

Land-use changes alter CO₂ flux patterns of a tall-grass *Andropogon* field and a savanna–woodland continuum in the Orinoco lowlands

JOSÉ SAN JOSÉ,^{1,2} RUBÉN MONTES,³ JOHN GRACE⁴ and NINA NIKONOVA¹

¹ Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas 1020-A, Venezuela

² Corresponding author (jsanjose@ivic.ve)

³ Departamento de Estudios Ambientales, Universidad Simón Bolívar, Apartado 89000, Caracas 1080-A, Venezuela

⁴ School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JN, U.K.

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Summary Land use changes in the savannas of the Orinoco lowlands have resulted in a mosaic of vegetation. To elucidate how these changes have affected carbon exchanges with the atmosphere, we measured CO₂ fluxes by eddy covariance and soil CO₂ efflux systems along a disturbance gradient beginning with a cultivated tall-grass *Andropogon* field (S1) and extending over three savanna sites with increasing woody cover growing above native herbaceous vegetation. The savanna sites included a herbaceous savanna (S2), a tree savanna (S3) and a woodland savanna (S4). During the wet season, maximum diurnal net ecosystem exchange (NEE) over the S1–S4 sites was 6.6–9.3, 6.6–7.9, 10.6–11.3 and 9.3–10.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The rate of CO₂ uptake over S1 was lower than that for C₄ grasses elsewhere because of pasture degradation. Soil respiration and temperature were exponentially related when soil water content (θ) was above 0.083 $\text{m}^3 \text{m}^{-3}$; however, soil respiration declined markedly as θ decreased from 0.083–0.090 to 0.033–0.056 $\text{m}^3 \text{m}^{-3}$. There were bursts of CO₂ emission when dry soils were rewetted by rainfall. During the wet season, all sites constituted carbon sinks with maximum net daily ecosystem production (NEP) of 2.1, 1.7, 2.1 and 2.1 $\text{g C m}^{-2} \text{day}^{-1}$, respectively. During the dry season, the savanna sites (S2–S4) became carbon sources with maximum emission fluxes of –0.5, –1.4 and –1.6 $\text{g C m}^{-2} \text{day}^{-1}$, respectively, whereas the tall-grass field (S1) remained a carbon sink with a maximum NEP of 0.3 $\text{g C m}^{-2} \text{day}^{-1}$ at the end of the season. For all measurement periods, annual NEP of sites S1–S4 was 366, 6, 116 and 139 g C m^{-2} , respectively. Comparisons of carbon source/sink dynamics across a wide range of savannas indicate that savanna carbon budgets can change in sign and magnitude. On an annual basis, gross primary production over the S1–S4 stands was 797, 803, 136 and 1230 g C m^{-2} , respectively. Net primary productivity (NPP) of the S1–S4 stands, calculated from eddy covariance measurements as the daily sum of NEE and day and night heterotrophic respiration was 498, 169, 181 and 402 $\text{g C m}^{-2} \text{year}^{-1}$, respectively. These values were slightly higher than NPP based on harvest measurements (432, 162, 176 and 386 $\text{g C m}^{-2} \text{year}^{-1}$, respectively), presumably because fine roots were incompletely harvested. Soil water content limited carbon uptake at all sites, and

water-use efficiency (WUE) was related to rainfall dynamics. During the dry season, all sites except the cultivated tall-grass *Andropogon* field (S1) had a negative WUE. Although our results are specific to the Orinoco vegetational mosaic, the effects of land-use practices on the controls and physiological functions of the studied ecosystems may be generalized to other savannas.

Keywords: carbon budget, eddy covariance, energy balance, land-use changes, soil CO₂ efflux.

Introduction

Savannas and seasonally dry tropical forests cover 30% of the world's vegetated surface and account for 15% of the annual global carbon sink impacted by human activities (Taylor and Lloyd 1992). Land use changes in savanna systems such as burning, livestock grazing, tillage and cropping have marked effects on carbon stocks in the soil and vegetation (Hall and Scurlock 1991, Ojima et al. 1993, Scholes and Hall 1996). In savannas, agricultural practices have degraded native vegetation or converted it to pasture and crops, and this has resulted in estimated carbon emissions in the range of 500–800 Tg C year⁻¹ (Seiler and Crutzen 1980). In contrast, when savannas are protected from fire and grazing, they undergo profound changes, often becoming carbon sinks (San José et al. 1998, Grace et al. 2006). Currently, there is interest in the potential of cultivated and native savannas as a sink for the incorporation and sequestration of anthropogenic CO₂ (Fisher et al. 1994, 1995, San José et al. 2003). However, the role of savannas as a carbon sink has rarely been evaluated. Based on periodic inventories and changes in land use, San José and Montes (2001) determined a sink of –17.5 Tg C year⁻¹ for the Orinoco lowlands ($0.4 \times 10^{12} \text{m}^2$).

Monitoring and understanding the existing CO₂ balance in savannas is vital for defining their carbon status. Monitoring carbon fluxes in vegetative mosaics is necessary for understanding the contribution of these fragmented systems to the global carbon budget. Land-use changes have marked effects on carbon storage and decomposition (Valentini 2003, Mel-

esse and Hanley 2005), which in turn affect climate by changing atmospheric climate forcings (Sellers et al. 1996). Information about the effects of land use changes can be useful in formulating environmental mitigation strategies.

Our objective was to analyze the effects of human-induced land-use changes on seasonal components of the carbon budget in a mosaic of disturbed savannas in the Orinoco lowlands of South America. Because of varying land use, the vegetation of this region exhibits contrasting canopy structure, albedo and physiological features that affect energy and water vapor fluxes (San José et al. 2008). Micrometeorological studies on CO₂ fluxes have been made over a limited range of savannas and grasslands, but often over only short time periods (San José et al. 1991, Verhoef et al. 1996, Hanan et al. 1998, Chen et al. 2003, Santos et al. 2003, Veenendaal et al. 2003, 2004, Xu and Baldocchi 2004, Jaksic et al. 2006, Beringer et al. 2007). We aimed to: (1) compare the role of land use on carbon fluxes and budgets as measured in a vegetation mosaic created as a result of human disturbance in the Orinoco lowlands using eddy covariance and soil respiration systems; (2) explore controlling factors on the gaseous exchange under different surface conditions as generated by land use; and (3) assess the capacity of the savanna mosaic to store carbon and maintain biodiversity as criteria of sustainability. We also report measurements of LAI, net primary production based on harvesting, soil organic matter and soil respiration.

Materials and methods

Study sites

The study was carried out in the Orinoco lowlands of South America. The research sites were established as part of the SAVAFLUX network (Grace et al. 1997) and are located on a disturbed vegetational mosaic in the Santa Barbara transect extending from 41 to 43° W and covering a gradient in mean annual precipitation from isohyet 1100 mm year⁻¹ in Santa Barbara to 1000 mm year⁻¹ in Aguasay. Differential intensity of land management has resulted in a mosaic of vegetation comprising a tall-grass (*Andropogon gayanus* Kunth) field (S1) that has been cultivated for 20 years and three sites (S2–S4) with increasing proportions of woody cover over native herbaceous vegetation. The savanna gradient encompasses a herbaceous savanna site (S2) with less than 3% tree cover, a tree savanna (S3) with 28% covered by woody species and a woodland savanna site (S4) with 78% tree canopy cover. The S2 and S3 sites were usually burned each year, but were not burned during the measurement period. The woodland savanna (S4) has been protected against cattle and fire since 1971. Data were collected over a 2-year period. At S1 and S3, all measurements were carried out simultaneously from May 1999 to April 2000. At S2 and S4, measurements were performed from May 2000 to April 2001. Thus, measurements encompassed wet and dry seasons at all sites.

Micrometeorological measurements

Over the study sites, simultaneous measurements of CO₂ and water vapor fluxes were made by the eddy covariance tech-

nique (Aubinet et al. 2000). Air-intake tubes were fixed to a metal mast at 12 heights above the vegetation and within foliage. These hoses were connected to a Type 161 gas handling system (Analytical Development Company, Hertfordshire, U.K.) and CO₂ in the air was measured with an infrared gas analyzer (LI-6262, Li-Cor, Lincoln, NE). The 1-h mean profiles were fitted with a β -spline function and differences between curves for successive 1-h periods were used to calculate hourly CO₂ storage (ΔS_c). 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 systems were used to analyze changes in gas exchange with distance downwind (i.e., advection) as described by San José (1992). Flux measurements were used to perform a footprint analysis as described by Schuepp et al. (1990) and Kaimal and Finnigan (1994). The components of the carbon budget were calculated as described by Ruimy et al. (1995). Downward fluxes into the system were considered positive and upward fluxes negative. Respiratory fluxes were treated as positive. The amount of CO₂ stored in the canopy air was treated as either positive, if S_c increased, or negative, if S_c decreased. The response of the apparent photosynthetic flux (APF) to absorbed photosynthetic photon flux (PPF) was fitted with a rectangular hyperbola. Statistical regression analysis and comparisons among datasets were made with Sigma-Plot curve fitter. To interpret the factors modulating the CO₂ fluxes over the sites, we decomposed net ecosystem exchange (NEE) into ecosystem respiration (R_{eco}) and gross primary production (GPP) by an algorithm that defines the short-term temperature sensitivity of R_{eco} (Reichstein et al. 2005). Net ecosystem exchange, which is the flux of the biota, was calculated as net ecosystem flux above the canopy (NEF) minus ΔS_c . In the studied savanna mosaic, the values of ΔS_c were small, so NEF was similar to NEE. Fluxes during periods with missing data were estimated by standard methods (Falge 2001, Reichstein et al. 2005).

Determination of the conductance path to the transfer processes and diagnoses

The pathway for H₂O diffusion between the canopy and the atmosphere was described by the surface (g_{st}) and aerodynamic (g_a) conductances. Aerodynamic conductance to water vapor and heat was estimated from the sonic anemometer measurements taking into account the additional boundary layer conductance to the momentum flux and the atmospheric stability (Thom 1972, Verma 1989):

$$\frac{1}{g_a} = \frac{u}{u_*^2} + \frac{1}{ku_*} \left(\ln \left(\frac{z_o}{z_H} \right) + \Psi_H - \Psi_M \right) \quad (1)$$

where u is longitudinal wind speed at the reference height, u_* is friction velocity, k is von Karman's constant, z_o/z_H is the ratio of the roughness lengths for momentum (z_o) and heat (z_H) transfers (Verma 1989), and Ψ_H and Ψ_M are the integrated adiabatic correction factors for heat and momentum, respectively (Paulson 1970). Equation 1 takes into account the differences

in transfer mechanism and the sink and source distribution for momentum, heat or mass. The ratio was taken as 10, a typical value for a homogeneous canopy (Garratt and Hicks 1973).

Surface conductance was calculated by the inverted form of the Penman-Monteith equation (Kelliher et al. 1993, 1995), using measurements of latent (λE) and sensible (H) heat fluxes as well as specific humidity deficit (D) in the formula:

$$\frac{1}{g_{sf}} = \left(\frac{\epsilon + 1}{g_a} \right) \left(\frac{\epsilon A}{(\epsilon + 1)(\lambda E)} \right) + \frac{\rho_a D}{E} \quad (2)$$

where ϵ is the dimensionless rate of change of saturated humidity with temperature, A is available energy for the canopy (A_c) and soil (A_s) (i.e., $A = A_c + A_s$) and E is surface evaporation rate.

Soil CO₂ efflux

At each site, hourly soil CO₂ efflux was measured with an infrared gas analyzer (Li-Cor, LI-6200) by sampling gas from a randomly positioned soil respiration chamber (Li-Cor, LI-6000-09). Every hour, four replicate samples were processed in the area. For each measurement, soil temperature was taken by placing a thermocouple 0.1 m below the soil surface. At each site, soil heterotrophic CO₂ flux was measured as described by Hanson et al. (1993). Two months before the onset of each season, four 16-m² subsites were randomly selected 400 m downwind from the instrument site. At each subsite, the soil was carefully excavated up to 0.3 m and the roots removed. The soil was then returned in reverse order of removal. The analyzed subsites were isolated from the system by introducing Plexiglas panels along each side to a depth of 0.5 m. Hourly measurements were carried out on each subplot as described for the soil CO₂ efflux measurements. Post-experiment sampling for residual root density was conducted, and results indicated that barriers excluded roots during measurements. At each site, two sets of four soil blocks (0.5 × 0.6 × 0.3 m) were dug out, placed in plastic containers and transported to the laboratory. In one set, the soil was separated from the roots and heterotrophic CO₂ flux was measured with a gas-exchange chamber. Comparison of heterotrophic effluxes from the field and laboratory determinations indicated that they differed by less than 14%. The second set of blocks were kept at 10 °C, and soil respiration (R_{10}) was measured as a function of soil water content (θ) with a respiratory chamber. For each seasonal mean of daily water content, R_{10} was calculated and soil CO₂ efflux (R_s) and absolute soil temperature (T ; K) were fitted as (Lloyd and Taylor 1994):

$$R_s = R_{10} e^{308.56 \left(\frac{1}{56.02} - \frac{1}{T - 227.13} \right)} \quad (3)$$

Net primary production

At each site, above- and belowground net primary productions (NPP; sum of weighted surface from the area covered by woody and herbaceous layers) were estimated as outlined by Long et al. (1992):

$$NPP = \Delta b + \Delta a + x_i \quad (4)$$

where Δb is the annual change in either standing crop green material or functional dry mass (for above- and belowground, respectively), Δa is the annual increment in dead mass and x_i is the annual change in disappearing dead material calculated as:

$$x_i = r_i \Delta a \quad (5)$$

where r_i is decomposition rate.

Carbon density in the dry mass of vegetation was calculated based on the proportion of carbon in woody and herbaceous vegetation (43%) reported by Hedges et al. (1986).

Annual changes in green material and aboveground dead mass

At each site, four permanent 50 × 50 m plots were established. At each plot, the heights of individuals of each species were measured, and the number of stems with heights above or equal to 0.05 m was recorded. Woody cover was calculated from the horizontal projection of the tree crown by taking the major and minor axes of an elliptical surface. Tree censuses were taken for 5-year height growth (1996–2001). Phytomass changes were calculated based on height–phytomass allometric regressions for each species (San José et al. 1998). Individual tree phytomass was estimated from tree height and averaged over the 2 years of the study. The annual growth increment was determined from the 5-year increment over the period 1996–2001.

At each plot, fifty 1-m² litter traps were randomly distributed, and aboveground litter was collected monthly for up to 1 year. Each trap was randomly relocated within the site after every collection. The traps were made of fine nylon nets mounted above ground level on a wood frame (Newbould 1970). The integration of monthly data represents the annual increment by death and shedding. After the last tree census at each plot, the annual changes in herbaceous phytomass (i.e., Δb and Δa) were calculated as the phytomass difference between the maximum and minimum herbaceous phytomasses. At each plot, the minimum herbaceous phytomass was determined at the end of the dry season (March–April) by measuring radiation interception (Li-Cor LAI-2000 plant canopy analyzer) at 1500 points selected at random. The number of sampling points provides a mean interception with a coefficient of variability of less than 10%. An independent calibration curve between herbaceous phytomass and radiation interception was obtained by comparing harvested herbaceous phytomass and herbaceous phytomass estimated by radiation interception. Thus, at each site, four 50 × 50 m plots were selected at random and radiation interception was determined at 1500 random points. Thereafter, the herbaceous phytomass was harvested, separated into green and non-green phytomass and oven dried at 80 °C to constant mass. A regression of radiation interception versus dry mass had a coefficient of determination of 0.61. At maximum phytomass development, the material was harvested with a mowing machine.

Disappearance of dead aboveground material For both herbaceous and woody species, the rate of decomposition of dead aboveground material was determined by the litter bag technique (Long et al. 1992). For the aboveground material, 120 50-g subsamples were taken randomly at the beginning of the growing season and enclosed in nylon bags of 2-mm mesh. The bagged samples were returned to their original positions. Ten bags were removed monthly throughout the growing season, the change in their mass calculated, and r_i estimated. A different set of subsamples was used to establish the dry-to-fresh mass ratio and to determine the initial dry mass in each bag.

Functional and nonfunctional belowground dry mass At each plot, maximum and minimum belowground functional phytomasses were determined. Fifty subplots were selected at random, and $1.0 \times 1.0 \times 0.3$ m soil-root monoliths were excavated. This soil volume contains more than 80% of the total belowground dry biomass (San José et al. 1985). Roots were separated by flotation (McKell et al. 1961). It was possible to distinguish tree roots from roots of herbaceous plants based on morphological characteristics and resistance to breakage of the woody roots (Böhm 1979). Root samples were dried at 80 °C to constant mass. Herbaceous and woody belowground phytomass samples of 50 g were taken at random. Functional and nonfunctional roots were separated based on the 2,3,5-triphenyltetrazolium chloride reduction assay (San José et al. 1982). Annual belowground increment (Δb) of the functional phytomass was calculated from the annual increment in functional phytomass. Annual increment of belowground nonfunctional dry mass (Δa) was calculated from the nonfunctional roots.

Changes in dead root disappearance The rate of decomposition of belowground phytomass was determined by the litter bag technique (Long et al. 1992). At the plots, 120 bags each containing 50 g of dead root mass were relocated in the soil horizon and 10 bags were removed monthly. Changes in masses were calculated.

Soil organic matter

At each site, triplicate soil samples were collected at depths of 0.00–0.10 (plant residues on the surface were removed), 0.10–0.15 and 0.20–0.30 m. The samples were analyzed for organic carbon percentage by the Walkley and Black method (Jackson 1958). The percentage of soil organic carbon was converted to percentage of total organic carbon by dividing the percentage of total organic matter by 1.724, assuming that carbon constitutes about 58% of soil organic matter (Cox 1972). Subsequently, the percent of total organic carbon was converted to g C m² by: (a) correcting the percentage of total organic carbon for readily oxidizable carbon by multiplying by 0.77 (Walkley 1947); and (b) relating the corrected values to soil volume by considering soil bulk density as determined from the volume occupied by 10 soil samples of 1 m² by the method described by Pla Sentis (1977).

Results and discussion

Net ecosystem flux

We examined environmental variables in an attempt to explain differences in NEF during typical dry and wet season days at the study sites (Figure 1). At all sites, variations in incoming shortwave radiation (San José et al. 2008) explained some of the variation in hourly NEF. The changes in incoming shortwave radiation were related to changes in air humidity mole fraction deficit at the sites. Maximum daytime NEFs (Figure 1) during the wet season, which can be useful for quantifying site function across the Orinoco mosaic, were 6.6–9.3, 6.6–7.9, 10.6–11.3 and 9.3–10.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for sites S1–S4, respectively, with the lowest values occurring in the herbaceous savanna (S2). Nighttime NEF to the atmosphere was greatest in the woodland savanna (S4) (3.9–4.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$) because of enhanced decomposition associated with litterfall and woody canopy cover. For S1–S4, maximum daytime NEF was similar to maximum values reported for mesic Neotropical and dry Paleotropical savannas of Brazilian cerrados (10–17 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Miranda et al. 1997, Santos et al. 2003), dry Paleotropical savannas of African plains (9–15 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Verhoef et al. 1996, Hanan et al. 1998, Veenendaal et al. 2003, Williams and Albertson 2004) and northern Australian savannas (10.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Eamus et al. 2001). In the tall-grass *Andropogon* field (S1), the maximum NEF value was similar to the range (10–15 $\mu\text{mol m}^{-2} \text{s}^{-1}$) reported for millet planted at the Hapex-Sahel southern super-site (Levy et al. 1997).

Comparison of the seasonal trends in daily NEF revealed that, during the growing season, maximum daytime NEF exceeded the dry season values as a result of increased activities of decomposers and vegetation function with temperature and θ . Daytime NEF during the wet season indicated net vegetation uptake over the daily course at all sites. Maximum NEF occurred around midday; however, the value was influenced by changes in radiation as a result of convective cloud formation, and the peak in NEF occurred before the afternoon increase in air humidity mole fraction deficit. With the onset of the dry season in the savannas, vegetative growth declined and there were reductions in the magnitude and timing of maximum NEF. As the dry season progressed, the S2–S4 sites experienced water stress, and maximum NEF decreased to 1.2–1.9, 3.5–4.0 and 3.4–3.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, as air humidity mole fraction deficit increased. A similar response has been reported for grasslands (Verma et al. 1992, Hunt et al. 2002), Brazilian campo sujo and cerrado (Miranda et al. 1996, Santos et al. 2003), broad-leaved semi-arid savannas in the Kalahari transect (Veenendaal et al. 2003) and Sahelian fallow savannas (Hanan et al. 1998).

Night flux error was assessed by considering the relative effects of storage and advection (cf. Grace et al. 1996, Aubinet et al. 2002, Kruijt et al. 2004). The results indicate that storage was negligible during the wet and dry seasons. For all sites, mean seasonal storage at night spanned 0.029 to 0.129 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Therefore, estimates of the storage flux ΔS_c were less than 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as has been reported for the Brazilian

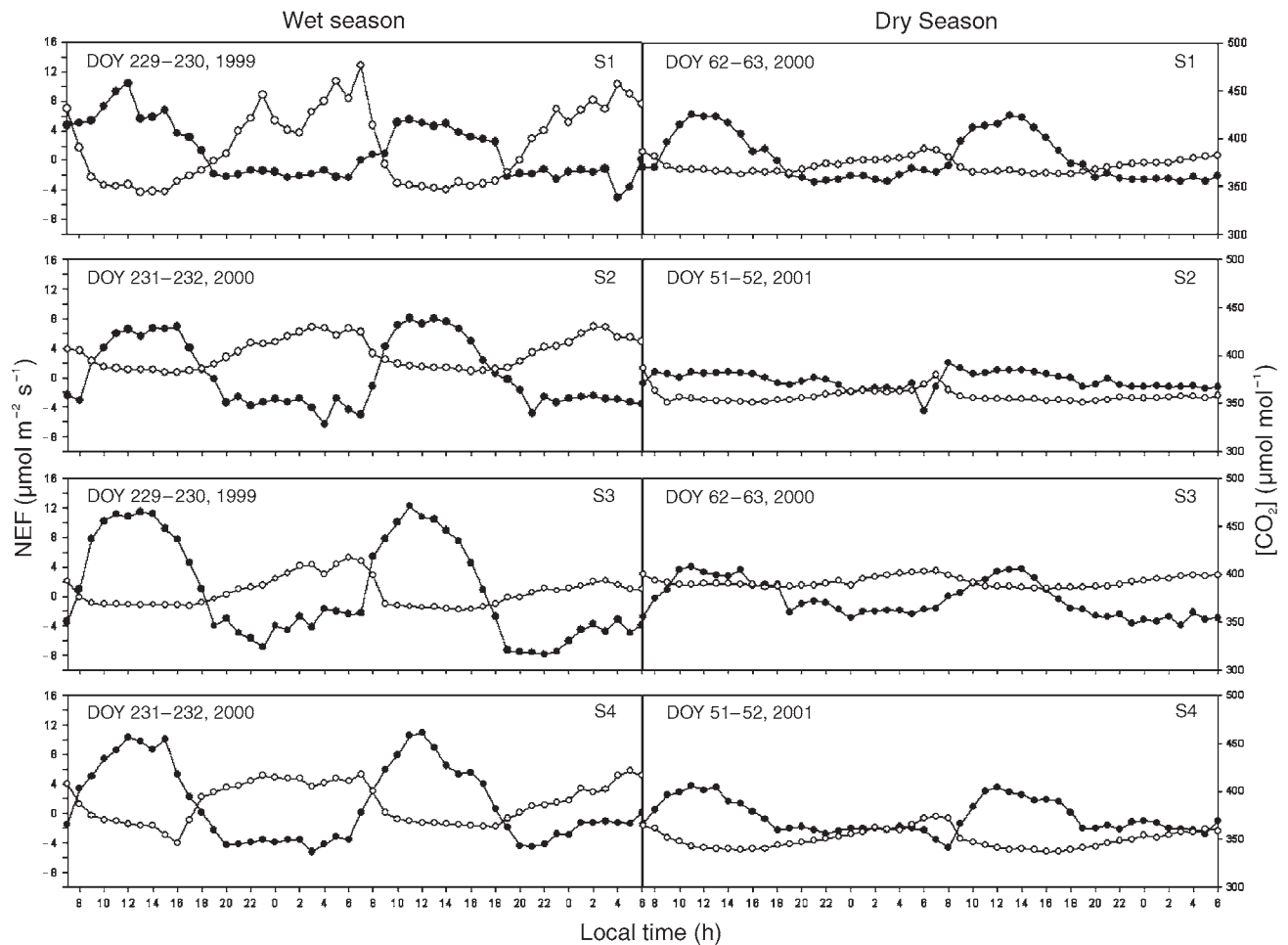


Figure 1. Wet and dry season net ecosystem flux (NEF; ●) and CO₂ concentration (○) in a vegetational mosaic of the Orinoco lowlands. Data correspond to the measurements taken from May 1999 to April 2001 over four sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna.

cerrado (Miranda et al. 1997). Thus, ΔS_c was not a significant proportion of mean hourly NEE and can be ignored in the open canopy. The relationship between ΔS_c and NEE was examined to determine if CO₂ fluxes were affected by advection when turbulence was low (Grace et al. 1996). As expected, ΔS_c increased with wind speed below 1 m s⁻¹; however, NEE showed no relationship with wind speed indicating that advection contributed nothing to the variation in CO₂ fluxes. The downwind flux difference resulting from stand heterogeneity and advection was less than 2.5%. For all sites, nocturnal flux measurements were considered unreliable when mean friction velocity (u_*) was below 0.1 m s⁻¹ (Grace et al. 1996). During both seasons of each study year, the percentage of nights with mean u_* below 0.1 m s⁻¹ was less than 8.5 and 0.0%, respectively. During calm nights, replacing data with parameterized values showed that the corrected fluxes varied between 0 and 3% of the uncorrected fluxes. Even on nights with low turbulence, error corrections were less than 4%, indicating little CO₂ build-up and that the relatively high wind speed reduced the development of a stably stratified nocturnal boundary layer.

Seasonally averaged nighttime NEF over the S1–S4 stands for the wet season (4.1, 2.9, 4.0 and 3.8 μmol m⁻² s⁻¹, respectively) was similar to the values measured over a cerrado and campo sujo in central Brazil as well as over *Brachiaria* fields in south-western Amazonia (Miranda et al. 1997, Grace et al. 1998, Santos 1999). During the dry season, daily NEF trends in the savannas (S2–S4) confirmed that nighttime NEF was the dominant component and that these ecosystems switched to being a net daily source of CO₂. The exception was the tall-grass *Andropogon* field (S1).

Apparent photosynthetic flux as a function of photosynthetic photon flux

For the entire dataset, wet and dry season hourly carbon fluxes for each site were used to analyze the hourly apparent photosynthetic flux (APF) as a function of PPF (Figure 2). We calculated APF as the sum of NEE and heterotrophic respiration (R_h). Each dataset was fitted with a rectangular hyperbola with a defined saturation at high PPF (APR_{sat} in Figure 2). The regression coefficients indicated that changes in PPF accounted for the variation in APF at all sites. A fitted hyperbolic func-

tion for NEF and photosynthetically active radiation (PAR) over the campo sujo and recently established pasture under the conditions of the central Brazilian plains has been reported previously (Santos 1999). Our results showed that the initial slope (α_a ; i.e., the apparent quantum-use efficiency) differed among sites. During the wet season in S1–S4, α_a values were lower than the mean reported for C_3 grasslands (0.004–0.007 versus 0.014–0.023; Ruimy et al. 1995, Flanagan et al. 2002, Xu and Baldocchi 2004). Low α has been related to water or nutrient stress, or both, limiting ecosystem production in the Orinoco savannas (San José 2001). Saturation of APF occurred at ambient PPFs. During the wet season in S1–S4, maximum APF was 12.4, 10.8, 15.8 and 19.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Despite the tall-grass *Andropogon* field (S1) being

a C_4 pasture, and the well-known lack of light-saturation in C_4 species (Black 1973), the response was related to its degraded state caused by continuous grazing without renewal practices. Soil analysis of S1 revealed that its nutrient status was well below that required for high production (Cochrane et al. 1985). The relatively low NEF over cultivated pasture in south-western Amazonia has been related to nitrogen deficiency (Grace et al. 1998). In S1–S4, the PPF required to saturate photosynthesis of the physiologically active canopy declined markedly from the wet to the dry season. During the dry season in S1–S4, the maximum APF capacity was markedly reduced to 8.3, 3.3, 4.9 and 6.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Over both seasons, estimated apparent nighttime respiration (i.e., the nocturnal sum of NEE and R_h) for the sites (0.4–2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$)

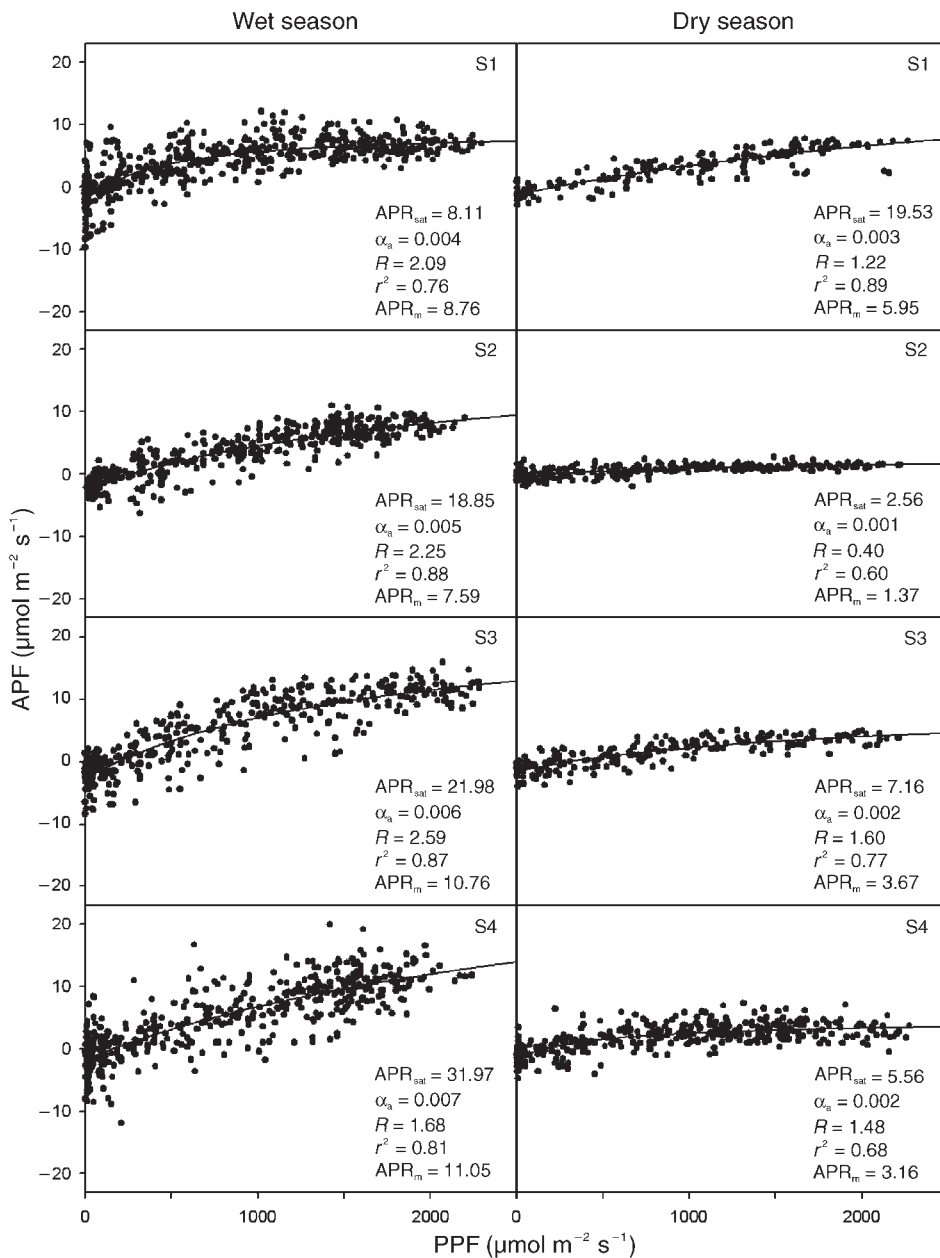


Figure 2. Wet and dry season apparent photosynthetic flux (APF) as a function of absorbed photosynthetic photon flux (PPF) in a vegetational mosaic of the Orinoco lowland. Data were collected from May 1999 to April 2001 at four sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna. Values were fitted with a rectangular hyperbola: APR_{sat} is APR at saturating PPF; α_a is apparent quantum yield; R is dark respiration; and APR_m is APR at maximum PPF ($1800 \mu\text{mol m}^{-2} \text{s}^{-1}$).

compared favorably with measured nighttime NEF.

Soil CO₂ efflux

For each season, the relationship between hourly soil CO₂ efflux (R_s) and soil temperature (T_s) showed different temperature sensitivities for R_h , autotrophic respiration (R_a) and turnover times of carbon pools (Figure 3). For all sites, the tendencies revealed two relationships, one significant for wet soil ($\theta > 0.148\text{--}0.168\text{ m}^3\text{ m}^{-3}$) and the other for dry soil ($\theta < 0.148\text{--}0.168\text{ m}^3\text{ m}^{-3}$). For the wet season in S1–S4, R_s ranged from -0.3 to $-21.3\ \mu\text{mol m}^{-2}\text{ s}^{-1}$. When soils were dry, R_s was smaller, ranging from -0.5 to $-11.5\ \mu\text{mol m}^{-2}\text{ s}^{-1}$. During the wet season, the temperature sensitivity encompasses effects on root and microbial activity and the incident effect of carbon uptake and partitioning to roots (Davidson et al. 1998, Bowling et al. 2002). During the dry season, the main proportion of respiration comes from the recalcitrant carbon that features low temperature sensitivity (Liski et al. 1999). When daily soil respiration was compared with the respiration curve as outlined by Lloyd and Taylor (1994), they showed bursts of CO₂ emission (i.e., the Birch Effect (Jarvis et al. 2007)). This response corresponds to a series of alternating rainless and rainy days. The effect of air-drying and rewetting on soil humus decomposition was originally reported by Birch and Friend (1956) and Griffiths and Birch (1961) for the East African soil of Kenya. They showed that R_h is stimulated by soil rewetting, and that respiration ceases when soil dries. Recently, this effect has been reported under field conditions (Hunt et al. 2002, Liu et al. 2002, and Rey et al. 2002). By contrast, soil respiration falling below Lloyd and Taylor's curves correspond to rainless days with θ below $0.148\text{--}0.168\text{ m}^3\text{ m}^{-3}$. In the Orinoco mosaic, soil CO₂ efflux was the main component of ecosystem respiration, because seasonal changes in θ and canopy structure allow high T_s values. During the dry season, low θ limited R_s and outweighed the temperature effect, indicating that these factors controlled R_s , as has been reported for Brazilian cerrados, northern Australia and African savannas (Holt and Coventry 1990, Meir et al. 1996, Zepp et al. 1996, Chen et

al. 2002). This dependence is associated with a change in the rate of carbon utilization (Knapp et al. 1998).

In S1–S4, mean annual soil CO₂ effluxes (5.2 ± 2.7 , 4.6 ± 2.7 , 5.4 ± 2.6 and $5.2 \pm 3.2\ \mu\text{mol m}^{-2}\text{ s}^{-1}$, respectively) were higher than the mean value estimated for a wide range of tropical savannas and grasslands ($1.6\ \mu\text{mol m}^{-2}\text{ s}^{-1}$; Raich and Schlesinger 1992). In the Brazilian cerrado, a mean of $3.0 \pm 0.8\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ has been reported for the early to late dry season (Meir et al. 1996). The higher mean annual soil CO₂ efflux values of the Orinoco sites appear to be associated with CO₂ bursts, which were accounted for in our calculations. For S1–S4, the turnover time of soil carbon, based on the soil carbon content and annual R_h , was 9.0, 4.3, 5.5 and 9.0 years, respectively. A value over 10 years has been calculated for a wide range of tropical savannas and grasslands (Raich and Schlesinger 1992). The differences in soil CO₂ efflux among the Orinoco sites (S1–S4) reflect variations in litter input and soil carbon content caused by disturbance (San José et al. 2003).

Net ecosystem production and gross primary production

The integration over time of hourly NEE gives net daily ecosystem production (NEP; Figure 4), which provides information on the effects of land use changes on the length of the period of active photosynthesis and respiration. Highest NEP occurred in the middle of the wet season when rainfall was more evenly distributed, with NEP in S1–S4 reaching maxima of 2.1, 1.7, 2.1 and 2.1 $\text{g C m}^{-2}\text{ day}^{-1}$, respectively. As the dry season progressed, phenological changes were evident as leaf shedding and grass marcescence. Consequently, the difference between wet and dry seasons in NEP was evident. The effect of water stress on NEP appeared soon after θ and λE decreased. During the dry season, maximum NEPs in S1–S4 (-1.4 , -0.5 , -1.4 and $-1.6\ \text{g C m}^{-2}\text{ day}^{-1}$, respectively) agreed with values reported for other systems exposed to similar drought conditions such as grasslands during summer and post-seeding (Ham and Knapp 1988, Verma et al. 1992, Dugas et al. 1999, Meyers 2001, Hunt et al. 2002) as well as deciduous forests

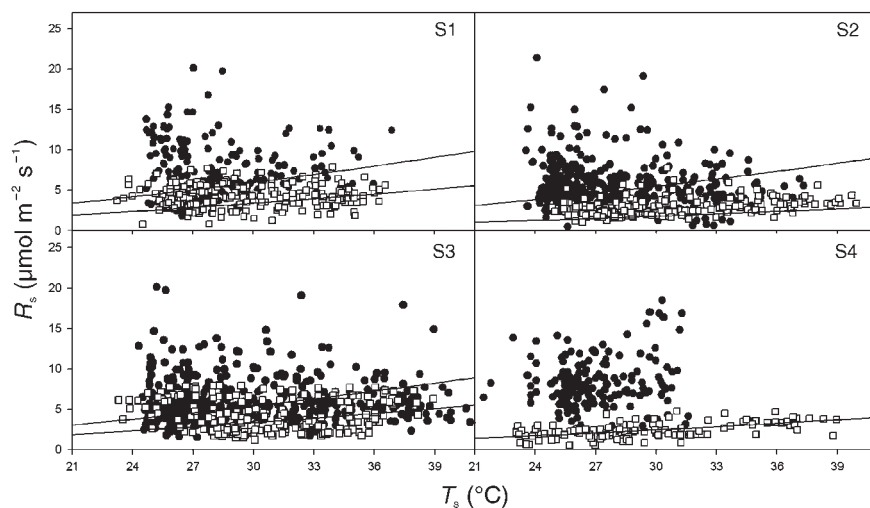


Figure 3. Soil CO₂ efflux (R_s) as a function of soil temperature (T_s) for the wet season (●) at a soil water content (θ) $> 0.148\text{--}0.168\text{ m}^3\text{ m}^{-3}$ and dry season (□) at $\theta < 0.148\text{--}0.168\text{ m}^3\text{ m}^{-3}$ in a vegetational mosaic of the Orinoco lowland. Data were collected from May 1999 to April 2001 at four sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna.

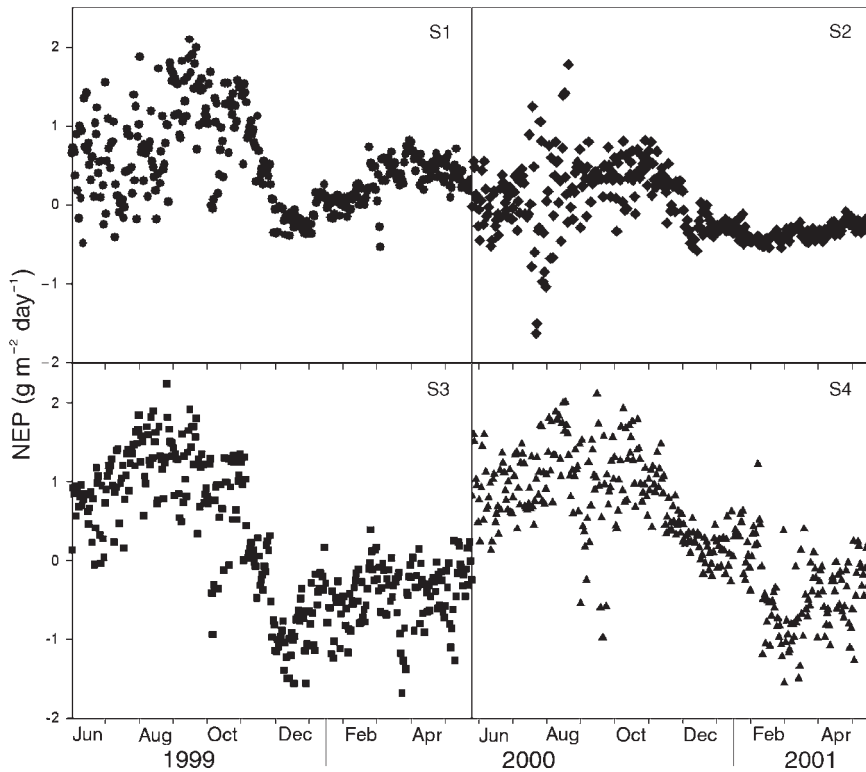


Figure 4. Net daily ecosystem production (NEP) over a vegetational mosaic of the Orinoco lowlands. Data were collected from May 1999 to April 2001 at four sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna.

(Hollinger et al. 1999, Goldstein et al. 2000, Schmid et al. 2000).

In the context of transition, the herbaceous savanna may be considered to be in a state of perpetual disturbance characterized by repetitive cycles of tree removal and cattle grazing. This system constituted a low carbon sink as a consequence of past landscape practices, particularly the reduction in plant biomass caused by animal grazing and invasion by low-productivity herbaceous weeds. This has resulted in savannas with low LAI and preferential allocation of carbon to roots, favoring respiration over photosynthesis. Our results indicated that, during the transition from woodland savanna to herbaceous savanna, R_{eco} increased following disturbance. In contrast, the transition between woodland savanna (S4) and tall-grass *Andropogon* field (S1) sites results in an increase in NEP and conversion toward a strong carbon sink.

In summary, the degraded savannas are converted to low annual carbon sinks, and variables such as temperature and water availability affect this conversion. In the transition from disturbed sites to woodland savanna, enhancement of NEP dominated respiration, as has also been reported for a mature secondary forest succession (Emanuel et al. 2006). In the four sites (S1–S4), annual NEP was 366, 6, 116 and 139 $\text{g C m}^{-2} \text{ year}^{-1}$, respectively, and R_{eco} was 439, 459, 744 and 654 $\text{g C m}^{-2} \text{ year}^{-1}$, respectively. In the herbaceous savanna (S2), annual NEP was similar to that for a Sahelian fallow savanna ($32 \text{ g C m}^{-2} \text{ year}^{-1}$; Hanan et al. 1998) and a New Zealand tussock savanna over the summer ($6 \text{ g C m}^{-2} \text{ year}^{-1}$; Hunt et al. 2002). However, the annual NEP values for the woody savannas (S3 and S4) were close to the lower limit reported for the

Brazilian campo sujo and cerrados and north Australian savanna ($122\text{--}290 \text{ g C m}^{-2} \text{ year}^{-1}$; Monteiro 1995, Miranda et al. 1996, Eamus et al. 2001, Santos et al. 2003).

The difference in annual NEP among savannas reflects the effects of limiting factors such as θ and the length of the growing season (San José et al. 1985, Meyers 2001). The importance of climatic changes on the length of the growing season has been considered by Houghton et al. (1996). For S1–S4, the difference in carbon sequestration was conditioned by the degree of human impact. Therefore, perturbation on long time scales has a long-lasting effect on NEP. Specifically, the higher annual NEP in the cultivated tall-grass *Andropogon* (S1) reflects its adaptation to savanna conditions and its potential in helping mitigate the greenhouse effect (Ojima et al. 1993, Fisher et al. 1994). In the savanna woodland continuum, the largest sink (i.e., NEP) accounted for woody and shrub growth, as reported for Australian savannas (Bowman et al. 2001, Fenshman et al. 2005, Beringer et al. 2007).

The difference in annual NEP between mesic and dry savannas contrasts with the similarity between savannas in maximum daytime NEE. Maximum NEE in the Orinoco sites ranged from 10 to 20 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. This range compared favorably with values reported for the Brazilian Neotropical savannas ($9\text{--}17 \mu\text{mol m}^{-2} \text{ s}^{-1}$) as characterized by oxisols and annual mean precipitation of 1500–2000 mm (Miranda et al. 1996, 1997, Santos et al. 2003). Furthermore, these values were similar to those reported for the Paleotropical mopane woodlands at the Kalahari transect ($10\text{--}14 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and Sahelian fallow savannas ($10\text{--}16 \mu\text{mol m}^{-2} \text{ s}^{-1}$) occurring with 306–464 mm of precipitation (Monteny et al. 1997,

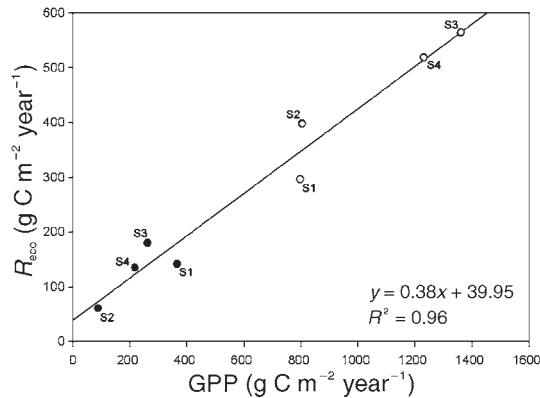


Figure 5. Ecosystem respiration (R_{eco}) as a function of gross primary production (GPP) in a vegetational mosaic of the Orinoco lowlands. Data were collected from May 1999 to April 1002 at four sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna.

Hanan et al. 1998, Veenendaal et al. 2003). Comparatively, NEE in the north Australian savannas ranged from 9 to 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Eamus et al. 2001). Therefore, the difference between savannas in annual NEP has a different explanation. It might be the length of the growing period. Across the Orinoco, cerrado and mopane savannas, there is a substantial difference in growing period: 8–8.5 months in the cerrados; 6–7 months in the Orinoco; and 3 months in mopane savannas. Therefore, changes in the savanna pattern can be considered as a mediating factor in ecosystem response to variation in production-related processes. This response can be related to drought adap-

tations and a quick growth response to improved water availability (Knapp and Smith 2001). The potential response of the carbon status of the savannas and grasslands can be considered as a vegetation adaptation to marked interannual differences in weather conditions.

There was a strong relationship between R_{eco} and GPP (Figure 5) as a result of cumulative carbon exchange throughout the seasons. These results are comparable with findings from European forests, where R_{eco} accounts for most of the variation in carbon balance (Valentini et al. 2000). Furthermore R_{eco} was more closely related to photosynthetic activity than to temperature. These results are in agreement with studies by Ekbald and Högberg (2001). Thus, site carbon status was driven by the effect of disturbance and seasonal impact of leaf area duration, g_{sf} and θ . For warm temperate grasslands, Novick et al. (2004) indicate that stomatal limitation is a primary factor determining net carbon status.

Net primary productivity

Net daily primary productivity was calculated by summing eddy covariance measurements of APF and apparent respiration flux. Eddy covariance-based measurements of NPP for the Orinoco sites were 498, 169, 181 and 402 $\text{g C m}^{-2} \text{year}^{-1}$, respectively. Harvest-based NPP measurements in the woodland savanna (S4; Table 1) with the highest tree cover and species diversity reached $386 \pm 30 \text{ g C m}^{-2} \text{year}^{-1}$. However, deforestation, burning and cattle raising have resulted in environmental patchiness of herbaceous (S2) and tree savannas (S3), reducing NPP by 57% ($162 \pm 13 \text{ g C m}^{-2} \text{year}^{-1}$) and 54% ($176 \pm 11 \text{ g C m}^{-2} \text{year}^{-1}$), respectively. In the tall-grass *Andropogon* field (S1), NPP reached a maximum value of 433

Table 1. Carbon content of above- and belowground vegetation and of the soil in the herbaceous and woody layers of each study site; net primary productivity (harvest-based measurements) of the herbaceous and woody layers of each study site; and leaf area index in the wet and dry seasons at each site in a vegetational mosaic of the Orinoco lowlands. Study sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna. Values are means \pm standard deviation. Site totals are the sums of the herbaceous and woody layers.

	S1	S2	S3	S4			
	Herbaceous	Herbaceous	Woody	Herbaceous	Woody	Herbaceous	Woody
<i>Vegetation carbon content (g m⁻²)</i>							
Aboveground	422 \pm 43	75 \pm 8	4.9 \pm 1.2	62 \pm 10	203 \pm 31	32 \pm 9	1011 \pm 175
Belowground	273 \pm 55	81 \pm 62	1.7 \pm 0.8	109 \pm 12	71 \pm 22	21 \pm 7	202 \pm 49
Layer total	695 \pm 79	157 \pm 22	6.6 \pm 2.6	170 \pm 24	274 \pm 44	52 \pm 10	1212 \pm 121
Site total	695 \pm 79	163 \pm 26		444 \pm 78		1265 \pm 143	
<i>Soil carbon content (g m⁻²)</i>							
0.0–0.3 m	3191 \pm 674	1468 \pm 202	70 \pm 1	1139 \pm 281	954 \pm 148	573 \pm 64	3030 \pm 534
Site total	3191 \pm 674	1539 \pm 214		2091 \pm 469		3602 \pm 694	
<i>Total system carbon content (g m⁻²)</i>							
Site total	3887 \pm 657	1702 \pm 236		2535 \pm 394		4866 \pm 642	
<i>Net primary productivity (g C m⁻² year⁻¹)</i>							
Individual layer	433 \pm 19	162 \pm 12	0.7 \pm 0.1	96 \pm 9	80 \pm 2	21.4 \pm 0.8	365 \pm 25
Site total	433 \pm 19	163 \pm 14		177 \pm 11		386 \pm 31	
<i>Leaf area index</i>							
Wet season	2.28 \pm 0.10	1.21 \pm 0.05		1.52 \pm 0.11		1.99 \pm 0.12	
Dry season	0.93 \pm 0.08	0.85 \pm 0.01		0.92 \pm 0.04		1.03 \pm 0.09	

$\pm 18 \text{ g m}^{-2} \text{ year}^{-1}$. The S1 site had been regularly grazed and burned under conditions representative of normal use without maintenance or renewal of the pasture cover. These long-term effects have markedly reduced annual dry matter production on S1 compared with recently established *Andropogon* fields ($863 \text{ g C m}^{-2} \text{ year}^{-1}$; Berroteran et al. 1986). Compared with the woodland savanna (S4), the soil carbon contents of sites S1–S3 (Table 1) are lower by 11, 57 and 41%, respectively. The harvest-based measurements of NPP may give systematically low results because of incomplete recovery of all below-ground components. However, values were within the range reported for the Orinoco savannas (San José and Montes 1997), providing validation of the eddy covariance measurements at the measurement scale.

Gross primary productivity was related to variations in LAI. Over 72% of the variance in GPP was explained by changes in LAI. Thus, GPP increased by $2.0 \text{ g C m}^{-2} \text{ day}^{-1}$ for

each unit increase in LAI. This relationship is consistent with grassland studies (Saigusa et al. 1998, Flanagan et al. 2002, Xu and Baldocchi 2004); however, the slopes ($3.9\text{--}9.0 \text{ g C m}^{-2} \text{ day}^{-1}$ per unit LAI) were comparatively greater.

Water-use efficiency

Water-use efficiency (WUE; $\text{NEP}/\lambda\text{E}$), a measure of the ability of vegetation to conserve water during CO_2 uptake, showed a seasonal trend (Figure 6). For the wet season in S1–S4, seasonally averaged daily WUEs were 5.2 ± 3.3 , 1.9 ± 3.2 , 4.6 ± 2.7 and $5.9 \pm 3.2 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$, respectively. Similar values were reported for a campo sujo (Santos 1999) and a cerrado (Monteiro 1995). For a C_4 pasture and a nearby *terra firme* forest site, Grace et al. (1998) found values of 4.4 and 2.3 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$, respectively. In our study, the large variations among sites in water and carbon exchanges with the atmosphere suggested that the variation in carbon uptake rate

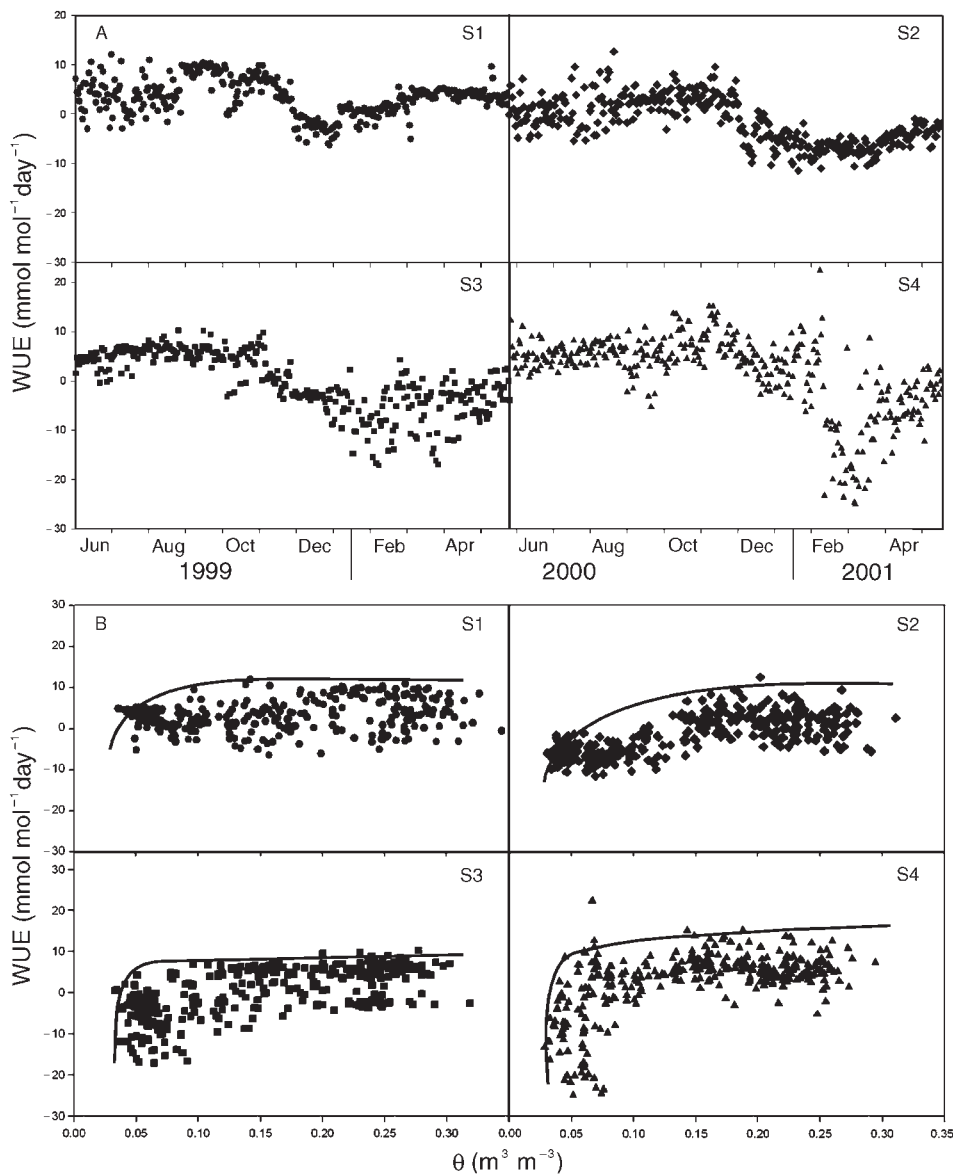


Figure 6. (A) Daily water-use efficiency (WUE) and (B) WUE as a function of soil water content (θ) with a fitted water boundary envelope in a vegetational mosaic of the Orinoco lowlands. Data were collected from May 1999 to April 2001 at four sites: S1 = tall-grass *Andropogon* field; S2 = herbaceous savanna; S3 = tree savanna; and S4 = woodland savanna.

differed from the variation in λE . Water-use efficiency showed an overall decline over the dry season as the air humidity mole fraction deficit (D_a) increased. However, the magnitude of WUE at a given D_a differed among sites. Thus, the S1–S4 sites at the wettest end of the θ range had the most efficient CO₂ uptake relative to water loss, whereas sites at the most arid end of the θ range were the least efficient. An exception was S1, although having a different magnitude of NEP and λE , the ratios of these fluxes were similar at different values of θ . Verhoef et al. (1996) and Williams and Albertson (2004) reported less than 10% difference in WUE between days with high versus low θ for African savannas. The WUE measured at our sites are stratified by θ according to their vegetative cover. Low WUE measured at S2 can be explained by different responses to soil respiration and soil evaporation. The soil respiration pattern indicates that soil respiration differences might have contributed to the WUE observed at the four sites. The sandy soil and low θ at each site resulted in soil evaporation about an order of magnitude smaller than transpiration.

Values of WUE were lower after a dry period than before a dry period. This could be a result of differences among species in drought response and could be considered a form of drought adaptation. Therefore, WUE not only reflects vegetation composition, but may be a determining factor in shaping vegetation composition.

Conclusions

The savannas are able to modify the annual global carbon exchange according to land use. The savanna mosaic of the Orinoco lowlands as a whole is sequestering carbon, and in the context of the carbon balance, it is a carbon sink with annual values of 366, 6, 116 and 139 g C m⁻² year⁻¹ for S1–S4, respectively. Across the physiognomic types of the Orinoco llanos, periodic inventories and changes in land use between 1982 and 1992 suggest a carbon sink of –17.53 Tg C year⁻¹ (San José and Montes 2001). In the Orinoco herbaceous savanna (S2), carbon accumulation is balanced by cattle management on the basis of adjustments in stocking rate, the frequency of prescribed fires, and resource extraction (San José and Montes 2001). As a result of human disturbance and the consequent environmental patchiness, a carbon sink does not obtain across the entire landscape. Moreover, human efforts to stabilize grazing lands have resulted in a loss of plant biodiversity. Consequently, management and equilibration of the carbon budget have minimized biodiversity of native grassland.

In mesic savannas, human disturbance causes profound biological changes. By contrast, recovery and lifespans of the tree and herbaceous life forms lead to a positive carbon balance. In the arid savannas, the frequency of disturbance is comparable to the lifespan and recolonization capability of the native life forms, which creates the impression of an ecosystem in equilibrium. However, in reality, the Orinoco savannas are always recovering from disturbance and are in non-equilibrium condition (Ellis and Swift 1988).

For S1–S4, the integrated annual values of GPP were 1162,

891, 1621 and 1447 g C m⁻², respectively, and were affected by the features of the threshold response of $\lambda E/\lambda E_L$ as a function of θ (San José et al., unpublished). The values for the tall-grass *Andropogon* field (S1) and the woody savanna (S4) were above those reported for an unburned Brazilian campo sujo (1293 g C m⁻² year⁻¹; Santos et al. 2003). Comparatively lower values ranging from 305 to 390 g C m⁻² year⁻¹ have been reported for the mopane savannas at the Kalahari transect and Sahelian fallow savannas (Hanan et al. 1998). Based on our results of net ecosystem carbon cycling in Orinoco savannas, we conclude that land use changes can turn the system into a small carbon sink or render it carbon neutral as a result of changes in assimilatory and respiratory fluxes, with the degree of perturbation and modification of the hydrological balance determining the outcome.

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