savanna stands. Measurements covered a one-year period from the beginning of the dry season (November 2008) to the end of the wet season (November 2009). During the wet season, the net ecosystem CO_2 exchange reached maximum values of 23 and 10 μmol(CO_2) m^{-2} s^{-1} in the *B. decumbens* field and in the herbaceous savanna stand, respectively. The soil CO_2 efflux for both stands followed a temperature variation during the dry and wet seasons, when the soil water content (SWC) increased above 0.087 m^3 m^{-3} in the latter case. Bursts of CO_2 emissions were evident when the dry soil experienced rehydration. The carbon source/sink dynamics over the two canopies differed markedly. Annual measurements of the net ecosystem production indicated that the *B. decumbens* field constituted a strong carbon sink of 216 g(C) m^{-2} y^{-1}. By contrast, the herbaceous savanna stand was found to be only a weak sink [36 g(C) m^{-2} y^{-1}]. About 53% of the gross primary production was lost as the ecosystem respiration. Carbon uptake was limited by SWC in the herbaceous savanna stand as evident from the pattern of water-use efficiency (WUE). At the *B. decumbens* stand, WUE was relatively insensitive to SWC. Although these results were specific to the studied site, the effect of land use changes and the physiological response of the studied stands might be applicable to other savannas.

Additional key words: Eddy covariance; soil CO_2 eflux; water-use efficiency.

Introduction

Globally, savanna covers the area of 22.5×10^{12} m^2 and accounts for approximately 13% of the total global terrestrial carbon stock (IPCC 2001) and 30% of the total terrestrial primary production (IPCC 1990). Recently, the socio-economic impact of high-input technologies has encouraged the extension of agricultural systems into the neotropical savannas, where organic matter production and the content of proteins and minerals are limited (Mullenax 1982, San José 2001). The African pasture grass, *B. decumbens*, is currently the most widely grown grass genus in the neotropics, yielding up to 1,931 g(dry mass) m^{-2} yr^{-1} (Miles *et al.* 1998, Rao *et al.* 1998). Furthermore, it has become well-adapted to use by large herbivores (Parsons 1972). On Oxisols and Ultisols, *B. decumbens* increases carbon allocation to roots (Rao *et al.* 1998). Therefore, the large land area occupied by

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Abbreviations: APF – apparent photosynthetic flux; Da – humidity mole fraction deficit; F_{10} – soil CO_2 efflux at 10°C; F_s – soil CO_2 efflux; GPP – gross primary production; LAI – leaf area index; NEE – net ecosystem CO_2 exchange; NEF – net ecosystem flux; NEP – net ecosystem production; PPF – photosynthetic photon flux; Q_i – photosynthetic photon flux density; R_{eco} – ecosystem respiration; u_* – mean friction velocity; WUE – water-use efficiency; α_a – apparent quantum yield (*i.e.*, initial slope); λE – evapotranspiration flux; ΔS_c – CO_2 storage; SWC – soil water content.

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B. decumbens pastures may be a substantial sink for global carbon uptake and carbon sequestration. So far, relatively little basic information is known about the effect of this major change in land use on the carbon balance (Santos *et al.* 2004). Understanding the processes controlling CO_2 fluxes in *B. decumbens* field is necessary for predicting how *B. decumbens* responds to environmental changes and how land management could affect those processes. The overall aim of this work was to compare the effect of seasonal conditions on CO_2 exchange and WUE in two contrasting types of land cover: the *B. decumbens* field and the herbaceous savanna in the Orinoco lowlands.

This study was carried out within the Orinoco basin (1.1×10^{12} m^2) of northern South America, which is characterized by oligotrophic soil and seasonal climate. These savannas are intermingled with *B. decumbens* pasture in an environmental patchiness ranging from new established stands to degraded fields. This landscape provides an excellent opportunity to undertake a paired study of cultivated pasture and herbaceous savanna, both subjected to the same environmental conditions, but impacted to different extent by human activities.

The purpose of this work was: (*1*) to analyze simultaneously the seasonal effect of Orinoco lowland conditions on the CO_2 exchange of the *B. decumbens* field and the nearby herbaceous savanna by using the eddy covariance method; (*2*) to assess the processes controlling CO_2 transfer under conditions generated by different forcing canopies; and (*3*) to evaluate the effect of replacement and expansion of these pasture systems on the carbon budget. With the rapid expansion of pastures in South America, this type of information could assist the sustainable management of the land.

Materials and methods

The research sites were located in a vegetational mosaic at the Experimental Station of the Eastern University (9°45'N, 63°27'W) in Monagas State, Venezuela. The vegetation was composed of the *B. decumbens* field, which was established in 1996 and grazed for nine years, and a herbaceous savanna with less than 3% of tree cover. The dominant herbaceous species were *Trachypogon spicatum* (L.f.) Kuntze*, Axonopus canescens* (Ness ex Trin.) Pilg., and *Bulbostylis funciformis* C.B. Clarke ex S. Moore. The conspicuous tree species were *Curatella americana* L., *Byrsonima crassifolia* L., and *Bowdichia virgilioides* Kunth. The height of the canopy for both herbaceous stands was about 120 ± 20 cm. The *B. decumbens* stand was ploughed, fertilized, and planted as a monoculture at a seed density suggested by Lapointe and Miles (1992) and Miles and Lapointe (1992). These stands were regularly grazed under conditions representative of those under normal use in the Orinoco lowlands. The climate is characterized by the mean annual precipitation of 1,055 mm, with 685 mm falling from May to November. Both stands were excluded from grazing during data collection over a one-year period from December 2008 to November 2009. Thus, measurements encompassed the dry (November–April) and wet (May–October) seasons at both sites.

Micrometeorological measurements: Simultaneous, micrometeorological measurements of CO_2 and water vapour fluxes were made over the study-sites (30 ha each) by the eddy covariance technique (Aubinet *et al.* 2000, 2002) during the consecutive dry and wet seasons. Footprint analysis followed Schuepp *et al.* (1990) and Kaimal and Finingan (1994). At each stand, air-intake tubes were fixed to a mast at six heights each above and within the canopy in *B. decumbens* and herbaceous savanna stands, respectively. These tubes were connected to a *Type 161* gas-handling system (*Analytical Development Company*, Hertfordshire, UK) and CO_2 in the air was measured with an infrared gas analyzer, model *LI-6262* (*LI-COR Bioscience*, Lincoln, NE, USA). Profiles of half-hour means were fitted with a β-spline function and differences between vertical curves were used to calculate half-hourly rates of CO_2 storage (ΔS_c). CO_2 flux measurements across the ecosystems, carbon budget, and best-fit equations for radiation response curves were followed as outlined in Ruimy *et al.* (1995). This paper followed the convention used in ecophysiology, *i.e.*, both photosynthetic and respiratory fluxes at the organ scale were treated as positive. At the system scale, downward fluxes into the system were considered as positive and upward fluxes as negative. The change in the ΔS_c in the canopy air was treated either as positive if ΔS_c increased or negative if it decreased.

Statistical regression analysis and comparisons among datasets were achieved by the *Sigma Plot* curve fitting software. The response of the apparent photosynthetic flux (APF) and soil heterotrophic respiration (R_h) were described as a function of incident photosynthetic photon flux (PPF) using a least-square fit to a rectangular hyperbola. The incident PPF was calculated as a factor (2.20) of incoming solar radiation (R_s) (Bégué *et al.* 1991, Frouin and Pinker 1995).

The net ecosystem flux (NEF) is the half-hour average flux over the canopy. The net ecosystem exchange (NEE), which is the flux attributable to biological activity, was defined as NEF – ΔS_c. The values of ΔS_c were small, thus NEF was nearly the same as NEE. To assess the factor modulating the CO_2 flux, we separated NEP (defined as the integration of NEE over the year) into ecosystem respiration (R_{eco}) and GPP by an algorithm that defines the short-term temperature sensitivity of R_{eco} (Reichstein *et al.* 2005). In addition to measuring the vertical changes in gas exchange, two masts were placed in the field at distances of 10 and 25 m from the central mast and eddy covariance system, and used to analyze changes in gas exchange with distance downwind (*i.e.*, advection) as described by San José (1992). Using daily data, we calculated the WUE of the evapotranspired water at the stand scale as the ratio of NEP to evapotranspiration flux (λ E). Fluxes during periods with missing data were estimated by standard methods (Falge *et al.* 2001, Reichstein *et al.* 2005).

At each study-site, soil moisture (SWC) was measured daily from 0 to 0.45 m depth by using time domain reflectometry, model *Trase System I – 6050X1* (*Soil Moisture Equipment Corp.*, CA, USA).

Soil CO₂ efflux: At both stands, hourly soil flux (F_s) was measured with an infrared gas analyzer, model *LI-6200* (*LI-COR Bioscience*, Lincoln, NE, USA) by using a randomly positioned soil respiration chamber, model *LI-6000-09* (*LI-COR Bioscience*, Lincoln, NE, USA). Every hour, four samples were processed and soil temperature was taken by placing a thermocouple 0.1 m below the soil surface. At each stand, R_h was measured as outlined by Hanson *et al.* (1993). Two months before the onset of the dry and wet seasons, four 16-m^2 plots were randomly selected 500 m downwind from the instrument site. At each plot, the soil was excavated up to 0.5 m and the roots were removed. The plot was isolated from the system by introducing a Plexiglas sheet along each side to a depth of 0.5 m. At each plot, hourly measurements were obtained as described. Post-experiment, sampling for residual roots was carried out and results showed that barriers were effective in excluding roots during measurements. At each stand, two sets of four soil blocks (0.5 m × 0.6 m × 0.3 m) were excavated and transported to the laboratory. In the first set, the soil was separated from the roots and R_h was measured with a gas-exchange chamber. Comparison of R_h from the laboratory and field indicated that they differed by less than 16%. The second set of blocks containing roots was kept at 10°C and soil CO_2 efflux at 10°C (F_{10}) was measured as a function of SWC. For each seasonal mean of daily water content, F_{10} was calculated. F_s and absolute soil temperature were fitted as outlined by Lloyd and Taylor (1994):

$$F_s = F_{10}\, e^{308.56}\left(\frac{1}{56.02} - \frac{1}{T - 227.13}\right)$$

Carbon stock and leaf area index in the stand: At each stand, above- and belowground carbon stock was determined. The carbon content in the dry mass of vegetation was calculated based on the proportion of carbon in the vegetation (43%) reported by Hedges *et al.* (1986).

At each stand, aboveground biomass was determined monthly by harvesting. Thus, at each stand, ten 4.0 m × 4.0 m plots were selected at random. Thereafter, the biomass was harvested, separated into green and nongreen biomass, and oven-dried at 80°C to constant mass.

At each stand, belowground biomass was also determined monthly where the aboveground biomass sample had been harvested. The soil of the plots was excavated in 4.0 m × 4.0 m × 0.5 m monoliths. The soil volume contained more than 80% of the total belowground dry mass. Roots were separated by flotation (McKell *et al.* 1961). Root samples were dried at 80°C to constant mass.

The leaf area index (LAI) was determined monthly by using a plant canopy analyzer, model *LAI-6200* (*LI-COR Bioscience*, Lincoln, NE, USA). The number of sampling points provided a coefficient of variability lesser than 10%.

Soil organic matter: At each stand, triplicate soil samples at only one time point were collected at depths of 0–0.1, 0.1–0.2, and 0.2–0.3 m. The samples were analyzed for organic carbon percentages by the Walkley and Black method (Jackson 1958). The percentage was converted to percentage of total organic carbon by assuming that carbon constitutes 58% of soil organic carbon (Cox 1972). Subsequently, the value was converted to g(C) m^{-2} by correcting the percentage for readily oxidable carbon (Walkley 1947) and relating the values to soil volume by using soil bulk density as determined from the volume occupied by 15 soil samples of 1 m^2 as outlined in Pla Sentis (1977).

Results

NEF: Changes in the NEF and F_s during typical days in the dry and wet seasons (Fig. 1) showed marked contrasts with more activity in the wet season. Variations in shortwave radiation and air humidity mole fraction deficit (D_a) (San José *et al.* 2014, unpublished) accounted partially for the divergence in the daily trends of the NEF. During the dry season, both stands experienced water stress and maximum daytime NEF (*i.e.*, *B. decumbens* and herbaceous savanna 4.3 and 2.3 μmol m^{-2} s^{-1}, respectively) was reached at noon, decreasing thereafter during the afternoon. During the wet season, NEF was influenced by the trend in R_s depending on convective cloud formation and increase in the humidity factor deficit during the afternoon with the onset of the season. Maximum NEF reached 19.2 and 9.4 μmol m^{-2} s^{-1} in *B. decumbens* and savanna, respectively. During the daytime dry season, the F_s in *B. decumbens* stand increased over that in the herbaceous savanna stand, whereas F_s was not different between stands during the wet season.

For all the dataset, nighttime flux error was evaluated on the basis of the effects of ΔS_c and advection as outlined in Grace *et al.* (1996), Aubinet *et al.* (2003), and Kruijt

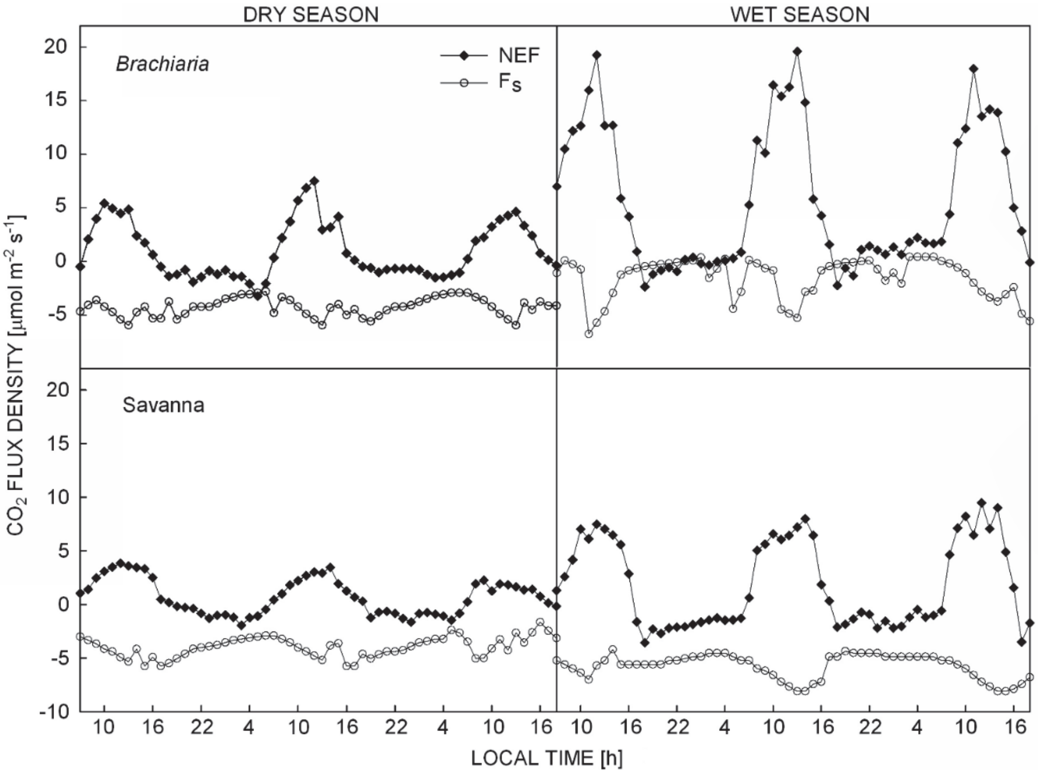

Fig. 1. Typical days of the dry and wet season net ecosystem flux (NEF; ●) and soil CO_2 efflux (F_s; ○) in a *Brachiaria decumbens* Stapf field and a savanna of the Orinoco lowlands. Data correspond to the measurements taken during the dry season of 12–14 March and during the wet season of 10–12 October.

et al. (2004). In relation to the storage, it was negligible; seasonally averaged night storage ranged from 0.030 to 0.137 μmol m^{-2} s^{-1}. NEE did not show a relationship with the wind speed, and therefore, advection did not contribute to the changes in the CO_2 fluxes. Advection and downwind flux difference were less than 1.7%. Nocturnal flux measurements were considered unreliable and were disregarded when the mean friction velocity (u_*) was below 0.1 m s^{-1}. During the dry and wet seasons, the percentage of nights with mean u_* below 0.1 m s^{-1} was less than 6.8 and 0.0%, respectively. The results indicated that during calm nights, the corrected fluxes with parameterized data varied between 0 and 2.8% of the uncorrected fluxes. On nights with low turbulence, the error corrections were lesser than 3.6%, indicating low CO_2 build-up with progression towards a stably stratified boundary layer. Consequently, the flat topography of the stands did not cause marked internal drainage flow at night.

During the night time of the typical days (Fig. 1), carbon losses corresponded to respiration of aboveground phytomass and soil respiration. During the dry season, NEF in the night was similar in both stands. However, during the wet season, the nighttime NEF was higher in the *B. decumbens* stand (–0.3 to –6.3 μmol m^{-2} s^{-1}) as compared with the herbaceous savanna stand (–0.4 to–3.5 μmol m^{-2} s^{-1}). For both stands, the maximum nighttime NEF was 33 and 38 % of maximum daytime NEF, respectively.

Densities of F_s from the *B. decumbens* and herbaceous savanna soils differed during the daytime. Thus, as the day proceeded, F_s measured in the *B. decumbens* field increased until midday hours, when it reached a maximum value of CO_2 release of –6.0 and –11.5 μmol m^{-2} s^{-1} during the dry and wet season, respectively. But in the herbaceous savanna soil, F_s was slightly variant with time until the mid-afternoon, when it reached –5.7 and –8.1 μmol m^{-2} s^{-1} during the dry and wet season, respectively. During the nighttime, F_s measured from both stands converged and were invariant.

APF as a function of incident photosynthetic photon flux: The APF as the sum of NEE in the daytime and R_h is presented as a function of the incident photosynthetic photon flux density (Q_i) (Fig. 2). From the fitted rectangular hyperbola equation, parametric values were obtained. The initial slope, considered as the apparent quantum yield (α_a), during both seasons was higher over the *B. decumbens* field than that in the herbaceous savanna. The difference might be related to the magnitude of LAI, which related the Q_i to stand bioproduction. Thus, in the wet season, the unavailable Q_i (*i.e.*, transmitted flux density) for CO_2 uptake was lower in the closed *B. decumbens* field canopy (13%) compared with that for the sparse savanna canopy (25%). The savanna was notably inactive in the dry season, while *B. decumbens* remained photosynthetically active.

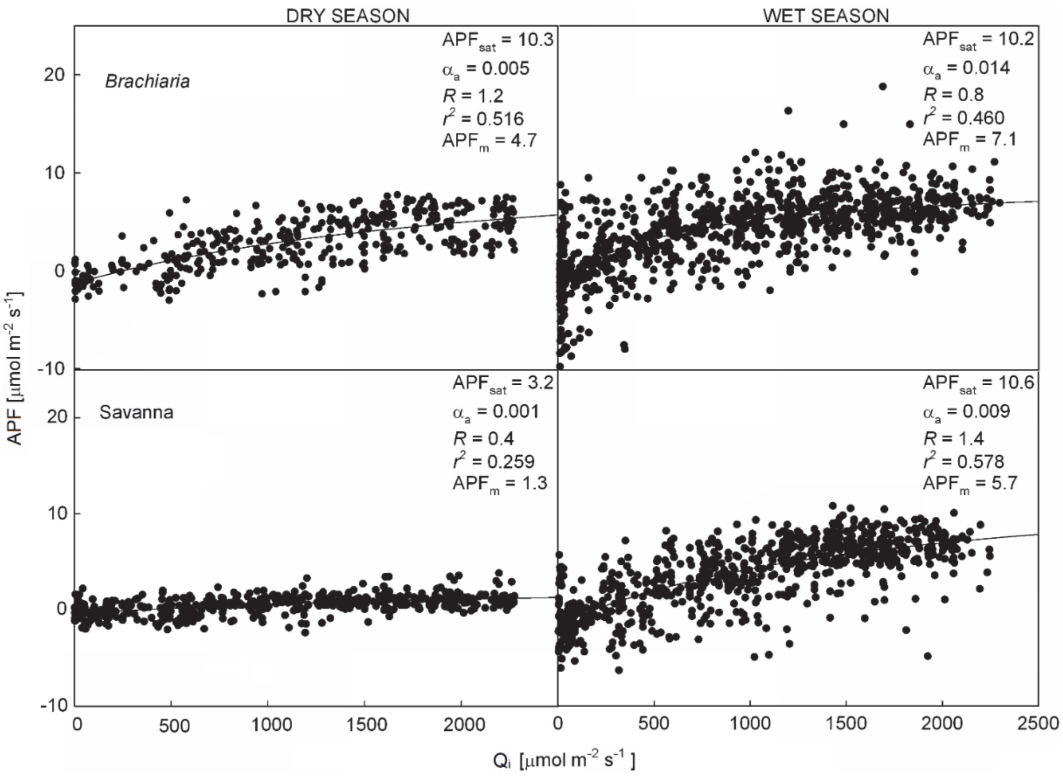

Fig. 2. Dry and wet season apparent photosynthetic flux (APF) as a function of the incident photosynthetic photon flux (Q_i) in a *Brachiaria decumbens* Stapf field and a savanna of the Orinoco lowlands. Values were fitted with a rectangular hyperbola: APF_{sat} is APF at saturating Q_i [μmol m^{-2} s^{-1}], α_a is apparent quantum yield [μmol(CO_2) μmol^{-1}(quantum)]; R is dark respiration (μmol m^{-2} s^{-1}); and APF_m is APF at maximum Q_i of 1,800 μmol m^{-2} s^{-1}.

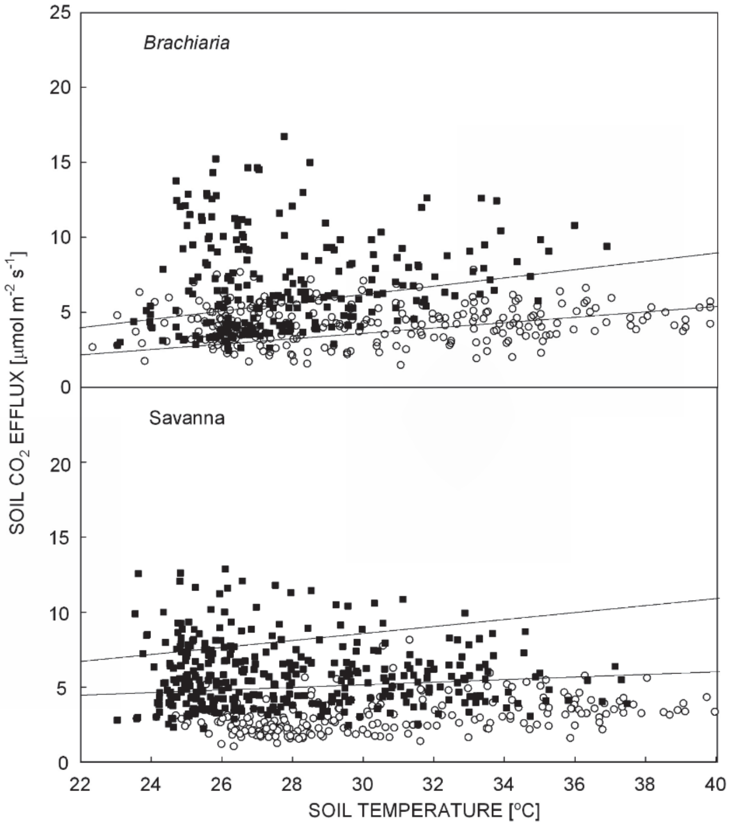

Fig. 3. Soil CO_2 efflux as a function of soil temperature for the dry (○) season at a soil water content (SWC) < 0.105–0.114 m^3 m^{-3} and wet (■) season at a soil water content (SWC) > 0.114 m^3 m^{-3} in the *Brachiaria decumbens* Stapf field and a savanna in the Orinoco lowlands. The fitted regression curves appear as outlined in Lloyd and Taylor (1994).

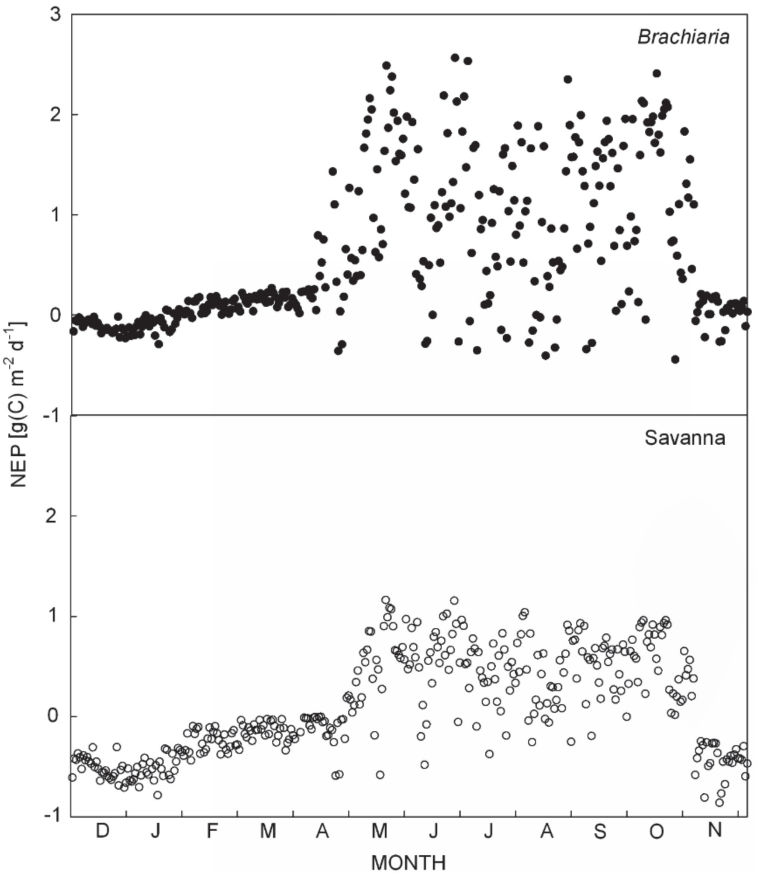

Fig. 4. Daily net ecosystem production (NEP) over a *Brachiaria decumbens* Stapf field and a savanna in the Orinoco lowlands.

F_s: For each season, the relationship between F_s and soil temperature showed different temperature sensitivities for R_h, autotrophic respiration (R_a), and turnover times of carbon pools (Fig. 3). For both stands, the trends revealed two tendencies corresponding to the dry and wet seasons. For the dry season (SWC < 0.064–0.079 m^3 m^{-3}), F_s in *B. decumbens* field ranged from –1.4 to –7.8 μmol m^{-2} s^{-1}, and in the herbaceous savanna stand, from –1.0 to –8.1 μmol m^{-2} s^{-1}. When the soil was wet (SWC > 0.064–0.079 m^3 m^{-3}), the value spanned from –1.8 to –16.7 μmol m^{-2} s^{-1} in the *B. decumbens* field, and from –2.2 to –12.8 μmol m^{-2} s^{-1} in the herbaceous savanna stand. The high values corresponded to bursts of CO_2 following rewetting of dry soil. These values markedly overshoot the expected relationship with soil temperature.

NEP and gross primary production (GPP): During the dry season, the *B. decumbens* and herbaceous savanna stands showed a seasonally averaged NEP of 0.09 and 0.29 g(C) m^{-2} d^{-1}, respectively (Fig. 4). During the wet season, both stands were a net sink of CO_2 until soil water began to decrease in November. Even in the dry season, with limited LAI, *B. decumbens* was a small sink when new leaves developed. By contrast, the herbaceous savanna was a small source of CO_2 during most of the dry season (*i.e.*, 90% of the days) with values ranging from –0.12 to –0.78 g(C) m^{-2} d^{-1}.

Annual NEP in the *B. decumbens* field was as high as 216 g(C) m^{-2} yr^{-1}. Therefore, the *B. decumbens* field was a markedly strong CO_2 sink whereas the herbaceous savanna was more or less in balance, being a sink of 36 g(C) m^{-2} yr^{-1} over the year-period. The annual GPP was 826 g(C) m^{-2} yr^{-1} for the *B. decumbens* field and 431 g(C) m^{-2} yr^{-1} for the herbaceous savanna. The seasonally averaged R_{eco} as a function of averaged GPP was fitted by a linear regression (seasonal GPP = 1.05 + 0.53 R_{eco}; r^2 = 0.84). Therefore, the R_{eco} was a high proportion of the GPP in the stands.

WUE: There was a marked seasonal trend (Fig. 5). For the dry season, the seasonally averaged daily WUE in the *B. decumbens* and herbaceous savanna stands were 0.6 ± 2.6 and –7.8 ± 6.1 mmol(CO_2) mol^{-1}(H_2O), respectively, and for the wet season, the values were 4.8 ± 4.3 and 2.2 ± 3.7 mmol(CO_2) mol^{-1}(H_2O), respectively. The magnitude of WUE at a given SWC differed between stands. In the *B. decumbens* fields, results showed that the values were similar as a function of SWC. By contrast, the WUE in the herbaceous savanna increased with SWC. Thus, at the wettest end of the range of SWC, the herbaceous savanna stand was the most efficient in CO_2 uptake relative to water loss, whereas at the driest end of SWC, it was the least efficient.

Discussion

NEF in the day and night: For both stands, the seasonally averaged daytime NEF was 2.5 ± 0.4 and 2.1 ± 0.2 μmol m^{-2} s^{-1}, respectively. Similar results have been reported for Brazilian campo sujo and cerrado (Miranda *et al.* 1997, Santos *et al.* 2003), Sahelian fallow savanna (Hanan *et al.* 1998), and broad-leaf, semiarid savanna in the Kalahari transect (Veenendaal *et al.* 2004). During the dry season, seasonal results indicated that the nighttime NEF trend over the *B. decumbens* stand decreased at the end of the dry season; however, the daily NEP was slightly positive. The nighttime NEF trend in the herbaceous savanna was the dominant component of the carbon ecosystem budget and, consequently, the system was a net daily source of CO_2. This result might reflect the differential sensitivity of the *B. decumbens* and herbaceous savanna stands to water stress causing reduction in effective LAI. Furthermore, the inhibition of the enzymes of C_4 metabolism as a result of water deficit might be also involved (Du *et al.* 1996, Lal and Edwards 1996).

Comparison of the seasonal tendency of NEF in the daytime revealed that during the wet season, NEF was higher than that for the dry season. This response was the result of canopy activity and decomposition, when both SWC and air temperature increased. The *B. decumbens* field and herbaceous savanna were appreciable sinks of CO_2 associated with maximum LAI development (*i.e.*, 2.4 and 2.1 m^2 m^{-2}, respectively). In the *B. decumbens* field, the maximum NEF in the daytime (*i.e.*, 23 μmol m^{-2} s^{-1}) was similar to that reported for *B. brizantha* (25 μmol m^{-2} s^{-1}) grown in southwestern Amazonia with LAI of 3.9 m^2 m^{-2} (Grace *et al.* 1998). However, these values were lower than the upper limit reported for *B. brizantha* growing in the cerrado (40 μmol m^{-2} s^{-1}) with a LAI of 4.0 m^2 m^{-2} (Santos *et al.* 2004). Such a difference could be related to the high bioproduction capacity of *B. decumbens* growing in soils with higher nutritional status and adequate cattle management. In the *B. decumbens* and similar pasture, there is considerable potential to increase the photosynthetic capacity by the application of fertilizer (Alvim *et al.* 1990). Lira *et al.* (1994) working with fertilized *B. decumbens* in northeastern Brazil reported a nearly 100% increase in dry matter over the control. Here, over the herbaceous savanna stand, the maximum NEF in daytime (*i.e.*, 10 μmol m^{-2} s^{-1}) across the upper boundary stand was similar to the maximum value reported for mesic neotropical savannas of Brazilian campo sujo, cerrado, and cerradão (9–20 μmol m^{-2} s^{-1}; Miranda *et al.* 1997, Vourlitis *et al.* 2001, Santos *et al.* 2003), northern Australian savannas (9–11 μmol m^{-2} s^{-1}, Eamus *et al.* 2001), Mopane woodlands at the Kalahari transect (10–14 μmol m^{-2} s^{-1}) and other African savannas and fallows (10–16 μmol m^{-2} s^{-1}; Monteny *et al.* 1997, Hanan *et al.* 1998, Verhoef *et al.* 1999, Veenendaal *et al.* 2004, Williams and Albertson 2004, Boulain *et al.* 2009).

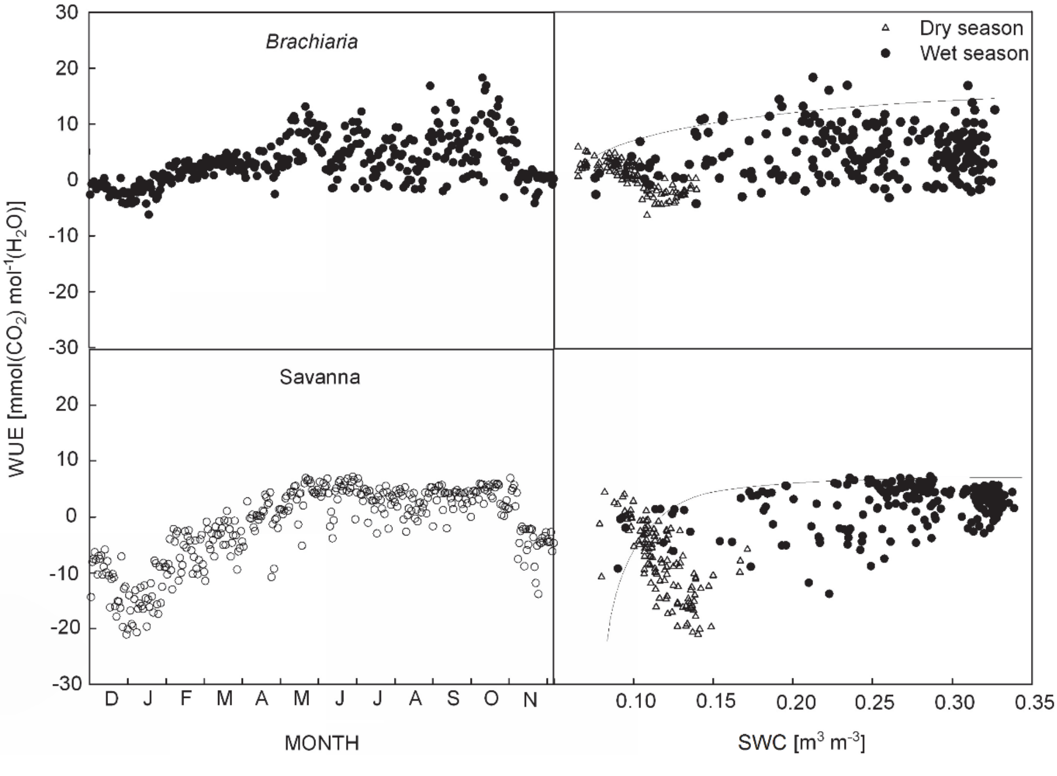

Fig. 5. Daily water-use efficiency (WUE) and WUE as a function of volumetric soil water content (SWC) with a fitted water boundary envelope in *Brachiaria decumbens* Stapf field and a savanna of the Orinoco lowlands.

During the wet season, the seasonally averaged NEF in the nighttime over the *B. decumbens* field (–2.1 ± 3.3 μmol m^{-2} s^{-1}) was higher than that in the herbaceous savanna (–1.7 ± 0.9 μmol m^{-2} s^{-1}). This was associated with accelerated decomposition of the marcescent leaves. The values for *B. decumbens* resembled the corresponding figures over *B. decumbens* fields in southwestern Amazonia (Grace *et al.* 1998). In the herbaceous savanna, the values were similar to those measured over campo sujos and cerrados (≥ –10 μmol m^{-2} s^{-1}) in Central Brazil (Miranda *et al.* 1997, Vourlitis *et al.* 2001, Santos *et al.* 2003). For the cerradão, the average rate of NEF in nighttime varied from –5 to –6 μmol m^{-2} s^{-1} during the wet season to < –4 μmol m^{-2} s^{-1} in the dry season (Vourlitis *et al.* 2001).

APF: For the whole data set, the hourly carbon flux for each stand was used to assess the hourly APF as a function of the PPF. This relationship has been analyzed by Hipps *et al.* (1983) and Baldocchi (1994). For both the *B. decumbens* and herbaceous savanna stands, the fitted hyperbolic functions like ours worked well for the established pasture of *B. decumbens* and campo sujo occurring in the Central Brazilian plains (Santos 1999, Santos *et al.* 2004) as well as for a millet plantation growing in a Sahelian fallows (Moncrieff *et al.* 1997). The absorbed energy, which is available for photosynthesis, is a function of LAI. Here, the closed *B. decumbens* stand absorbed more PAR than did the open herbaceous savanna canopy. The seasonal changes in APF were associated with variations in SWC. During the dry season, SWC was below wilting point (0.087 m^3 m^{-3}) for 36 and 4 days in the *B. decumbens* and herbaceous savanna stands, respectively. The moisture was insufficient to maintain the respiration and photosynthesis.

In spite of the fact that *B. decumbens* pasture and herbaceous savanna are dominated by C_4 grasses with well-known lack of radiation saturation in C_4 species (Black 1973), the APF became PPF-saturated in both stands. A similar response has been reported for *B. brizantha* growing in western Amazonia (Grace *et al.* 1998). The assimilation became increasingly PPF-saturated as the dry season progressed. Saturation has been reported in a north Australian savanna only during the dry season (Eamus *et al.* 2001). These low responses in both stands could be related to constraints in available resources and environmental conditions (Veenendaal *et al.* 1993, Le Roux and Mordelet 1995, Grace *et al.* 1998). Also, the low response might be related to differences in the CO_2 uptake and additional losses of CO_2 *via* edaphic respiration (Baldocchi and Meyers 1998). Consequently, these results call for improving agronomical practices and genetic material as related to carrying capacity and pasture management. Promising marker selection has been carried out to improve agronomic traits (Tohmé *et al.* 1998).

The variation between stands and seasons in their photosynthetic activity might be inferred from the flux/irradiance curve. For the *B. decumbens* and herbaceous savanna stands, the α_a was 0.005–0.014 and 0.001–0.009 μmol(CO_2) $μmol^{-1}$(quantum), respectively. Those values were within the range reported for C_4 grasslands [0.009 –0.052 μmol(CO_2) $μmol^{-1}$(quantum)], millet growing in the Sahel [0.020 μmol(CO_2) $μmol^{-1}$(quantum)], savanna fallow [0.018 μmol(CO_2) $μmol^{-1}$(quantum)] and Brazilian cerrado [0.012–0.014 μmol(CO_2) $μmol^{-1}$(quantum)] as derived from micrometeorological measurements (Ruimy *et al.* 1995, Miranda *et al.* 1997, Moncrieff *et al.* 1997).

F_s values ranging from 1.0 to 8.1 μmol m^{-2} s^{-1} were characteristic of savannas in the dry season (Miranda *et al.* 1997, Eamus *et al.* 2001, Wilsey 2002, Santos 2003, Veenendaal *et al.* 2004) and lower than those found in rain forests (Sotta *et al.* 2004), presumably becasue of water deficits inhibiting microbial and root activities, and a restriction in rhizodeposition. The seasonal difference in the sensitivity of F_s to temperature was associated with the nature of the processes. However, F_s was the main component of the ecosystem respiration as the seasonal effect of the SWC and canopy structure outweighed the temperature effect. This effect has been shown for grasslands (Luo *et al.* 1996, Craine *et al.* 1999), cerrados in Central Brazil (Meir *et al.* 1996), African savannas (Zepp *et al.* 1996), and the wet-dry tropical savannas of northern Australia (Chen *et al.* 2002). During the dry season, a major portion of F_s is coming from the recalcitrant carbon that features low sensitivity to temperature (Liski *et al.* 1999), whereas during the wet season, the temperature effect reflected root and microbial activities as well as carbon uptake and partitioning to the roots (Davidson *et al.* 1998, Bowling *et al.* 2002). When the respiration curves as outlined in Lloyd and Taylor (1994) were incorporated into the respiration data, bursts of CO_2 emissions were evident during alternating series of rainless and rainy days. This effect was originally reported by Birch and Friend (1956) and Griffiths and Birch (1961) for the East Africa soils of Kenya. Recently, the "Birch effect" has been reported for Sahelian fallow savannas (Boulain *et al.* 2009), Sudanian savannas (Brümmer *et al.* 2009), tussocks (Hunt *et al.* 2002), and tall-grass prairies (Liu *et al.* 2002).

In addition to aforementioned factors, the daily difference between stands in F_s might be related to the variations in carbon input from litter and soil carbon content (Table 1). The mean annual F_s for the *B. decumbens* and savanna stands were 5.1 ± 2.3 and 4.5 ± 2.1 μmol m^{-2} s^{-1}, respectively. Here, the values were higher than the mean values reported for tropical savannas and grasslands (1.6–3.0 μmol m^{-2} s^{-1}) (Raich and Schlesinger 1992, Meir *et al.* 1996, Verhoef *et al.* 1999). The high values could be associated with CO_2 bursts.

Table 1. Vegetation and soil carbon content, net primary production, and leaf area index in a *Brachiaria decumbens* Stapf field and a herbaceous savanna in the Orinoco lowlands. Values after ± are the limits for means of 10 samples (95% probability).

	Brachiaria field		Savanna	
	Dry season	Wet season	Dry season	Wet season
Vegetation carbon content [g(C) m^{-2}]				
Aboveground				
Assimilatory	84 ± 23	132 ± 36	46 ± 6	69 ± 22
Nonassimilatory	106 ± 52	209 ± 74	106 ± 28	71 ± 27
Belowground (0.0 – 0.5 m depth)	197 ± 30	309 ± 65	76 ± 24	162 ± 26
Stand total	387 ± 64	650 ± 85	228 ± 62	302 ± 73
Soil carbon content [g(C) m^{-2}] (0.0 – 0.3 m depth)	3,616 ± 382		2,589 ± 252	
Total system carbon content [g(C) m^{-2}]	4,266 ± 592		2,946 ± 382	
Net ecosystem production [g(C) m^{-2} yr^{-1}]	216		36	
Leaf area index [m^2 m^{-2}]	1.55 ± 0.14	2.44 ± 0.23	0.93 ± 0.08	2.14 ± 0.20

The turnover time of soil carbon as the ratio of soil carbon content to annual R_h was nine and seven years for the *B. decumbens* and savanna stands, respectively. Therefore, the carbon in the soil is replaced with time in a manner similar to that in other tropical savannas and grasslands (Raich and Schlesinger 1992).

NEP, R_{eco}, and GPP: Assessments of carbon balance, especially when monitored in the long term, can help us to evaluate the sustainability of a system and lead to improved management strategies.

In the *B. decumbens* field, annual NEP was 216 g(C) m^{-2} yr^{-1}, whereas in the herbaceous savanna, the value [*i.e.*, 36 g(C) m^{-2} yr^{-1}] was close to equilibrium. Therefore, the activity and length of the period of active photosynthesis and respiration was greater in the *B. decumbens* field than in the herbaceous savanna.

Results indicate that the replacement of a herbaceous savanna by a *B. decumbens* pasture resulted in a strong carbon sink. This high NEP reflects the adaptation of *B. decumbens* to lowland conditions and its potential in helping to mitigate the greenhouse gas emissions. By contrast, the herbaceous savanna may be considered to be in a disturbed state characterized by cycles of cattle grazing and tree renewal. As a consequence, the savanna system was a low carbon sink with low LAI (Table 1). Thus, the ecosystem respiration to NEP ratio was favored when woodland savanna was replaced by herbaceous savannas following disturbance (San José *et al.* 2008). The annual NEP in the herbaceous savanna was similar to that in a Sahelian fallow savanna [12–32 g(C) m^{-2} yr^{-1}] (Hanan *et al.* 1998) and southern African savannas [25–32 g(C) m^{-2} yr^{-1}] (Lloyd 1999, Veenendaal *et al.* 2004). By contrast, in the woody savannas of the Orinoco llanos, Brazilian campo sujo and cerrado, and north Australian savanna, the sink was strong [106–380 g(C) m^{-2} yr^{-1}] (Monteiro 1995, Miranda *et al.* 1997, Eamus *et al.* 2001, Chen *et al.* 2003, Santos *et al.* 2003, San José *et al.* 2008).

The difference between savannas in NEP reflected the effects of the length of the growing period, environmental conditions, and land-use changes (Meyers 2001, San José *et al.* 2008). The highest reported NEP for savannas was measured in Brazilian neotropical savannas and north Australian savannas [NEP = 122 – 380 g(C) m^{-2} yr^{-1}] (Monteiro 1995, Miranda *et al.* 1997, Eamus *et al.* 2001, Chen *et al.* 2003, Santos *et al.* 2003) with a growing season of 6–8.5 months and precipitation ranging from 1,500 to 2,000 mm per year. In the Orinoco tree savannas, NEP ranged from 116 to 139 g(C) m^{-2} yr^{-1} during a growing period of 6–7 months and precipitation of 1,300 mm (San José *et al.* 2008). The lowest value was reported for the paleotropical, Sahelian fallow savanna and Mopane woodlands at the Kalahari transect [NEP = 12–32 g(C) m^{-2} yr^{-1}] (Hanan *et al.* 1998, Veenendaal *et al.* 2004) with a growth period of only 3–4 months and precipitation of just 306–464 mm. The influence of the environmental conditions on NEP as reflected by the drought effect was shown in the Australian savannas (Eamus *et al.* 2001, Leuning *et al.* 2005). Thus, in the tropical wet/dry savannas in Australia, Leuning *et al.* (2005) estimated a net loss of 44 g(C) m^{-2} yr^{-1}. Burrows *et al.* (2002) monitored 57 sites and they found that the net aboveground carbon increment in the *Eucalypt* woodlands in Queensland was 53 g(C) m^{-2} yr^{-1}. By contrast, Eamus *et al.* (2001) reported a gain of 280 g(C) m^{-2} yr^{-1} in much wetter savannas near Darwin in Australia tropical north.

Here, effects of land-use changes on NEP were evidenced, when the herbaceous savannas were replaced by *B. decumbens*.

NEP increased 6-fold. In the Orinoco lowlands, the replacement of the herbaceous savanna by the African grass *Andropogon* lead to an increase in the NEP of 61-fold (San José *et al.* 2008). In the North Australia, the management of open-forest savannas by using fire reduced the NEP from 430 to 360 g(C) m^{-2} yr^{-1} due to fuel combustion, land use impact on productivity, and changes in the surface-atmosphere coupling. Here, the carbon status was driven by the land-use changes and seasonal impact as conditioned throughout by LAI development, SWC, and D_a.

The ecosystem respiration of *B. decumbens* and herbaceous savanna stands was 306 and 198 g(C) m^{-2} yr^{-1}, respectively. The R_{eco} was related to the GPP and therefore it accounted for the carbon balance. Thus, the fitted linear equation indicated that seasonal R_{eco} was 53% of the GPP, determining the seasonal trend of changes. In the unburned and burned campo sujo, the ratio reached higher values (*i.e.*, 71 and 77%, respectively) (Santos *et al.* 2003). This different outcome is probably due to high abundance of shrubs with woody cover in the campo sujo (Ribeiro and Walter 1998).

WUE as a measure of the ability of vegetation to conserve water during CO_2 uptake showed at both stands a divergent seasonal tendency (Fig. 5). During the wet season, the averaged WUE was 4.8 ± 4.3 and 2.2 ± 3.7 mmol(CO_2) mol^{-1}(H_2O) in the *B. decumbens* and herbaceous savanna stands, respectively. For a *B. brizantha* stand and a terrafirme forest, Grace *et al.* (1998) reported values of 4.4 and 2.3 mmol(CO_2) mol^{-1}(H_2O), respectively. In the drought-prone areas of Sahelian plains, the WUE of millet reached up to 8.0 mmol(CO_2) mol^{-1}(H_2O) due to the management and breeding of better cultivars. Here, the efficiency in the *B. decumbens* field was similar at different values of SWC. This species possesses drought resistance traits that allow balancing of transpiration and CO_2 uptake, which avoids extreme internal water deficit. The results indicated that under the same environmental conditions, the major determinant was the difference between stands in their drought resistance associated to root exploration and leaf area development. The fertilized *B. decumbens* could maintain high evapotranspiration by exploring larger soil volume (*i.e.*, 339 g m^{-2}) as compared with that in the herbaceous savanna (*i.e.*, 115 g m^{-2}). Imposed fertility has increased WUE of annual ryegrass (Stewart 2001). In the *B. decumbens*, the high LAI reduced the effect of water shortage on grass water status and allowed a growth and survival for considerable periods that was evidenced by the NEP trend. By contrast, the WUE in the herbaceous savanna stand varied with seasonal SWC. Particularly, in African savannas, the difference in WUE between days with high *vs.* low SWC was lesser than 10%. Similar results were found for the campo sujo (Santos 1999), the cerrado (Monteiro 1995), and the African savanna at Ghanzi, Botswana (Williams and Albertson 2004). The response in WUE to SWC might result from species adaptation to drought.

Conclusion: Based on the analysis of net ecosystem carbon cycling, we may conclude that replacement of the savannas by the *B. decumbens* pasture can turn the system into a carbon sink of 216 g(C) m^{-2} yr^{-1} as a result of changes in CO_2 uptake and respiratory fluxes. Similarly, the African grass *Andropogon* was a carbon sink of 366 g(C) m^{-2} yr^{-1} (San José *et al.* 2008). However, this stand combined higher carbon intake with greater annual evapotranspiration. As a consequence, a trade-off of carbon storage for water loss was likely. Therefore, this work identified potential problems and management needs associated with sequestration. The climate feedback could potentially offset the increase in transpiration and convective rainfall following the replacement of savannas by the *B. decumbens* fields. This feedback must be assessed to estimate the projected effect of conversion to the *B. decumbens* fields for cattle grazing and carbon sequestration payments. On the basis of simulating the afforestation of crop and pasture lands, there is no evidence for increased rainfall from local convection (Jackson *et al.* 2005). However, under cattle grazing, this rate of carbon accumulation does not occur. Assessing the long-term effects of cattle grazing with *B. decumbens* field and savanna indicate that soil organic carbon remained in equilibrium for 30 years (San José *et al.* 2003). Carbon accumulation is managed by adjustment of the stocking rate, fire frequency, and resource extraction. However, in reality, the Orinoco savannas constitute a nonequilibrium system since they are always recovering from cattle and fire disturbance (San José and Montes 2007).

References

Alvim, M.J., Botrel, M. de A., Verneque, R.da S., Salvati, J.A.: [Nitrogen application in accessions of Brachiaria. 1. Effect on dry matter production.] – Pasturas Tropicales **12**: 2-6, 1990. [In Portuguese]

Aubinet, M., Grelle, A., Ibrom, A., *et al.*: Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. – Adv. Ecol. Res. **30**: 113-175, 2000.

Aubinet, M., Heinesch, B., Longdoz, B.: Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability. – Glob. Change Biol. **8**: 1053-1071, 2002.

Aubinet, M., Heinesch, B., Yernaux, M.: Horizontal and vertical CO_2 advection in a sloping forest. – Bound-Lay. Meteorol. **108**: 397-417, 2003.

Baldocchi, D.: A comparative study of mass and energy exchange over a closed (wheat) and an open (corn) canopy: II. Canopy CO_2 exchange and water use efficiency. – Agr. Forest Meteorol. **67**: 291-321, 1994.

Baldocchi, D., Meyers, T.: On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and gaseous deposition fluxes over vegetation. – Agr. Forest Meteorol. **90**: 1-25, 1998.

Bégué, A., Desprat, J.F., Imbernon, J., Baret, F.: Radiation use efficiency of pearl millet in the Sahelian zone. − Agr. Forest Meteorol. **56**: 93-110, 1991.

Birch, H.F., Friend, M.T.: Humus decomposition in East African soils. – Nature **178**: 500-501, 1956.

Black, C.C.: Photosynthetic carbon fixation in relation to net CO_2 uptake. – Ann. Rev. Plant Phys. **24**: 253-286, 1973.

Boulain, N., Cappelaere, B., Ramier, D., *et al.*: Towards an understanding of coupled physical and biological processes in the cultivated Sahel - 2. Vegetation and carbon dynamics. – J. Hydrol. **375:** 190-203, 2009.

Bowling, D.R., McDowell, N.G., Bond, B.J., Law, B.E., Ehleringer, J.R.: ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. – Oecologia **131:** 113-124, 2002.

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

Burrows, W.H., Henry, B.K., Back, P.V., *et al.*: Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications. – Glob. Change Biol. **8**: 769-784, 2002.

Chen, X., Eamus, D., Hutley, L.B.: Seasonal patterns of soil carbon dioxide efflux from a wet-dry tropical savanna of northern Australia. – Aust. J. Bot. **50**: 43-51, 2002.

Chen, X., Hutley, L.B., Eamus, D.: Carbon balance of a tropical savanna in northern Australia. – Oecologia **137**: 405-416, 2003.

Cox, G.W.: Laboratory Manual of General Ecology. Pp. 272. W.O.C., Iowa 1972.

Craine, J.M., Wedin, D.A., Chapin, F.S.: Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland. – Plant Soil **207**: 77-86, 1999.

Davidson, E.A., Beck, E., Boone, R.D.: Soil water content and temperature as independent or confound factors controlling soil respiration in a temperature mixed hardwood forest. – Glob. Change Biol. **4**: 217-227, 1998.

Du, Y.C., Kawamitsu, Y., Nose, A., *et al.*: Effects of water stress on carbon exchange rate and activities of photosynthetic enzyme in leaves of sugarcane (*Saccharum* sp.). – Aust. J. Plant Physiol. **23**: 719-726, 1996.

Eamus, D., Hutley, L.B., O´Grady, A.P.: Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. – Tree Physiol. **21**: 977-988, 2001.

Falge, E., Baldocchi, D., Olson, R., *et al.*: Gap filling strategies for defensible annual sums of net ecosystem exchange. – Agr. Forest Meteorol. **107**: 43-69, 2001.

Frouin, R., Pinker, R.T.: Estimating photosynthetically Active Radiation (PAR) at the Earth's surface from satellite observations. – Remote Sens. Environ. **51:** 98-107, 1995.

Grace, J., Lloyd, J., Miranda, A.C., Miranda, H., Gash, J.H.C.: Fluxes of carbon and water vapour over a C_4 pasture in south-western Amazonia (Brazil). – Aust. J. Plant Physiol. **25**: 519-530, 1998.

Grace, J., Malhi, Y., Lloyd, J., *et al.*: The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. – Glob. Change Biol. **2**: 209-217, 1996.

Griffiths, E., Birch, H.F.: Microbiological changes in freshly moistened soil. – Nature **189**: 424, 1961.

Hanan, N.P., Kabat, P., Dolman, A.J., Elbers, J.A.: Photosynthesis and carbon balance of a Sahelian fallow savanna. – Glob. Change Biol. **4**: 523-538, 1998.

Hanson, P.J., Wullschleger, S.D., Bohlman, S.A., Todd, D.E.: Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest. – Tree Physiol. **13**: 1-15, 1993.

Hedges, J.I., Clark, W.A., Quay, P.D., *et al.*: Compositions and fluxes of particulate organic material in the Amazon River. – Limnol. Oceanogr. **31**: 717-738, 1986.

Hipps, L.E., Asrar, G., Kanemasu, E.T.: Assessing the interception of photosynthetically active radiation in winter wheat. – Agr. Meteorol. **28**: 253-259, 1983.

Hunt, J.E., Kelliher, F.M., McSeveny, T.M., Byers, J.N.: Evaporation and carbon dioxide exchange between the atmosphere and a tussock grassland during a summer drought. – Agr. Forest Meteorol. **111**: 65-82, 2002.

IPCC: Climate change: the IPCC Scientific Assessment. – In: Houghton, J.T., Jenkins, G.J., Ephraums, J.J. (ed.): Report by Working Group I Pp. 410. Cambridge University Press, Cambridge, New York, and Melbourne 1990.

IPCC: Intergovermental panel on climate change. climate change 2001. – In: Watson, R.T. and the Core Writing Team (ed.): Synthesis Report. Third Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge Univ. Press, New York 2001.

Jackson, M.L.: Soil Chemical Analysis. Pp. 380. Prentice, New York 1958.

Jackson, R.B., Jobbagy, E.G., Avissar, R., *et al.*: Trading water for carbon with biological carbon sequestration. – Science **310**: 1944-1947, 2005.

Kaimal, J.C., Finnigan, J.J.: Atmospheric Boundary Layer Flows. Their Structure and Measurement. Pp. 289. Oxford University Press, Oxford 1994.

Kruijt, B., Elbers. J.A., von Randow, C., *et al.*: The robustness of eddy correlation fluxes for Amazon rain forest conditions. – Ecol. Appl. **14**: S101-S113, 2004.

Lal, A., Edwards, G.E.: Analysis of inhibition of photosynthesis under water stress in the C_4 species *Amaranthus cruentus* and *Zea mays*: electron transport, CO_2 fixation and carboxylation capacity. – Funct. Plant Biol. **23**: 403-412, 1996.

Lapointe, S.L., Miles, J.W.: Germplasm case study: *Brachiaria* species. – In: Miles, J.W., Maass, B.L., do Valle, C.B., Kumble, V. (ed.): CIAT Pastures for the Tropical Lowlands: CIAT´s Contribution. Pp 43-55. CIAT, Cali, Colombia, 1992.

Le Roux, X., Mordelet, P.: Leaf and canopy CO_2 assimilation in a West African humid savanna during the early growing season. – J. Trop. Ecol. **11**: 529-545, 1995.

Leuning, R., Cleugh, H.A., Zegelin, S.J., Hughes, D.: Carbon and water fluxes over a temperate *Eucalyptus* forest and a tropical wet/dry savanna in Australia: measurements and comparison with MODIS remote sensing estimates. – Agr. Forest Meteorol. **129**: 151-173, 2005.

Lira, M.D., Farias, I., Fernandes, A.D.M., Soares, L.M., Dubeux, J.C.B.: Response stability of signal grass (*Brachiaria decumbens* Stapf.) with increasing nitrogen and phosphorus levels. – Pesqui. Agropecu. Bras. **29**: 1151-1157, 1994.

Liski, J., Ilvesniemi, H., Mäkelä, A., Westman, C.J.: CO_2 emissions from soil in response to climate warming are overestimated. The decomposition of old soil organic matter is tolerant of temperature. – Ambio **28**: 171-174, 1999.

Liu, X.Z., Wan, S.Q., Su, B., Hui, D.F., Luo, Y.Q.: Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem. – Plant Soil **240**: 213-223, 2002.

Lloyd, C.R.: The CO_2 dependence of photosynthesis, plant growth responses to elevated CO_2 concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO_2 concentrations and increased nitrogen deposition at a global scale. – Funct. Ecol. **13**: 439-459, 1999.

Lloyd, J., Taylor, J.A.: On the temperature dependence of soil respiration. – Funct. Ecol. **8**: 315-323, 1994.

Luo, Y.Q., Jackson, R.B., Field, C.B., Mooney, H.A.: Elevated CO_2 increases belowground respiration in California grasslands. – Oecologia **108**: 130-137, 1996 .

McKell, C.M., Wilson, A.M., Jones, M.B.: A flotational method for easy separation of roots from soil samples. – Agron. J. **53**: 56-57, 1961.

Meir, P., Grace, J., Lloyd, J., Miranda, A.C.: Soil respiration in a rain forest in Amazonia, and in cerrado in Central Brazil. – In: Gash, J.H.C., Nobre, C.A., Roberts, J.M., Victoria, R.L. (ed.): Amazonian Deforestation and Climate. Pp. 319–329. John Wiley & Sons, UK 1996.

Meyers, T.P.: A comparison of summertime water and CO_2 fluxes over rangeland for well watered and drought conditions. – Agr. Forest Meteorol. **106**: 205-214, 2001.

Miles, J.W., Lapointe S.L.: Regional germplasm evaluation: A portfolio of germplasm options for the major ecosystems of tropical America. – In: Miles, J.W., Maass, B.L., do Valle, C.B., Kumble, V. (ed.):. Pastures for the Tropical Lowlands: CIAT´s Contribution. Pp 43-55. CIAT, Cali, Colombia, 1992.

Miles, J.W., Maass, B.L., do Valle, C.B., Kumble, V.: [*Brachiaria*: Biology, Agronomy and Improvement.]. Pp. 312. CIAT-EMBRAPA, Colombia 1998. [In Spanish]

Miranda, A.C., Miranda, H.S., Lloyd, J., *et al.*.: Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. – Plant Cell Environ. **20**: 315-328, 1997.

Moncrieff, J.B., Monteny, B., Verhoef, A., et al.: Spatial and temporal variations in net carbon flux during HAPEX-Sahel. – J. Hydrol. **189**: 563-588, 1997.

Monteiro, J.M.: [CO_2 fluxes in a cerrado sensu stricto.] – Master Dissertation, Univ. Brasilia, Brasilia 1995. [In Portuguese]

Monteny, B.A., Lhomme, J.P., Chehbouni, A., *et al.*: The role of the Sahelian biosphere on the water and the CO_2 cycle during the HAPEX-Sahel Experiment. – J. Hydrol. **189**: 516-535, 1997.

Mullenax, C.: [Adequacy and management of natural grasslands in the high plains of the Eastern Plains of Colombia.] – Carta Agraria **278**: 2, 1979. [In Spanish]

Parsons, J.J.: Spread of African grasses to the American tropics. – J. Range Manage. **25**: 12-17, 1972.

Pla Sentís, I.: [Methodology for the physical characterization to diagnose problems in management and conservation of soils in tropical conditions.] – Graduate course in Soil Science, UCV. Pp 112. Maracay 1977. [In Spanish]

Raich, J.W., Schlesinger, W.H.: The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. – Tellus B **44**: 81-99, 1992.

Rao, I.M., Kerridge, P.C., Macedo, M.C.M.: [Nutritional requirements and adaptation to acid soils *Brachiaria* species.] – In: Miles, J.W., Maass, B.L., do Valle, C.B., Kumble, V. (ed.): [*Brachiaria*: Biology, Agronomy and Improvement]. Pp. 58-78. CIAT, EMBRAPA, Colombia 1998. [In Spanish]

Reichstein, M., Falge, E., Baldocchi, D., *et al.*: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. – Glob. Change Biol. **11**: 1424-1439, 2005.

Ribeiro, J.P., Walter, B.M.: [Vegetation physiognomies of the Cerrado biome]. – In: Sano, S.M., de Almeida, S.P. (ed.): [Cerrado: Environment and Flora.] Pp. 89-168. EMBRAPA-CPAC, Planaltina, Brazil 1998. [In Portuguese]

Ruimy, A., Jarvis, P.G., Baldocchi, D.D., Saugier, B.: CO_2 fluxes over plant canopies and solar radiation: a review. – Adv. Ecol. Res. **26**: 1-68, 1995.

San José, J.J.: Mass and energy transfer within and between burned and unburned savanna environments.– Int. J. Wildland Fire **2**: 153-160, 1992.

San José, J.J.: Contribution of rangelands to animal production in the tropics. – In: Sotomayor-Rios, A., Pitman, W.D. (ed.): Tropical Forage Plants: Development and Use. Pp. 269–294. CRC Press, New York 2001.

San José, J.J., Bracho, R., Montes, R., Nikonova, N.: Comparative energy exchange from cowpeas [*Vigna unguiculata* (L.) Walp cvs. TC-9-6 and M-28-6-6] with differences in canopy architectures and growth durations at the Orinoco llanos. – Agr. Forest Meteorol. **116**: 197-219, 2003.

San José, J.J., Montes, R.: Resource apportionment and net primary production outcome across the Orinoco savanna-woodland continuum. – Acta Oecol. **32**: 243-253, 2007.

San José, J.J., Montes, R., Grace, J., Nikonova, N.: Land-use changes alter CO_2 flux patterns of a tall-grass *Andropogon* field and a savanna-woodland continuum in the Orinoco lowlands. – Tree Physiol. **28**: 437-450, 2008.

Santos, A.J.B.: [Fluxes of energy, carbon and water in a vegetation of campo sujo.] – Master Dissertation, Univ. Brasilia, Brasilia 1999. [In Portuguese]

Santos, A.J.B., Da Silva, G.T., Miranda, H.S., Miranda, A.C., Lloyd, J.: Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in Central Brazil. – Funct. Ecol. **17**: 711-719, 2003.

Santos, A.J.B., Quesada, C.A., Da Silva, *et al.*: High rates of net ecosystem carbón assimilation by *Brachiaria* pasture in the Brazilian cerrado. – Glob. Change Biol. **10**: 877-885, 2004.

Schuepp, P.H., Leclerc, M.Y., MacPherson, J.I., Desjardin, R.L.: Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation. – Bound.–Lay. Meteorol. **50**: 353-373, 1990.

Sotta, E.D., Meir, P., Malhi, Y., Nobre, A.D., Hodnett, M.: Soil CO_2 efflux in a tropical forest in the central Amazon. – Glob. Change Biol. **10**: 601-617, 2004.

Stewart, W.M.: Balanced fertilization increases water use efficiency. News and views. A regional newsletter published by Potash & Phosphate Institute (PPI). Pp. 2, www.ppi-far.org. Lubbocks, Texas 2001.

Tohmé, J., Palacios, N., Lenis, S., Roca, W.: [Applications of biotechnology to *Brachiaria* genus.] – In: Miles, J.W., Maass, B.L., do Valle, C.B., Kumble, V. (ed.): [*Brachiaria*: Biology, Agronomy and Improvement.] Pp. 216-225. CIAT-EMBRAPA, Cali, Colombia 1998. [In Spanish]

Veenendaal, E.M., Kolle, O., Lloyd, J.: Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa. – Glob. Change Biol. **10**: 318-328, 2004.

Veenendaal, E.M., Shuschu, D.D., Scurlock, J.M.O.: Responses to shading of seedling of savanna grasses (with different C_4 photosynthetic pathway) in Botswana. – J. Trop. Ecol. **9**: 213-229, 1993.

Verhoef, A., Allen, S.J., Lloyd, C.R.: Seasonal variation of surface energy balances over two Sahelian surfaces. – Int. J. Climatol. **19**: 1267-1277, 1999.

Vourlitis, G., Priante, N., Hayashi, M.M.S., *et al.*: Seasonal variations in the net ecosystem CO_2 exchange of a mature Amazonian transitional tropical forest (cerradao). – Funct. Ecol. **15**: 388-395, 2001.

Walkley, A.: A critical examination of a rapid method for determining organic carbon in soils–effect of variations in digestion conditions and of inorganic soil constituents. – Soil Sci. **63**: 251-264, 1947.

Williams, C.A., Albertson, J.D.: Soil moisture controls on canopy-scale and carbon fluxes in an African savanna. – Water Resour. Res. doi:10.1029/2004WR003208, 2004.

Wilsey, B.: Clonal plants in a spatially heterogeneous environment: effects of integration on Serengeti grassland response to defoliation and urine-hits from grazing mammals. – Plant Ecol. **159**: 15-22, 2002.

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