Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa

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Abstract

We studied the seasonal variation in carbon dioxide, water vapour and energy fluxes in a broad-leafed semi-arid savanna in Southern Africa using the eddy covariance technique. The open woodland studied consisted of an overstorey dominated by ***Colophospermum mopane*** with a sparse understorey of grasses and herbs. Measurements presented here cover a 19-month period from the end of the rainy season in March 1999 to the end of the dry season September 2000.

During the wet season, sensible and latent heat fluxes showed a linear dependence on incoming solar radiation (I) with a Bowen ratio (β) typically just below unity. Although β was typically around 1 at low incoming solar radiation (150 W m^{-2}) during the dry season, it increased dramatically with I, typically being as high as 4 or 5 around solar noon. Thus, under these water-limited conditions, almost all available energy was dissipated as sensible, rather than latent heat.

Marked spikes of CO_2 release occurred at the onset of the rainfall season after isolated rainfall events and respiration dominated the balance well into the rainfall season. During this time, the ecosystem was a constant source of CO_2 with an average flux of 3–5 μmol m^{-2} s^{-1} to the atmosphere during both day and night. But later in the wet season, for example, in March 2000 under optimal soil moisture conditions, with maximum leaf canopy development (leaf area index 0.9–1.3), the peak ecosystem CO_2 influx was as much as 10 μmol m^{-2} s^{-1}. The net ecosystem maximum photosynthesis at this time was estimated at 14 μmol m^{-2} s^{-1}, with the woodland ecosystem a significant sink for CO_2. During the dry season, just before leaf fall in August, maximum day- and night-time net ecosystem fluxes were typically -3 μmol m^{-2} s^{-1} and 1–2 μmol m^{-2} s^{-1}, respectively, with the ecosystem still being a marginal sink.

Over the course of 12 months (March 1999–March 2000), the woodland was more or less carbon neutral, with a net uptake estimated at only about 1 mol C m^{-2} yr^{-1}. The annual net photosynthesis (gross primary production) was estimated at 32.2 mol m^{-2} yr^{-1}.

Keywords: carbon balance, *Colophospermum mopane*, eddy covariance, energy balance, savanna, semi-arid, soil respiration

Introduction

Over the last few years, considerable attention has been given to the potential contribution of temperate and tropical forest ecosystems to the net incorporation of anthropogenic CO_2 into the terrestrial biosphere (Lloyd, 1999a; Malhi & Grace, 2000; Malhi *et al.*, 2000; Schulze *et al.*, 1999; Valentini *et al.*, 2000). Much less attention, however, has been paid to the carbon balance of savanna ecosystems, despite savanna ecosystems covering an area of 17×10^6 km^2 of the earth's surface, a greater area than is occupied by either temperate or boreal/temperate forests. They are therefore potentially

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a significant carbon sink. For example, Taylor & Lloyd (1992) estimated that 15% of the annual global carbon sink might be attributable to savannas and seasonally dry tropical forest ecosystems. Moreover, large increases in woody biomass in savanna ecosystems of the latter part of the last century have been reported as a result of intensifying land use (Van Vegten, 1983; Archer *et al.*, 2001). But there is a lack of field data to support these observations.

Fluxes of energy, water and carbon, as measured with eddy covariance techniques, can nowadays be used to estimate net ecosystem photosynthesis responses directly to variations in environmental conditions and annual ecosystem carbon balance (Moncrieff *et al.*, 1997). However, in savanna ecosystems, such measurements have been, until now, limited. From West Africa, results have been reported from a regrowing fallow savanna (abandoned arable field) over a short measurement period (Verhoef *et al.*, 1996; Hanan *et al.*, 1998). Subsequent modelling suggested only a marginal sink for atmospheric CO_2 in this system. Miranda *et al.* (1997) presented data for wet and dry seasons for Brazilian cerrado savanna characterized by a relatively high rainfall, but prone to regular fires. These data suggested a potential substantial sink, while measurements in C_4-dominated pastures have indicated a potential for a relatively high CO_2 fixation rate (Grace *et al.*, 1998).

Ecosystems along the Kalahari Transect present a diversity of broad- and fine-leaved savanna types on a relatively homogeneous substrate of aeolian sand deposits (Thomas & Shaw, 1991; Scholes & Parsons, 1997). The annual rainfall varies from 200 mm to more than 900, resulting in widely differing tree densities from open shrub savanna to dense Miombo woodland (Wild *et al.*, 1967; White, 1983). Despite these differences in the annual average rainfall, all sites along the transect are characterized by a distinct dry period of at least 4–5 months during the Austral winter. In this study, we report on interannual seasonal variation in carbon, water and energy fluxes from a semi-arid mopane (*Colophospermum mopane*) woodland located in the midpoint of this transect. *C. mopane* woodland is one of the dominant savanna forms in Southern Africa, extending across much of northern Botswana, through southern Zimbabwe/north-east South Africa and into central Mozambique (Wild *et al.*, 1967; White, 1983; Coates Palgrave, 1988). It is one of the most distinctive vegetation groups in Southern Africa, often forming pure stands (Coates Palgrave, 1988) with a limited grass understorey (Wild *et al.*, 1967).

Methods

Site

The research site was located in a broad-leaved *C. mopane* (Kirk ex Benth.) savanna woodland, located about 20 km east of Maun, Botswana (23°33′E, 19°54′S). The long-term climate of this site is semi-arid, with a mean rainfall of 464 mm (Table 1). There is a distinct dry season during the winter months from May to September. Appreciable rainfalls are normally limited to between December and March. The coefficient of variation for the midrainy season, January and February, is 60% (Bhalotra, 1987). Intermittent dry spells during the rainy season are common.

A micrometerological tower (height 12.6 m) was erected in the middle of a homogeneous tall mopane stand with a maximum canopy height of about 8 m, but with patches of short (shrub) mopane (maximum canopy height 2 m) located about 300 m to the north-east and to the west of the tower. This vegetation pattern stretched in all directions for at least 2.5 km. The *C. mopane* trees were often associated with the hemi-parasitic shrub *Ximenia americana*. The canopy cover of the mopane trees in the stand has been estimated at 30–40% (Bird *et al.*, 2002). The marginal understorey consisted of grasses with a canopy cover of at most 15%, with *Panicum maximum*, *Schmidtia pappophoroides*

Table 1 Long-term climatic data of the Maun area: monthly rainfall, maximum recorded monthly rainfall, mean maximum daily temperature, mean minimum daily temperature and potential evapotranspiration (potential evapotranspiration according to Penman. Source: Bhalotra, 1987)

Climatic variable	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Annual
Rainfall (mm)	0.1	0.3	3	17	50	79	110	100	73	25	6	1	464
Max. rainf. (mm)	5.4	9.6	31.9	101.1	169.6	262.2	395.9	365.7	273.8	120.4	62.3	17.1	1183.9
Max temp (°C)	25.3	28.5	32.5	33.6	33.3	32.7	32.1	30.8	31.2	30.1	27.8	25.1	30.3
Min temp (°C)	7.1	9.9	14.7	18.6	19.5	19.2	19.6	19.2	18.2	15.1	7.1	7.1	14.9
PET (mm)	111	147	185	211	197	196	180	155	165	139	123	101	1910

PET: potential evapotranspiration.

and *Urochloa trichopus* being the dominant species. Some herbs were also present, the most abundant being *Commelina benghalensis* and *Solanum panduriforme*. The soil slope in the area was $<0.5\%$. The study area is under communal land use and for many decades has been primarily used for cattle grazing and firewood collection. During the period of this study, March 1999–September 2000, few cattle were, however, present. This was a consequence of a complete slaughtering of all cattle in the area as a disease control measure 2.5 years prior to the commencement of the study. *C. mopane* is a drought-deciduous tree with an almost total absence of leaves during the dry season. The maximum leaf area index (LAI) for the stand varies at the peak of the growing season between 0.9 and 1.3 (Mantlana, 2002).

Meteorological instruments

Wind speed, air temperature, water vapour pressure and CO_2 concentration were measured with a closed eddy covariance system consisting of a Gill Sonic anemometer with an omnidirectional head (Solent R3, Gill Instruments, Lymington, UK) installed at 12.6 m height on the north-east corner of the tower in the prevailing wind direction and a Licor 6262 closed path infrared gas analyser (LI-COR Lincoln, NE, USA). Air was drawn through 1/8 in BEV-A-LINE tubing and pushed through the analyser at approx. 7 L min^{-1}. A pressure transducer (PTP101B, Vaisala, Helsinki, Finland) was used to correct for pressure fluctuations. The analyser was used in absolute mode. Pure N_2 was used to continuously flush the reference cell. The gas analyser was checked weekly and recalibrated every 2–3 weeks, or more often, when deemed necessary. Calibration was carried out with a calibration gas using a known CO_2 concentration (between 340 and 380 ppm) and with air using a known H_2O concentration, generated with an LI 610 dewpoint generator (LI-COR). Drift, in the measurements between calibrations, was, however, mostly below 1% and never more than 3% of the range. Sensible heat (H) and latent heat (λE) were calculated on-line after co-ordinate rotation (Aubinet *et al.*, 2000). Signals from the sonic anemometer and the gas analyser were digitally synchronized. Loss of high-frequency signals in the closed path system was accounted for by aligning the λE and CO_2 cospectra with that of H, while accounting for differences in time lag between the anemometer and gas concentration measurements (Eugster & Senn, 1995, Moncrieff *et al.*, 1997, Grace *et al.*, 1998).

The tower was also equipped with a data logger (CR23X, Campbell Scientific, Logan, Utah, USA) with additional micrometeorological sensors for short- and long-wave radiation (CM3, Kipp & Zonen, Delft, Netherlands) air temperature and humidity (HMP 45a Vaisala, Uppsala, Sweden) and photon flux density (LI 190 SA LICOR, Lincoln, NE, USA). These sensors were attached to 2 m long aluminium masts on the opposite side of the tower from the sonic anemometer. Rainfall, soil temperature and soil heat flux were measured to the east of the tower at a distance of ca. 20 m. Soil temperature was measured at 0.02, 0.05, 0.10, 0.50 and 1.00 m with platinum resistance thermometers (at each depth $n = 3$) (Geratherm, Geschwenda, Germany). Heat flux plates were measured at 0.05 m (Rimco HP3, McVan Instruments, Victoria, Australia) ($n = 5$) and soil moisture by volume at 0.10, 0.50, 100 and 115 m (Theta probe; Delta T Devices, Burwell UK; at each depth $n = 3$). The relation between volumetric soil water content and soil matric potential was determined by sampling the drying curve water release characteristic, using the filterpaper method (Deka *et al.*, 1995).

Data analysis

Eddy covariance measurements were taken with a frequency of 20 Hz and integrated as half-hour means with the EDISOL software (Aubinet *et al.*, 2000; Knohl *et al.*, 2002, Kolle & Rebmann, 2002). Derived variables, such as aerodynamic and surface conductance and canopy-to-air vapour pressure deficit, were calculated using the formula in Miranda *et al.* (1997) and Grace *et al.* (1998). Fetch distances were calculated according to Schuepp *et al.* (1990) and Kolle & Rebmann (2002). Missing data due to equipment failure in the data set amounted to ca. 15% during the period of measurements presented here and were either replaced through interpolation (for periods of maximum 2–3 h) or by using a Michaelis–Menten formula for daytime fluxes, or Lloyd and Taylor's equation for night-time fluxes (Lloyd & Taylor, 1994).

Results

Rainfall and soil moisture conditions

Measurements commenced towards the end of the wet season in March 1999. With the exception of occasional small showers in September and October, rains did not again occur until mid-November (Fig. 1). The highest total monthly rainfall of 198 mm was recorded in February 2000; this being twice the long-term average for that month. Soil moisture profiles measured between December 1999 and September 2000 reflect this rainfall pattern having a still dry profile in the beginning of the wet season (early December 1999), a moist profile during the peak of the rainy season (March 2000), and again, a largely depleted profile by

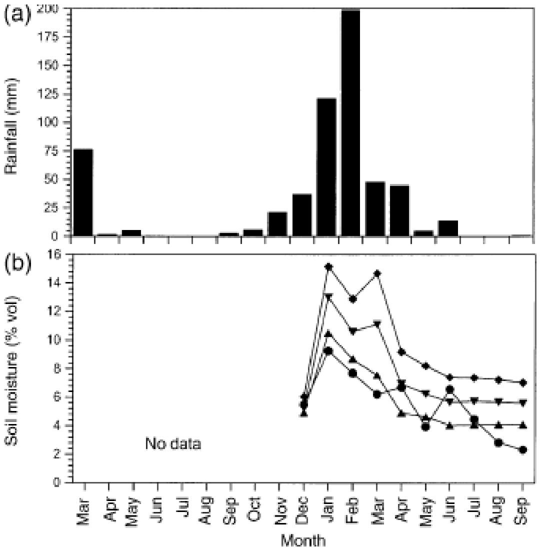

Fig. 1 Monthly rainfall (a) and soil moisture percentage (b) during the period (soil moisture depths 10 cm = ●, 50 cm = ▲; 100 cm = ▼; 150 cm = ◆).

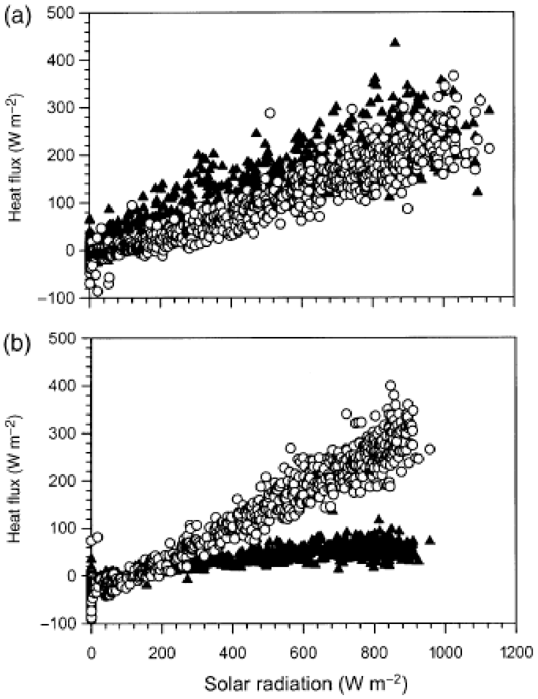

Fig. 2 Solar (or shortwave downward radiation) latent and sensible heat flux in the wet (a, March) and dry (b, August) season (sensible heat exchange = ○, latent heat exchange = ▲).

the beginning of the middle of the next dry season (August 2000). The minimum soil moisture values (50–100 cm) equate approximately to matric potentials of −1.0 MPa (3.2%) and −0.1 MPa (4.5% soil moisture), respectively. These presumably reflect the soil matric potentials at which water becomes unavailable for the vegetation.

Energy balance

Incoming solar radiation (I) reached maximum values of 1100 W m^{-2} during the wet season (April 2000), with maximum I being less during the dry season (960 W m^{-2}: August 2000). Despite similar rates of incoming insolation, the partitioning of the available energy differs dramatically for the two periods (Fig. 2). During the wet season, both sensible (H) and latent heat fluxes (λE) showed a linear dependence on I, with λE tending to be slightly higher than H. Bowen ratios (β) were therefore generally just below unity. A markedly different pattern was observed, however, in the dry season. Although β was generally around 1 at low I (< 150 W m^{-2}), λE never rose above about 60 W m^{-2}, with almost all available energy at high I being dissipated as sensible, rather than latent heat. Daytime β was therefore typically between 4 and 5 during periods of the highest insolation.

The extent to which the measured sensible and latent heat fluxes accounted for the available energy is shown in Fig. 3, where ($H + \lambda E$) is plotted against ($R_n - G$), R_n being the net radiation and G being the soil heat flux as measured at 0.05 m depth. These data, taken from March 2000, show incomplete energy balance closure with the sum of H and λE, as measured by the eddy system, being typically up to around 25% lower than ($R_n - G$), this imbalance tending to be greatest during periods of high insolation. The mean 50% and 90% fetch distances of the eddy system for this period were during daytime 114 and 520 m.

One explanation for this may be an underestimation of G due to substantial heat gradients in the upper layers of the soil, but with the placement of the soil heat flux sensors below the 5 cm below the soil surface (Kurbatova *et al.*, 2002). For example, during mid-day G reached 23% of R_n, a value typical for sparse canopy vegetation (Jones, 1992). The mean daily soil temperature for March was 27.90 °C at 0.02 m, this being 0.23 °C higher than the average temperature at 1.00 m depth. The highest half-hour mean soil temperature at 0.02 m (39.61 °C) was reached at 14.15 h. By then the temperature difference between 0.02 and 1.00 m had increased to 12.04 °C. The differences between 0.02 and 0.05 m and 0.05 and 0.10 m were 3.97 and 3.63 °C, respectively,

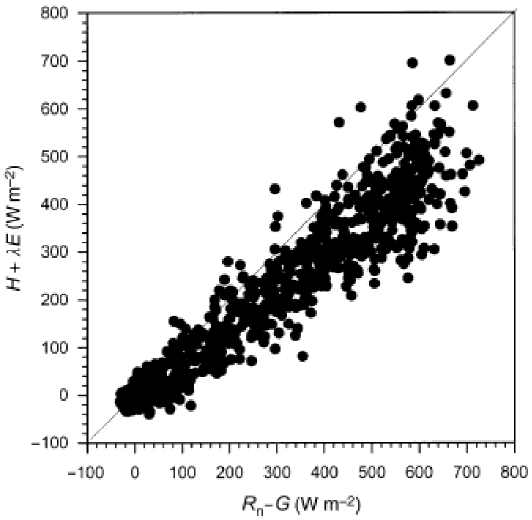

Fig. 3 Comparison of the energy balance closure of eddy covariance measurements of sensible (H) and latent (LE) heat exchange and radiation measurements: net radiation (R_n)–soil heat flux (G). The solid line indicates $x = y$.

at this time period. The buildup of a large soil temperature gradient during high insolation must result in an extra energy storage term S in the soil above the soil heat flux plates ($S_{0\text{–}5\,\mathrm{cm}}$). Given the mean observed maximum temperature change in March of up to 5 °C h^{-1} in the top 0.02 m of soil during high insolation and assuming a specific heat capacity (c_p) of 800 J kg^{-1} K^{-1} (sandy soil; mean bulk density 1.8 kg dm^{-3} with 0.05 kg kg^{-1} water, Jones, 1992; Mantlana, 2002) $S_{0\text{–}5\,\mathrm{cm}}$ should reach peak values in the order of 100 W m^{-2}. Adding S to the balance would more or less bring the gap in the energy balance at high insolation into the range usually observed in eddy measurements (Moncrieff *et al*., 1997). We thus believe that our data are of a generally high quality in terms of the energy balance.

Representative diurnal patterns for fluxes at the beginning, middle and end of the wet season

At the commencement of the wet season in early December 1999, new leaf development was still in progress after the first rains with volumetric soil moisture at the surface fluctuating at around 5% (not shown). Figure 4 shows diurnal patterns in energy fluxes (Fig. 4a) along with changes in air temperature and vapour pressure deficit (Fig. 4b) and CO$_2$ fluxes and conductances (Fig. 4c) for 2 consecutive days of contrasting weather conditions at this time. For 1 December, the weather was overcast and relatively cool, whereas for 2 December, conditions were generally clear (except for some cloud around mid-day), with both temperatures and vapour pressure deficits (D) substantially greater than the day before. Incoming solar radiation values as high as 1100 W m^{-2} were observed for 2 December (Fig. 4a), but maximum λE values were low, being only around 100 W m^{-2}. Maximum photosynthetically active radiation (PAR) reached 800 μmol m^{-2} s^{-1} on the first cloudy day and 2050 μmol m^{-2} s^{-1} on the second sunny day (not shown). Air temperature (T_a) varied between 20 on the first and 30 °C above the tree canopy by midafternoon and minima were around 19 °C at night. Vapour pressure deficits (D) reached 1.6 KPa on day 1 and 3 KPa on day 2. Associated canopy-to-air vapour pressure differences ($D_{\text{can–air}}$) varied from 2.8 KPa on the first day to as much as 5 KPa on 2 December (not shown). On day 2, the maximum aerodynamic conductance for heat and vapour transfer (g_a) varied between 2 and 2.5 mol m^{-2} s^{-1} during daytime and 0 and 0.5 mol m^{-2} s^{-1} at night, while the surface conductance (g_s) for the developing leaf canopy was around 0.25 mol m^{-2} s^{-1} during daytime, and 0 mol m^{-2} s^{-1} at night. Despite marked day-to-day differences superimposed on the expected diurnal patterns in T_a, $D_{\text{can–air}}$ and I, ecosystem CO$_2$ fluxes were more or less constant and positive over this period, with rates usually between 3 and 5 μmol m^{-2} s^{-1} both during the day and night. Despite a limited leaf area, no distinct diurnal pattern in net CO$_2$ exchange was observed and the ecosystem was clearly a constant source of CO$_2$ at this time. Whatever fluctuations in ecosystem CO$_2$ fluxes that were observed seemed to be more related to changes in turbulence at night, with high efflux rates being related to higher g_a and vice versa. This was probably a simple phenomenon being related to the intermittent flushing of CO$_2$ accumulated within the canopy at night when occasional high nocturnal turbulence intensities occurred. The average CO$_2$ concentrations just above the tree canopy varied between 376 ppm around 14:30 hours and 424 ppm around 4:00 hours.

By early March 2000, foliar development had been completed and the canopy had attained its maximum LAI of around 1.0. Soil moisture was much greater than had been in December, reaching a volumetric soil water content of 10% at the soil surface, reflecting a large rainfall, 198 mm, recorded in February (twice the long-term average). The data shown in Fig. 4d–f for this period (1 and 2 March) reflect high insolation days, with I reaching 1100 W m^{-2}. Latent heat fluxes were now appreciably larger than in December, being as high as 270 W m^{-2}. These higher values occurred despite

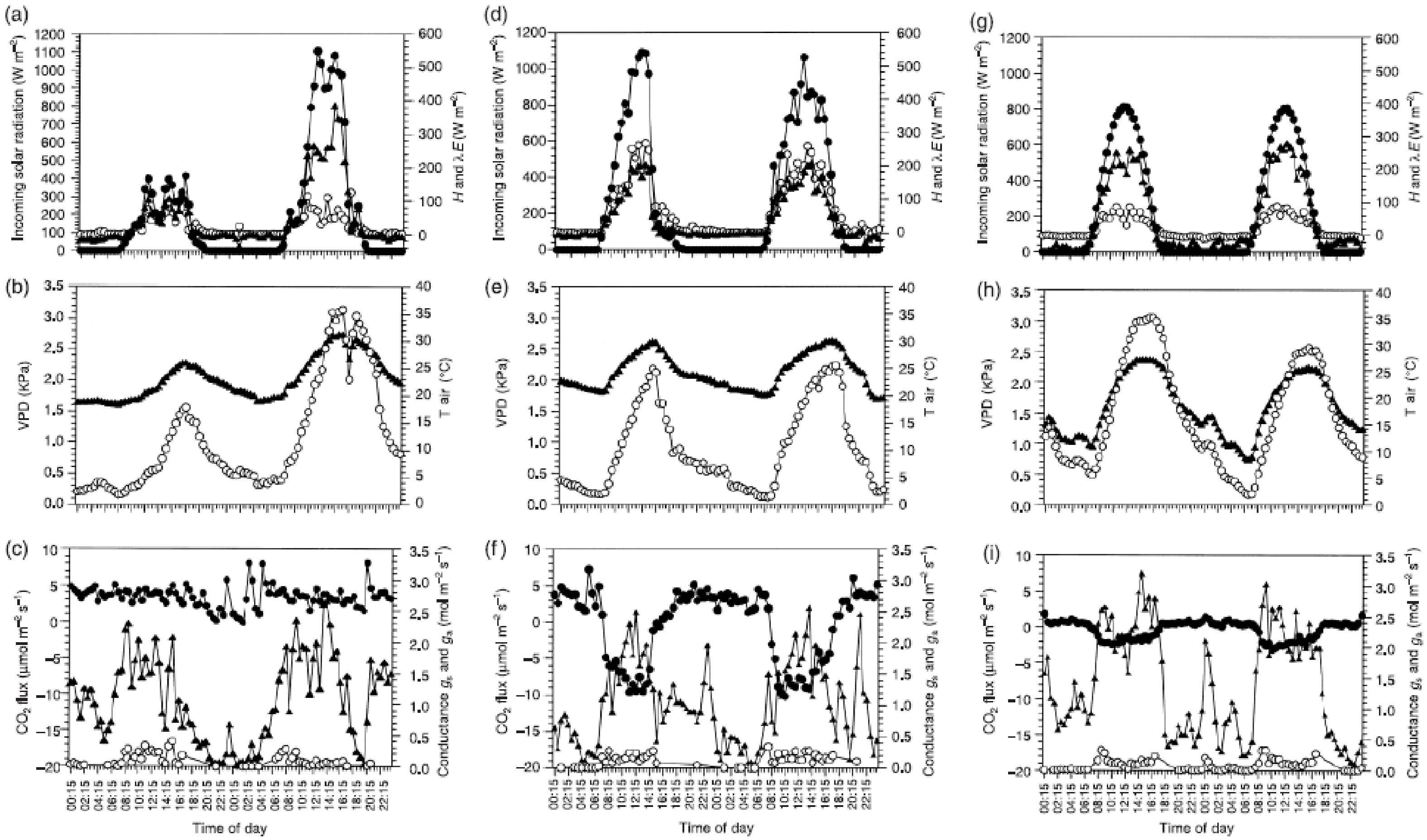

Fig. 4 Variation in (a) incoming solar radiation (●), sensible heat flux (H) (▲) and latent heat flux (▼); (b) air temperature (●), vapour pressure deficit (▲) and (c) CO$_2$ flux (●), Aerodynamic conductance for heat and vapour transfer (g_a) (▲) and canopy stomatal conductance (g_s) (○) on 1 and 2 December 1999 (Julian days 335 and 336). (d–f) As for (a–c), but for 1 and 2 March 2000 (Julian days 31 and 32). (g–h) As for (a–c), but for 6 and 7 August 2000 (Julian days 219 and 220).

maximum I being similar to that observed for clear sky days in December. Incoming PAR for these days was accordingly also similar to those occurring for Fig. 3. Maximum T_a was also similar to December at around 30 °C, but night temperatures were higher. Maximum D was around 2.3 KPa, with $D_{can-air}$ around 3 KPa: less than earlier on in the dry season. The values for g_a and g_s were similar to those obtained in December, although the relative contribution of soil and canopy to g_s would have shifted. Night-time fluxes were similar to December, averaging around 3 µmol m^{-2} s^{-1}. During daytime, a maximum CO_2 flux into the canopy of 10 µmol m^{-2} s^{-1} was observed. Clearly, at this time of the year, the site is an appreciable sink for CO_2. The average CO_2 concentrations just above the tree canopy now varied between 354 ppm around 14:30 hours and 426 ppm around 4:00 hours. Our third example (Fig. 4g–i) comes from the beginning of August, by which time the rains had ceased and soil water contents were already low (Fig. 1). Trees had not yet started to shed leaves, but the grass and herb understorey had dried out. As this period was only 1 month after the winter solstice, incoming solar radiation values were lower compared with December or March, even on cloudless days, attaining maximum values of only 800 W m^{-2}, with maximum incoming PAR of around 1500 µmol m^{-2} s^{-1}. Latent heat fluxes were already much reduced, compared with the middle of the wet season, maximum λE was generally less than 90 W m^{-2}, but maximum H was close to 300 W m^{-2}. Air temperature reached maxima at around 27 °C. Canopy conductances were often reduced below 0.25 mol m^2 s^{-1}.

Night-time CO_2 fluxes were lower than in either December or March. The average values varied mostly between 1 and 2 µmol m^{-2} s^{-1}. During daytime some limited uptake of CO_2 by the vegetation was clearly discernible, with a maximum uptake of around 3 µmol m^{-2} s^{-1} being observed. The average CO_2 concentrations just above the tree canopy now varied between 370 ppm around 14:30 hours and 381 ppm around 4:00 hours.

Coupling with the atmosphere

In order to obtain a reliable estimate of the carbon balance of an ecosystem using the eddy covariance technique, it is necessary to ensure that no systematic biases in the measurements occur (Goulden *et al.*, 1996; Moncrieff *et al.*, 1997). In this context, it is of concern that quite often ecosystem CO_2 efflux rates seem to be reduced under conditions of low turbulence, especially under stable atmospheric conditions at night (Goulden *et al.*, 1996; Grace *et al.*, 1998). To assess the magnitude of this effect for our site, we examined the relationship between friction velocity (u^*) and the night-time CO_2 flux for the periods examined in Figs 4d–f and g–i viz 1 and 2 December 1999 and 1 and 2 March 2000, this is shown in Fig. 5. The decline in the measured fluxes below a friction velocity of around 0.1 m s^{-1} suggests that there is then insufficient coupling. These conditions may occur mainly at night totalling only a few hours daily. Differences that were observed in the carbon flux on a daily (sunset to sunset) basis could not be linked to night-time periods of the previous day with reduced wind velocity. In our site, we did not measure CO_2 profiles and it is therefore not completely possible to separate biotic and storage fluxes in the eddy covariance signal. However, due to the open canopy, coupling is better than in other ecosystems and comparable with a boreal windthrow (Knohl *et al.*, 2002). The height of the tower is also only 12.5 m. If significant night-time storage would occur, this could be visible in high early morning fluxes, but is not the case (Fig. 4). In the absence of topographical features that might cause internal drainage flow at night, correction of carbon balance calculations for lack of coupling at low (u^*) values was considered inappropriate as biotic and minor storage fluxes will at any rate have compensated for each other, when occasional flushing of the canopy occurred. Therefore, we made no further corrections in the carbon balance calculations to avoid double counting (Dolman *et al.*, 2002; Knohl *et al.*, 2002).

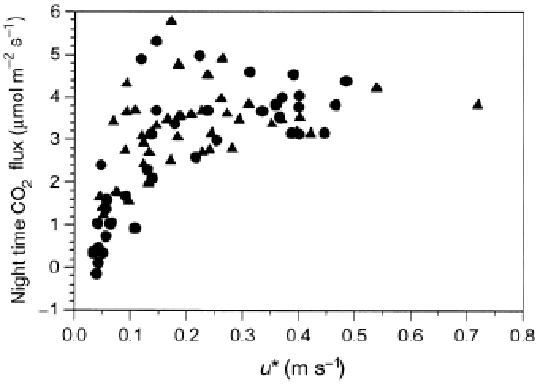

Fig. 5 Relationship between night-time CO_2 flux and the friction velocity for December 1999 (●, Julian days 336 and 337) and March 2000 (▲, Julian days 219 and 220).

Ecosystem photosynthesis

The photosynthesis and respiration components, which constitute the net ecosystem flux, were separated by modelling daytime system respiration with night-time data and soil temperature using the equation of Lloyd & Taylor (1994). In this case, soil temperature at 0.1 m depth was taken as the independent variable. Using this approach, light response curves for January 2000, March 2000 and August 2000 are presented in Fig. 6. January was the first month for which the stand had developed a canopy (foliar development started in early December). March represents the peak of the rainy season with the canopy having its maximum LAI of around 1.0. August represents the mid-dry season, just before leaf fall had commenced.

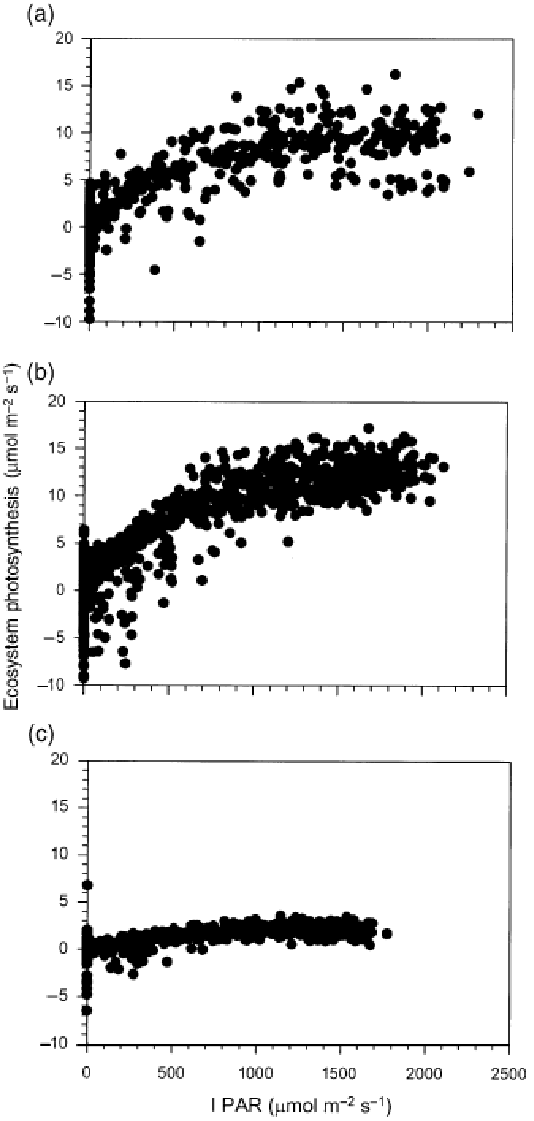

Fig. 6 Light response curves of ecosystem photosynthesis for January (a), March (b) and August (c) 2000.

For January, the mean maximum rates of ecosystem photosynthesis increased with PAR to about 1200 µmol quanta m^{-2}s^{-1}, with a maximum rate (A_{max}) of about 10 µmol CO$_2$ m^{-2}s^{-1}. Higher ecosystem photosynthesis rates were then observed in March, with both the initial slope of the light response curve and A_{max} being greater than in January, A_{max} in March being around 14 µmol m^{-2}s^{-1}. By August, however, the photosynthetic capacity was much reduced, A_{max} only being about 2 µmol m^{-2}s^{-1}.

The correction for ecosystem respiration allows for an estimate of gross primary productivity (GPP) on an annual basis. After estimating daytime respiration on a monthly basis, we found for the period March 1999 to February 2000, which includes the relatively dry months of March, April and May 1999, a GPP CO$_2$ uptake of 25.6 mol m^{-2}. For the period September 1999 to August 2001, which includes a wet February and March 2000 period and late rains in June, the annual total rainfall was 32.2 mol m^{-2}.

Ecosystem carbon balance

At the start of the measurement period, in the latter part of the wet season (March 1999), the mopane woodland showed a consistent net ecosystem CO$_2$ uptake rate of between 0.05 and 0.2 mol m^{-2}day^{-1}. As the dry season progressed, the rate of net carbon uptake rate decreased, with the woodland being a slight source of CO$_2$ to the atmosphere from August to November (Fig. 7). Nevertheless, superimposed upon this long-term seasonal change in the carbon balance of the woodland were high-frequency 'spikes' of CO$_2$ efflux immediately after the isolated rainfall events characteristic of this environment. This was observed in both March and September and, most markedly so, immediately after the first heavy rains at the commencement of the wet season in November. Ecosystem respiration continued to dominate the carbon balance even after rainfall became more regular in November and December resulting in a strong release of CO$_2$ during the early wet season. Only by February 2000, when foliar development was nearly complete, did the woodland again become a net sink of CO$_2$; remaining so virtually until all available soil water had been depleted and leaf fall had commenced in early September. Over the period March 1999–March 2000, the ecosystem was more or less in balance, being estimated to be accumulating only about 1 mol of CO$_2$ m^{-2} over this 12-month period.

Discussion

Our savanna is located within a patchwork of tall mopane trees with intermittent shrub stands. Recently

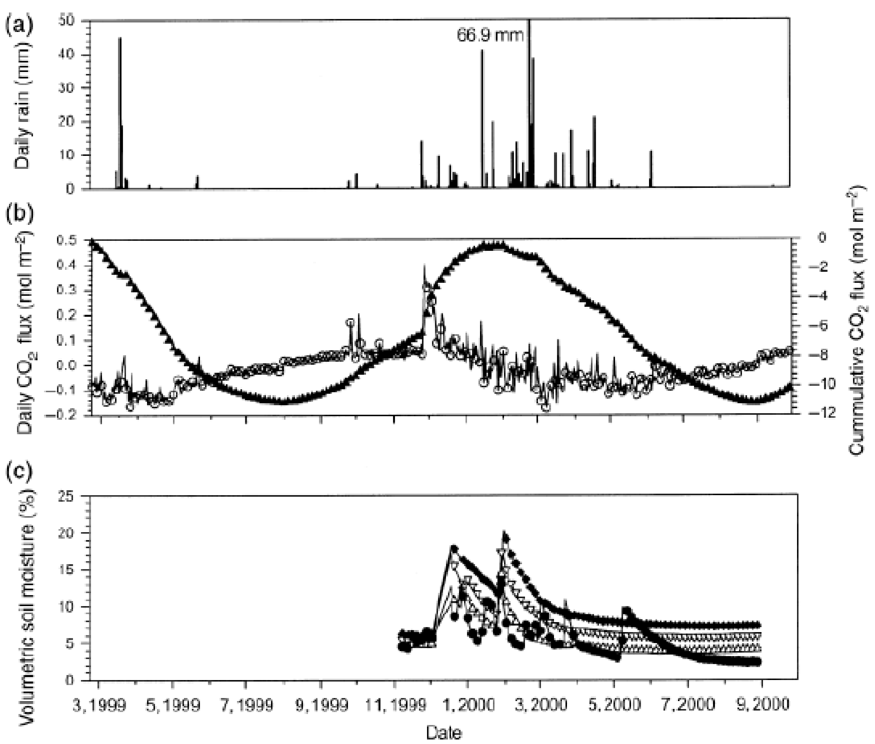

Fig. 7 Daily rainfall (a), daily (○) and cumulative (▲) CO_2 flux (b) and soil moisture conditions at different depths during the study period. Symbols are shown at each fifth data point (depths: 20 cm = ●, 50 cm = ▲, 100 cm = ▼, 150 cm = ◆).

acquired Iconos imagery of the study site suggests a higher reflectance and presumably lower R_n of the shrub patches than the taller mopane stands in the area (S. Ringrose, unpublished results). This is of relevance because at our site, the eddy system integrates measurements over a larger area, of up to 520 m (90% fetch), which includes some shrub patches while the radiation sensors are, due to their smaller area coverage, mostly directed at tall mopane alone. This, in addition to the soil heat flux measurement problem already discussed, could contribute to the small difference in the energy balance measurements by the eddy system as compared with the radiation and soil heat flux. Thus, we are confident that the current study has quantified the land atmosphere exchange of H_2O and CO_2 in our savanna system with an accuracy similar to other seasonally dry tropical ecosystems (Miranda *et al.*, 1997; Grace *et al.*, 1998).

The deciduous semi-arid mopane woodland studied here showed a clear seasonal pattern in its CO_2 exchange characteristics. At the onset of the rainy season, the system was a net source with a low system respiration and, once the rainfall pattern had become regular, the net uptake increased until March, this also being the period of continual foliar development. Maximum rates of CO_2 uptake of around 10 μmol m^{-2} s^{-1} and maximum ecosystem photosynthesis rates of around 15 μmol m^{-2} s^{-1} are achieved 2–3 months after the commencement of regular rains. In the dry season just before leaf fall, net photosynthetic rates are already low, about 2 μmol m^{-2} s^{-1}, and after leaf fall there is a long period, where the ecosystem is a small, but significant, source of carbon to the atmosphere. The maximum rates of ecosystem CO_2 uptake are similar to those reported for Brazilian cerrado *sensu stricto* (Miranda *et al.*, 1997) and Sahelian fallow savanna (Verhoef *et al.*, 1996; Hanan *et al.*, 1998). Both these systems have a maximum leaf area similar to the woodland studied here: 1.2–1.4. The value for annual ecosystem photosynthesis of between 25.6 mol m^{-2} yr^{-1} (drier period) and 32.2 mol m^{-2} yr^{-1} (wetter period) is similar to the modelled figure of 27.5 mol m^{-2} yr^{-1} reported by Hanan *et al.* (1998) for the Sahel, but appreciably lower than an estimate of 106 to 125 mol m^{-2} yr^{-1} (depending on fire history) obtained for *campo sujo* savanna in central Brazil (Santos *et al.*, in press).

The C_4-dominated grass layer is a potentially highly productive component in savanna ecosystems (Grace *et al.*, 1998; Santos *et al.*, unpublished results) and may also significantly contribute to their total evapotranspiration (Schulze *et al*., 1994; Hutley *et al*., 2001). On the basis the isotopic composition of CO_2 evolution from their woody savanna in Brazil, Miranda *et al*. (1997) estimated that about 40% of ecosystem productivity may have been derived from C_4 plants. They also noted that this could be an overestimate as their study site was in a phase of regrowth after fire, when C_3 biomass is being stored as structural carbon in tree stems. The $^{13}C/^{12}C$ ratio of soil carbon for the woodland site studies at our site has been determined at $-21‰$ (Bird *et al*., 2002). This suggests that over longer timescales, in the order of 45–50% of net primary production (NPP) derives from C_4 plants. With our instrumental set-up, it was not possible to separate the carbon uptake in the tree layer and the understorey. However, our site has a sparse understorey of herbs and grasses with less than 15% ground cover. Leaf photosynthesis in grasses and herbs in the area stops effectively with the drying out of the surface layer below 4% soil moisture by early May (P. Weber and E.M. Veenendaal, unpublished results of leaf level measurements on *P. maximum* and *C. benghalensis*). This observation, together with the prolonged net carbon uptake during the dry season, which can only be attributed to the woody layer, suggests that an estimate of the relative contribution to NPP based on the soil carbon inventory at our site may be an overestimate of the present situation. The ecosystem light saturated response at the peak of the rainy season also supports the suggestion of a C_3-dominated flux in this woodland.

Ecosystem respiration responded rapidly to rainfall and soil moisture changes. The high respiration bursts at the beginning of the wet season may reflect the seasonality of both leaf and fine root production in these savanna types (Rutherford, 1984; Scholes & Walker, 1993) as well as local soil physical conditions. Soil respiration (autotrophic and heterotrophic) is likely to constitute the principal component of the overall ecosystem respiration rate (Malhi & Grace, 2000). Sensitivity of soil respiration to changes in soil matric potential has often been reported (e.g. Bhaumik & Clark, 1948; Wildung *et al*., 1975; Orchard & Cook, 1983). An immediate large increase in soil respiration after rainfall has also been observed for boreal forests and may be typical for sandy soils (Kelliher *et al*., 1999; Shibistova *et al*., 2002). Soil water release characteristics for a sandy soil such as in our mopane site show small volumetric increases in dry soil matric potential to ≤ 100 KPa. Thus, a relatively minor rainfall event triggers a large change in soil matric potential, affecting conditions in which heterotrophic microbiota can be active. The maximum rates of ecosystem respiration recorded were again of similar order to those reported for the Sahelian fallow savanna and Brazilian cerrado studies. The biggest difference between the savanna ecosystem in this study and the cerrado system examined by Miranda *et al*. (1997) is the much longer dry season typically experienced for the woodland here (on average 6 months with rainfall with less than 20 mm per month vs. only 3 months in Brazil). The importance of variable dry periods has been highlighted even for moister regions (Malhi & Grace, 2000; Prentice & Lloyd, 1998; Lloyd, 1999b). Although the woodland here remained a sink for CO_2 for about 4 months after the rains ceased, it was a sustained source of carbon from September through to January.

The net uptake estimate of $1\ \mathrm{mol\ CO_2\ m^{-2}\ yr^{-1}}$ does not take into account the fact that some wood is carried away from the site for firewood use. Therefore, in contrast to the results reported for fire-prone cerrado (Miranda *et al*., 1997), our savanna is more or less at balance, similar to modelled results reported for the Sahel (Hanan *et al*., 1998) and Southern Africa (Lloyd, 1999a).

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